

Perception and Processing of Illusory Contours

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Barbara Dillenburger
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Dekan: Prof. Dr. F. Schöfl

1. Berichterstatter: Prof. Dr. C. Wehrhahn

2. Berichterstatter: Prof. Dr. H. Mallot

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1. INTRODUCTION

Seeing things which are not physically existent is normally thought to be a sign of mental problems rather than part of our normal perception. Schumann, however, described in 1900 with "Scheinkanten" (apparent edges) a percept of borders, which had no physical counterpart in the visual scene. Along with descriptions of many other illusions at this time, including geometric or brightness illusions, the percept of virtual edges indicated that we are not seeing a true pictorial copy of the world. Instead, our visual system appears to interpret the physical information available in an image.

How might this illusion be useful? Virtual contours might, for example, prove helpful to detect low contrast object borders, thereby enabling object perception and structuring of a visual scene under most lighting conditions.

One example for this is shown in Fig.1.1. Observers usually see here a photograph of three kittens curled together: a grey tiger, a black, and a black kitten with white legs.



Fig. 1.1: Three Kittens. The left picture shows three kittens curled together. Most current edge detectors (Sobel algorithm, Gimp 2.0) fail to segregate them. Especially in the case of the black and black-white kitten, the latter's white leg is 'detected' by the algorithm to be a separate object.

As shown in the right part of Fig.1.1 the physical content in the original photograph does not contain sufficient edge information to physically support the percept of three kittens. Comparing the results of a currently available computational edge detector (Sobel algorithm, Gimp 2.0) with human perception shows some of the differences between physical content and our perception of the scene. Large parts of the two black cats are not distinguishable from each other by computational edge detection. Physically, the picture contains one object in form of a cat's head: the grey tiger's face is clearly segregated. One larger object of an unusual form is furthermore detected by the edge detector. This object is perceived by humans to be the bodies of three cats partially occluding each other. A smaller object is lying in front of the larger one, recognized by us to be the white leg of Charlie the cat (if we know him by name). Thus, we can easily detect three kittens by perceptually extracting their body contours which are not supported by the physical reality in the image. It is obvious from this example how important good edge detection can be under suboptimal lighting conditions. In the case of three kittens curled together in a dark corner, it is a vital task, for example, for a mouse to perceptually

extract edges, corners, and body contours. Using a better edge detector than those currently available might decide between seeing the predator hiding in dark corners, or running right into sleeping cats which looked like a big, dark blob with a strange white little thing in front of it.

This, might virtual edges be more than just erroneous side effects of vision? Could they even be rather useful interpretations of a visual scene and its cues? If the latter was true, we would expect our system to use many of the different cues available in natural scenes, thereby providing us with the flexibility to not only react to a regular, well-trained picture, but also to the possibly important exceptions. Experimental examination of the percept in the years following Schumann's first description showed that various contexts can induce illusory contours. Kanizsa-type stimuli (Kanizsa 1976, Kanizsa 1979, von der Heydt & Peterhans 1989), abutting line patterns (Peterhans & Von der Heydt 1989), abutting textures (Lamme et al. 1995), depth (Hirsch et al. 1995) and motion cues (Julesz 1981) can lead to the very same percept. Furthermore, the illusory contour percept might in general be important, as described in the cat-mouse-scenario, for animals using vision to detect objects and distinguish them from the surround. Illusory edges are indeed perceived by a wide variety of species, including mammals (Schumann 1900, Bravo et al. 1988, Zimmermann 1962), birds (Nieder et al. 1999, Zanforlin 1981, Frost et al. 1988), and insects (Van Hateren et al. 1990, Horridge et al. 1992).

Thus, illusory contours can be understood to be a vital construct of our visual system. Objects in our environment may be only partially visible due to poor contrast or obstructed view.

The visual context of an object embedded in its scene bears additional information about probable object borders and the structure of the visual scene. Perceptual construction of physically non-existent contours by using contextual information might thus be a crucial step towards object perception.

Our visual system thus provides perceptual certainty about physically uncertain information, interpreting incoming information to construct a possibly useful percept. This interpreter simplifies our scene perception by clustering boundaries to objects. That way, giving us less options how to rationally structure and interpret our visual input, this system possibly enables us to make fast decisions in any visual environment. One example for this idea is shown in Fig.1.2.

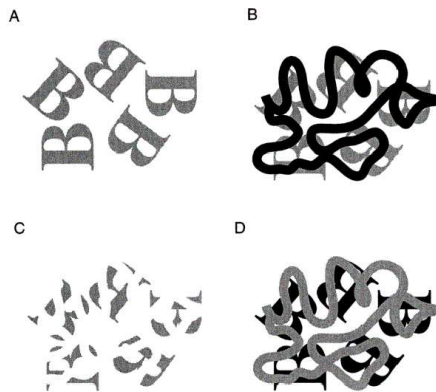


Fig. 1.2: Grossberg 1997. Letters (A) are (B) still easily recognized when they are occluded. It is more difficult, however, to discriminate the same letter fragments without visible occluder (C). This effect is not due to a changed contrast sign between fragments and occluder (D).

Using the contextual information of an object which covers part of the picture, we can combine object parts which belong together. By doing this we are able to recognize the partially hidden objects, in this case letters. The same letter parts

without information about the occluding object, however, are astonishingly difficult to decipher, even though we already consciously know both the occluded objects and their meaning.

Luminance defined contours play a major role in processing the virtual construct, as they provide the contextual information inducing illusory contour process and percept. Illusory contour perception depends solely on real elements, the inducers. Every change of the illusory contour percept is thus necessarily based on changes in the contextual real elements. Understanding how changes in the context affect illusory contour perception is thereby essential to understand the processes underlying illusory contour perception.

As is already known, illusory and real contours share processing resources (Von der Heydt et al. 1984). Real contours as contextual stimuli should thereby interact with illusory contour processing. This interaction and its impact on illusory contour perception is dependent on how real and illusory processes are interleaved and on the properties of contour processing mechanisms in the primate cortex. In this thesis I measured contextual influence of real contours on illusory contour perception. I tested the dependency of these interactions on real line orientation and contrast, and on the timing of real-illusory interaction. Based on these studies, I propose a mechanism of illusory contour construction in areas V1 and V2. In preliminary physiological experiments in macaque visual cortex I measured contextual modulations of neuronal activity showing that part of the real-illusory contour interactions similar to those measured psychophysically can also be found in neural responses in area V1 of the macaque.

1.1 History of Illusory Figures

Different types of illusory contours and their inducers have been found and studied since the first description of “Scheinkanten” was published by Schumann in 1900. The following paragraph will give an overview about the large variety of illusory contour stimuli and their influence on our current understanding of the underlying processes.

Ehrenstein modified 1941 the brightness illusion originally published by Herrmann in 1870 (the Hermann grid) such, that it induced the illusory contour percept known today as ‘Ehrenstein figure’. It is composed of lines arranged in a circular pattern like rays abutting to the sun. The outline of the empty central, circular region in this figure is usually clearly perceived, although the physical stimulus does not contain this outline, but only a few lines abutting to it. The inner circle is usually perceived to be brighter than the background, or it is even perceived as a transparent disc in front of the bright background.

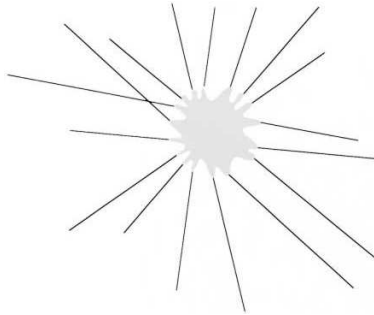


Fig. 1.3: Albert et al. 2001. The Ehrenstein figure in a recent variant. The figure shows a transparent, illusory disk which apparently occludes the abutting lines. This is perceived despite the existence of a real occluder which can be cognitively sufficient to structure the scene.

One variant of this illusion by Albert et al. 2001 is shown in Fig.1.3. Here the Ehrenstein-figure is combined with an irregular patch. Occlusion by the central patch would be sufficient to explain the abutting line pattern. The perception of an illusory transparent disk outlining the occluder is, however, still very strong. The authors of this illusion conclude from this example that top-down, i.e. cognitive explanations are not sufficient to understand illusory contour construction. Even in cases where object completion is unnecessary to explain a scene’s structures, illusory contours can be perceived.

Kanizsa presented in 1976 a variety of new types of the illusion, including an Ehrenstein figure which is collapsed into an abutting line pattern. This figure thus contains only two surfaces which are separated by an illusory border. No brightness effect is induced in this illusion. Another figure presented by Kanizsa was the so-called Kanizsa-triangle. An illusory triangle is induced by three partial disks which are arranged at the corners of the figure. Combining abutting line patterns and the partial disk arrangement, he also created the stimulus later used by Poom (2001), as shown in Fig.1.4. Evidence has been found that contours of opposite contrasts can be used pooled together to induce an illusory figure completion process. Poom tested whether completed figures can also be induced by different, combined stimulus attributes, in this case line offset, as shown alone in the first part of Fig.1.4, and disparity information in the random dot patches, as can be seen in the combined stimulus in Fig.1.4. Cross-fusion of the two combined inducer arrangements leads to a completed figure floating over the inducers, showing that even the combination of different stimulus attributes can lead to a typical illusory contour percept.

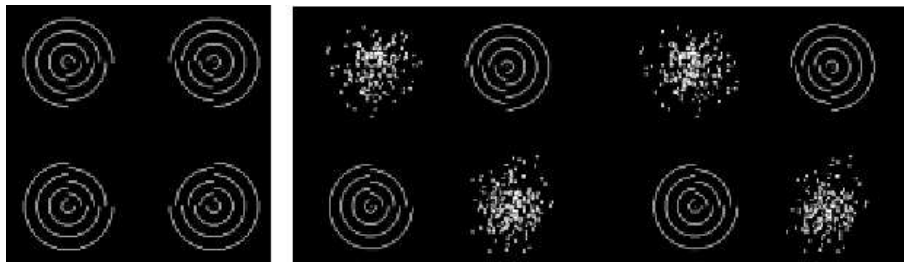


Fig. 1.4: Poom 2001. The first stimulus, after Kanizsa 1976, induces an illusory figure with only one inducer type, i.e. line offset. The second stimulus set combines different inducer types: line offset and disparity information. Cross-fusion leads to the typical illusory figure.

Poom's random dot patterns are based on Julesz work from 1960. He designed random dot patterns which induced illusory figures either stereoscopically, or by using coherent dot motion. Julesz' experiments showed that monocular form perception is not essential for binocular matching and depth perception. Moving random dots were used later by Cunningham et al. 1998, who studied spatiotemporal boundary formation and found that no static spatial differences were needed to induce borders and surfaces. The dynamic information alone was completely sufficient for illusory contour construction.

Depth information was also used by Heider & Peterhans (2002), who employed a spontaneously splitting figure which induces, if cross-fused, an even much clearer illusory contour and separation between two surfaces, as can be observed in Fig.1.5.

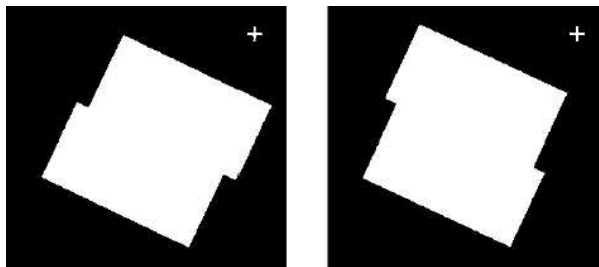


Fig. 1.5: Heider & Peterhans 2002. Even without fusion two separate white rectangles touching each other, i.e. a spontaneously splitting figure, are perceived. Cross-fusion of the two figure parts leads to a stronger separation of the two rectangles.

Heider & Peterhans (2002) studied human perception with this type of stimulus as well as neural responses in macaque V2, showing that neurons can even use stereoscopic cues very distant from their receptive fields (up to 8 deg). They furthermore found that the averaged best stimulus settings for the neurons were also those settings that lead to the strongest illusory contour percept in human observers. Thus, they showed a strong correlation between early visual cortical activity and human perception, indicating that the neural substrate for depth induced illusory contours might indeed lie in area V2.

Illusory contours can thus, as outlined above, be induced by a variety of stimulus attributes as a figure being incomplete[45], line ends and offsets[15], binocular disparity information[43], or dynamic coherence[10]. These single inducing elements can induce brightness illusions, illusory borders, and surfaces. They can even also be combined to lead to an illusory percept[45, 82, 29]. The perception of illusory contours disregarding of the attributes inducing them suggests an early pooling of illusory contour processes. The variety of illusory contour inducers and percepts as well as their robustness indicates their importance for structuring scenes.

1.1.1 *Erroneous Side Effects, or important Feature?*

Are illusory contours an important feature of the visual system, or can they be viewed as merely a specialty of animals with higher cognition, even possibly only a side effect of mechanisms concerned with stimuli of “real” importance? I would like to give here an outline of the various experiments conducted with animals of very different species. These studies indicate that the perception of illusory contours is a phenomenon widespread in the animal kingdom, thereby supporting the idea of virtual contours being a vital construct for visual animals.

Animal experiments concerning illusory contour perception and processing started in 1962 with Zimmermann’s discrimination tasks with baby monkeys. He trained the monkeys with real, solid figures and tested their perceptual performance with outlined or incompletely outlined figures. The animals were able to do the task similarly well with the partial figures as with the complete and solid figures, indicating perceptual completion of the physically incomplete structures. The perception of Kanizsa-type illusory figures has later been also studied in a comparative study with humans and chimpanzees by Fagot & Tomonaga, reporting indications for illusory figure perception in chimpanzees. This perceptual similarity between humans and monkeys supports monkey physiology as a tool to study processes leading to perception also in humans.

Based on the assumption of monkey physiology being a good model for human processing, von der Heydt & Peterhans carried out experiments in 1984 in which they studied the neural signals in early visual cortex of awake macaques to illusory contour stimulation. They reported single neurons in V2 responding to illusory contour stimulation. V2 neurons responsive to virtual contours were orientation selective and responded stronger to the optimally oriented real line than to the illusory contour of the same orientation. In the following studies [109, 78] Von der Heydt & Peterhans could replicate these first findings and showed not only V2-responses to Kanizsa-type illusory figures, but also to illusory contours induced by abutting lines. Most interestingly, neurons did respond to Kanizsa-figures even if the inducers did not touch the cell’s receptive field, indicating feedback from higher areas or complex horizontal computations leading to the cell’s responses.

In these studies Peterhans & Von der Heydt found only very few V1 cells responding selectively to illusory contours, whereas about 32 to 44% of the V2 cells tested were selective for illusory contours. They concluded that V2 is the first area to ‘bridge gaps’, and that V1 is primarily a contrast edge detector [79].

Grosf et al. 1993, in contrast to the ‘V2 bridges gaps’- hypothesis, reported V1 responses to illusory contours of the abutting line type. Their study was in critique as the stimuli contained low-level contrast information which could have led to a real contour response (Van der Zwan & Wenderoth 1994). The finding of V1 responding to illusory contours, however, has been reproduced by other groups. Lee & Nguyen 2001 conducted recordings of single cell responses in both areas V1 and V2 to squares which were, in partial disc arrangement, either outlined, modally or amodally completed. They found both primary and secondary visual cortex responses to real and completed figures, but reported these signals to appear in an unexpected sequence. The earliest responses were found in V2 cells, followed by the V1 responses which were not very strong until over 100 msec after V2 had signalled the illusory figure. These results show that Peterhans and Von der Heydt (1989) were correctly assuming that V2 is the first area to respond to illusory contours. It might, however, send its information about the virtual contour back to V1.

Another report of primary visual cortex activity to illusory contours was published by Ramsden et al. (2001). Using optical imaging in the anaesthetized macaque they measured cortical activity to illusory (induced by abutting line pattern) and real contour stimulation. Orientation domain patterns in V2 to illusory contours

were found to be similar to the real contour domains. In V1 too, illusory contours resulted in different activation patterns dependent on orientation, thus indicating that illusory contours activate V1 as well as V2. Orientation domains, however, were different from real contour orientation domains: domains activated best by vertical real contours were activated best by horizontal illusory contours. As no illusory contour responses have been reported earlier than V1, this orientation reversal in V1 is one further indication of a complex computation involving areas higher than V1. This higher area possibly feeds back illusory contour information via a different path than real contour information.

These recent findings (Lee & Nguyen 2001, Ramsden et al. 2001) indicate that primate V1 does not only detect physical (real) edges, but also receives information related to or leading to edge completion.

Other mammals studied besides primates are primarily cats. Single cell responses in cat visual cortex to illusory contour stimulation with abutting gratings were first recorded by Redies et al. 1986. They found neural responses to illusory borders to be similar to real contour activity, confirming the results by Von der Heydt & Peterhans (1984) in macaques, but reported not only responses in the cat correlate to primate V2, but also V1.

Cat visual cortex thus appears to have processes which are similar to primates and contain information about completed edges. But do they also perceive illusory contours like primates do? That they probably do has been shown by Bravo et al. (1988). They trained cats in a 2AFC task to detect real figures in two displays. They then tested their ability to detect illusory figures of the Kanizsa type in similar displays, where one sides partial discs were rotated to not induce an illusory figure. The two cats tested were significantly above chance rate in this experiment, indicating that they were able to discriminate the illusory figure from the randomly rotated partial disc arrangement.

Cats' performance in orientation discrimination of illusory contour has been tested by DeWeerd et al. in 1990. They used contours induced by abutting line patterns as introduced by Vogels (1987) in a human psychophysics experiment. In this experiment subjects (or cats) had to decide in a just noticeable difference task whether an oriented line or illusory contour was tilted leftwards or rightwards relative to a reference orientation presented before. Humans were found to be as good with illusory as with real contours in this task [108]. Cats were able to do the task too, but had a better performance with the real than with the illusory stimulus [12].

From these reports it is apparent that mammals might in general be able to process and perceive illusory contours and figures. Edge completion, however, would be useful for every animal trying to structure a visual scene, not only cats and primates. Supporting this view, also other species were found to perceive virtual contours.

Chickens, for example, were found to perceive illusory contours in 1981 by Zanforlin (1981). In 1988 a study by Frost et al. (1988) followed, showing neural activity in pigeons to illusory contours in a kinematogram.

Nieder & Wagner recorded 1999 single cell responses in alert barn owls primary visual system (visual Wulst) to illusory contour stimulation. They tested abutting gratings with a gap (i.e. with real contrast border), and without gap at different spatial frequencies of the grating. Single-unit activity to illusory contours was then compared to real contour responses. They found that almost all contour-sensitive cells responded also to illusory contours independent of local information like grating spacing. In the same study they also investigated the barn owls' perception of illusory contours. The owls were found to be able to transfer from practice sessions with real contour figures to performing a task with illusory contour figures. This results indicated that the animals were well able to perceive illusory figures comparable to stimuli defined by luminance contrast.

Most surprisingly, illusory contour perception has been demonstrated even in honey

bees. Van Hateren et al. 1990 trained bees in a discrimination task with tilted solid rectangles. To get a sugar-water reward, the insects had to choose one of two ways in a Y-maze, based on the tilt of the presented rectangle. The bee's performance in the test with Kanizsa-type rectangles was better than chance. The performance with partial discs rotated such that they did not induce an illusory figure, in contrast, was clearly at about chance.

A similar experiment was conducted 1992 by Horridge et al. (1992). They trained honey bees with real lines (vertical and horizontal) and tested them with an illusory line induced by abutting gratings. They found that when the training lines were embedded in a pattern similar to the abutting grating, the bee's performance in both tasks was comparable, thereby suggesting that also honey bees can perceive illusory contours induced by various contexts.

These reports show illusory contour processing and perception crossing over species as different as mammals, birds, and insects. The studies thus suggest that construction of an illusory contour is an important feature of visual systems in general, as hypothesized above. That the perception of virtual contours is comparable in animals as different as bees and monkeys, with independently evolved visual systems, indicates the importance of mechanisms for edge completion (see also the review by Nieder 2002).

From these studies a picture of processes in early cortical stages emerges. In primates, the earliest illusory contour selectivity has been found in areas V1 and V2 (Von der Heydt et al. 1984, Lee & Nguyen 2001, Ramsden et al. 2001), in barn owl responses have been recorded in the visual Wulst (the analogon to our primary visual cortex) (Nieder & Wagner 1999). How might these mechanisms work, and are they really low-level computations, as the animal experiments reported here might suggest? In the following sections I will focus on primate psychophysics and physiology, summing up our current knowledge about perception and neural correlates of illusory contours.

1.1.2 Psychophysics of Illusory Contours

Psychophysics is a method to measure the relationship between physical events and perception. But how can the perception of something which does not have a physical counterpart be measured psychophysically? Following section, different ways to study illusory contour perception will be described and discussed. I will focus on the two type of illusory contour stimuli which have been studied most extensively and which will also be employed in this thesis: Kanizsa figures, and abutting line patterns.

Kanizsa Figures

Kanizsa presented 1976 among other examples of perception of contour completion a new illusory figure: 'Pacmen', i.e. three partial disks which were arranged such that they span an illusory triangle between them, as depicted in Fig.1.6. This stimulus was since then used in similar form by many psychophysical as well as physiological experiments.

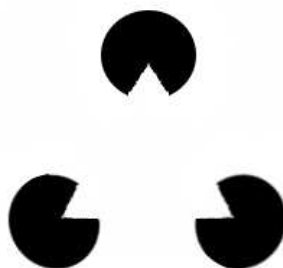


Fig. 1.6: Kanizsa 1976. Three partial discs are arranged in such a way that they span an illusory triangle between them.

Kanizsa-figures induce simultaneously illusory contours, an illusory figure, illusory brightness of the figure, and mostly even an illusory depth percept, along with the percept of amodal completion of the inducers. This makes them at the same time one of the most volatile and problematic stimuli in illusory contour examination. Their complexity leads to many uncertainties of how to understand experimental results. Therefore, studying illusory contour perception was for many years mostly concerned with the search for ways to measure and modulate illusory contour strength, and, most importantly, to control for the many different possible explanations of modulatory effects.

One step forward in these efforts was achieved by Shipley & Kellman (1992), who reported the 'support ratio' to be a modulator of illusory contour strength in Kanizsa-figures. While measuring perceived contour clarity in a rating task, they changed inducer diameter and distance, thereby changing size of the inducers and length of the illusory contour. They found that subjects rated illusory contours with small inducers, but also small illusory contour length, to be similar strong as longer contours induced by bigger inducers. They concluded that the support ratio, the ratio between length of the inducing contours and the length of the induced contour, was the most important factor for perceptual strength of Kanizsa-type illusory figures. Thus, it is possible to gradually modulate the perceptual strength of illusory figures by controlled changes of the physical information provided by the inducers.

A completely different way to study illusory contour perception is based on the form of the Kanizsa figure and the possibility to change this illusory form with little changes in the inducers. Reynolds (1981) introduced Kanizsa-triangles with either curved or straight sides. After short presentation of these figures, subjects had to indicate whether they perceived the illusory figure, and whether this figure was perceived to be curved or straight. Using backward masking of the inducers at different times after stimulus presentation, Reynolds found that about 120 msec of uninterrupted processing time is needed to perceive the illusory figure. For discrimination between curved and straight figure the stimulus has to be processed for about 20 msec more. Besides giving new insights in the temporal evolution of illusory contour processing, this study introduced form discrimination and backward masking as new tools to measure illusory contour perception.

Based on Reynold's experiments (1981), Ringach & Shapley (1996) developed a fat/thin task with Kanizsa-type illusory squares. The inducing partial discs were slightly rotated to induce vertical illusory contours which were bent inward (thin), or outward (fat). In Fig.1.7 the fat illusory figure is shown as a stimulus in a backward masking paradigm. Subjects had to discriminate between these two possible forms in a two alternative forced choice experiment with constant stimuli. Perceptual thresholds in this task were measured in dependence of presentation time and mask type.

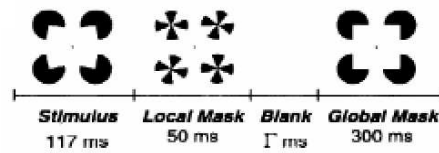


Fig. 1.7: Ringach & Shapley 1996. Partial discs in a Kanizsa square were rotated to induce a fat, or thin figure. Backward masks interfering with the inducers ('local mask') and masks interfering with the illusory percept ('global mask') were presented at different times after stimulus onset.

Backward masking was done using a 'local mask', which was designed to interfere with the inducers, or a 'global mask', designed to interfere with the illusory figure. Testing mask effects on discrimination thresholds over different mask onset times, Ringach & Shapley (1996) found that interference by local masking occurred significantly earlier than interference by global masking. With these experiments, they were able to support reports about the temporal development of illusory contours (Reynolds 1981, Westheimer & Li 1996), and extended that knowledge about the point that early on (until up to 117 msec presentation time) 'local masking' was possible by interference with the inducers, but later on 'global masks', in their case uncurved illusory squares, were needed to interfere with the illusory percept. Interaction with this later step was impossible after 250 msec. Processes occurring at the later time appear not to be involved in real contour processing (Imber et al. 2005). Part of the experiments I present in this thesis (chapter 4 & 5) are based on the fat/thin task introduced by Ringach & Shapley (1996).

One additional idea about how to study illusory contour strength has been used by Dresch & Bonnet (1995), who did not directly modulate the Kanizsa-figure illusory contour, but superimposed a subthreshold real line on it. In detection experiments they found that the subthreshold real line was detectable, i.e. suprathreshold, in combination with the illusory contour. This effect was not due to an uncertainty reduction as they showed in a control experiment. They concluded that subthreshold summation occurred between illusory and real contours. The results Dresch & Bonnet obtained in their study, however, were criticized 1994 by McCourt & Paulson, who found in a similar study variable and inconsistent effects over different observers. Real stimuli were only found to be more or less detectable dependent on their distance to the illusory contour. I will present in chapter 4 new data which support the critique by McCourt & Paulson and furthermore indicate that detectability of real elements superimposed on illusory contours is not a valid experiment to study the perceptual strength of illusory contours.

A very recent technique using Kanizsa-figures has been published by Guttman & Kellman (2004). They presented a Kanizsa figure in Ringach's fat/thin configuration [88] and positioned a small dot either out- or inside of the figure. Subjects had to discriminate the dot's position relative to the illusory figure. With this concept, Guttman & Kellman not only gained information about the perceived form of the illusory figure, but also about the precision of the illusory edge percept. By measuring the locational error and, using outside and inside thresholds, the imprecision of the dot localization in a backward masking paradigm, they could show that illusory contours reached highest precision after 120 msec of processing, about 40 msec later than real contours [27]. This again supports the 117-120 msec time point of illusory contour processing as also found by Reynolds (1981), Ringach & Shapley (1996), and Westheimer & Li (1996). Control stimuli inducing either weak or no illusory contours needed significantly longer (up to 170 msec) to reach similar accuracy, indicating the use of different and more cognitive strategies in those stimuli. This study thus provides with the dot localization task a new powerful tool to study

illusory contour perception and especially precision of the underlying processes.

Abutting Line Patterns

Vogels & Orban studied 1987 whether orientation discrimination of illusory contours was similarly good as with real contours, and whether illusory contours showed early cortical properties of oriented lines such as the oblique effect. In a 'Just Noticeable Difference' task (JND) they presented a pattern of semicircles of different radii abutting to its mirror image, as shown in Fig.1.8. The induced illusory contour could be rotated by rotating the pattern of half circles.



Fig. 1.8: Vogels & Orban 1987. Semicircles of different sizes are arranged with mirror-symmetrical semicircles to induce an illusory contour between them. Rotation of the circular pattern leads to tilt of the illusory contour.

Vogels & Orban showed with their experiment that orientation discrimination of illusory contours in humans is as good as for real contours. Moreover, they found that also illusory contours show the oblique effect: discrimination thresholds were much better at vertical and horizontal orientations, than at the oblique orientations. These experiments thereby not only opened a new set of options for quantitative assessment of perceptual strength of illusory contours, but also showed that illusory contours are perceptually very similar to real contours and share some of their properties.

Also using orientation discrimination, Westheimer & Li (1996) further optimized the stimulation by studying the influence of abutting line orientation and presence of a gap versus directly abutting line patterns on the illusory percept. They showed that orthogonal abutting lines were optimal to induce illusory lines. Furthermore, they presented evidence for a difference between directly abutting line patterns and patterns separated by a gap, with the gap stimulation being more robust against masking and orientation changes of the inducing lines.

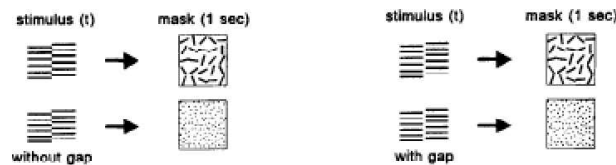


Fig. 1.9: Westheimer & Li 1996. Illusory contours are backward masked in an orientation discrimination task. Masks found to be most effective were random line pattern.

As shown in Fig.1.9, they also tested illusory contours in a backward masking paradigm. If illusory contours are cortically represented similar to real lines, similar masking effects should occur. Oriented real lines can be optimally masked by real lines rather than by any other masking pattern (Li et al. 2000). This study could indeed show that illusory contours are masked better by random lines than by a random dot pattern of the same overall contrast [114]. Masking effects decrease after illusory contour processing of about 100 to 120 msec, comparable to the studies cited before [87, 88, 27]. The stimuli and experimental paradigm used in chapter 3 are based on the study by Westheimer & Li (1996).

Thus, illusory contours induced by abutting line patterns can be treated and studied similar to Kanizsa figures. This includes the possibility to design psychophysical tests using small changes in the inducing elements which lead to clearly distinguishable perceptual changes in the illusory contour (Ringach & Shapley 1996, Vogels & Orban 1987, Westheimer & Li 1996, Guttman & Kellman 2004). Illusory contours of both types employed here show interactions with real contours (Kanizsa 1976, Paradiso et al. 1989), including masking effects which change over time and which depend on the mask type (Reynolds 1981, Ringach & Shapley 1996, Westheimer & Li 1996). Thus, various experimental tools to study illusory contour perception and the underlying processes have been reported previously. These tools allow to measure the perceptual strength and contextual modulation of both virtual contour stimuli which I will focus on in this thesis.

1.1.3 Localisation of Illusory Contour Processing in Primates

Which are the neural correlates of illusory contour perception? Psychophysical investigations suggest at least in part common mechanisms of real and illusory contour processing, which are to some extent assumed to reside in early visual cortex. Support for this idea has been reported by von der Heydt et al. 1984, who showed single cell responses in primate V2 to illusory contour stimulation to be comparable to real contour related activity.

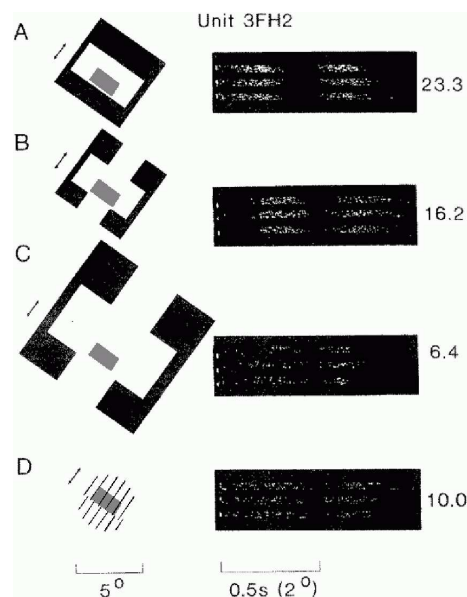


Fig. 1.10: Von der Heydt & Peterhans 1989. A V2 single unit responds to real edges moving over its receptive field (A) as well as to illusory edges (B-D) with different inducing elements, which even can be outside the RF.

These cells were found to be relatively cue-invariant (Von der Heydt & Peterhans 1989, Peterhans & Von der Heydt 1989). They responded to illusory contours induced by stimuli similar to the Kanizsa-triangle as well as to abutting line patterns, as can be observed in Fig.1.10. The recorded illusory contour units responded even when the inducing elements were clearly outside their receptive fields [109], showing that contextual effects lead to illusory contour responses early in the visual processing pathways in cells also signalling real contours.

Indication of neural signals to illusory contours in even earlier stages have been reported by Grosf (1993), who showed that macaque area V1 responds to abutting

line stimuli. This result has also been found by other groups, showing single cell responses to disparity based occlusion, flashed Kanizsa-figures (Lee & Nguyen 2001), as well as intrinsic activity to abutting line patterns (Sheth et al. 1996, Ramsden et al. 2001).

Besides macaque or cat visual cortex, also human early visual cortical areas respond to illusory contours, as shown by Hirsch et al. (1995). They acquired fMR images of subjects viewing either an outlined square, a Kanizsa-type square or the variant shown before in Fig.1.4 with partial discs consisting of concentric rings. In comparison to luminance controls (i.e. rotated inducers, or luminance defined square in the inducer arrangement) Hirsch et al. found first, that illusory contours led to different activation pattern than no-contour stimulation. Second, activity related to illusory contour stimulation was found in extrastriate areas (V2 and higher), but might also involve striate cortex (i.e. V1) [31].

Similar results were obtained using PET. ffytche et al. (1996) measured regional cerebral blood flow to presentation of a Kanizsa-triangle and a real triangle in comparison to a rotated control in human observers. Blood flow changes in higher areas, i.e. outside the occipital lobe, would support theories of higher order cognitive processes for illusory contour processing. If, on the other hand, activity was found mainly in the occipital lobe, the low-level processing hypothesis would be supported. ffytche et al. (1996) found illusory contour activation only in early areas, especially in the central visual field in V2, but also possibly in V3. These results indicate that no higher cognition is needed for illusory contour extraction. The areas activated by the illusory figure were activated by the real triangle. Activation was, however, diminished in this case. This suggested that the completion process might have been active in this condition, but attenuated by the addition of real contours. On the other hand, this results might show that V2 is involved in the processing of simple shapes but recruits more, and other cell pools to complete the illusory figure [18].

Are the reported activations in early visual cortices related to illusory contours, or rather to their inducers? Sheth et al. (1996) tested this by measuring intrinsic activity to subjective and real contour stimulation in cat V1 and V2. Using oriented luminance gratings they measured orientation maps, which were compared with orientation maps obtained with subjective gratings, induced by orthogonally oriented real lines. They found real and illusory orientation maps widely overlapping in V2, indicating neural activity selective to subjective contour orientations comparable to real contour orientations. In V1, in contrast, they found the subjective orientation map to differ by up to 90° to the real orientation map, suggesting that V1 is more responsive to the inducing real than to the induced illusory orientation. Single cell recordings showed the ambiguity of these results: 42% of the tested V1 cells carried illusory contour information, in part in combination with responses to the real contours [96].

Also higher visual areas might be involved at least in illusory figure processing, as shown by Mendola et al. (1999) in an fMRI study. BOLD change in human visual cortex was measured in conditions with illusory versus real figure stimulation, or to illusory figures versus control stimuli without figural elements. They found higher activity to abutting line figures than to a simple grating along the whole visual cortical pathways (V1 up to V7 and LOR). Activity to abutting gratings changed with spatial frequency of the grating, showing possibly changes in strength of the illusory figure with changes in the inducing real elements.

Further evidence for involvement of higher-level processes at least in amodal completion has been found by Corballis et al. 1999 by studying two 'split-brain' patients. Testing the subject's performance in form discrimination tasks they found illusory contours to be perceived using both hemifields separately, suggesting low-level mechanisms common to both hemispheres for illusory contour construction.

Both subjects were considerably worse in discrimination of an amodally completed figure, indicating more higher-level, lateralized processes. These results supported other indications for early cortical mechanism for basic illusory contour processes, while suggesting that amodal completion might be based on more complex, higher level processes [9].

Larsson et al. (1999) criticized that most studies did not compare real and illusory contour activation in one subject. Furthermore, attentional states and their possibly important role in illusory contour perception were mostly neglected. Moreover, real and illusory stimuli mostly differed in saliency, thereby possibly influencing attention and neuronal activity not related to contour completion. Larsson et al. thus performed a PET study with subjects either performing a discrimination task with a real, or an illusory form, or while simply fixating, using aligned line ends as inducers. They found wide overlap of areas activated by real and illusory contours, including V1 and V2. One region in the right fusiform gyrus, however, was activated stronger by illusory contour stimulation, suggesting higher-area involvement in illusory contour processing. In a principal component analysis they found in addition a decoupling of areas V1 and V2 in illusory contour processing. Both areas correlated significantly in fixation and real contour conditions, but not in the illusory contour condition. This might reflect different neuronal mechanisms in the same areas for processing real and illusory contours [57].

Additional evidence for robust V1 activation by illusory contours has been provided by Seghier et al. (2000), who carried out an fMRI study stimulating human subjects with moving illusory contours. They found activation in V5, but also, and stronger, in V1 and V2. Primary visual cortex activation was also confirmed with static illusory contours, however weaker than with moving stimuli. This might be an indication for a possible feedback from higher-level areas which enhances segregation of figure and ground (Hupé et al. 1998). These results suggest that low-level visual areas including V1 are involved in perceptual grouping and illusory contour processing [95].

Following the earlier study by Sheth et al. (1996) in cats, Ramsden et al. (2001) measured intrinsic activity using optical imaging in macaque V1 and V2. Differential activity between real gratings and abutting gratings with obtuse or acute real lines showed V2 real and illusory contour orientation maps that were widely overlapping. In V1, however, orientation maps were shifted by 90°. Sheth et al. obtained similar results, but concluded that the V1 activity was due to the inducing lines. Ramsden et al. showed that V1 was specifically activated by the illusory contours, yet with reversed orientation maps [84].

Along with the results by Lee & Nguyen 2001, who showed single cell responses to Kanizsa-figures in both V1 & V2, but with higher latency in primary visual cortex than in secondary, these results suggest not only that V1 indeed is involved in the processing of illusory contours, but that also feedback from V2 or higher areas might be the major source of illusory contour information in V1 [58, 84].

In contrast to this, Murray et al. (2002) showed with EEG and fMRI evidence for illusory contour signals not occurring earlier than in higher-level object recognition areas of the LOC. They thus replicated the earlier results by Mendola et al. (1999). Measuring latencies to illusory figure response onset, Murray et al. found earliest VEP modulation at 88 msec after stimulus onset, which was about 40 msec after the initial visual cortical response. They concluded that illusory contour information in early visual areas might be due to feedback from higher areas such as the LOC. The same group later furthered their study in the temporal domain comparing modal and amodal completion (Murray et al. 2004), showing a common initial mechanism for both completion processes at 140 msec after stimulus onset. This process manifested itself as a modulation in response strength within higher visual areas, including the LOC and parietal structures. Differential mechanisms to

amodal and modal completion were evident only from 240 msec on with amodal completion relying on continued strong responses in these structures.

Neural correlates of illusory contour processing can thus be found in earliest cortical stages, including V1 (Grosf et al. 1993, Seghier et al. 2000, Lee & Nguyen 2001, Ramsden et al. 2001) and V2 (von der Heydt & Peterhans 1989, Peterhans & von der Heydt 1989, ffytche et al. 1996, Seghier et al. 2000), but have also, possibly dependent on more complex stimulus attributes, been found in higher areas (Hirsch et al. 1995, Mendola et al., Murray et al. 2004). Low- and high-level processes are possibly linked by recurrent processes (Lamme et al. 2000, Lee & Nguyen 2001, Murray et al. 2004).

1.1.4 Physiological Studies of the Neural Correlate

The characterisation of neural signals in cat and monkey primary visual cortex by Hubel & Wiesel starting in 1962 (Hubel & Wiesel 1962, Hubel & Wiesel 1968, Hubel & Wiesel 1977) showed that oriented lines are the optimal stimuli for most V1 neurons. In their studies they revealed the functional architecture of areas V1 and V2 that gave rise to a new understanding of the processes leading to visual perception. The visual system has been understood since then as hierarchical structure with functionally highly specific domains which process different attributes of visual stimuli in parallel. This functional segregation allows for 'low-level' computation of retinal input that might be sufficient to explain many aspects of visual perception. In 1984, von der Heydt et al. found that V2 in monkeys does not only preferably respond to oriented physical contours, but also to illusory contours. Cells selective for virtual contours appeared not to be dependent on the type of inducer leading to the virtual contour (Von der Heydt & Peterhans 1989). Cells were, for example, activated by abutting gratings with different line distances if only the induced contour was oriented optimally for the respective cell. Also the perceptually completed edges of Kanizsa-type figures were found to activate these neurons. In this case neurons fired even when the inducers were outside their classical receptive field, suggesting information processing outside of strictly hierarchical bottom-up structures.

Neuronal responses can be modulated by contextual stimuli outside the classical receptive field, as has been shown by Knierim et al. (1992). Contextual modulation of the earliest cortical processes might allow early visual cortex to be involved in complex perceptual processes, such as pop-out effects (Knierim et al. 1992 or figure-ground segregation (Lamme et al. 2000). The latter study tested cell's responses in V2 to an illusory figure which was induced by abutting textures. Cells responded differentially if lying on an illusory figure or on the background of the identical texture, even though the illusory borders were outside of the cell's classical receptive field. This supported not only the idea of illusory contours as an important part of object construction and figure-ground segregation, but also that early cortical cells contain complex information about objects outside their reach [54]. The neural substrate of these contextual modulations might be connections to neighbour neurons of the same area (horizontal connections) as well as feedback from neurons of higher areas (Lamme et al. 1998).

Even earlier responses to illusory contours than in area V2 have been reported by Grosf et al. 1993, who found V1 responses to these stimuli in the macaque. The stimulus employed in this study, however, has been criticized for containing low-level information in the cell's preferred orientation. Illusory contour responses in V1 might thus not be existent, unless induced accidentally by real stimulation.

Leventhal et al. 1998 probed neural correlates of boundary perception, stimulating cells of areas V1 and V2 in cats and macaques with edges induced by various cues,

including gratings, textures, and motion. Especially in V2, but also in area V1, they found many cue invariant cells, containing information about orientation and direction of borders regardless of the cues inducing these borders. Cue-invariant cells were found to be less orientation-specific than cue-dependent, luminance contour cells, which is consistent with Westheimer & Li's finding (1997) of poorer orientation discrimination ability with illusory than with real contours. Leventhal et al. concluded that cue-invariant cells might signal the presence of an edge already in earliest processing stages, thereby building an important bridge between the highly variable stimulation of our physical world and our need to construct simple borders to recognize objects in their surround [59].

Sugita studied 1999 the complexity of primary visual cortex 'simple' cells and their responses to amodally completed bars, as shown in Fig.1.11. He presented either a completed bar crossing the receptive field of the recorded cells, or the same bar occluded by a visible or invisible (i.e. background) patch in the range of the RF. Cells did only respond to complete bars, unless, however, disparity information was added such that the patch appeared to lie in front of the bar. Thus, the bar was perceived to be occluded, and V1 cells responded similarly strong to it as to the luminance contrast bar. If the disparity information led to the percept of two separated bar segments in front of the patch, cells did not fire. Controls showed that the cells did not respond to the disparity information or the patches themselves. Response latency to amodally completed bars was not found to be different than that to normal bars crossing the RF.

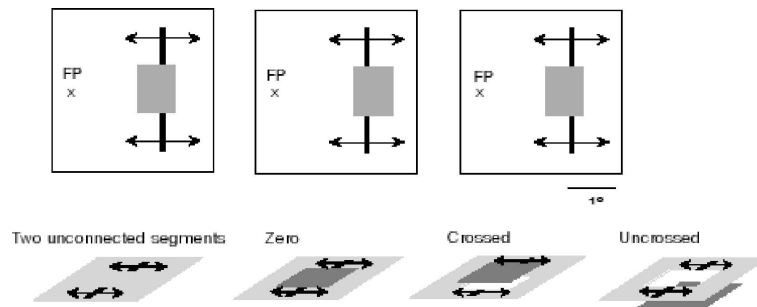


Fig. 1.11: Sugita 1999. Bar fragments are perceived as amodally completed if a cross-fused patch separating them lies in front of them, but not if the patch lies behind.

Sugita thereby could show that information about completion based on disparity cues is available as early as V1, probably fed to the cells via lateral connections or feedback from an area very close to V1.

Similar recordings were conducted in area V2 by Bakin et al. (2000). Using flank facilitation as a measure for contextual influences on neural responses they could show that V2 neuronal responses in the macaque differed when the receptive fields were lying on illusory surfaces or outside of them. They presented a bar in the cell's receptive field and modulated its response with a collinear flank outside of the RF. By modulating depth cues outside of the classical receptive field they induced the percept of central bar and flank lying either in the same plane of depth, or in different distances from the viewer. Cells responded stronger to collinear facilitation in the same depth plane, while showing no decrease in the response to orthogonal inhibitory flanks which were in a different plane than the central bar. Responses modulated by contextual depth cues had the same latency as responses to the bar alone. As no disparity information was presented inside of the neurons receptive fields, these results indicate complex processing already in V2, leading to single cells being informed not only about real or illusory contours in their receptive fields, but also about the illusory figures the neurons are 'looking' at [5].

Using optical imaging of intrinsic activity Ramsden et al. (2001) could show activation of V2, but also V1 to abutting line illusory contour stimulation, thus supporting earlier reports of primary visual cortex belonging to the processing chain for illusory contours (Grosf 1993, Sugita 1999). Ramsden et al. found, however, a surprising relationship between illusory and real contour activation in V1: illusory and real orientation maps were found to be reversed, as can be seen in Fig.1.12, whereas V2 did not show such a reversal.

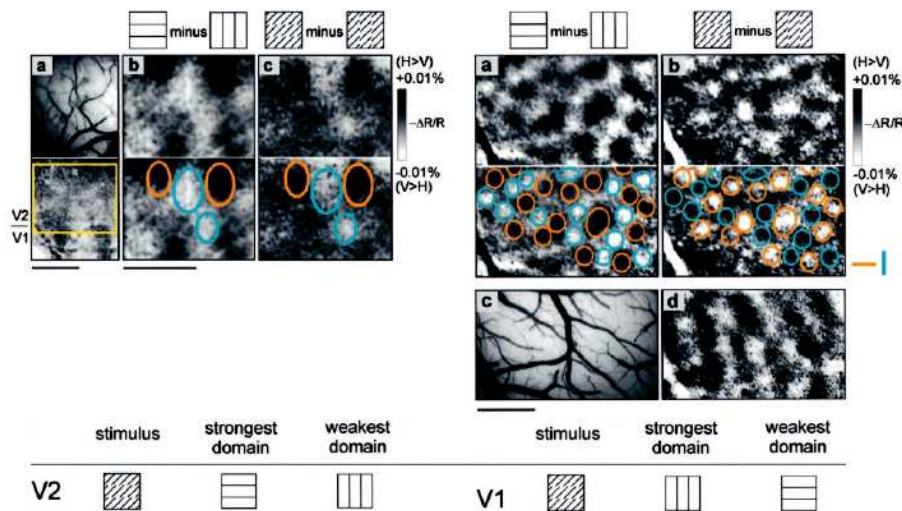


Fig. 1.12: Ramsden et al. 2001. Differential optical imaging in V2 shows overlapping orientation maps to illusory and real contour stimulation. Real orientation maps in V1, however, overlap with the activity evoked by the orthogonal illusory contours.

V2 domains activated best by horizontal real contours overlapped with domains activated strongest by horizontal illusory contours. In V1 those domains showing highest activity to horizontal real contours were found to respond best to illusory contours of the vertical orientation, and vice versa. Similar results were found 1996 by Sheth et al. in cat area V1 [96], but were ambiguous in their meaning because of the stimulus configuration. As primary visual cortex has been shown not to carry the first illusory contour signal (von der Heydt et al. 1984, Lee & Nguyen 2001), the reversed activation in V1 might be due to feedback information, possibly from V2 [84].

Further indication for V1 involvement in illusory contour processing and a possible feedback mechanism has been shown by Lee & Nguyen (2001). They studied single cell responses in V1 and V2 of macaques to Kanizsa-type illusory figures, real outlines and amodally completed figures. They found V1 clearly signalling to different types of completed contours, but its responses were delayed relative to the V2 responses. Control stimuli (rotated partial disks) did not induce single cell responses.

Response latencies in V2 were with 70 - 90 msec found to be comparable to earlier reports about illusory and real contour related activity in V2. V1 responses occurred in the superficial layers first, responding at about 100 msec, followed by deeper layers from 125 msec on. Deep layer responses were not significant before 190 msec after stimulus onset. Lee & Nguyen concluded that the illusory contour signal found in V1 was probably due to feedback from higher areas like V2 [58].

It has been shown that the earliest single cell responses to illusory contours occur in V2 (von der Heydt et al. 1984, Lee & Nguyen 2001) in mostly cue-invariant cells

(von der Heydt & Peterhans 1989, Peterhans & von der Heydt 1989, Leventhal et al. 1998). Primary visual cortex has also been found to signal illusory contours (Grosfof et al. 1993, Sugita 1999, Lee & Nguyen 2001, Ramsden et al. 2001). This response occurs later, however, than the one in area V2 (Lee & Nguyen 2001) and orientation reversed to real contour activation (Ramsden et al. 2001). Masking effects (Macknik & Livingstone 1998, Li et al. 2001) as well as contextual modulation outside the receptive field (Li et al. 2000, Li et al. 2001, Kapadia et al. 2000, Sugita 1999) have been shown to affect V1 responses in close correlation to perceptual effects. Therefore, it can be speculated that primary visual cortex activity is an active and vital part in the processing of illusory contours.

1.1.5 Connectivity: Feedforward, Feedback, or Horizontal?

The visual cortical system is largely understood as a hierarchically structured system. Early areas like V1 extract basic stimulus features, feeding forward information via different pathways according to stimulus attributes to higher areas which reconstruct increasingly complex objects. Connections providing the neural substrate for local feature processing might be intrinsic horizontal connections which combine neural signals from distant neurons preferring similar stimulus attributes. Feedback connections, on the other hand, might build the basis for adjusting the processing of physical inputs with higher-level information such as complex stimulus properties, knowledge, and expectation.

Which of these anatomical structures might underlie illusory contour processing? First attempts to understand the underlying mechanisms resulted in cognitive or higher level explanations, implying that neural signals were processed in a feedforward manner with increasing complexity up to cognitive processes recognizing figures. Gregory introduced 1972 the term 'cognitive contours' to imply already with the name the mechanisms supposedly leading to the percept. Kanizsa proposed 1976 his completion hypothesis, according to which our cognitive system completes figures and their borders in otherwise incomplete objects. Many examples of illusory contour perception appear to support these ideas, as illusory contours often outline physically invisible occluders. Completing the occluder, as can be seen in Sugita's example in Fig.1.11, leads to perceptual completion of an otherwise fragmented object. The example by Albert et al. (2001) in Fig.1.3 shows, though, that illusory contours can be perceived even without explanatory need for completion.

Marr, on the other hand, suggested 1976 that first order discrimination and grouping leading to figure-ground segregation might act on the 'primal sketch' of the physical input. He proposed top-down influences from higher areas onto low-level processing stages to act later to control and adjust visual processing based on knowledge and purpose. This model thus suggested early visual processing to be sufficient for many operations thus far understood as 'cognitive'.

Cognitive or high-level theories of illusory contour perception dominated until the first neural responses to illusory stimulation were recorded in area V2 of the macaque (von der Heydt & Peterhans 1989). These recordings clearly showed the involvement of low-level structures in contour completion. Von der Heydt & Peterhans assumed that horizontal connections provided the information from outside of the receptive field which led to illusory contour responses in V2 single cells.

Horizontal connections coincide with cross-correlated activity of cells of similar orientation selectivity separated by several mm, as has been shown in cat primary visual cortex by Ts'o et al. (1986). Neurons in V1 might thus be able to integrate stimuli over wider areas than their receptive field size would allow. Similar network properties and connectivity have been shown in the macaque monkey (Livingstone & Hubel 1984, Gilbert 1992) and hence might provide also in humans a possible neural substrate for collinear contour integration. These connections have been shown

between V1 cells with non-overlapping receptive fields (Salin & Bullier 1995), thus building a large network able to process global in addition to local information.

More support for a horizontal network for contour extraction and completion came from Stettler et al. (2002), who labelled V2 domains with the retrograde tracer GFP (green fluorescent protein) using transfection via an adenovirus. They found that V2 feedback extends the same area as V1 intrinsic horizontal connections. Feedback connections, however, appeared to be less dense, and sizes of iso-orientation domain periodicity in V1 and V2 were inconsistent, leading to the notion that the V2-feedback to V1 might be uncorrelated with orientation. Horizontal connections in V1, in contrast, were found to be highly orientation specific. These results would not support an contour integration system based on feedback under the assumption that such a system would need iso-oriented or at least uni-oriented feedback from V2 to V1.

In contrast to Stettler et al. (2002), Angelucci & Bullier (2003) found iso-oriented feedback from V2, which, in addition, also covered a larger area than horizontal connections. They concluded from their results that surround properties of V1 cells might be mainly due to feedback. They furthermore tested the effect of V2 inactivation using GABA injections and found decreased responses in V1 to flashing bar stimulation. Angelucci & Bullier concluded from their work [8, 3, 2] that feedback from V2 enhances V1 center responses and surround suppression.

That feedback connects V1 not only with neighbouring extrastriate area, but also with higher level areas had already been shown 1994 by Rockland & Van Hoesen in a tracing study. They found feedback connections to V1 in macaque from several close areas from V2 up to MT, but also from distal, higher-level areas like TEO. Anatomical results would thereby support the possibility of recurrent networks feeding back higher-level signals about complex, possibly illusory objects to low-level areas such as area V1.

Is there also evidence for physiological relevance of feedback? Cortical feedback indeed modulates neural response of areas V1, V2, and V3 in figure-ground segregation, as has been reported by Hupé et al. (1998), who recorded single cell responses while reversibly inactivating area V5/MT. They found neural responses to a central moving bar on a stationary background reduced by cooling, suggesting V5 feeding back motion information and thereby rendering the bar more visible on its background. Responses to the bar moving together with the background, however, were increased, indicating that background suppression might be under feedback influence. All effects were strongest for low-salience stimuli, silencing in absence of feedback from V5 some neurons in V1, V2, and V3 completely. Feedback has thus been shown to shape and modulate early visual cortical signals in a mostly excitatory fashion, specifically enhancing figure-ground segregation of low salience stimuli [38].

One further argument for a feedback and against a horizontal network as major component in contour completion is the difference of their conduction velocity. Girard et al. showed 2001 that feedback connections have a conduction velocity similarly fast as feedforward connections, whereas horizontal connections are considerably slower. The high velocity of feedback coincides with almost undelayed effects of inactivation of areas MT or V2 onto V1 (Hupé et al. 2001) as well as with earliest V1 responses to illusory contour stimulation following V2 by only 10-20 msec (Lee & Nguyen 2001).

Is the primary visual cortical activity essential for illusory contour perception, or is it a mere side effect of a highly intertwined and recurrent system?

Supèr et al. showed 2001 that the difference between psychophysical visibility and invisibility of a target illusory figure on textured background was reflected in modulations of the neural signal in V1. These modulations were shown before to be relevant in figure-ground segregation (Lamme et al. 1995, Zipser et al. 1996, Hupé

et al. 1998), with signals to figure being stronger than those to ground after about 90 msec. Manipulating saliency of the stimulus led to consistent changes in neuronal response patterns. If modulation was not present in the signal, the target was not detected, comparable with earlier results by Macknik & Livingstone (1998) who disrupted the transient off-response of V1 neurons using backward masking, leading to invisibility of the target. Combining backward masking with a forward mask, thus interrupting the onset response, they created a 'standing wave of invisibility' reflected in V1 neural responses. A similar approach was used by Lamme et al. (2002) who trained macaque monkeys to detect a target on a textured background. Backward masking resulted in the target being psychophysically invisible. Recording single cell responses they found that the mask interrupted figure-ground segregation in V1, as seen by Supèr et al. (2001). This suggests not only that masking interferes with feedback from higher areas, but also that this V1 activity due to feedback is essential for perception, at least in figure-ground segregation. In contrast to contextual modulation by stimuli outside of the receptive field that were found to be affected by feedback (Hupé et al. 1998, Lamme et al. 1998), effects on center-surround properties of V1 neurons appear not to be mediated through feedback, as has been found by Hupé et al. 2001 by inactivating V2 with GABA injections and recording of V1 responses to different stimuli.

Processing in primary visual cortex is a highly complex combination of feedforward streams and recurrent processing, which interact modulated by task and stimulus properties (Hupé et al. 1998). Recent anatomical data are ambiguous and support both feedback (Angelucci & Bullier 2003) and horizontal connections (Stettler et al. 2002) as possible carriers for a contour integration system. A process possibly involved in illusory contour and surface formation, figure-ground segregation, is a primarily feedback-driven process that acts on the later part of V1 neural responses (Lamme et al. 1995, Hupé et al. 1998). This modulation of V1 activity due to feedback appears to be crucial for psychophysical detectability of a stimulus (Macknik & Livingstone 1998, Supèr et al. 2001, Lamme et al. 2002). A feedback system can thus be thought to be a good candidate for a major part of a contour integration and completion network.

1.2 Contextual Effects on Illusory Contour Processing

Illusory contours are induced by real contextual information. Changes in the illusory percept are thus necessarily related to changes in the context.

Kapadia et al. showed 1999 dynamically changing receptive field structures of orientation selective cells in V1 to contextual stimulation, which was later shown to also have a perceptual correlate in orientation discrimination tasks (Kapadia et al. 2000). Contextual effects are found to depend on contrast (Kapadia et al. 1999), orientation (Li et al. 2000), but also timing (Macknick & Livingstone 1998) and even mental states (Ito et al. 1999).

It appears thereby to be important to study a solely contextually defined structure like illusory contours dependent on the respective context, giving us possibly insights into the processes leading to the illusory percept.

The following section will summarize the current knowledge about contextual effects on illusory contour perception and processing.

1.2.1 Spatial Interaction

Best known and studied spatial interactions with illusory contours are the tilt aftereffect and tilt illusion (simultaneous orientation contrast), spatial summation, and masking effects. Spatial contextual modulation has been shown to depend on contrast, which will be discussed separately in this section.

Tilt Aftereffect and Tilt Illusion

Many geometrical illusions, like the Ponzo or the Poggendorf illusion have been reported as examples of interaction between real and illusory contours. One example I want to describe here in more detail is the tilt illusion (TI), and its temporally separated version, the tilt aftereffect (TAE).

Paradiso et al. demonstrated 1989 the tilt aftereffect in illusory contours comparable to real contours, suggesting that the same cortical loci might give rise to real as well as to illusory contours. They found, however, an asymmetry in interactions between real and illusory contours in the TAE. Real contour adaptation leads to strong effects in both illusory and real test contours, whereas adaptation to illusory contours affects real test contours much less, suggesting that either the illusory contour is comparable to a low contrast contour, or that real and illusory contour processes are only in part overlapping with earliest processes being purely real. Also is the interocular transfer of the TAE stronger with illusory than with real contours, consistent with physiological reports about illusory contour cells in V2 being mostly binocular, while the proportion of monocular cells in purely real contour selective neurons is much higher.

Van der Zwan & Wenderoth (1995) further examined tilt aftereffect (TAE) and tilt illusion (TI) with illusory contours in an orientation discrimination task using a staircase procedure, studying 'direct' and 'indirect' effects similar to those observed with real contours (Gibson & Radner 1937): a target contour is perceptually pushed away from an adaptation stimulus, if they differ in an angle of less than $50 - 60^\circ$. If the difference angle is larger than $50 - 60^\circ$, however, the target contour appears to be tilted towards the adapting contour. This effect has been discussed as related to local processes as possibly lateral inhibition (Blakemore et al. 1970), or real interaction between end-stopped cells (Von der Heydt & Peterhans 1989) in the direct case, and 'higher-order' processes in the indirect case. Van der Zwan & Wenderoth (1995) were able to show both direct and indirect effects also with illusory contours, showing the same distinctive asymmetrical angular function as was previously found with real contours. Manipulations of direct and indirect effects

in TAE and TI with illusory contours showed the same results as would be expected with real contours, supporting the idea of common mechanisms for real and illusory contours (Van der Zwan & Wenderoth 1995).

Spatial Summation and Interference

Kanizsa published in 1976 an example for real-illusory contour interaction, showing figures with partially open borders in one case, leading to the perception of an illusory figure occluding part of the real objects, and the same figures with closed borders, that did not give rise to the illusory percept. He interpreted this effect as support for his completion hypothesis.

In contrast to that description of real lines interfering with the illusory percept stands more recent work from Dresch & Bonnet (1995), who studied detectability of real contours superimposed on illusory contours. They found that real lines at subthreshold were detectable if presented superimposed and parallel to Kanizsa-type illusory contours. Ruling out uncertainty reduction as an explanation for the result, they concluded that illusory and real contours must be processed at least in part by the same low-level line detectors, that thus can show summation effects with illusory and subthreshold real input [14]. This study has been criticized by McCourt & Paulsen (1994). They also studied detectability of real elements (dots) in close proximity of illusory contours and found high variability of results over subjects and no consistent summational effects. Real component detectability was, however, dependent on distance to the illusory contour, still suggesting some possible interactions between real and illusory contours [69]. The summational effects reported by Dresch & Bonnet (1995) might possibly be explained by collinear facilitation, which has been reported between real contours by Wehrhahn & Dresch (1998). Further evidence for that idea has been provided by Danilova et al. (2001), who presented Gabor patches along with illusory contours and found collinear facilitation.

Kanizsa's original idea of completion of figures and the interference of closure lines with the illusory percept [45] has been picked up again by Ringach & Shapley (1996). They measured form discrimination thresholds in a fat/thin task with Kanizsa-type illusory figures. Thresholds drastically increased when suprathreshold lines, that were shorter than the illusory contour, were superimposed on the sides of the illusory figure. These results supported Kanizsa's notion of real lines interfering with the illusory contour percept, but not with his completion hypothesis, that expected real line interference only if they provided an alternative cognitive explanation, like a complete real figure outline, for the partial disks.

Contrast Effects

Studies on contrast dependency of contour processing and perception are mostly concerned with real rather than illusory contours. One reason for this is probably that the processes inducing illusory contours appear to be widely cue-invariant (Poom 2001), and even inducers of different luminance polarity lead to the illusory percept, if no contrast polarity changes occur at partial disc intersections (Spehar 2000). Furthermore, illusory contours pose various problems for testing their perceptual strength as well as for defining their 'contrast'. Therefore, I will here not focus solely on contextual effects on illusory contours, but try to depict contrast influences on contour processing in general.

One approach used to study real-illusory interaction is the measurement of detection thresholds for real elements superimposed on illusory contours. Employing this method, indications for subthreshold summation with illusory contours have been reported by Dresch & Bonnet (1995). Their data suggest that illusory contours and superimposed subthreshold real lines summate to stimulate the neural mechanisms

processing oriented contours stronger than the illusory contour or the subthreshold line alone, comparable to summation of real lines (Kulikowski & King-Smith 1973). This study has been, however, criticized by McCourt & Paulsen (1994), who found summation of real and illusory contours to vary strongly over subjects. Further attempts to study subthreshold summation with illusory contours have been conducted by Poom (2001), who compared effects of real and illusory contour flanks on real line detection thresholds and found in both cases (real and illusory) improved thresholds with collinear contours. The subthreshold summation effect found by Dresp & Bonnet (1995) might thereby be more likely due to collinear flank facilitation, which has been shown both psychophysically and physiologically (Kapadia et al. 1995, Wehrhahn & Dresp 1998).

Possible summation effects with subthreshold real lines stand in contrast to masking effects of superimposed suprathreshold real lines. Already Kanizsa presented (1976) an example for interference of real with illusory lines. Ringach & Shapley (1996) were able to show this masking effect psychophysically in an illusory figure shape discrimination task. Thus, real and illusory lines can perceptually interfere, but might possibly also support each other dependent on real line contrast.

Single cell responses in primary visual cortex have been shown to change with contrast not only of their centre stimulus, but also of their surround. Levitt & Lund (1997) studied the dependency of contextual modulation of neurons in macaque V1 on contrast. They recorded single cells while stimulating with optimally oriented and directed gratings in the cell's minimum response field. Adding surround gratings that did not elicit responses themselves reduced spike rates to optimal stimuli drastically. This effect was much stronger at low centre stimulus contrast. Facilitatory effects with the nonpreferred oriented surround were shown at high contrast centre stimulus, but were diminished or reversed into suppression at low contrast in the centre [60].

Recording single cell responses in V1 to gabor patch stimulation under different contextual modulations Polat et al. (1998) also showed contrast dependency of context effects. Suprathreshold collinear flanks facilitated cell responses if the central target was at low contrast. At high centre activity, on the other hand, flanks suppressed neural activity compared to the centre-alone responses.

Dragoi & Sur modelled in 2000 contextual modulations of V1 cells at different contrasts, implementing excitatory as well as inhibitory inputs and their influence on receptive field properties. Recurrent inhibition was in that model the major assumption ensuring contrast-dependent contextual suppression (high contrast & iso-oriented surround) and facilitation (low contrast & iso-oriented surround).

A perceptual correlate of the physiological effects has been reported by Mareschal et al. (2002). They measured orientation discrimination thresholds of a central grating that was surrounded, separated by a gap, by a grating of variable orientation. Thresholds were increased by iso- or near-oriented surround at high centre contrast. At low contrast also cross-oriented surrounds (of the same low contrast) were suppressive.

Contrast is thus an important factor for contextual modulation of processing and perception of contours. Its effects are not yet clearly understood, but have been shown to shape receptive field sizes and structures as well as to influence perceptual decisions.

Spatial interactions of real elements with illusory contours depend on orientation. Effects of real contour orientation on illusory contours have been well studied, with findings indicating a close relationship between real and illusory contour processing, but also showing deviations between them. Contrast effects, on the other hand, are not well understood yet, partially because of difficulties to approach the problem experimentally. Recent physiological and psychophysical studies indicate though

the importance of contextual and target contrast on receptive field structure that might be shaped by dynamically changing inhibitory and excitatory inputs.

1.2.2 Timing Effects

What is the temporal development of illusory contour processing and perception, and how do contextual interactions change over time?

Reynolds tested 1981 the temporal evolution of Kanizsa-type illusory edges by interrupting the processing at 50, 75, 100, 125, and 150 msec after stimulus onset with a backward mask. Subjects then had to indicate whether they perceived an illusory figure, and whether the figure had straight or curved completed edges. Masks were solid circles at the positions of the Kanizsa inducers. Reynolds found that subjects started to persistently report the illusory contour percept after 100 msec. The discrimination performance stabilized at 125 msec after stimulus onset, suggesting completion of the illusory contour processes by that time.

Westheimer & Li (1996), too, used a backward masking paradigm, but with an abutting grating stimulus; presenting a random line pattern at various times after stimulus offset (which was presented for 50 msec), they found that masking did not affect illusory contour orientation discrimination thresholds after 120 msec. At this timepoint the illusory contour thus appears to be completed both in the Kanizsa figure and the abutting grating type.

Ringach & Shapley (1996) supported this completion time point. They showed using backward masking of local (real) and global (illusory) features of the Kanizsa-type square, that local masking could be effectively used until about 117 msec after stimulus onset, thus replicating Reynolds results. Global masks, however, were affecting perceptual thresholds between 250 and 400 msec after stimulus onset. Illusory figures were later shown to globally mask more effectively than real figures (Imber et al. 2004). Together this suggests that illusory contours are completed locally in a low-level computation until about 125 msec. Following the edge completion the complex Kanizsa-type illusory figure itself may be build up between 250 and 400 msec in higher level processes.

What is the possible physiological basis of the reported masking effects? Macknik & Livingstone (1998) reported maximal effects of backward masking in macaque primary visual cortex neurons at about 100 msec after stimulus onset. Backward masks affected mainly the after-discharge of orientation selective cells. This study indicates that the masking at 120 msec SOA found in illusory contour perception (Ringach et al. 1996, Westheimer & Li 1996) might also be related to neuronal activity modulation in V1.

That illusory contour stimulation elicits neuronal activity not only in V2 (Von der Heydt et al. (1984)), but also in V1, has been reported by Grosf et al. (1993) and, more convincingly, by Lee & Nguyen (2001). In the latter study timing of illusory contour responses in macaque V1 and V2 were recorded. Lee & Nguyen found first neural activity indeed in V2, as also shown by von der Heydt & Peterhans (1989). Responses in superficial V1 occurred by 30 msec after the V2 responses, suggesting that source of the V1 response might be feedback from V2 or even higher areas [58]. V1 activity to illusory contour stimulation occurred thus at about 100 msec after stimulus onset, in deep layers even at over 125 to 190 msec. In this temporal scheme, it is interesting to note that 'local' backward masking effects (Ringach et al. 1996) occur until about 125 msec after stimulus onset. Interaction of the mask with the illusory contour process might thus indeed be situated in primary visual cortex, thereby suggesting that a feedback from higher areas to V1 might be a crucial part of illusory contour perception.

A similar time frame for illusory contour development has been shown for amodal completion by Murray et al. (2001): they found stabilization of the amodal percept

after around 100 msec. Completion times can, however, vary dependent on spatial configuration of the stimulus. Guttman et al. (2003) reported prolonged completion processes with increased occluders.

Spatial dependency of temporal development of contour completion has been tested also by Kojo et al. (1993). They presented partial disks of an Kanizsa-type triangle sequentially, with each disk being present for 33 msec. They found that increasing time between partial disk presentation decreased perceptual strength of the illusory figure in comparison to a control with simultaneously flashed inducers. This effect could be reversed by increasing the support ratio of the figure, i.e. by presenting bigger partial discs, or by reducing the spatial distance between the inducers.

Similar temporal evolution of abutting grating stimuli (Westheimer et al. 1996), modally and amodally completed figures (Murray et al. 2001, Lee & Nguyen 2001), and comparable dependency on spatial configuration (Kojo et al. 1993, Guttman & Kellman 2003) for the Kanizsa-type completions suggest that one common mechanism is responsible for these different virtual contour percepts. Their maskability (Westheimer et al. 1996, Ringach et al. 1996) furthermore shows the possibility to interact with the illusory contour processes possibly even in their earliest cortical stages (Macknik & Livingstone 1998, Li et al. 2000, Li et al. 2001).

1.2.3 Attentional Effects

Cues and changes in context which bring a stimulus in our focus of attention are important clues to select task-relevant structures in a scene and to facilitate feature detection. Attention has been shown to influence visual processing in early stages (Reynolds & Chelazzi 2004) and thus might also interact with illusory contour processing. The following section will summarize some of the effects of attention on visual processing.

As has been shown by Motter (1993), attention has physiologically measurable effects in areas V1, V2, and V4 of macaques. Directing a behaving monkey's attention to an oriented bar located in the RF of the recorded neuron increases the activity of that neuron. Attending away from the RF decreases neural activity to the physically identical stimulus. Effects were dependent on the number of competing stimuli. More competition was needed in V4 than V1 or V2 to result in differences between neural activity in attend-to and attend-away conditions. This might indicate that attention affects the influence of contextual stimuli on single cell responses [71].

The perceptual correlate of attentional effects on visual perception has been psychophysically tested by Ito et al. (1998). Subjects were asked to discriminate whether a target line was brighter or dimmer than a reference. Target line position was either indicated by a single locational cue, thereby focussing attention on the target, or four cues indicated that the target could be at one of four different positions, thus distributing attention rather than focussing it. Along with brightness thresholds also contextual effects in form of collinear flank facilitation were tested under the two attentional conditions. Ito et al. (1998) found not only higher thresholds in brightness discrimination in the distributed than in the focussed attention condition, but also that flanks facilitated the task much more in the distributed attention condition than in the focussed condition, indicating, as already assumed by Motter (1993), that attention possibly interferes with the surround suppression. Exploring the same phenomenon physiologically in the behaving macaque, Ito & Gilbert (1999) found that contextual effects changed with attentional state, but not responses to the target alone. Contextual effects decreased, however, with training the task and were opposite in the two monkeys tested, indicating that they used different strategies. But still, neural activity correlated with each monkey's be-

havioural results in dependence on attentional state. The results show that already earliest cortical processing stages can be dynamically modulated by attention [40]. How attention affects not contextual effects, but neuronal responses alone has been studied by McAdams & Maunsell (1999). They recorded neuronal activity in area V4 of macaque to attended or ignored stimuli. Monkeys had attend either to a colored, or oriented stimulus, and they had to indicate whether two stimuli appearing in the same location had the same orientation, or color dependent on the current attentional condition. Oriented stimuli (gabor patches) were always in the RF, thus stimulating the recorded neuron in either an attended or unattended condition. MacAdams & Maunsell found that attention to the receptive field location improved neuronal ability to respond to a stimulus, including enhanced orientation discrimination, by increasing the response amplitude. Attention thus has effects comparable to stimulus changes that enhance its saliency [68].

Friston & Büchel (2000) tested in an fMRI study possible attentional modulation of connectivity between V2 and V5/MT in humans. They presented radially moving dots and asked subjects to either detect velocity changes in the pattern (attended condition), or to passively view the stimulus (unattended condition). Speed changes did actually not occur during scanning, but were expected by the subjects. During attended conditions responses in MT were enhanced, attentional effects that were also supported by endured motion aftereffects the attended vs. the unattended condition. Friston & Büchel (2000) used a nonlinear model testing effective connectivity between V2 and MT, finding that V2-driven input over conditions was explanatory for modulatory effects in MT, thereby supporting attentional changes in early visual cortex and its effects on processing also in higher areas [19].

In contrast to the previously cited studies, Marcus & Van Essen (2002) found no modulatory effects of attention on scene segmentation in V1. This might possibly be because attentional influence on stimulus context might be only needed to perform high-resolution spatial tasks and thus might not affect early cortical activity in different experimental designs. In V2, attention had a slight facilitatory effect comparable to the one reported by previous studies.

Attention has thus been shown to affect perception (Motter 1993, Ito et al. 1998) and processing already in early visuocortical stages, including V1, V2, V4, and MT (Ito & Gilbert 1999, McAdams & Maunsell 1999, Friston & Büchel 2000), and might thus also be relevant in illusory contour processing. Effects vary, however, with behavioural strategy (Ito & Gilbert 1999), task (Marcus & Van Essen 2002), and experimental design (McAdams & Maunsell 1999). Stimulus-related effects might thus be difficult to separate from attentional effects, and experimental design has to take care of this possible trap.

1.3 Proposal of this Thesis

Illusory contours are constructed based on real, contextual information, the inducers. Every change of the illusory contour percept is thus necessarily based on changes in the contextual real elements. Understanding how changes in the context affect illusory contour perception is thereby a major step towards understanding the processes underlying illusory contour perception.

Recent physiological reports showed neural signals to illusory contour stimulation as early as in primary visual cortex (Ramsden et al. 2001, Lee 2001). Signals were, most interestingly, orientation reversed to the real contour signal, and appeared later in V1 than in V2. The physiological results mentioned suggest that a feedback mechanism from primate V2 to V1 is involved in illusory contour processing (see also Roe 2003).

Is there perceptual evidence for interactions between real and illusory contours?

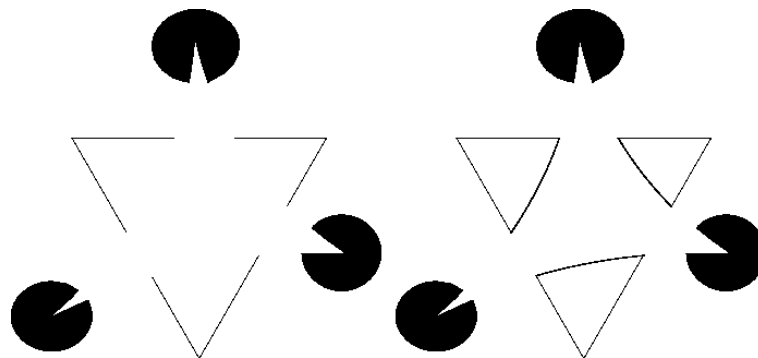


Fig. 1.13: Examples for perceptual effects of real lines of different orientations on an illusory contour percept, here Kanizsa-type triangles. The Kanizsa-triangle with abutting real line elements appears to be perceptually stronger than the same triangle with parallel real elements.

As can be observed in Fig.1.13, contextual real elements in a scene appear qualitatively to be able to change the perceptual strength of illusory contours dependent on their orientation: the perception Kanizsa-type triangles is enhanced by abutting lines, but weakened by parallel real lines. Parallel interference by high contrast lines has also been shown psychophysically (Ringach et al. 1996), while facilitation by orthogonal lines has not been tested so far.

Various other signs of interaction between real and illusory contours have been shown by Paradiso 1989, Westheimer et al. 1996, Dresch & Bonnet 1995, and McCourt & Paulsen 1994. Some of these interactions can be attributed to early visual cortex.

Feedback from V2 (Lee & Nguyen 2001) and orientation reversal in V1 (Ramsden et al. 2001) as part of the illusory contour mechanism, as proposed by Roe 2003, would lead to specific real-illusory interactions that could be psychophysically and physiologically measurable.

First, interactions between real and illusory contours should be orientation dependent, as shown before (Paradiso et al. 1989). These orientation dependent contextual effects should, however, be clearly attributed to either interaction with the real inducers, or with the illusory contour itself. So far most experimental designs are not able to distinguish between these two options.

Second, contextual effects onto illusory contours should be measurable even at sub-threshold contrasts, but might show contrast dependent effects possibly related to changes in receptive field properties in early processing stages. For example, psychophysical correlates of contrast-dependent receptive field changes have been

shown by Mareschal et al. (2002).

Third, if V1 as computational stage is important for illusory contour perception, orientation dependency of real contour interaction with the illusory contour should change over time. A feedback mechanism (Lee & Nguyen 2001) with orientation reversal (Ramsden et al. 2001) would lead, as an example, to early interference by one orientation, but later to summation effects of the same oriented stimulus.

I will test here whether interactions between illusory and real contours depend on real line orientation, contrast, and on the timing of real-illusory interaction. To this end I will measure the saliency of illusory contours as modulated by contextual stimuli.

2. GENERAL METHODS

In this chapter the methods employed in the behavioural experiments will be described shortly to provide a common background for the different experimental sections.

2.1 Psychophysics

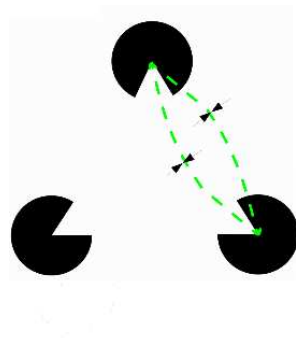
Psychophysics is a concept of measuring and quantifying the relationship between physical events and perception. The processing apparatus is assumed to be a 'black box'. The formula describing behavioural responses to sensory stimuli allows to derive properties of the underlying processing mechanisms.

The idea to test perceptual strength relative to intensity of a physical stimulus was first developed by E.H. Weber in 1834, who noticed that to discriminate two heavy weights was more difficult than to discriminate two light weights. He measured the relation between stimulus intensity (i.e. weight) and just noticeable difference thresholds (i.e. difference of two weights that lead to the subjects ability to discriminate between them), and derived the *Weber fraction*: the relation between stimulus intensity and perceptual difference threshold.

Following Webers results and his own ideas about matter and mind as two sides of the same coin, G.T. Fechner developed in 1860 methods to relate physical stimulation and conscious perception, to thereby measure mental processes. Fechner designed the main strategies to psychophysically measure thresholds: the *Method of Adjustment*, the *Method of Limits*, and the *Method of Constant Stimuli*. In the following sections, I will give a short overview about these methods (see also Gescheider 1985).

Method of Adjustment

The method of adjustment is based on the subjective appearance of a stimulus. A subject is asked to adjust a predefined stimulus parameter such that the stimulus reaches a certain perceptual quality. The average setting chosen to reach the percept is the adjustment threshold.



Average Setting

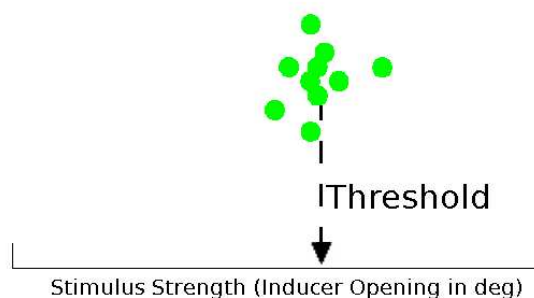


Fig. 2.1: Exemplary depiction of the method of adjustment. An uncurved Kanizsa-figure is displayed. Subjects are asked to adjust the inducer opening to produce a reliable percept of an outward curved illusory contour. The average of several of these adjustments is the perceptual threshold in this method.

An example for the method is illustrated in Fig.2.1. In this case, a Kanizsa-figure is presented. Changing the width of the inducer opening changes the curvature of the illusory contours in the figure. A subject is asked to adjust the inducer openings such that one side of the figure appears to be bent outward. The weaker the perceptual strength of the illusory percept, the wider the opening of the partial discs to produce a clearly bent illusory contour.

Method of Limits

In the method of limits, today mostly used as staircase procedure, the stimulus intensity is constantly adjusted to the subject's performance in a perceptual task. If performance is suprathreshold, intensity is decreased, if the performance sub-threshold, intensity is increased until the threshold is reached.

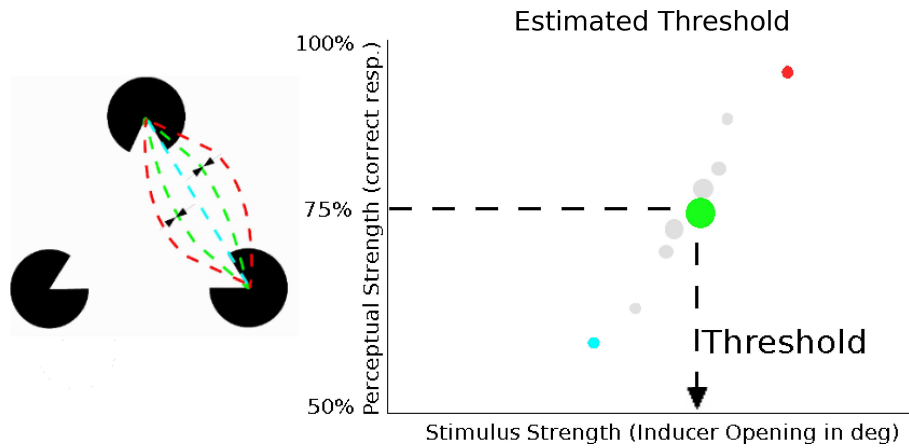


Fig. 2.2: Depiction of the method of limits. Kanizsa-figures of a certain curvature are displayed. Subjects are asked to discriminate the curvature of the illusory contour (bent outward or inward). After several correct responses to a stimulus of the same curvature, curvature (i.e. opening of the partial discs) is decreased. Wrong responses lead to an increase of curvature. Curvatures at which subjects respond correctly in 75% of the cases are the thresholds in this procedure. Stimuli presented are thus adjusted to the subject's responses.

To give an example (Fig.2.2): a curved Kanizsa-figure is presented. The subject has to indicate whether this figure is curved inward or outward. If the responses in more than 25% of several trials are wrong, the opening of the inducers is increased to increase the curvature. Are responses in more than 75% of the trials correct, the curvature of the illusory contour is decreased. The inducer opening at which the subject responds correct in 75% of the trials is defined as the subject's perceptual threshold. This procedure leads in a short time to an estimate of the perceptual threshold.

Method of Constant Stimuli

Using the method of constant stimuli perceptual strength at several predefined stimulus intensities is tested repeatedly to measure the relation between physical intensity and perception.

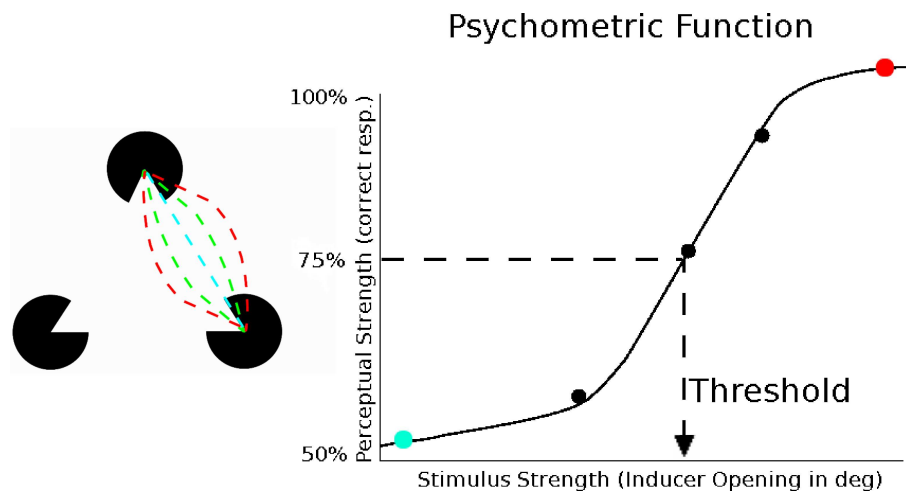


Fig. 2.3: Depiction of the method of constant stimuli. Kanizsa-figures of a predefined set of different curvatures are displayed in a random order. Subjects are asked to discriminate the curvature of the illusory contour (bent outward or inward). Responses to each stimulus are collected and the percentage of correct responses to each stimulus condition is calculated. These percentages are fitted to a sigmoidal function (psychometric function). Thresholds are e.g. at the 75% level of correct responses.

In the illusory contour example (see Fig.2.3), a Kanizsa-figure is presented with one of several predefined inducer openings, leading to uncurved, weakly curved and strongly curved illusory contours. Each condition is displayed several times in a random order. The subject has to indicate in each trial whether the induced illusory contours appear to be bent outward or inward. The percentage of correct responses at each inducer opening is fitted to a psychometric function to find the perceptual threshold at the level of 75% correct responses.

In the psychophysical experiments presented here the method of constant stimuli was applied. This method gives an overview over the perceptual space spanning from not perceiving to always perceiving a sensory quality of the stimulus. The method of constant stimuli has a higher precision in estimating perceptual thresholds than the method of limits.

All experiments were designed in a *Two-Alternative-Forced-Choice-paradigm* (2AFC), which is a widely used way to quantify the perception of a subject. Following the presentation of a physical stimulus the subject is here asked to decide between two possible perceptual alternatives. In the curved illusory figure example, this could mean that the contours are either bent inwards or outwards.

Given two options the probability to respond correctly just by guessing lies at 50%. The perceptual threshold at which it is assumed that the subject is just able to discriminate between the two given stimulus qualities is here by definition at 75% correct responses. By fitting a *psychometric function* (here a gaussian distribution) to the perceptual data obtained the threshold can be calculated.

To analyse the relation between sensory input and perception, stimuli have to be manipulated in a controlled way. Here I am interested in the interaction of real and illusory contours. Possible stimulus manipulation to study real line influence on the illusory percept include changes in orientation of the real contours, in their physical intensity (i.e. their contrast), or in the temporal relationship between illusory and real contour presentation. The *Stimulus Onset Asynchrony* (SOA) is one term to describe the relative timing of one stimulus and another, indicating the time from

stimulus onset to onset of a second stimulus. One further term is the *Inter Stimulus Interval* (ISI), that describes the time between offset of the first and onset of the second stimulus.

2.1.1 Subjects

Subjects, between 20 and 32 years old, were informed about the experimental procedure and gave their informed consent. Some subjects were paid for the time invested into the experiments, some were students participating in a labrotation. All subjects were allowed to have as many breaks between stimuli as they felt was necessary for relaxed view.

All subjects had normal or corrected to normal acuity and no known visual deficits. Before experimentation started, several trials were presented to them. Subjects were asked to report what they were perceiving, and whether they felt comfortable viewing the stimuli. All subjects reported clear perception of the illusory contour or figure (dependent on the experiment). First trials of the experiments were done under my supervision, assuring that the subjects understood the task and how to respond.

Subjects practiced the experiments for at least two to three days before the data presented here were collected.

2.1.2 Procedure

All experiments were carried out in a 2AFC paradigm with constant stimuli. Subjects had to indicate via mouse button click, whether they perceived one alternative, or the other. In an orientation discrimination task, as an example, an illusory contour either tilted to the left, or to the right was presented. An untilted (vertical) contour or a tilt too small to be perceived by the subject led to guessed responses. Optimally, this would result in 50% correct and 50% wrong responses in a two alternative task. This served as a control for biases in the subject's response.

For most experiments the method of constant stimuli, unless stated otherwise in the individual chapter, was used to measure discrimination thresholds for illusory contour curvature, or orientation. The 75% correct responses threshold was used. All thresholds are based on at least 300 trials that were collected over several days.

2.1.3 Analysis

Psychometric functions were fit to the subject's responses to the stimuli using Mathematica's (Wolfram Research) Nonlinear Regress, which finds a least-squares fit to the data for a given model (Gaussian function in this case). Based on this the threshold (at 75% correct responses) and its asymptotic standard error can be assessed, giving an estimate for the goodness of the fit.

We compared the subjects' pooled thresholds for the parallel and orthogonal real line condition respectively with the no line condition in a paired t-test for every real line contrast. A second test involved alignment of the individual data to detection threshold for the real lines, thus pooling the data not over each contrast, but at positions in contrast range relative to detection threshold. This alignment allows a comparison of data at perceptually similar contrasts (i.e. subthreshold versus suprathreshold contrasts), thus taking into account the variability between individual subjects.

2.2 Apparatus

All experiments were programmed using OpenGL and C/C++, in part under Windows98 (Microsoft), in part under Linux (Mandrake 9 and 10) on a pentium computer. Stimuli were displayed on different monitors as specified in the respective chapters. All monitors were calibrated against a Minolta CS-100, one monitor was calibrated additionally against a CS-1000. The calibration procedure is explained in detail below. Experiments were always carried out binocularly in a dark room, viewing distances were depending on the experiment either 3 m and 57 cm. Data were analyzed with Mathematica 4 (Wolfram Research).

2.2.1 Monitor Calibration

Testing the performance of a subject in a perception task requires that we know the properties of our stimulus. That includes especially the properties of the system we use to present this stimulus, i.e. for visual stimuli we need to know the brightness of our monitor, and the luminance contrast of the stimuli used. Every monitor, however, is individual in its luminance and spectral output. Two monitors from the same company, production line, and even production day can differ significantly. Those differences are not only based on the complex and difficult building process leading to a CRT monitor, but also on the monitor's 'history': electro-magnetic fields in the surround can change the monitor's behaviour.

If no monitor is identical to another, identical input (Grey/RGB-values) can lead to different output (luminance/spectral composition) and thus to a different perception (brightness/color). Comparison of perceptual data collected with different monitors would thus be impossible.

Measuring perception psychophysically also demands precise knowledge about the stimulus that leads to the tested perception. Knowing the input to our monitor does not give us per se precise information about our stimulus' properties. We thus have to calibrate the monitor, i.e. measure the output at a given input.

RGB-space of a monitor is a cube of equal sides, with the grey scale being the diagonal, defined by identical numbers of Red, Green, and Blue (see fig. 2.4).

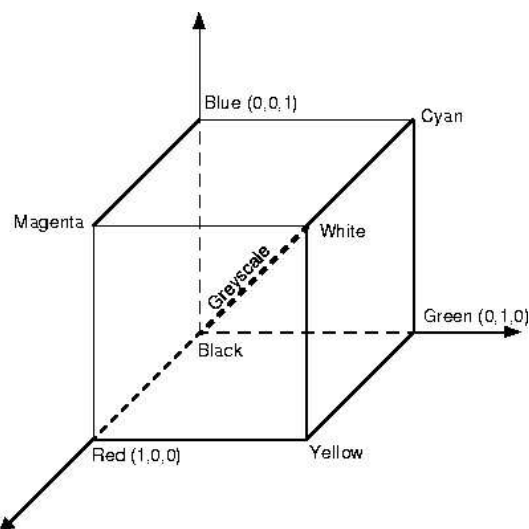


Fig. 2.4: RGB space: a monitors input space is defined as a cube with axes Red, Green, and Blue. Equal input of Red, Green, and Blue changes the greyscale of the monitor from black (RGB: 0,0,0) to white (RGB: 1,1,1).

The monitor's output to each grey value, i.e. the amount of light emitted (luminance, $[cd/m^2]$), however, cannot be described by a straight line anymore, but rather by a square-function (see fig.2.5). Increase of grey values in RGB-space thus cannot be translated 1:1 into increase in luminance.

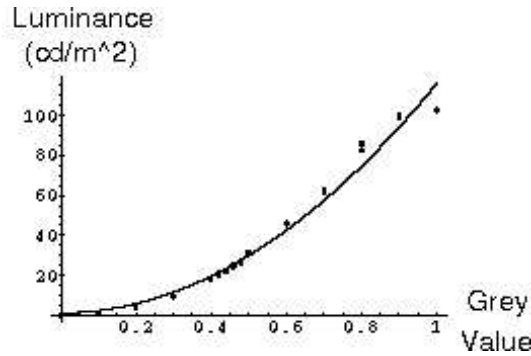


Fig. 2.5: Luminance calibration of a CRT monitor: at given grey values the luminance output of the monitor is measured. The output function is fitted best by a square function.

Data of a luminance calibration are fitted best by a square function:

$$Y = a + b * x^2 \quad (2.1)$$

Y: luminance (cd/m^2)

a: offset - how bright is the monitor when it is black?

b: maximal luminance value obtainable with the monitor

x: grey value

For perceptual tasks it is of more use to know the contrast of a stimulus than it's absolute luminance. The definition for the Weber contrast is:

$$ContrastStim = \frac{LumStim - LumBackground}{LumBackground} \quad (2.2)$$

Contrasts used in the experiments presented here are 0.03, 0.05, 0.1, 0.15, 0.3, and 0.95.

3. BACKWARD MASKING OF ILLUSORY CONTOURS WITH ORIENTED REAL LINES

3.1 Introduction

Illusory contours can be induced by various stimuli. Different types of illusory contours are, nonetheless, perceptually and physiologically comparable to each other. Interestingly, the neural representation of both stimuli is identical in early processing stages [109, 78]. Processing of illusory contours even overlaps in primate area V2 with the mechanisms leading to real contour perception, as has been shown physiologically by von der Heydt & Peterhans 1989.

If virtual contours are treated in early processing stages as if they were real contours, they should have similar properties as real lines. Indeed, illusory contours perceptually behave in a way comparable to real contours, as has been shown using psychophysics with the tilt after effect (Paradiso et al. 1989), or backward masking (Westheimer & Li 1996). In the latter study the following hypothesis was tested: if the illusory contour is represented in orientation specific domains of visual cortex (see [109, 78]), its perception should be masked specifically by oriented patterns rather than by any other pattern. This hypothesis was supported by Westheimer & Li (1996), who found strong backward masking effects by random oriented lines, but much weaker perceptual interference by circular or random dot patterns [114]. One remaining question, however, is whether the masking effect they found has been due to masking of the inducing real lines, or rather due to masking of the illusory contour, as Westheimer & Li assumed. I therefore want to test here whether illusory contour perception can be masked differentially with real lines of different orientations. Specifically, I will test whether backward masking of an illusory contour stimulus with real contours affects the inducing real lines, or whether it rather interferes with the induced illusory contours.

Backward masking studies with Kanizsa-type illusory figures (Reynolds 1981, Ringach & Shapley 1996) tested the temporal development of illusory contour perception. The latter study found that Kanizsa-figures can be masked by stimuli interfering with the inducers ("local" mask [88]) until about 120 msec of processing time. Following this induction time, illusory contour perception can be masked only by stimuli interfering with the illusory percept ("global" mask [88]). Westheimer & Li (1996) found a similar time constant (120 msec) for the induction of illusory contours with abutting line stimuli. Similar timing of perceptual development suggests similar underlying processing mechanisms for Kanizsa-type and abutting line type illusory contours, as already indicated by the physiology studies by von der Heydt & Peterhans 1989. As pointed out above, it is unclear whether backward masking of abutting line patterns affects the inducing real lines or the illusory contour. It is thus so far not possible to identify the hypothesized early and later processing steps in the temporal development of abutting line illusory contours. I therefore test here whether backward masking effects on illusory contours reveal temporally segregated induction and establishment processes.

Illusory contours of the abutting line type include different luminance contrast cues that might lead to or strengthen the contour percept. One possible luminance contrast cue can be found in the relationship between the distance of real lines and the

gap size between the abutting line pattern. With high spatial frequency of the real lines the overall average contrast of the stimulus increases. A gap between two high spatial frequency pattern thus can be understood as a low contrast line separating two higher contrast objects. Therefore contours induced by abutting line patterns with gap are not thought to be “illusory”, second order contours[108, 114]. On the other hand, abutting line patterns without gap can be perceived rather as abutting textured surfaces, than as an illusory contour stimulus. Westheimer & Li (1996) showed, however, that introduction of depth information does not improve perception of abutting line patterns without gap. This suggests that these stimuli do not necessarily subserve the processing of surfaces, but rather induce “real” illusory contours.

The processing stages leading to an illusory contour percept, as pointed out above, are temporally segregated. It should thus be possible to interact early on with the inducing processes, while later on solely the induced processes remain. Backward masking at different times after stimulus onset can therefore be used as a tool to distinguish between inducing and induced processes. Masking effects on real contours have not been reported to change over time. Temporally segregated masking effects can therefore be expected to indicate second order processes. If abutting line pattern with gap belong to the category of real contour stimuli, we thus would expect oriented masking effects that do not change over time. If, however, these stimuli induce second order contours, we would expect masks to first interfere with the inducers, and only later with the induced contour. To test that hypothesis, I will measure here masking effects over time on both abutting line stimuli with and without gap.

3.2 Methods

3.2.1 Apparatus

Experiments were programmed using OpenGL and C/C++ under Windows98 (Microsoft) on a pentium computer. Stimuli were displayed on a 21 inch CRT color monitor (Sony GDMF500R) with a refresh rate of 75 Hz. The monitor was calibrated against a Minolta CS-1000. Experiments were carried out binocularly in a dark room at a viewing distance of 3 m. Data were analysed with Mathematica 4 (for details see below).

3.2.2 Subjects

All 6 subjects (5 female, 1 male, age 22-33) had normal or corrected to normal acuity. Subjects practiced the experiment for at least three days or 1500 trials before the data shown here were collected.

3.2.3 Stimuli

Experiments were conducted on a grey background at a luminance of $41\text{cd}/\text{m}^2$. The stimulus consisted of an abutting line pattern inducing a virtual contour. The line pattern was visible through a circular Gaussian filtered window. This stimulus is designed in several ways to minimize information content based on real cues. In the following text, these aspects are described in detail.

Abutting line patterns typically are mirror-symmetrical (e.g. Vogels 1987, Westheimer & Li 1996, von der Heydt & Peterhans 1989). In the case of a vertically oriented illusory contour, stimuli are mirror-symmetrical both along the vertical (along the illusory contour) and the horizontal (dividing the stimulus in two halves). In a circular stimulus, reorienting the illusory contour leads to a rotation of both the vertical and the horizontal reflection lines. In rectangular stimuli, however, changes in illusory contour orientation from the vertical coincide with loss of the vertical reflection line, unless the whole abutting line pattern is rotated along with the illusory contour. Presence of symmetry has been reported to be easily detected by humans if presented for only 150 msec (for review, see Wagemans 1998). The changes in symmetry, which are inherent to rectangular stimuli, might therefore be strong additional cues as to whether an illusory contour is tilted from the vertical or not. By presenting the stimulus in a circular arrangement (as e.g. used by Vogels 1987), the symmetry of the real line pattern does not change despite changes in illusory contour orientation.

Another possible cue to illusory contour orientation is the length of inducing lines in the abutting line pattern. A rectangular window, as employed by Westheimer & Li (1996) as well as by von der Heydt & Peterhans (1989), is problematic, as line length on each side of the stimulus pattern changes with illusory contour orientation. Here I applied a Gaussian filter to the stimulus to blur the border of the circular window. It is thereby very difficult to discriminate individual line length differences at varying illusory contour orientations.

The real lines used here had a thickness of 0.04 min of arc, which corresponded to 1 pixel in the display. At this width no oriented luminance contrast border was perceived, but the point end of a very thin line.

Line pattern were separated by a gap of 4 min of arc. This gap size was chosen to use a stimulus comparable to those employed by Westheimer & Li 1996 in their backward masking experiments. Introducing a gap in illusory contour stimuli has been discussed as providing additional low-level luminance contrast information, thus leading to real contour rather than illusory contour processing [114, 109, 108]). In the stimulus presented here this information was minimized by using a large

distance between real lines in the line pattern (>14 min of arc) relative to the gap width (4 min of arc).



Fig. 3.1: Abutting grating stimulus. High contrast abutting gratings inducing an oriented virtual contour are visible through a circular gaussian filter. The figure is saved from a screenshot from the actual program.

Illusory contour length was 75 min of arc, corresponding to the diameter of the circular window minus the width of the filtered border (5 min of arc).

Inducing gratings were either oriented at 45° or 135° . Both orientations were randomly presented to ensure identical spatial configuration of illusory contour and real lines at all illusory contour orientations. Subjects reported to mostly not perceive different real line orientations during the normal experiment, unless they concentrated on it rather than on the illusory contour. Real line information thus changed from trial to trial, thereby minimizing the impact of local luminance cues.

In some experiments backward masks were presented. Masking patterns consisted of a line pattern identical to the inducing line pattern. Masks were either presented at an orientation of 45° , 135° , 90° (horizontal) or 0° (vertical) to study the orientation dependency of masking effects. A control condition was a blank screen that was presented instead of the masks after illusory contour presentation.

3.2.4 Procedure

Subjects were comfortably seated in a dark room. A chin rest assured constant viewing distance of 3 m. In all experiments, a fixation spot was presented for 500 msec followed by the stimulus. The stimulus was shown for 75 - 150 msec, as stated in the respective results section (see Fig.3.2). The fixation spot disappeared with stimulus presentation onset. Following stimulus presentation, either a blank screen or a line pattern identical to the inducing abutting lines was presented for 200 msec. The program waited for the subject's response.

The experiment was conducted in a 2AFC paradigm with constant stimuli. Subjects had to indicate via mouse button click whether the illusory contour appeared to be tilted to the left or to the right. No error feedback was given.

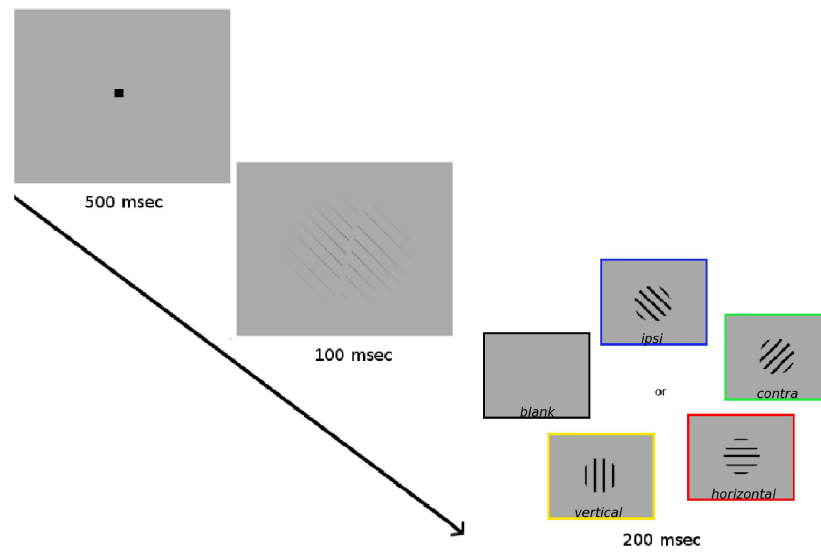


Fig. 3.2: Discrimination Task. A fixation period of 500 msec was followed by the stimulus (75, 100, 125, or 150 msec), which was then backward-masked by an oriented line pattern for 200 msec. Subjects had to decide in a 2AFC paradigm whether the illusory contour was tilted to the left or to the right from vertical.

Orientation discrimination thresholds were measured in each stimulus condition. Thresholds are based on at least 300 trials that were collected over at least two days.

3.2.5 Analysis

Psychometric functions were fitted to the subject's responses using Mathematica's (Wolfram Research) Nonlinear Regress, which produces a least-squares fit to the data using a given model. Here a Gaussian function was used. Based on the fit the threshold (at 75% correct responses) and its asymptotic standard error were calculated.

3.3 Results

3.3.1 Baseline Measurements

To present an illusory contour I used here a new abutting line stimulus. In this stimulus, the influence of cues other than the line end information is minimized. First, line patterns presented here are oblique. Inducing lines are thereby never orthogonal to the vertical illusory contour. Orthogonality has been shown to be a strong cue in orientation discrimination in humans. The stimulus presented here therefore minimizes the risk of subjects judging the orthogonality of the abutting line patterns to the illusory contour. This possibility is furthermore reduced by presenting both acute and obtuse line patterns in a pseudo-random fashion. Secondly, the stimulus is presented in a circular window. Tilt of the illusory contour changes the symmetry in a rectangular pattern, but not in a circular pattern. Symmetry has been found to be easily detected by human subjects[111]. The symmetry of a pattern might thus be used as an additional cue in rectangular abutting line stimuli. The use of the symmetry cue can be excluded here.

The stimulus used here has furthermore the advantage of minimizing luminance contrast cues by various means. First, I applied a circular Gaussian filter to the abutting line pattern. The Gaussian filter prohibits the use of cues such as real line length to the window border. Secondly, real line width is about 2 sec of arc, thus further reducing the amount of real edges in the stimulus.

Luminance contrast cues still inherent in the stimulus depend on gap size and line distance. To minimize the impact of these cues, line distances should be chosen to be as wide as possible while still providing good perceptual strength of the stimulus. Different gap sizes (i.e. with and without gap), however, will be compared experimentally. Stimulus parameters should thus be set to be as similar as possible in both gap and no-gap conditions. To ensure both good perceptual strength independent on gap size, and minimal luminance contrast information, I first assessed the perceptual strength of the stimuli without masking. To find optimal settings, I measured orientation discrimination thresholds of stimuli with different gap sizes and different spatial frequencies of the line pattern.

Dependency of Illusory Contour Strength on Inducer Line Distance and Gap Size

Illusory contours were presented for 125 msec as shown in the method section, followed by a blank screen for 200 msec. The subject's task in a 2AFC paradigm was to decide whether the illusory contour appeared tilted to the left or right.

Gap sizes tested were 0, 2, and 4 min of arc. Parameters were chosen to be comparable to the study by Westheimer & Li (2001). Line distances tested were 11.3, 14.1, 16.9, and 19.7 min of arc. They were set to be about three times as wide as the maximal gap to minimize real contrast information. Two subjects participated in this experiment, measuring orientation discrimination thresholds with the new illusory contour stimulus under the different conditions described.

As can be observed in the results of subject BD (Fig.3.3), perceptual strength of the illusory percept varies with gap size and line distance. At big line distances (i.e. low spatial frequencies) discrimination thresholds are highest in all gap size conditions. Thresholds decrease towards line distances of 14 and 17 min of arc. At these settings, thresholds of different gap size conditions are not significantly different. Further decrease of line distance again leads to increased discrimination thresholds in the no gap condition. Thus, different gap size conditions consistently depend on spatial frequency of the abutting line pattern, with an optimal line distance of about 14 - 17 min of arc.

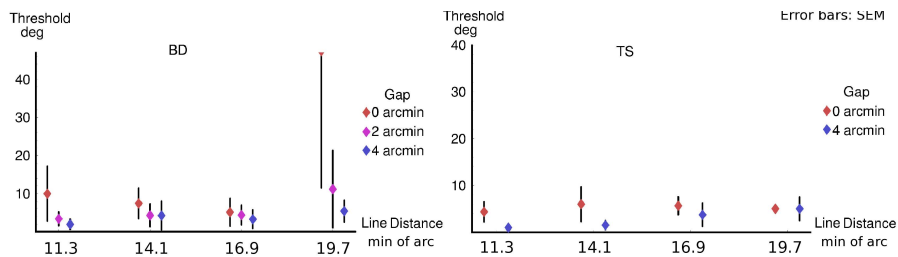


Fig. 3.3: Discrimination thresholds (in deg) of two subjects at different gap sizes (0, 2, and 4 arcmin) and line distances, as indicated on the X-axes. Error bars shown are Standard Errors.

Thresholds of subject TS, on the other hand, are only marginally dependent on line distance and gap size in the range of parameters tested here. Thresholds of stimuli without gap are in general slightly higher than thresholds of stimuli with gap. While stimuli without gap lead to the same thresholds in each condition, stimuli with gap (4 min of arc) tend to have higher thresholds with increasing line distance. Lowest thresholds in the gap stimulus were measured at line distances of 11.3 and 14.1 min of arc.

Comparison of the different gap size conditions shows over all higher thresholds with smaller gap size. This results has already been indicated by Westheimer & Li 1996, who showed lower perceptual strength of abutting line patterns without gap than with gap [114]. As can be seen here, thresholds gradually increase from no gap, over gap size 2 min of arc, to gap size 4 min of arc in subject BD's results.

Based on these results, the line distance used in the following experiments was 14.1 min of arc. This setting was found to lead to similarly good perceptual strength of stimuli with and without gap. Stimuli were shown at a gap size of either 0 and 4 min of arc, as indicated in the respective section.

Perceptual Strength over Time

The processing of illusory contours, as described in the introduction, occurs in two major steps: first, induction by contextual stimuli, and secondly, establishment of the illusory contour as a neural representation comparable to that of a real contour. Masking interrupts stimulus processing. In which processing state the stimulus processing is interrupted depends on the timing of the mask presentation. Results in the experiments therefore depend on the processing state reached by the end of the stimulus presentation.

To get an impression of how similar the time dependency of illusory contour processing is over the subjects participating in this experiment, orientation discrimination thresholds were measured at three different presentation times (100, 125, and 150 msec). After stimulus presentation, a blank screen was presented for 200 msec.

Fig.3.4 shows the individual results of four observers in the blank condition at different presentation times. Subject AW only participated in the experiments with presentation times of 100 and 125 msec.

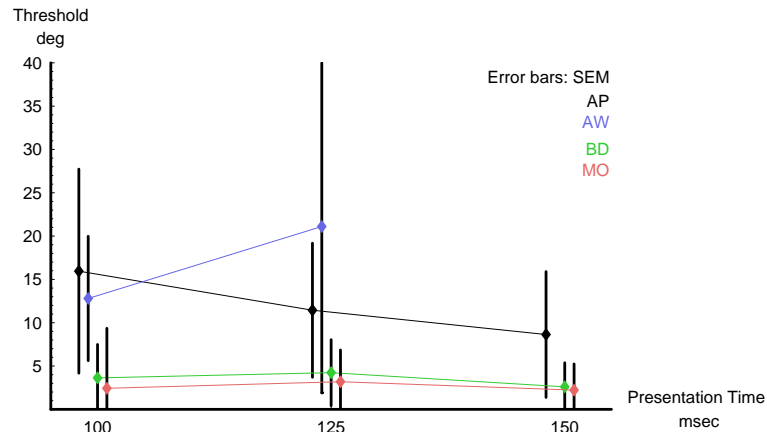


Fig. 3.4: Discrimination thresholds (in deg) of four subjects in the blank condition at presentation times of 100, 125, and 150 msec. Error bars shown are standard errors of the mean.

As can be seen, thresholds vary tremendously between subjects. Unmasked illusory contours have to be tilted by about 21° for subject AW to be discriminated correctly in 75% of the trials, while a tilt of only 11° is needed for subject AP. Even better discrimination ability is found in subjects BD (4°) and MO (3°). Lower thresholds are not the only sign of a different orientation discrimination ability: subjects also vary strongly in the consistency of their responses, and thus in their error. Big error bars, as seen in the results of subjects AW and AP, correspond to their respective problems to perform the task reliably. Both subjects reported to sometimes not be able to perceive the illusory contour. This inability to perceive the induced contour was in their impression due to the short presentation times. Especially for subject AP longer presentation times were needed to reliably induce the illusory percept: thresholds decreased here with increasing presentation time, as can be seen in Fig.3.4.

As stimulus conditions should be as similar as possible to be comparable between subjects, stimuli were not adjusted for subjects with apparent need for longer presentation times. Masking effects were, furthermore, less variable over subjects than might be expected from the baseline results.

3.3.2 Backward Masking of Illusory Contours

Westheimer & Li (2001) showed masking of their illusory contour to be comparable to masking of real contours. They found oriented line masks to interfere stronger with the illusory percept than circular or random dot patterns. The masking effect in their experiment could be, however, both due to interference with the inducing real components of the stimulus or the induced illusory component. I thus ask here whether an illusory contour itself, or rather its inducing patterns can be masked with real lines.

Illusory contours are neurally represented as early as in area V2 in orientation specific domains that also respond to real contours[109]. As backward masking has been found to affect early visual cortical processing (Macknik & Livingstone 2001), masking of illusory contours might be similar to masking of real lines. Masking of real lines is strongest with parallel oriented mask patterns (Li et al. 2001).

If an oriented line mask affects the inducing lines, a line pattern oriented parallel to the inducers would be expected to be an effective masking tool. If, however, masking interferes with the virtual contour itself, a line pattern parallel to the illusory

contour would be expected to have the strongest masking effect. Measuring the perceptual strength of illusory contours masked with real lines of different orientations can thus possibly clarify whether masks interfere with inducing or induced processes in the illusory contour stimulus.

Experiments were conducted as shown in the method section, using the optimal settings established in the last section. Line distances were 14.1 min of arc, while abutting line pattern were separated by a gap of 4 min of arc. Illusory contours were presented for 125 msec. At this time, illusory contour induction processes are thought to be completed (Reynolds 1981, Ringach & Shapley 1996, Westheimer & Li 1996, Lee & Nguyen 2001). The stimulus was followed by real line masks of different orientations. Masking patterns resembled the inducing line pattern of the illusory contour stimulus, but did not induce an illusory contour. Masks were either oriented parallel to the inducing line pattern (ipsi), or rotated by -45° (horizontal), 45° (vertical), or 90° (contra). The vertical pattern was oriented parallel to the illusory contour, while the horizontal pattern was oriented orthogonally to the illusory contour.

Four subjects participated in this experiment. Discrimination thresholds of single subjects in each masking condition are shown in Fig.3.5.

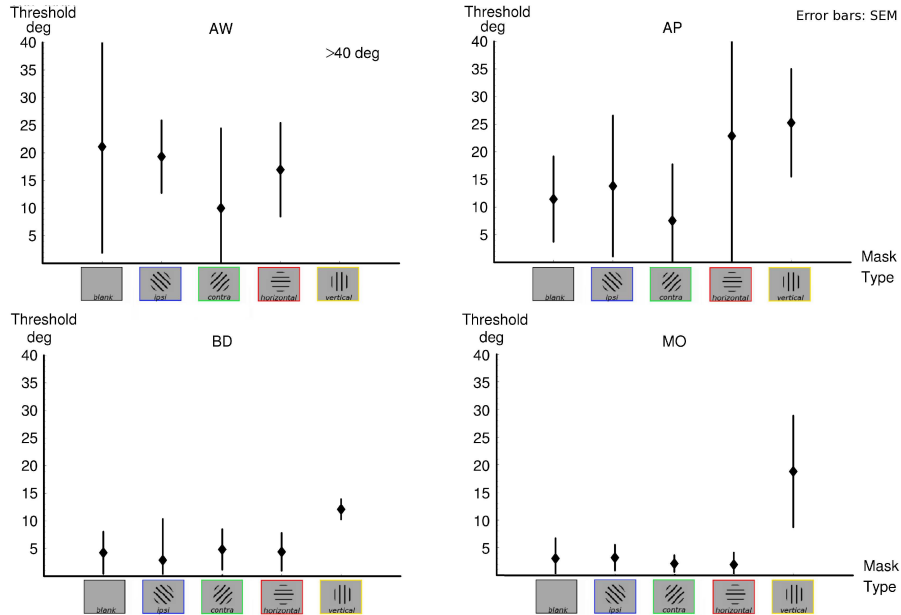


Fig. 3.5: Discrimination thresholds (deg) of four subjects under different masking conditions at a presentation time of 125 msec. Mask types (blank, ipsi, contra, horizontal, and vertical) are depicted on the X-axes. Error bars shown are standard errors of the mean.

For easier comparison, blank condition thresholds at the respective presentation time are included in the individual data plots.

In agreement with the thresholds in the blank condition, thresholds in the masking conditions vary between subjects. While subjects AW and AP need the illusory contour to be tilted at least about 10° to 20° in the masked conditions, subjects BD and MO have consistently lower thresholds (up to 10°) which drastically increase only in the vertical mask condition. Individual ability to perform the task is also similar in the blank and masking conditions. Thresholds of subjects AW and AP show large error bars over all conditions, indicating the general difficulties of these subjects in the experiment. In contrast, error bars of subjects BD and MO

are consistently smaller in all conditions, increasing only in the vertical masking condition for subject MO.

The vertical condition, which contains real lines parallel to the illusory contour, shows strong masking effects over all subjects. Individual thresholds are here at least about 2 times larger than thresholds in the blank or even other masking conditions. Only subject AP shows a masking effect in the horizontal condition as strong as in the vertical condition. Besides this single effect, masks of other than vertical orientations have little effect on the thresholds in comparison to the blank condition.

As pointed out before, real line length might be one possible cue to judge illusory contour orientation in a rectangular stimulus. Inducing lines on the upper left side of the stimulus are shorter than those on the upper right if the illusory contour is tilted to the left. A reference frame, like the rectangular borders of a line pattern, is needed to judge real line length. In the circular Gaussian stimulus used here this reference frame is per se not present. If, however, the vertical mask is presented following the stimulus, real lines of the stimulus and real lines of the mask overlap perceptually. Indeed, subjects reported to sometimes perceive line crossings between the inducing lines and the vertical mask. The vertical mask therefore might be a reference frame to judge real line length in the stimulus. Thus, it would theoretically be possible in this masking condition to judge the inducing line length on one side of the stimulus and thereby deduce the illusory contour orientation. Interestingly, the subjects apparently could not use this information in the task, as can be observed in the results.

To emphasize the consistency of masking effects between observers, averaged results of the four subjects are shown in Fig.3.6.

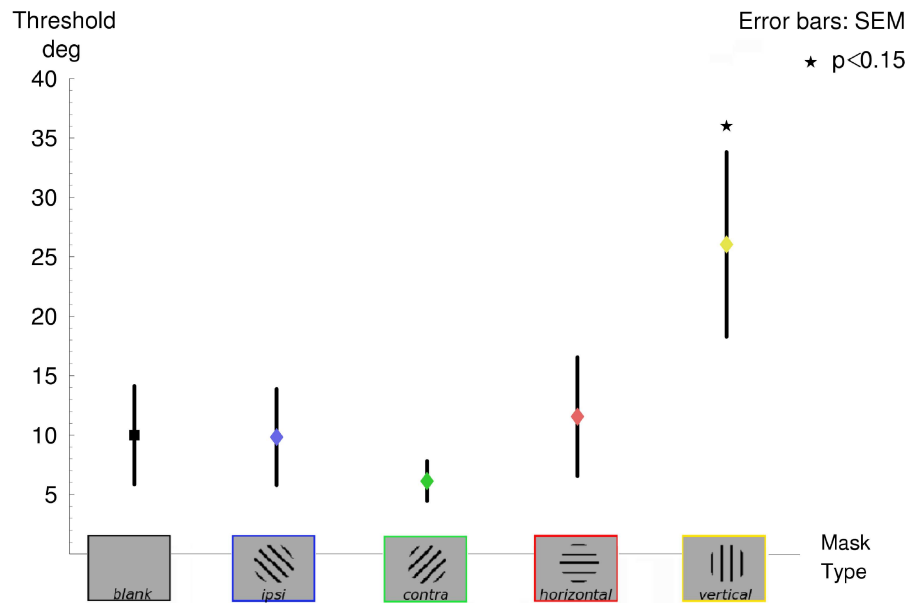


Fig. 3.6: Average of the individual discrimination thresholds (see Fig.3.5) at presentation time 125 msec over mask type in deg. Mask types are depicted on the X-axes. Error bars shown are standard errors of the mean. The star indicates a trend of the results to differ from the blank condition as assessed in a paired t-test.

Results show strong masking by the vertical line pattern. Results in the vertical condition show a trend to be different from the blank condition (paired t-test, $p < 0.15$). This trend is in agreement with single subject's results (see Fig.3.5). Every other masking pattern does not interfere significantly with the illusory contour

percept. Also, the vertical masking effect was perceived to be clearly different from other masking conditions. Subjects found it extremely difficult to do the task in the vertical masking condition, mostly having the impression of not perceiving anything but the vertical lines. In contrast, in the other conditions subjects reported to mostly perceive the illusory contour as a line shining through the masking pattern. This percept was never reported to occur in the vertical condition.

Interestingly, the contra condition appears to be less interfering than other masking conditions. Variability over subjects in this condition is furthermore less than in the blank condition. These differences, however, turned out not to be significant.

In summary, at a presentation time of 125 msec lines parallel to the illusory contour turned out to be the strongest masks, leading in average to thresholds of more than twice the threshold in the blank or even other masking conditions. Effects of other masks were not significantly different from the blank condition.

3.3.3 Time Dependency of Masking Effects

Effects of masking change over presentation and thereby processing time, as has been shown in studies using Kanizsa-type illusory figures (Reynolds 1981, Ringach & Shapley 1996). In the latter study, a temporal segregation of masking effects was found. First, local masking affected the inducing stimuli, and secondly, global masking interfered with the illusory figure. The transition between both stages occurred at a stimulus presentation time of about 120-130 msec, at which time the induction of illusory contours both of the Kanizsa-type, and the abutting line type is thought to be completed [114, 88]. Similar processing times suggest that processes of comparable complexity lead to the different illusory contour percepts. We might thus expect basic processing stages, like induction versus establishment of the illusory contour, to also be comparable between different types of illusory percepts. I test here whether masking effects on illusory contours change over time consistent with the hypothesized two stage processing.

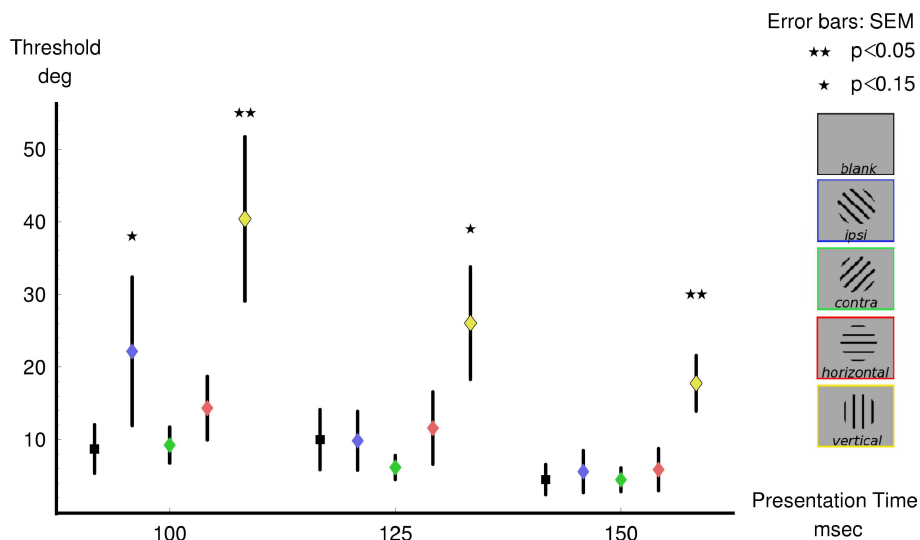


Fig. 3.7: Averaged discrimination thresholds in deg at different mask types, as depicted in the legend, and presentation times (100, 125, and 150 msec). Error bars show standard errors of the mean. Stars indicate results that significantly differ from the blank condition of the respective presentation time as assessed in a paired t-test.

The illusory contour stimulus was presented for 100, 125, and 150 msec. Abutting line gap size was 4 min of arc, line distances were 14 min of arc. Masks of differ-

ent orientations were presented following the stimulus for 200 msec. As described before, subjects had to indicate whether the illusory contour was tilted to the left or to the right. Four subjects were tested with presentation times of 100 and 125 msec, only three subjects with a presentation time of 150 msec. Averages of thresholds over subjects were calculated at each presentation time and mask type and are plotted in Fig.3.7.

Comparison of average masking effects at different presentation times shows a clear decrease of masking over time. Illusory contours, if presented for 100 msec, are strongly masked by both the ipsi pattern (parallel to the inducers) and the vertical pattern (parallel to the illusory contour). Interferences increase the averaged thresholds up to about two times the baseline thresholds (ipsi, trend to differ from baseline with $p < 0.15$) and even up to about four times the baseline thresholds in the vertical mask condition (significantly different from baseline with $p < 0.05$). At this shortest presentation time masking with horizontal patterns shows furthermore slightly increased thresholds in comparison to the blank condition. Masking effects, however, did not reach significance in this case.

In the central section of the plot are the data at presentation time 125 msec, which have been discussed above. Here only the vertical mask strongly interferes (trend with $p < 0.15$) with the illusory percept and increases the average threshold to up to twice the baseline threshold. Other mask conditions do not interfere with the illusory contour. In comparison to other conditions, in fact, the contra mask does even appear to be helpful: average thresholds are here about half the baseline threshold. This effect, however, did not turn out to be significant.

At an even longer presentation time of 150 msec, thresholds are overall lower than at shorter presentation times. This indicates the processing of the illusory contour to be clearly advanced, as already suggested by previous masking studies (Reynolds 1981, Ringach & Shapley 1996, Westheimer & Li 1996). Similar to the presentation time of 125 msec, only the vertical mask pattern has an effect on illusory contour perception. Thresholds in the vertical mask condition are significantly different from baseline ($p < 0.05$).

In summary, masks presented for 100 msec show interferences both with the inducing lines as well as with the illusory contour, as indicated by masking effects by real lines both parallel to the inducing lines, as well as to the induced contour. In contrast, at presentation times later than 125 msec solely the vertical line pattern interferes with the illusory contour percept.

3.3.4 *Dependency on Gap Size: Real or Illusory Contours?*

The two stages of masking effects shown here indicate that the stimulus used induced an illusory contour rather than a real contour for which, in contrast, two stages of masking effects have not been reported so far. One critical point in this experiment, however, is that it might not induce an illusory, but a real, luminance contrast contour[114]. I therefore test in the following experiment whether both contours induced by stimuli with and without gap are similarly affected by masking.

If an illusory contour induced by abutting line patterns without gap underlies different processes than the illusory contour induced by patterns with gap, timing and strength of masking effects would be expected to be different between both stimuli.

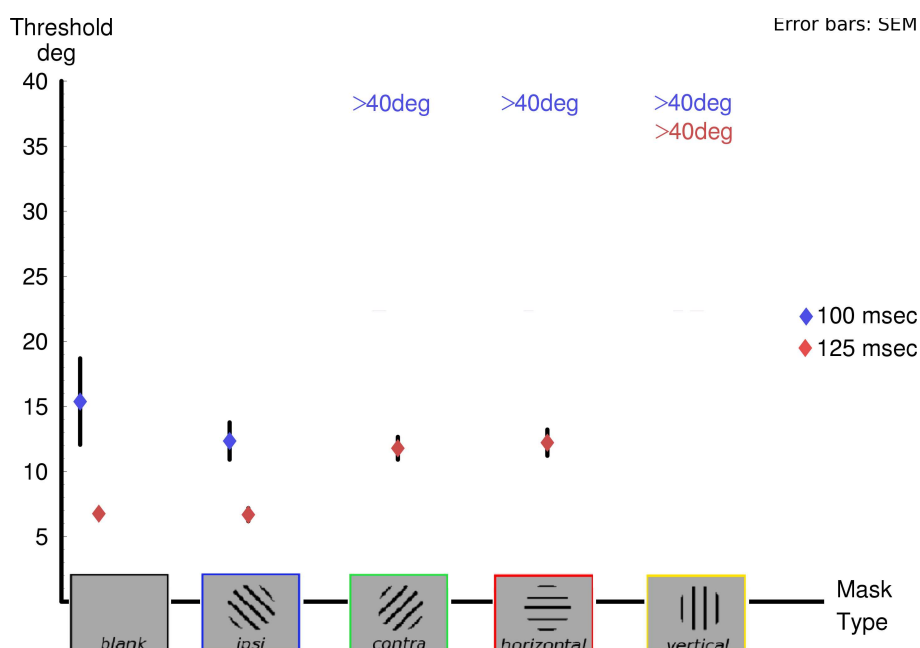


Fig. 3.8: Averaged discrimination thresholds in deg at different mask types and presentation times. Inducing lines were directly abutting (no gap). Data shown are results from two subjects. Error bars show standard errors of the mean.

An illusory contour induced by abutting line patterns without gap was presented for 100 or 125 msec, followed by the different mask types described earlier. Line distances were 14 min of arc, which was shown in section 3.3.1 to induce contours of perceptual strength comparable to the stimulus with gap. Averaged results of two subjects are shown in Fig.3.8.

At a presentation time of 125 msec, thresholds at different masking conditions show a similar pattern as seen before in the gap stimulus at the same presentation time (compare Fig.3.7). Main interfering effects are seen with the vertical mask, which leads to thresholds of more than 40° . Contra and horizontal mask patterns, however, increase thresholds much stronger than they did in the gap stimulus. Both stimuli were adjusted to have similar perceptual strength (Fig.3.3). Masking, however, has been shown by Westheimer & Li 1996 to generally affect the no gap stimulus stronger than the gap stimulus[114]. Also presentation of the gap stimulus mask patterns oriented other than vertical showed either elevated thresholds or higher variability (Fig.3.7). Stronger interference by all mask patterns might therefore be expected with the no gap stimulus.

One real difference, though, is the ipsi masking condition, which in the gap condition resulted in more drastically increased thresholds than was seen in the contra or horizontal condition. In the no gap stimulus, however, thresholds in the ipsi condition are identical to those in the blank condition. While this seems to be rather surprising, it is evident from the stimulus settings why the ipsi mask might even strengthen the illusory contour percept in the no gap stimulus. The ipsi masking line pattern is oriented parallel to the inducing pattern. By directly presenting the mask following the no gap stimulus, a strong motion percept is induced, sliding both halves of the inducing pattern towards each other. This motion occurs along the illusory contour, that is thereby induced first, by the stimulus, and secondly, by the motion effect due to the mask presentation. Subjects indeed reported to perceive a strong movement along the illusory contour in this condition. In contrast, this percept was never reported in the gap condition, suggesting that the distance

of the abutting line patterns prevents a second illusory contour induction and thus allows for masking effects of the ipsi masking pattern.

At 100 msec presentation time, thresholds are overall increased in comparison to a presentation time of 125 msec, as has been found with the gap stimulus too (Fig.3.7). While strongest masking effects at 125 msec were only seen in the vertical masking condition, at 100 msec almost every masking pattern leads to poor perception of the illusory contour. The only exception is the ipsi condition, which shows thresholds similar to the blank condition. As pointed out above, this effect is most probably due to the strong motion effect perceived in this condition.

Besides the motion effect induced by the ipsi mask, backward masking of the no gap stimulus thus leads to results similar to those presented before in the gap condition. Early on (100 msec), almost every oriented mask pattern interferes with the illusory contour perception. Later on (125 msec), only real lines parallel to the illusory contour show strong masking effects. Results presented here thereby indicate that both abutting line stimuli with and without gap lead to the induction of an illusory contour.

3.3.5 *Illusory Contours as Mask*

In the previous sections I showed that illusory contours can be selectively masked with lines parallel to them. Similar masking effects have been shown with real contours (Li et al. 2001). Illusory contours are represented in neurally orientation specific domains in area V2 also activated by real lines of the same orientation (von der Heydt & Peterhans 1989). Orientation specific interference of real lines with the illusory contour might be due to direct interaction of induced illusory activity and newly incoming real signals in the oriented domains in V2. As these domains are both activated by real and illusory contours, also an illusory contour of the same orientation might lead to masking effects similar to those of parallel real line masks. A masking pattern which by itself does not significantly interfere with the illusory percept, would be expected to mask stronger if it additionally induces an illusory contour parallel to the target contour. The backward masking illusory contour, however, would naturally be started to be processed later than the target illusory contour. Masking effects by illusory contours would therefore be expected to be considerably smaller than effects by luminance contrast contours at the same presentation times.

To test whether masking patterns with illusory contour lead to stronger interference than the same patterns without illusory contour, I conducted the same backward masking experiment with different masking patterns with and without vertical illusory contour. Results shown in Fig.3.9 are averages over three subjects at presentation times 100 and 125 msec.

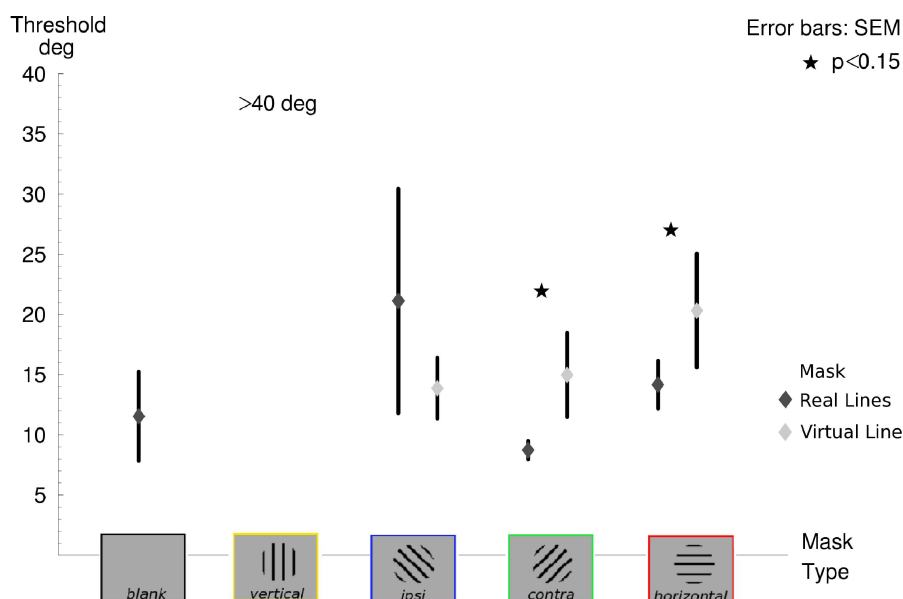


Fig. 3.9: Averaged discrimination thresholds in deg at different mask types, as depicted in the legend. Ipsi, contra, horizontal pattern were presented with or without a vertical illusory contour (i.e. central vertical gap). Results of three subjects with presentation times 100 and 125 msec were averaged. Error bars show standard errors of the mean. Stars indicate results that significantly differ in the virtual line condition from the real line pattern condition, as assessed in a paired t-test.

To allow for comparison with the blank and the vertical masking condition, the respective averaged results are also presented in the graph. Blank thresholds are at about 12° , while the averaged threshold in the vertical mask condition is at over 40° . Thresholds in the ipsi and horizontal masking conditions using real lines only are increased as compared to the blank condition, while being significantly lower than the threshold in the vertical masking condition. As seen before (Fig.3.7), the contra pattern appears to rather help than interfere with the percept.

Comparing thresholds in mask conditions with vertical illusory contour, we can see two effects. First, the ipsi mask pattern leads to better performance with the illusory contour than without. Yet, this effect turned out not to be significant. Why is the ipsi masking effect not increased by including an illusory contour? One possible interpretation of the masking effects of the ipsi pattern in the real line condition is that real lines in the mask directly mask the parallel real lines in the stimulus (compare to Li et al. 2001). On the other hand, real lines parallel to the inducing lines might also interfere with the illusory percept by “closing the gap”, which the illusory contour would have to bridge, as termed by Peterhans & Von der Heydt 1989. Induction would thus possibly not be initiated because of inhibition of end-stopped cells in V1, which might mediate the early stage of illusory contour processing [109]. The masking effect would therefore not necessarily be due to interference with the real contours, but with the inducing process. By “adding” a vertical illusory contour (i.e. a gap) to the ipsi pattern, one of the interfering moments of this pattern is deleted. The masking effect of this pattern is thereby diminished.

Secondly, thresholds in the contra and horizontal condition are increased in the illusory contour mask as compared to the real line mask. Both these effects were trends with $p < 0.15$. Interference by the vertical illusory contour was, as predicted, smaller than the masking effect found with vertical real lines. This can be due to processing time differences between target and masking illusory contours. The masking illusory contour would be expected to be perceptually much weaker

than the target illusory contour. Masking effects should thereby be decreased in comparison to other masking lines. Furthermore, perceptual strength of real contours is per se stronger than that of illusory contours (compare Westheimer & Li 1996, Ringach & Shapley 1996). Illusory contours might thus in any case be less effective masks than real contours of the same orientation.

To summarize, illusory contours can mask illusory contours: mask patterns that were only weakly (horizontal mask) or not interfering (contra mask), showed the tendency of increased thresholds ($p < 0.15$) when containing an illusory contour as compared to the real contour masking pattern alone. Thresholds were considerably lower than those found in the vertical mask condition, indicating lower perceptual strength of the masking illusory contour in comparison to the masking vertical real lines. In contrast, the ipsi mask patterns did not show higher thresholds when containing an illusory contour. This suggests that the ipsi pattern more efficiently than other masks “closes the gap” and thereby interferes with the inducing processes. When the ipsi mask itself contains an illusory contour, i.e. a gap, inducing processes can proceed to bridge the stimulus’ gap and thus induce an illusory contour.

3.4 Discussion

3.4.1 Masking of Illusory Contours depends on Orientation

Illusory contours are neurally represented in primate area V2 in orientation selective neurons which also respond to real lines of the same orientation (von der Heydt & Peterhans 1989).

Real lines are masked best by real parallel lines (Li et al. 2001). There has been evidence that also Kanizsa-figure illusory contour can be masked by parallel real lines (Ringach & Shapley 1996). Abutting line type illusory contours, however, have so far only been shown to be masked by real lines in general, as compared to effects of circular masking pattern, or random dot masks (Westheimer & Li 1996). As abutting line induced illusory contours are neurally represented in the same V2 cells as Kanizsa-figure contours and real lines, interactions between real and all these illusory contours should be highly orientation specific. Problematic in the case of abutting line pattern is only, that it is not possible to separate oriented real lines from oriented illusory lines in the stimulus. Masking of the abutting line pattern by presenting a random line pattern [114] does not allow to infer on masking effects on illusory contours. The line pattern could have masked the inducing real lines as well.

I tested here whether masking of abutting line stimuli by real lines indicates interference with inducing, or rather with induced contours. I tested this by measuring orientation discrimination thresholds of illusory contours. As abutting line pattern were presented for 125 msec, completed induction of the illusory contour was assured [87, 88, 114, 58]. Illusory contours were backward masked with oriented line pattern either parallel to the inducing contours (ipsi), parallel to the illusory contour (vertical), oriented horizontally, or rotated by 90° to the inducing lines (contra). By assuming that the rule “parallel lines mask best” holds both for real and illusory contours, expectations were the following. If real lines specifically interfere with the inducing contours, the ipsi pattern should show maximal masking effects. If, on the other hand, real lines interfere directly with the illusory contour, the vertical pattern should strongly interfere with the percept.

The averaged results presented in Fig.3.6 reveal clearly support for real line interference with the illusory contour rather than with the inducers. Vertical line patterns, i.e. lines parallel to the illusory contour, strongly increase discrimination thresholds. Subjective experience of most subjects in this masking condition is even to “see nothing”. Other real line orientations do on average not interfere with the percept, indicating that illusory contour induction is completed at this time. Thus, solely interference with the neural representation of the illusory contour is possible at presentation times of 125 msec. Although single subject’s results are less clear (Fig.3.5), they all show the same major effect: vertical lines interfere with the percept, leading in some cases to performance at chance rate. Masking effects of other than the vertical lines might indicate some variability in processing time of illusory contours over subjects.

Data provided here therefore provide evidence for orientation specific masking effects of illusory contours. Parallel real lines strongly interfere with the illusory contour. The assumption that “parallel lines mask best” can thus be supported to also hold for illusory contours of the abutting line type.

3.4.2 Masking of Illusory Contours changes over Time

Illusory contours are second order contours, which are induced by contextual stimuli, leading to a neural representation as oriented lines without having a direct physical counterpart in the stimulus. Illusory contours are thus necessarily at least in part processed differently from real contours: first, they are induced, and second,

their neural representation has to be established.

The segregation of illusory contour processing into two major steps has been indicated by several studies. Von der Heydt & Peterhans 1989 found oriented single cell activity to illusory contour stimulation in primate area V2, but not in V1 cells of the same orientation selectivity. This suggested that the contour information cannot be inferred by V1 from low level contrast information. Rather illusory contour information has to be induced in different structures early on, leading to the contour itself being not represented before V2. Recent physiology studies by Lee & Nguyen (2001) and Ramsden et al. (2001) even suggested feedback signals from area V2 to V1 to be part of the illusory contour processing. This indicates that establishing the illusory contour related activity involves complex processes distributed over different areas. A psychophysical study by Ringach & Shapley (1996) also provided evidence for temporal segregation of inducing and induced processes. They showed that local masks (masking the inducers) can interfere with Kanizsa-type illusory contours early after stimulus presentation, while global masks (masking the illusory contours) interfere later. Local and global processes were divided in this study at processing times of about 120 msec. Similar time constants were reported in masking experiments by Reynolds (1981), Westheimer & Li (1996), and Guttman et al. (2004), suggesting that perceptual transition between induction and establishment of the illusory percept occurs at about 120 msec.

Physiologically, slightly shorter times are reported. A study by Lee & Nguyen (2001) showed that illusory contours of the Kanizsa-figure type are represented in V2 earliest at about 90 msec. Furthermore, von der Heydt & Peterhans (1989) reported V2 latencies to abutting line stimulation of about 70-80 msec, suggesting that the transition from inducing to induced processes occurs at this time. Of course, the timing of neural and perceptual events does not have to be identical. Even if some single cells respond to a stimulus, perceptual strength of this stimulus does not necessarily reach levels at which the stimulus or its properties are clearly perceived by a subject.

Illusory contours induced by abutting lines, as discussed in the previous section, are masked by real lines parallel to them at presentation times of 125 msec. The orientation specificity of these masking effects suggests that at this time real lines interfere with the illusory contour processes rather than with the inducing processes. I tested whether earlier on masking of the inducing processes can be shown. Measuring the change of masking effects over time I thus tested whether two steps of processing, induction and establishing, lead to the percept of illusory contours in the abutting line stimulus.

As presented in the results section in Fig.3.7, the orientation specificity of masking of illusory contours indeed changes drastically over time. Lines parallel to the illusory contours strongly interfere at all times, but lines parallel to the inducing contours interfere at 100 msec presentation time. As stated before, this indicates that early on inducing processes can be masked, while later on solely the illusory contour itself, i.e. the establishing processes, can be interfered with.

Why do vertical lines still interfere at earlier times? As the transition between induction and establishing of the illusory contours certainly is not a sharp, but rather a gradual process, both stages are expected to overlap to some extent in the rather short time period tested here (100 to 150 msec). Furthermore, the perceptual strength of illusory contours increases over presentation time (see Fig.3.4). That means that after a presentation time of 100 msec stimulation is sufficient to induce an illusory percept, which is, however, weaker than after a presentation times of 150 msec. Interference with the illusory contour itself would thus be expected to occur at both times, but to be stronger early on. Exactly this can be seen in the results (Fig.3.7): vertical line pattern interference decreases with increasing presentation time.

The experiments conducted here thus show that interaction between real and illusory contours, specifically backward masking of illusory contours by real lines, changes over time. Data indicate that abutting line stimuli first induce illusory contour processing, which then leads to the establishing processes probably related to neural representation of the illusory contour in V2. Transition between the two stages occurs at about 125 msec presentation time. At that time especially the induction phase appears to be completed, as suggested previously by other studies [87, 114, 88, 27]. As similar results have been already shown for Kanizsa-figures [88], I suggest that the separation of inducing and induced processes as well as its timing are general properties of second order contour processing.

3.4.3 Possible Mechanisms of Real-Illusory Contour Interaction

How might an oriented line pattern interfere with the illusory contour percept? In the following sections, two possibilities to interpret the stimulus used here and its effects on the visual system are described and related to the results obtained here.

Line Crossings leading to new Luminance Contrast Contours

Oriented line pattern masks result in a very distinct pattern of line crossings between the inducing and the masking lines. This overlap might lead to contrast enhancement in early visual processing at single locations in the pattern. Such an effect would perceptually change the luminance contrast pattern of the stimulus dependent on mask orientation, as depicted in Fig.3.10. For the processing of the illusory contour especially contrast changes in close proximity to the illusory contour could be important: these new contrast borders can be processed as real contours, or change the way the illusory contour is induced.

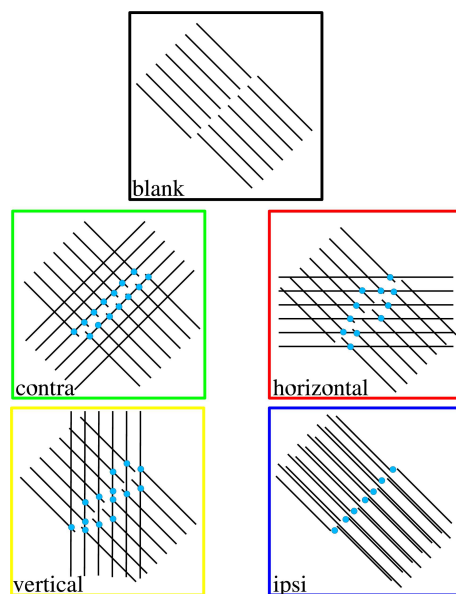


Fig. 3.10: Depiction of possible effects of line crossings by inducing and masking pattern of different orientations. Blue dots indicate line crossings in close proximity to the illusory contours.

In the blank condition, only the line ends and the overall contrast difference between line patterns and gap indicate location and orientation of the target contour. In the contra mask condition, line crossings almost coincide with line ends, thereby enhancing the contrast border to the target contour. Horizontal and vertical line

patterns, however, lead to a much more complicated pattern of line crossings and line ends. In the horizontal condition this pattern is still mostly consistent with target contour orientation. In the vertical condition, on the other hand, a clear shift in the contrast pattern occurs, which might perceptually obscure the target contour orientation. Ipsi-oriented line patterns, finally, do not lead to line crossings and thus do not enhance any contrast border. The contrast pattern visible in this condition would therefore be comparable to the blank condition.

Oriented line pattern masks thereby might induce contour percepts of other orientations than that of the illusory contour simply by changing the overall contrast patterns. Are the data presented here consistent with these effects?

This hypothesis is supported by the consistently strong interference by the vertical line pattern, and, furthermore, by the result that contra masks interfere slightly less than other mask types.

Opposing to the predictions of the contrast model, however, I did not find the ipsi pattern to be comparable to the blank condition. In fact, at early interaction times (100 msec, see Fig.3.7) the ipsi mask was on average strongly interfering with the percept. The horizontal pattern, however, did not lead to comparable masking effects, even though we would expect it to interfere stronger than the ipsi pattern.

One further prediction of the luminance contrast based model is depicted in fig.3.11. By masking with another illusory contour instead of masking with a real line the contrast pattern to be processed is changed drastically. The effect is illustrated with the contra mask, which normally appears to rather help than interfere with the illusory contour percept. Changing the masking pattern such that it itself induces an illusory contour leads to lines along which contrast borders are enhanced by crossover of stimulus lines and mask lines. First, the pattern as shown in Fig.3.10(contra) is still induced by stimulus and mask, but second, an additional pattern induced by the gap in the mask pattern is visible. Both, indicated by the blue dots in Fig.3.11(contra virtual) lead to an ambiguous percept of one vertical and one contour of a different orientation. In comparison to the vertical mask effect, as shown in the same figure, the illusory contour in the contra mask appears to obscure the illusory contour percept much more. Orientation discrimination with this “illusory” masking pattern would thus be expected to be considerably worse as compared to the vertical masking condition.

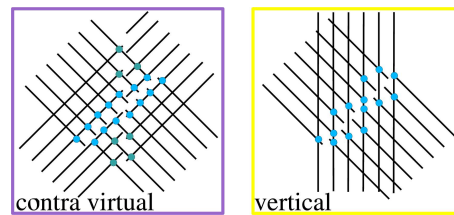


Fig. 3.11: Depiction of possible effects of line crossings by inducing and masking pattern. Compared are here vertical line pattern and contra pattern with a vertical illusory contour. Blue dots indicate line crossings in close proximity to the illusory contours.

The results presented in Fig.3.9 do not support the model described above. Interferences by masks with illusory contours are increased as compared to effects of real line masks alone. Thresholds, however, are considerably lower than those measured in the vertical mask condition. Interestingly, the ipsi mask even shows an unexpected decrease of the average threshold (Fig.3.9).

I therefore conclude that the masking effects presented here are not solely due to the changes in the overall contrast pattern which are generated by presenting mask patterns of different orientations.

Real Contours interact with Inducing Processes and Illusory Contours

An alternative model of interactions between real and illusory contours is based on the neural representation of both contours in the same orientation selective cells in V2[78, 109]. Interactions between real contours and the illusory processes might be understood by real line interaction with the inducing mechanism in abutting line stimuli, namely with end-stopped cells in V1[78, 109]. A different explanation of real contour effects on illusory contour processes is based on real-real contour interactions, specifically on real line masking by parallel lines, as reported in V1[61, 62, 64]. Experimental results will now be discussed in the light of these neural mechanisms. I found early masking effects (<125 msec) by most oriented line pattern. Especially masking with vertical lines and patterns oriented parallel to the inducers showed strong effects. Horizontal patterns were also weakly interfering with the illusory contour percept. This broad, but tuned interference could be explained by interference of the masks with the inducing processes such that patterns oriented similar to the inducers “close the gap”. An abutting line illusory contour is most probably induced by activation of oriented end-stop cells in V1[109]. These cells converge on cells in V2 that are activated as well by simple/complex cells of the opposite orientation specificity[34]. End-stopped cells typically are inhibited by lines extending over their receptive fields (Hubel & Wiesel 1968). Lines parallel to the inducers, but extending over the gap, thus might decrease the activation of V2 by inhibiting end-stopped cells in V1.

At presentation times of at least 125 msec only vertical line patterns show strong interference with the percept. Their masking effects can be understood by a direct interaction of real lines with the illusory contour in orientation specific cells, probably in V2. Real lines can be masked best by lines parallel to them, even if the masks are outside the receptive field of the studied cell, as has been shown by Li et al. 2001. This masking effect has also been shown psychophysically in the same study. Similar effects were reported by Macknik & Livingstone 1998, who showed changes in V1 single cell activity due to backward masking with parallel lines, leading to a complete invisibility of the target line. Comparable interferences with single cell activity might also occur in V2, thereby allowing real lines to interfere with illusory contour activation in V2 oriented single cells. These effects, however, have not been reported in V2 so far. As a feedback mechanism from V2 to V1 has been suggested to be part of the illusory contour mechanism[58, 84, 90], masking of illusory contours by parallel real lines might even simply occur in V1 similar to the masking of real lines reported by Li et al. (2001) and Macknik & Livingstone (1998). This would imply that illusory contour related V1 activation is necessary to perceive illusory contours.

Finally, I conducted an experiment using illusory contours as masks to test the following predictions. As there is no reason to think that the illusory contours from target and mask would be processed by different mechanisms, the masking illusory contour would be expected to interfere with the target illusory contour. In principle, this interference should be as strong as that found with vertical real lines. In the backward masking experiment, though, the mask is naturally presented after the target. Processing of the target illusory contour would thereby be advanced by the time of induction of the masking contour. The target illusory contour would thus be perceptually stronger than the masking illusory contour by the time the latter would be presented. Interference of the the illusory contour mask would thus be very weak in the beginning and increase over time. The vertical real line pattern, on the other hand, can interfere with the target in a much faster and stronger way. The contra pattern with illusory contour would thus be expected to show considerably less interference than the vertical line pattern. As the illusory contour, however, still would interfere with the target stimulus, we would expect increased thresholds

by masking with a vertical illusory contour as compared to the contra mask alone. Experimental results support the latter assumption: contra masks which contained an illusory contour interfered stronger than contra masks without an illusory contour. Thresholds, however, never reached levels seen in masking with vertical lines (Fig.3.9). The same results were found with the horizontal pattern, indicating that an additional vertical illusory contour in a stimulus tends to increase mask strength of otherwise only weakly masking pattern.

A very different result was obtained with the ipsi pattern which resulted in slightly lower thresholds with illusory contour than without.

The ipsi mask itself interferes stronger with the illusory percept than the contra or horizontal masks (Fig.3.7). This interference was especially found at shorter presentation times (100 msec) and decreased at later times (150 msec). The ipsi mask is thus probably not interfering with the illusory contour, but rather with the inducing processes. As the ipsi pattern is oriented parallel to the inducing pattern, it might directly mask the cortical processing of the inducing real contours, as suggested by masking studies by Macknik & Livingstone 1998 and Li et al. 2001. Both studies showed that even parallel lines only surrounding the stimulus line can mask its perception efficiently. An illusory contour (i.e. a gap of 4 min of arc) in the masking pattern is thereby not expected to drastically reduce any parallel masking effects. Rather, we would expect increased interference similar to the effects in the contra and horizontal masks, because an additional mask component, the illusory contour, interferes with the percept. Interference of the ipsi pattern with illusory contour, however, is relatively smaller than interference of the ipsi pattern alone (Fig.3.7). As pointed out above, masking by lines parallel to the inducers might, though, be possibly related to “closing the gap”. Parallel lines, which extend over the receptive fields of cells inducing the illusory contour would inhibit their activity. The masking illusory contour represents a gap, at which parallel lines do not extend over the receptive fields of cells activated by line ends. End-stop cell activity would thus be less inhibited in an ipsi mask with illusory contour pattern than in the real line mask alone.

Taken together, the results of the experiments conducted here support direct interactions of real contours with both inducing processes and the illusory contour. The data are consistent with known or proposed neural mechanisms underlying these interactions, such as end-stop cell driven induction of abutting line illusory contours, and integration of stimulus and target activation in oriented single cells in either V1 or V2.

3.4.4 *Conclusion*

This chapter described backward masking of illusory contours by real lines. Backward masking effects are orientation selective and change over time. The evidence presented here indicates that abutting line induced illusory contours are processed in two steps. First, they are induced, and second, their neural representation is established. Induction processes are completed at a time of about 125 msec, while establishing the illusory contour extends at least over 150 msec.

I found evidence for two processing stages for abutting line stimuli with and without gap, suggesting that these stimuli induce a second order contour. Changes of masking over time very similar to the effects described here were also found with Kanizsa-figure stimulation, which were masked early on locally (inducing processes), and later on globally (induced processes)[88]. I therefore suggest that illusory or second order contours are processed in general via inducing processes extending over the first 125 msec, followed by processes establishing the neural representation of the induced contour.

I furthermore suggest the following mechanisms to explain orientation selective in-

teractions between real and abutting line illusory contours. Real contours can interfere early on (< 125 msec) with the processes inducing the illusory contour, namely by probably inhibiting end-stopped cells in early visual cortex[109]. Later on (≥ 125 msec), real contours interfere with the illusory contour, showing parallel line masking effects that might be comparable to masking of real lines as showed in V1[64, 61, 62]. This would indicate that either similar masking effects also occur in V2, or that illusory contours are represented and masked in V1, as suggested by other studies[58, 84, 90].

4. CONTRAST DEPENDENT MODULATIONS OF ILLUSORY CONTOUR PERCEPTION

4.1 Introduction

Our environment is structured by luminance defined and context defined contours, both of which provide vital information about object borders. Context defined contours include abutting line induced contours and Kanizsa figure contours. Illusory contour perception depends solely on real elements, the inducers. Every change of the illusory contour percept is thus necessarily based on changes in the contextual real elements. Understanding how changes in the context affect illusory contour perception is therefore a major step towards understanding the underlying processes. A number of neurophysiological studies have indicated the presence of neurons responsive to illusory contours in the early visual cortical areas. The first observations of neural responses to illusory contours in visual cortex were made in macaque area V2, but not V1 (Von der Heydt & Peterhans 1989, Peterhans & Von der Heydt 1989). Single cell responses to illusory contour stimulation were found to be similar to real contour responses. Neurons were activated both by moving partial rectangles arranged such that they spanned an illusory rectangle between them (Kanizsa type figures), and by abutting line stimuli. Cells responded even when real edges were clearly outside the receptive fields, showing context induced gap closure in area V2 [109, 78].

Neural signals and intrinsic activation, however, have recently been shown also in primary visual cortex (Ramsden et al. 2001, Lee & Nguyen 2001). These studies suggested a possible feedback mechanism from primate V2 to V1 might be involved in illusory contour processing. So found Lee & Nguyen (2001) single cell activity to flashed Kanizsa figures in macaque V1 and V2. Primary visual cortex responses were delayed, however, relative to V2 activation. In contrast, real contour activation arises first in V1, followed by V2 (Schmolesky et al. 1998).

Ramsden et al. (2001) also showed primary visual cortex activity to illusory contour stimulation. Using optical imaging they measured orientation maps to abutting line pattern and real line stimuli. In V2, maps were found to widely overlap, in accordance with previous reports [109, 78]. Activation in V1, however, was strongest to illusory contour orientations opposite to optimal real contour orientations. V1 has been shown not to carry the earliest illusory contour signal [109, 78, 58]. The orientation reversal in primary visual cortex thus must be due to feedback, possibly from V2.

As illusory contours are induced by contextual stimuli, their properties rely on elements defined by luminance contrast. Real contour information fedforward from LGN to cortical areas is thus a crucial part of illusory contour processing. Based on this and the results cited above [109, 78, 58, 84], Roe 2003 proposed orientation dependent interactions between real (feedforward) and illusory (feedback) contour processing in primate V1 and V2.

The hypothesized system would lead to possible perceptual interactions between extracted illusory contours and additional real contour information. Are there perceptual evidences for interactions between real and illusory contours?

As can be observed in Fig.4.1, contextual real elements in a scene appear qualita-

tively to be able to change the perceptual strength of illusory contours dependent on their orientation (Kanizsa 1976): Kanizsa-type triangles apparently are perceptually strengthened by lines abutting to the illusory outlines, but weakened by lines superimposed on the illusory contours. Psychophysical experiments so far only provided evidence for interference by high contrast parallel lines. So measured Ringach & Shapley 1996 form discrimination thresholds with illusory figures of the Kanizsa type. Superimposing real contours on the illusory outlines significantly increased thresholds showing interference of parallel real lines with the illusory percept. In contrast, Dresch & Bonnet (1995) tested detectability of real lines, and found subthreshold lines being detectable if superimposed on illusory contours. This subthreshold summation effect of parallel real and illusory lines [14], together with high-contrast parallel line interference [88] indicate possible contrast-dependent real-illusory interactions.

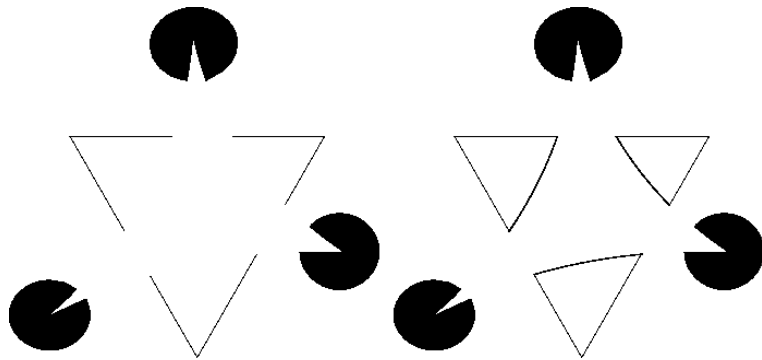


Fig. 4.1: Examples for perceptual effects of real lines of different orientations on an illusory contour percept, here Kanizsa-type triangles. The Kanizsa-triangle with abutting real line elements appears to be perceptually stronger than the same triangle with parallel real elements.

Feedback from V2 and orientation reversal in V1 as part of the hypothesized illusory contour mechanism (Roe 2003) would lead to specific real-illusory interactions that should be psychophysically measurable.

First, interactions between real and illusory contours are expected to be orientation dependent.

Second, contextual effects onto illusory contours should be measurable even at sub-threshold contrasts, if interactions occur at early processing stages.

Measuring perceptual strength of illusory contours under contextual modulation it was tested here whether interaction between illusory and real contours depends on orientation and contrast.

4.2 Methods

4.2.1 Apparatus

Experiments were programmed using OpenGL and C/C++ under Linux (Mandrake 9.2) on a pentium computer. Stimuli were displayed on a 17 inch CRT color monitor (Gateway 2000 Vivitron) with refresh rate 75 Hz. The monitor was calibrated with a Minolta CS-100. Experiments were carried out binocularly in a dark room at a viewing distance of 25 in. Data were analyzed with Mathematica 5 (for details see below).

4.2.2 Subjects

Four female subjects, between 20 and 27 years old, participated. Three of the subjects were naïve to the purpose of the experiments. All subjects had normal or corrected to normal acuity.

4.2.3 Stimuli

Discrimination Task (Illusory Contour)

The stimulus consisted of three black partial disks ($0.5\text{cd}/\text{m}^2$) with a diameter of 37 min of arc that induced a Kanizsa-type illusory triangle (see Fig.4.2). The illusory contour tested (right side of the illusory triangle) was 2° long with a support ratio of 0.4. Opening angles of the partial disks inducing this contour were randomly changed ($\pm 0-4^\circ$) to produce a percept of the contour being bent either outwards or inwards (cf. Ringach & Shapley 1996).

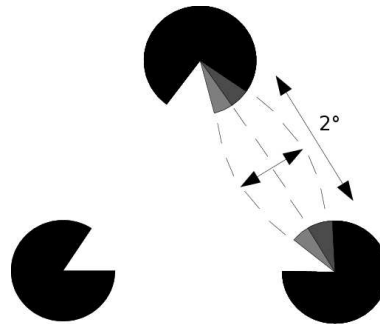


Fig. 4.2: Two of the inducers of a Kanizsa-type illusory triangle were changed randomly (opening $\pm 0-4^\circ$) to produce a percept of the illusory contour tested being curved in- or outwards. The illusory contour's length was 2° . Appearance of inwards and outwards bending contour is exaggerated in this depiction.

The effects of real lines onto illusory contour perception were tested by presenting a short real contour simultaneously to the illusory contour. To test whether real line effects depend on orientation, real lines were presented either parallel (superimposed) or orthogonal (abutting) to the illusory contour. These two conditions were randomly interleaved with a baseline condition, in which no additional real line was presented.

The real contour was a sixth of the illusory contour's length (18 min of arc). It was presented in the middle of the upper half of the tested illusory contour. Both positioning and length of the real contour were chosen to ensure stable stimulus conditions. They assured minimal changes of distance between the real and illusory contour under each bending condition, as distance between real and illusory stimuli has been shown to affect detectability of real components superimposed on illusory

contours (McCourt & Paulsen 1994).

Interactions between real and illusory contours have been found to be possibly dependent on real line contrast (Dresp & Bonnet 1995, Ringach & Shapley 1996). This was tested by presenting oriented real lines at Weber contrasts of 3%, 5%, 10%, 15%, and 30%, covering the whole perceptual range from subthreshold to suprathreshold contrasts. Lowest (subthreshold) contrasts furthermore allowed to test whether real-illusory contour interactions depend on conscious perception of the interacting real line.

Detection Task (Real Contour)

Perceptual strength, i.e. detectability, of real stimuli superimposed on illusory contours is known to vary considerably over subjects (McCourt & Paulsen 1994). Stimuli of identical contrasts in the same experimental setup can be clearly visible to one subject, but subthreshold for another subject. To allow comparison of data across subjects despite these perceptual differences, detection thresholds were measured for the real stimuli used in our experiment. Discrimination data were then aligned to the subject's detection threshold, as described in detail in the analysis section.

Detection thresholds for real lines were measured for each subject. The stimulus consisted of two Kanizsa-type squares presented left and right from the fixation spot. The illusory contours had the same length and support ratio as the illusory contour tested in the discrimination experiment. Real lines identical to lines used in the discrimination task were presented either superimposed on the left or right Kanizsa-square. Lines were shown on the illusory contours next to the fixation spot. Why was the stimulus design changed for this task? Pretests were carried out with stimuli identical to the discrimination task design. Real lines were presented in the upper or lower half of the bent illusory contour. Subjects had to detect where the real line was shown. Results in these pretests (not shown) were similar to the data shown here. Subjects, however, reported difficulties concentrating on where they detected the real line in the triangle stimulus (both possible locations of the real line were very close to each other). The design was therefore changed, placing the real lines to the left or to the right of the fixation spot, thereby perceptually clearly separating both options.

I chose Kanizsa-type squares (instead of the triangles used before) and real line location on the illusory contour (centrally instead of closer to one inducer) to allow comparison of our detection experiments with previously reported data by Dresp & Bonnet (1995) and Ringach & Shapley (1996).

Parallel and orthogonal real lines were tested at contrasts of 0% (i.e. no line), 3%, 5%, 10%, 15%, and 30%. Contrasts were identical to contrasts used in the discrimination task, enabling us to precisely know whether a real-illusory interaction found in the discrimination experiment was due to subthreshold or suprathreshold real line effects.

Real lines were 18 arcmin long (identical to the discrimination task) and were placed in the center of the illusory contour. Separate experiments were conducted with straight illusory contours, bent inwards ($\pm -4^\circ$), and bent outwards ($\pm +4^\circ$) illusory contours, to provide an estimate of the perceptual strength of real contours used in the discrimination task with illusory contours of varying curvature.

4.2.4 Procedure

Subjects were seated at 25 in viewing distance in a dark room. In all experiments, a black fixation spot was presented for 500 msec followed by the stimulus, that was shown for 250 msec (see Fig.4.4). The fixation spot remained visible throughout the stimulus presentation. The program then awaited the subject's response. No

error feedback was given.

Subjects practiced the experiments until thresholds were stable for at least three days (i.e. about 1500 trials) before thresholds shown here were collected.

Discrimination Task (Illusory Contour)

In a 2 alternative forced choice paradigm with constant stimuli subjects had to indicate via mouse button click, whether the illusory contour on the right side of the stimulus appeared to be curved to the left or to the right.

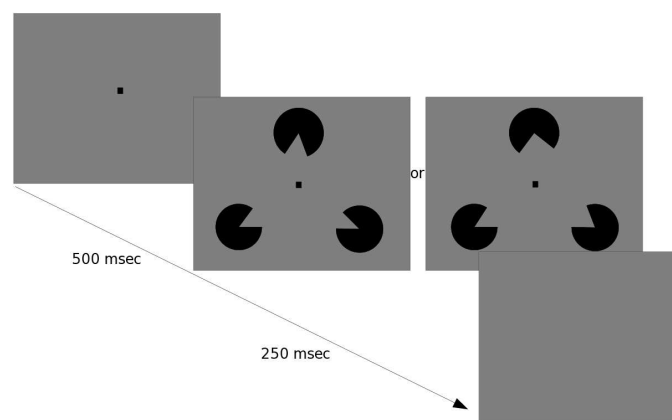


Fig. 4.3: Discrimination Task. A fixation period of 500 msec was followed by the stimulus (250 msec), whose right side was perceived to be either bent out- or inwards. Subjects had to decide in a 2AFC paradigm, to what side the illusory contour was bent.

I used the method of constant stimuli, measuring perceptual strength of illusory contour curvature at 5 different settings (partial disk opening change at 0, 1, 2, 3, or 4° inwards or outwards respectively). These different stimuli were presented in a pseudo-random fashion. Percent correct responses at each curvature setting are fitted to a psychometric function. Thresholds were calculated at 75% correct responses. Thresholds presented here are based on a total of at least 300 trials that were collected over several days.

Detection Task (Real Contour)

Detection thresholds for orthogonal and parallel real lines were measured for each subject separately.

After fixating for 500 msec two Kanizsa-type squares were presented side by side for 250 msec, with the subject holding fixation centered between them. Real lines were presented on either the left or right virtual contour (closest to fixation spot). Contrasts and orientations were randomized. Subjects had to report whether the real line had been presented to the left or the right of the fixation spot (2AFC procedure).

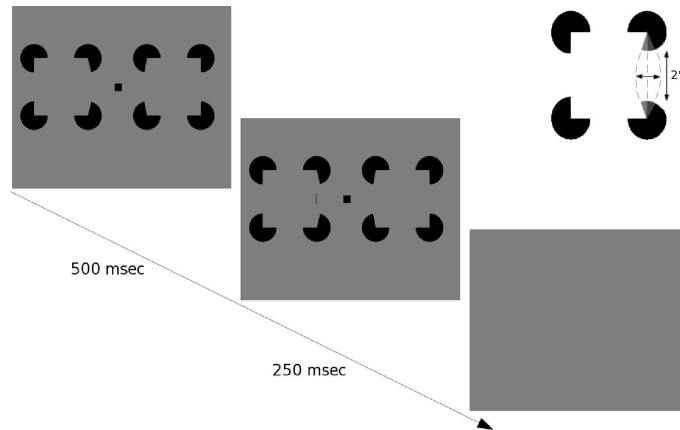


Fig. 4.4: Detection Task. During a fixation period of 500 msec two illusory squares were presented to the left and right of the fixation spot. A real line was then presented for 250 msec superimposed on one of the illusory contours next to the fixation spot. In a 2AFC paradigm subjects had to indicate on which side they perceived the real line.

The method of constant stimuli was used to determine psychometric functions and thresholds at the 75% correct response point. Thresholds are based on at least 300 trials.

Detection thresholds for real lines were used for aligning the individual data in contrast space (see analysis).

4.2.5 Analysis

Psychometric functions were fit to the subject's responses to the stimuli using Mathematica's (Wolfram Research) Nonlinear Regress, which finds a least-squares fit to the data for a given model. A gaussian function was employed to fit the psychometric function. Based on this the threshold (at 75% correct responses) and its asymptotic standard error can be calculated.

The subjects' pooled thresholds in single real line conditions (parallel or orthogonal at different contrasts respectively) were compared with the no line condition using a paired t-test. As the absolute contrast thresholds differed across subjects, data across subjects were pooled by normalizing to each subject's detection threshold. This alignment thus allows a comparison of data at perceptually similar contrasts (i.e. subthreshold versus suprathreshold contrasts).

4.3 Results

4.3.1 Detectability of Real Lines

It has been reported before that illusory contours influence the detectability of real lines (Dresp & Bonnet 1995). Detectability of real components in close proximity to illusory contours has been shown to vary drastically between subjects (McCourt & Paulson 1994). Therefore, to permit comparisons across individuals, it is necessary to equate across perceptual thresholds by adjusting experimental settings to each subject's perception (i.e. to the individual's real line detection threshold). Thus, detection thresholds for real contours superimposed on the illusory contour were measured for each subject (see methods section for details).

McCourt & Paulson (1994) have shown that the detectability of real lines is affected by distance between the illusory and real line. Therefore, I tested thresholds for three different real/illusory conformations. Illusory contours were bent inward, straight, or bent outward. Real contours always remained in the same position: the orthogonal line always abutted the straight virtual contour, and the parallel line was always superimposed on the straight virtual contour. In the case of the orthogonal line, the real line slightly crosses the virtual contour but this is negligible because the real line is positioned so close to the inducers. Thus, each subject was tested on 6 different conditions (two real line orientations for each of the three inward, straight, and outward illusory contour configurations). Each condition was tested with 5 levels of contrast, 3 subthreshold contrasts and 2 suprathreshold contrasts.

Subjects-specific Detection Thresholds

Real line detection thresholds for each of the four subjects (BD, IK, NB, and CM) are shown in Fig.4.5.

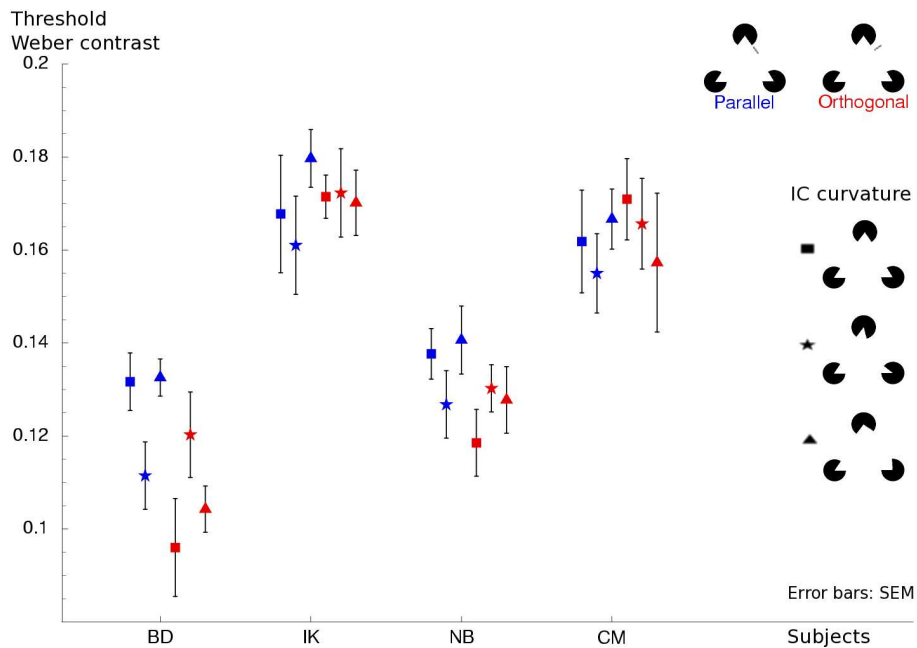


Fig. 4.5: Detection threshold of real contours superimposed on illusory contours of different shapes. Shown are the individual contrast thresholds for four subjects, with red data points corresponding to orthogonal line detection, and blue data points showing parallel line detection. Symbols depict illusory contour shapes (box: straight, star: bent inwards, triangle: bent outwards). Error bars show standard errors.

Detection thresholds were found to vary considerably between subjects (see McCourt & Paulson 1994 for comparison). As can be observed in Fig.4.5, the results show lower detection thresholds over all testing conditions for subjects NB ($13.0\% \pm 0.3$) and BD ($11.6\% \pm 0.6$) in comparison to subjects IK ($17.0\% \pm 0.2$) and CM ($16.3\% \pm 0.2$). These threshold data were then used to for comparison between individuals (see Subjects Averages below). To permit comparison across subjects, the data were aligned according to perceptual threshold and categorized measurements into 4 subthreshold and 2 suprathreshold levels. Thus, for example, real line contrasts of 15% were classified as 'subthreshold' for CM and IK, and 'suprathreshold' for BD and NB (see Tab.4.1).

Although real line detection threshold varied across subjects, for each individual, detection thresholds were found to vary only mildly across experimental conditions. The ranges of detection thresholds for subjects NB, BD, IK, and CM were 12 - 14%, 10 - 13%, 16 - 18%, and 16 - 17%, respectively. Thresholds for different experimental conditions varied across subjects. In subjects BD and NB lower detection thresholds were found for orthogonal (red symbols) than for parallel (blue symbols) real lines. This effect was found under the straight (squares) as well as the outwards bending (triangles) illusory contour condition. Subjects CM and IK, however, did not show differences in thresholds for orthogonal and parallel real lines, supporting the high variability reported by McCourt & Paulson (1994). Thresholds for parallel lines varied with subject and experimental condition. Unlike the report by Dresch & Bonnet (1995), I found no indication of summation between parallel real and illusory lines. Thus, there was little effect of illusory contour bending on real line perception. Therefore, a single averaged threshold value (averaged over all conditions) for each subject was used for the analysis of the discrimination task data (see below).

4.3.2 Perceptual Strength of Illusory Contours

Perceptual strength of the illusory contours was tested with superimposed parallel real line, superimposed orthogonal line (abutting), and no line. As different real-illusory contour interactions have been reported at sub- and suprathreshold contrasts (Dresch & Bonnet 1995, Ringach & Shapley 1996), the influence of real components was tested at different subthreshold and suprathreshold real line contrasts. Tests with real lines at subthreshold contrast furthermore allowed us to test whether real-illusory contour interactions are possible without subjects perceiving the interacting stimulus.

I therefore aimed to test, a) whether real-illusory contour interaction depends on real line contrast, and b) whether real-illusory interactions are evident at subthreshold contrasts.

Baseline: Perceptual Strength of Illusory Contours

Perceptual thresholds for the illusory contours were measured by asking subjects whether the illusory contour was bent inward or outward. Illusory contour conditions with and without presentation of additional real lines were interleaved. These 'no line' trials were randomly interleaved within blocks which tested for a fixed orientation and contrast of a superimposed real line. Subjects responded by clicking the right or left button on a mouse.

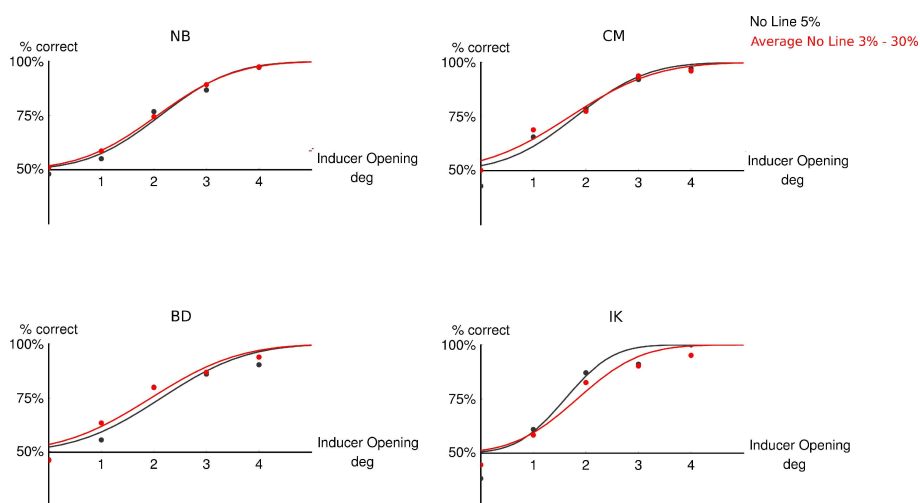


Fig. 4.6: Psychometric functions of four subjects in the 'no line' condition. Shown in blue are results from stimuli interleaved with real line conditions at a contrast of 5% and the average results over all contrast blocks (red).

Fig.4.6 illustrates the psychometric functions for illusory contour perception ('no line' condition) for each of the four subjects. Subject data for inward and outward percepts showed no difference, so these data are averaged together in Fig.4.6. As can be seen, larger outward or inward bends (e.g. more than 3 deg) were easy to discriminate (near 100%), whereas smaller bends (e.g. less than 2 deg) were more difficult (near 50% performance). Since 'no line' conditions were identical in every block, it is expected that performance on this task would not change across different 'real line' blocks. As expected, measurements from single real line condition blocks (black dots, data from 5% real line contrast shown) did not differ from the average across different real line conditions (red dots, averaged data from 3-30% real line contrasts). I used thresholds at the 75% correct response level for discrimination as a measure of illusory contour perception.

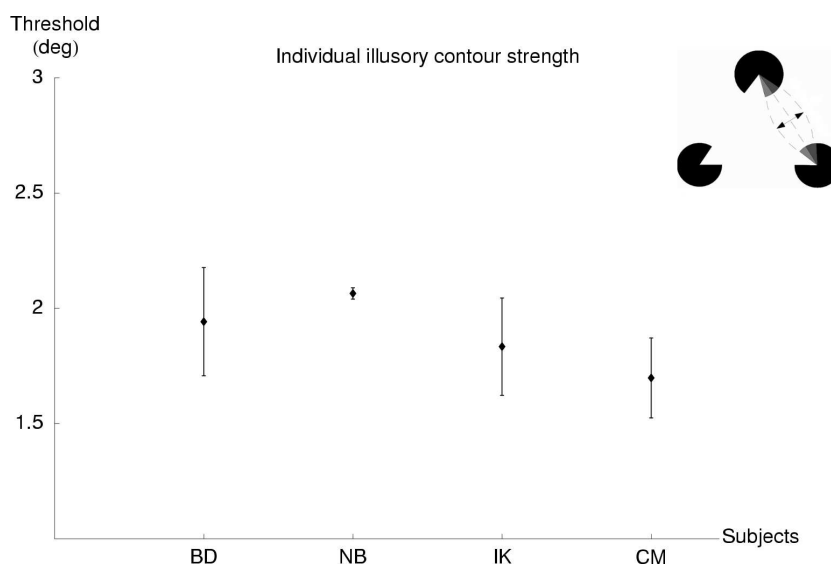


Fig. 4.7: Baseline of illusory contour strength for each subject. Shown are shape discrimination thresholds in degrees of inducer change. Error bars show standard error of the mean.

These 75% thresholds for the 'no line' condition are plotted in Fig.4.7. Mean thresholds of all 'no line' conditions for each subject are shown.

Illusory contours are similar in their perceptual strength across subjects. Inducer opening has to be bent by at least 1.5 to 2.2 deg for subjects to clearly perceive whether the illusory contour is bent outwards or inwards (mean = 1.9 deg).

Variability over different experimental conditions differs across subjects. Subject NB has almost identical baseline values for every condition, leading to a low standard error, whereas the three other subjects show different thresholds depending on the real line condition tested in the same sessions with the respective "no line"-condition. Subjects BC, IK, and CM tended to have higher variability for the 'no line' condition in blocks with high contrast real lines. Of course "no line"-conditions are identical across blocks. Small differences in 'no line' thresholds could reflect within-subject performance instability or influence of expectation or attention. Performance on 'real line' conditions were then compared to each subject's averaged "no line"-thresholds.

Single Subjects

Data from two subjects are presented here, one subject with a low perceptual threshold and one with a high perceptual threshold. Both subjects exhibit similar trends. Thresholds of subject NB (Fig.4.8(A), in degrees of inducer angle difference) are presented over different contrasts of the superimposed real line. The black triangle on the x-axis indicates the detection threshold for the real lines (13%, cf. Fig.4.5). Shown are three conditions: thresholds with a superimposed parallel real line (gray stars), thresholds with an orthogonal, i.e. abutting real line (black diamonds), and the threshold for illusory contour alone (white dot). Gray bars indicate standard error of the mean.

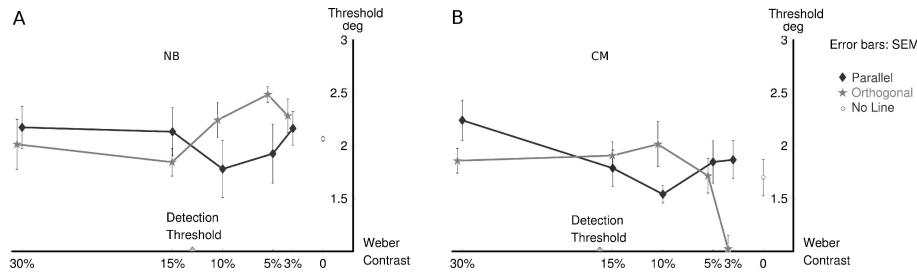


Fig. 4.8: Discrimination thresholds of illusory contour shape over contrast for subjects NB (A) and CM (B). Three conditions were tested: superimposed parallel line (diamond), orthogonal line (star), and without real line (circle, at contrast 0). Error bars show SEM, real line detection thresholds are indicated by the triangle on the x-axes).

At most contrast levels, superimposed orthogonal real lines significantly affect illusory contour perception. Although suprathreshold orthogonal lines at high (30%) contrast do not change illusory contour perception, when presented at suprathreshold contrast near threshold (15%), orthogonal lines enhance the illusory percept. Interestingly, at subthreshold contrasts (3%, 5%, and 10%), superimposed orthogonal lines significantly interfere with illusory contour perception. Thus, near the real line detection threshold, there is a reversal of orthogonal real line influence from enhancing to diminishing the illusory percept.

Although at most contrast levels the performance of subject NB is not affected by superimposed parallel real lines, there is also a reversal effect near the detection threshold. Unlike orthogonal lines, parallel lines tend to interfere at suprathreshold and enhance the illusory percept at subthreshold contrasts. Thus, the influence

of orthogonal and parallel lines are quite distinct and show opposing influences at subthreshold contrasts.

Subject CM exhibits similar trends, although different absolute thresholds as can be seen in Fig.4.8(B). The perceptual threshold for real lines is 16.3% (black triangle on x-axis). For orthogonal lines, similar to subject NB, at the high contrast level (30%) little effect is seen and at subthreshold levels there is some interference (10%). For parallel lines, subject CM exhibits interference at highest contrast (30%) and enhancement at subthreshold contrast (10%). As for subject NB, the crossover point is near the real line threshold. These effects disappear at very low subthreshold contrasts (5%) and even reverse at the lowest contrast. The subthreshold summation by orthogonal lines at a contrast of 3% observed in subject CM's data was not found in any other subject.

Thus, the individual data sets are highly similar in their overall pattern of real line effects on illusory contour perception. Orthogonal real lines interfere with the illusory percept at low contrasts, while parallel real lines tend to interfere at higher contrasts. The orientation reversal of real-illusory interaction occurs at contrast at the individual detection threshold.

Subject Averages

Methodology

In this section the method of averaging the data will be described in detail. Although it is possible to simply average raw data across the same absolute contrast values across subjects, this is based on the assumption that the conditions tested are similar across subjects. However, since contrast perception can vary considerably between subjects across experimental conditions, averaging across subjects at the same absolute contrast level may actually combine data that reflect perceptually very different stimuli.

Thus, a method was used which averages perceptually comparable data. In this method, I used each subject's detection threshold for real lines as a zero point for comparison across subjects. Data from each subject were then categorized into 4 different subthreshold levels (Sub 1-4) and 2 suprathreshold levels (Supra 1-2). In this way, individual data were aligned to permit averaging of data with similar perceptual strength. Two subjects BD and NB had low detection thresholds (between 10% and 15%), whereas detection thresholds of IK and CM were higher than 15%. Data were aligned to take these differences into account as shown in Tab.4.1). For example, for subject NB, contrast levels 3%, 5%, and 10% were subthreshold, whereas, for subject IK, contrast levels 3%, 5%, 10%, and 15% were subthreshold.

Alignment of Individual Data						
Perceptual Range	Sub 1	Sub 2	Sub 3	Sub 4	Supra 1	Supra 2
BD	-	3%	5%	10%	15%	30%
CM	3%	5%	10%	15%	30%	-
IK	3%	5%	10%	15%	30%	-
NB	-	3%	5%	10%	15%	30%

Tab. 4.1: Individual data were aligned to detection threshold for oriented real lines to average data of perceptually similar conditions. Four of the tested contrasts were subthreshold (Sub 1 to 4) for subjects CM and IK (3% to 15%), whereas only three contrasts (3% to 10%) were subthreshold for subjects BD and NB. Only one contrast was suprathreshold (supra1) for subjects CM and IK, but two for subjects BD and NB.

Results

Alignment resulted in an asymmetric pooling of the data, with Sub1 and Supra2 categories containing data from only two subjects, respectively, whereas the other points of similar perceptual strength (Sub2, Sub3, Sub4, and Supra1) were averaged over all four subjects. This approach is conservative by assuming, for example, that contrasts in the category Sub1 are distinctly different from contrasts in the category Sub2. Because the Sub1 and Supra2 categories contain data from only two subjects, significance levels are reduced at these values. Also raw non-aligned data were examined. If the results are robust, they should be consistent across different pooling methods for contrast levels that are clearly sub- or supra-threshold.

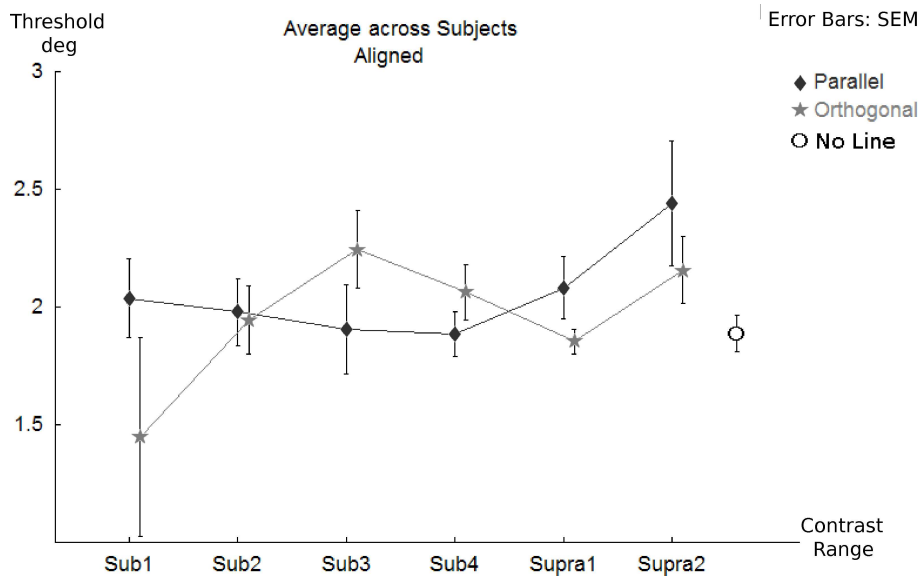


Fig. 4.9: Average of four subjects' aligned data. Thresholds in the orthogonal (star) and parallel (diamond) conditions are shown over contrast range relative to detection threshold. The 'no line' threshold is shown as open circle. Error bars indicate the Standard Error of the Mean.

Fig.4.9 illustrates the average of aligned data from all four subjects. In general, the influence of real lines on illusory contour perception is either absent or interfering (all thresholds are similar or higher to the 'no line' condition threshold, open circle). Evidence for enhancement is evident for only one subject (CM) at the lowest contrast of 3%. Since all other subjects showed no effect in this condition, this point is no confirmation of subthreshold summation (Dresp & Bonnet 1995).

Parallel Effects: Suprathreshold Interference

These data show interference effects of parallel lines on illusory contour perception. Parallel lines tend to have little effect except at suprathreshold contrasts (Supra1, Supra2) where the effect is clearly interference. In contrast to previous reports[14], no significant summation effect was observed. Parallel lines interfered at subthreshold (3%) as well as at suprathreshold (30%) contrasts. No parallel line influence on illusory contour perception was found around detection threshold (10% & 15%). The overall pattern of effects is with tendencies to interfere at subthreshold and no influence of parallel lines onto illusory contour perception at detection threshold.

Orthogonal Effects: Interference at and below Threshold

The effect of orthogonal real lines on illusory contour perception differs from that of parallel real lines. Orthogonal real lines tend to have an interfering effect at subthreshold contrasts (Sub2, Sub3, and Sub4) and a weak facilitatory effect at low

suprathreshold contrast levels (Sub1). As pointed out above, however, this facilitation effect was found only in one subject. At the contrast level Sub1, orthogonal lines did not show any significant effect on illusory contour perception in the other subjects. At contrast levels above detection threshold, the effect becomes that of interference.

Note that there is a crossover point between orthogonal and parallel line effects at near-threshold contrast levels. Importantly, these data show that all four subjects exhibit a pattern similar to that of the single subjects shown above (Fig.4.8).

Threshold Differences

To more clearly display interference versus facilitation effects, the differences of thresholds in the real line conditions and the 'no line' condition are plotted below. Threshold differences greater than zero show interference effects and differences below zero show facilitatory effects. The effects of parallel real lines on illusory contour perception are plotted over contrast ranges in Fig.4.10(A), orthogonal line effects are shown in Fig.4.10(B). Paired t-tests for the averaged data were conducted, with 2 degrees of freedom (DoF) for Sub1 and Supra2 categories, and 6 DoF for all other categories. Stars in the data plot indicate significant differences between the real line condition and the 'no line' condition, with stars showing p values < 0.1 .

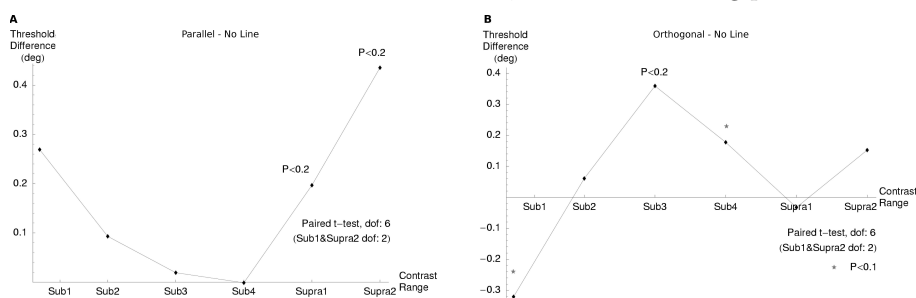


Fig. 4.10: Average of aligned data of four subjects. Shown is the threshold difference to the no line condition over contrast range relative to detection threshold. Real lines parallel (A) and orthogonal (B) to the illusory contour were tested. Stars indicate paired t-test results (star: $p < 0.1$).

As shown in Fig.4.10(B), parallel real lines show weak tendencies at suprathreshold contrast levels (Supra1 & Supra2, $p < 0.2$). At these contrasts, parallel lines in general interfere with the illusory contour percept. Parallel lines have no significant effect on performance in the task at contrasts below detection threshold.

Orthogonal lines, in contrast, exhibit tendencies to interfere at contrast levels at sub-threshold or close to detection threshold (Fig.4.10(B), Sub3, $p < 0.2$, Sub4, $p < 0.1$). At even lower contrast levels, weak trends to facilitation are found (Sub1, $p < 0.2$). No significant effects of orthogonal lines were found at suprathreshold contrasts.

Taking together both orthogonal and parallel line effects in this task, overall interaction of real lines with illusory contour perception occurs even at very low, subthreshold contrasts. Real line interactions with illusory contour perception are dependent both on orientation and contrast of the real component.

Predominant Effect of Oriented Lines on Illusory Contour Perception is Interference

The results reported above were found to be only tendencies. Comparison of individual data and averaged results showed, however, the overall consistency of the real-illusory interaction measured. Are the effects found in the averaged data results of few strong effects in the individual data combined with no or even opposite effects in most data points? To resolve this question, the following way to look at this

data was tried. To examine the data without regard to the strength of the effect, for each data point I used a 1, 0, and -1 index to indicate interference, no effect, and facilitation, respectively. Here, data were not clustered to points of perceptually similar contrast. Rather individual data were aligned exactly to detection threshold by shifting individual contrast values (x-axes) by the difference between individual detection threshold and average detection threshold, thus having single data points covering the whole tested contrast range. Values at each contrast were then calculated as sum of the respective number, half of the direct neighbours and one fourth of the second neighbours. Data smoothed in that way show how consistent the effects are over different, perceptually similar contrasts, with indices between -0.25 and 0.25 indicating no or inconsistent effects at the respective condition and contrast range, whereas higher or lower indices (interference: > 0.5 , facilitation: < -0.5) indicate consistent effects. Smoothed data are shown in Fig.4.11.

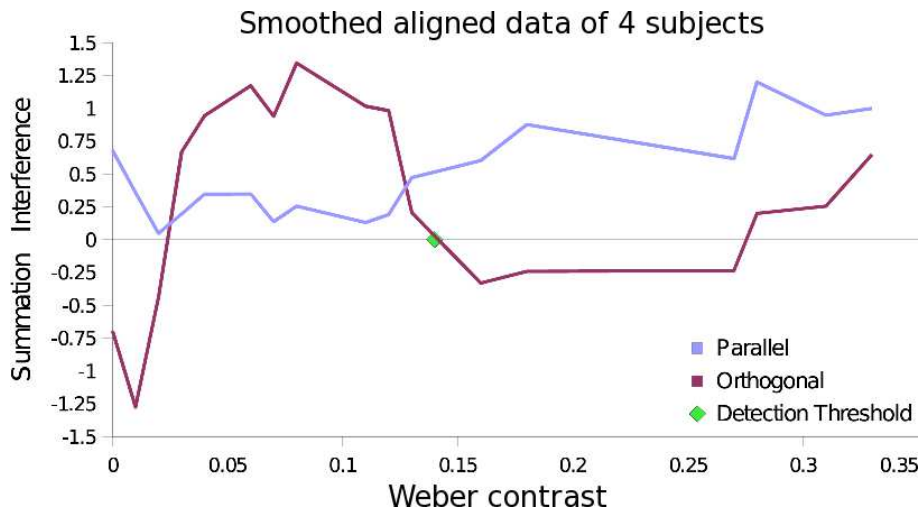


Fig. 4.11: Smoothed aligned data of 4 subjects. Interference was initially set to 1, facilitation to -1. At every contrast the individual effect was summed with the weighted neighbour effects (see text). Parallel line effects are shown in blue, orthogonal in red. Detection threshold is depicted as green dot.

Despite this very different method of examining the data, similar effects are seen as in the averaged results. Real lines influence illusory contour perception in an orientation-dependent and contrast-dependent manner. In general real lines (both parallel and orthogonal across most contrasts) were found to interfere (most average indices > 0.5). Parallel lines have little consistent effect at subthreshold contrasts and interfere primarily at suprathreshold contrasts. Orthogonal lines interfere below detection threshold, but facilitate at suprathreshold levels.

4.4 Discussion

Illusory contours are induced by real contextual stimuli. Different types of inducers can lead to differently oriented illusory contours. For example, a vertical real edge in a partial disk supports the perception of a vertical illusory contour. Vertical lines in an abutting line pattern, however, lead to the perception of a horizontal line along the disruption in the real line pattern. The same real element, that is, the vertical real line, can thus lead to contour percepts of opposite orientations dependent on additional cues in the scene.

This suggests that additional real elements can interfere with the processing and perception of illusory contours, thus supporting one interpretation of the cues available in a visual scene over another.

Here, I reported perceptual interactions between real and illusory contours that support this suggestion. Interaction was found to be dependent on orientation as well as on contrast of the real lines. Parallel real lines interfere with the illusory contour percept at suprathreshold contrasts, whereas orthogonal lines interfere predominantly at subthreshold. Lines of very high contrasts (95%), however, appear to interfere disregarding of orientation in our experimental setting.

4.4.1 *Measuring Illusory Contour Strength - which Method is preferable?*

Illusory contours are solely induced by contextual real elements. Every change of the illusory contour is necessarily based on changes in the contextual inducers. Understanding how changes in the context affect illusory contour strength is thus a major step towards understanding the perception of illusory contours and its underlying processes.

One class of tests for perceptual strength of illusory contours uses the effect of illusory contours onto real stimuli by measuring detectability of real elements superimposed on illusory contours (Dresp 1996, McCourt 1994). Is this approach valid for testing perceptual strength of illusory contours? Directing attention to or away from a stimulus has effects on stimulus processing (Motter 1993) and on the effects of contextual influences (Ito 1999). In the cited detectability experiments attention was directed towards the stimulus to be detected, not towards the illusory contour. The effects measured might thus be different from effects onto the perceptability of illusory contours.

In the experiments conducted here, detection thresholds were measured for real lines which were superimposed on an illusory contour. Using different real line contrasts as constant stimuli psychometric functions could be measured, with real line detectability decreasing with decreasing contrast. The results did not indicate subthreshold summation. No consistent effect of real line detectability on either line orientation or illusory contour shape was observed. I furthermore found high variability in real line detectability over subjects, as has previously been reported by McCourt & Paulson 1994. These results show that the perceptual strength of real lines does not depend on the form, location, or orientation contrast of an illusory contour. Thus, real line detectability is not a valid measure for illusory contour strength and the effects of real lines onto illusory contour perception.

To test whether real lines of different contrasts have different effects on illusory contour perception, perceptual strength of illusory contours was tested with and without superimposed real lines of various contrasts. Illusory contour strength was tested in a shape discrimination task comparable to that employed by Ringach & Shapley (1996).

Results from this experiment showed that real lines superimposed on an illusory contour affect the perceptual strength of this illusory contour. These perceptual interactions depend on real line contrast and orientation. This result stands in

contrast to the highly variable detectability results found here and also reported by McCourt & Paulson (1994). These results thereby support the view that detectability measurements of real lines in illusory contour stimuli do not provide the same information as measurements of illusory contour strength with contextual modulation of the same real lines.

In contrast to the results reported by Dresch & Bonnet (1995), no indication of sub-threshold parallel summation of real and illusory contours was found, neither in the detectability nor in the discrimination experiments. The stimulus was controlled such that the real line was not directly adjacent to the inducer contours. The possibility to induce collinear facilitation, as reported by Wehrhahn & Dresch 1998, was thereby minimized. This stands in contrast to the experiment by Dresch & Bonnet (1995) in which real lines spanned the complete gap between two inducing stimuli in the Kanizsa-figure. Their 'subthreshold summation' results might therefore rather be due to collinear facilitation of real line detection as reported by Wehrhahn & Dresch (1998).

The data presented here thus indicate that detectability of real lines is not a valid measure of perceptual strength of illusory contours. Direct assessment of illusory contour strength via discrimination tasks provides different information than detectability measurements, and was found to be more reliable and consistent over subjects and different conditions.

4.4.2 Interaction of Real and Illusory Contours

Contextual real stimuli induce the percept of an illusory contour or object. Changes in the inducing stimuli leads to changes in the illusory contour percept. Additional real elements in close proximity to the illusory contour thereby can have effects onto the processing and perception of this illusory contour.

What is this possible interaction of luminance contrast information and illusory contours based on? The first processing stage at which neural responses to illusory contours were found in macaques is the secondary visual cortex (von der Heydt & Peterhans 1989). Single cell and intrinsic activity in area V2 is similar under real and illusory contour stimulation (von der Heydt 1989, Peterhans 1989, Ramsden 2001, Lee 2001). This overlap suggests that orientation dependent interaction of both contour types can exist at least at the level of V2. Real-illusory contour interactions can be measured using psychophysical methods and have been shown using the tilt illusion (Paradiso 1989), different backward and simultaneous masking paradigms (Reynolds 1981, Westheimer & Li 1996, Ringach & Shapley 1996), or detectability measurements of superimposed real elements (Dresch & Bonnet 1995, McCourt & Paulson 1994). Orientation dependency of these interactions have been indicated by some of these studies [?, 88, 14]. Most experiments so far were only conducted with high contrast real lines. Interaction effects might therefore be influenced by higher level processes such as attention. Stimuli of subthreshold contrast are, in contrast, not detectable by a human subject, yet neurons in early visual cortex can still respond to them. If real-illusory contour interactions occur in the early cortical processing stages, these interactions should also be measurable with real lines of subthreshold contrast.

The predictions were thus, first, that the perceptual strength of illusory contour would differ between a control condition (no real element added) and different real line conditions, thus confirming an interaction between our real elements and illusory contours. Interaction effects are furthermore predicted to arise with real lines of sub- and suprathreshold contrasts, indicating low-level processes as the mediators of these effects. Second, performance in the illusory contour shape discrimination task was hypothesized to differ between the two real line orientations, thereby supporting the view that real-illusory contour interaction occurs in orientation-selective

domains such as in area V1 or V2. And finally, third, real lines parallel to the illusory contour were previously reported to interfere with illusory contour perception [88]. This result was expected to be replicated by the experiments conducted here.

Real-Illusory Contour Interaction at Sub- and Suprathreshold

Measuring the perceptual strength of an illusory contour with and without superimposed real lines of different contrasts showed that real-illusory contour interaction occurs both at sub- and suprathreshold. While suprathreshold interaction can be interpreted in terms of attentional or other higher level effects, subthreshold interaction is probably due to low-level processes. This general result thus indicates that real-illusory contour interactions can occur in early stages of visual cortical processing.

At suprathreshold predominantly parallel real lines were interfering, but also orthogonal lines showed some interfering effects at these contrasts. Both parallel and orthogonal interference might be due to direct interaction of real and illusory processes, suggesting orientation-independent mechanisms at high contrast. On the other hand, they also might be due to attentional effects of the high contrast stimulus. This is supported by the subjects' reports, saying that 'real lines are confusing' or that they 'were sometimes automatically looking to the real line'. In general, these difficulties were reported only at the highest contrast used in the experiment. Orthogonal lines were only found to interfere at this contrast. This suggests that orthogonal real lines at suprathreshold interacted with the illusory contour percept alone by interfering with the subjects' attention. Parallel lines, in contrast, interfered with the percept over a wide range of suprathreshold contrasts. The difference between high contrast lines of different orientations indicates that parallel real lines, in contrast to orthogonal, might in fact interact orientation selectively with the illusory contour processes, thus confirming the results reported by Ringach & Shapley (1996).

Interestingly, real line effects on illusory contour perception were found to change with contrast. While parallel lines interfered at high contrasts, they had no effect on the percept at contrasts below detection threshold. This results alone might indicate that mechanisms mediating real-illusory contour interaction do not reside in low-level structures. However, orthogonal real lines, which were only interfering at the highest suprathreshold contrast, again interfered at subthreshold. This shows that real line interaction with the illusory contour is not solely a higher-level interaction. The results thus confirm both interaction at lowest contrasts as well as its orientation dependency, thereby suggesting that real-illusory contour interaction is mediated by early visual cortical structures that show orientation-selectivity, thus probably areas V1 and V2.

What mechanisms could underly the contrast-dependent change in real-illusory contour interaction?

V1 cells of all layers were found to respond differentially to a stimulus of varying relative contrasts to its surround (Levitt & Lund 1997), showing not only changes in orientation selectivity for contextual interaction, but also in the sign (suppression versus facilitation) of these interactions. Decreasing contrast has furthermore been shown to lead to an increase in receptive field sizes (Sceniak et al. 1999), an effect which also has been found psychophysically (Mareschal 2002). These size changes might lead to a change of which part of the stimulus information affects center and surround of a neuron, thereby possibly resulting in inhibition at one contrast and facilitation or no effects at a different contrast.

Physiological facilitation effects were found in only a very narrow range of contrasts with stimuli close to threshold and with low contrast surrounds (Polat et al. 1998, Kapadia et al. 2000). High contrast surrounds were found to be mostly suppressive.

This effect was found to be independent on orientation (Levitt & Lund 1997, Polat et al. 1998). These studies together indicate changes in excitatory versus inhibitory connections of the same cell pools rather than different pool sizes at different contrasts.

The results of the psychophysical experiments thus are consistent with physiological studies. The difference in real line effects at subthreshold and suprathreshold contrasts reported here might be due to changes in receptive field sizes of single cells in early visual cortex as well as to a change of interaction between cell pools in the areas processing illusory contours. To draw further conclusions, physiological studies of the contextual effects of real lines on illusory contour processes will have to be conducted.

Orientation Dependency of Real-Illusory Contour Interaction

Psychophysical and physiological similarity between real and illusory contours suggests in part common processing mechanisms in early visual cortex [109, 78, 108, ?, 84]. Real-real line interactions might thereby serve to some extent as a model for real-illusory contour interactions.

Interactions between real contours show both inhibition and facilitation effects. Presentation of real lines in the surround of a contour stimulus interferes with the perceptual strength when the surround lines are parallel to the target line (Li et al. 2000, van der Smagt et al. 2005). The same effect was also found in backward and forward masking studies (Macknik & Livingstone 1998). Lines orthogonal to the target line, in contrast, predominantly facilitate perception or have no effect at simultaneous presentation (Li et al. 2000, van der Smagt 2005).

Are there evidences for similar effects in illusory contour perception? Westheimer & Li (1996) found a general backward masking effect of real lines of random orientations, while Ringach & Shapley (1996) even reported suppression of the illusory contour percept specifically by real lines parallel to the illusory contour. They, however, did not compare the results to masking effects at different orientations. The data reported in this thesis, however, show exactly the same result with illusory contours of the abutting line type and the Kanizsa-figure type: parallel lines at suprathreshold contrast interfere with an illusory contour percept.

Masking by high contrast parallel lines thus appears to be a general principle for real and illusory contours. A neural correlate of parallel masking effects with real lines has been shown in area V1 (Macknik & Livingstone 1998, Li et al. 2000). The earliest illusory contour response, however, has been reported to arise in area V2 (von der Heydt & Peterhans 1989), while neural signals to the same stimulus in V1 appear delayed (Lee & Nguyen 2001) and orientation-reversed (Ramsden et al. 2001). Parallel real line interference with illusory contour thus probably occurs in area V2, where contour-responsive neurons signal both real and illusory contours of the same orientation (von der Heydt & Peterhans 1989, Peterhans & von der Heydt 1989).

In the introduction to this chapter a Kanizsa-figure was shown with interfering parallel lines and supporting orthogonal lines (Kanizsa 1976). Interference was experimentally supported, while no facilitation by orthogonal lines was found. However, looking at a drawing of lines abutting to an illusory figure probably leads to higher level, or cognitive, inferences about occlusion cues and figure-ground segregation. In the experiment, in contrast, illusory figures and lines were presented for only 250 msec. This presentation time is apparently too short to let the visual system use possible cues such as additional abutting lines. This interpretation might thus support the hypothesis that the real-illusory contour interactions studied here are processed in early visual cortex.

In the experiment conducted here, however, orthogonal lines sometimes overlapped

with the illusory contour. Real lines were thus only truly abutting when the illusory contour was straight. At this point the illusory contour was neither curved inward or outward, the perceptual task could thus only be conducted at chance rate. Facilitation by really abutting lines was thus not measured in this experiment. Rather, the percept of a straight illusory contour might have been supported by the abutting real line. Abutting lines would thereby not have facilitated the percept, but instead interfered with it in any case. Interestingly, this result was only found at the highest contrast as well as at subthreshold contrasts. While the high contrast effect can be explained by attentional interferences as described above, the subthreshold interference might in fact be due to the enhancement of a straight illusory contour percept.

Facilitation effects have been reported by Dresch & Bonnet (1995) who reported subthreshold summation of parallel real lines with illusory contours. This effect was not observed in the data obtained here. The high inter-subject variability (McCourt & Paulson 1994) in the detection task used by in that study might have resulted in an overestimation of the observed effects. Furthermore, the experimental design employed by Dresch & Bonnet (1995) can lead to apparent summation effects which can in fact be explained by collinear facilitation (Wehrhahn & Dresch 1998).

With lines orthogonal to the illusory contour subthreshold interference was observed. The differential effects at low and high contrasts have been discussed in the previous section. In general, a reversal of effects from subthreshold to suprathreshold is consistent with recent physiological findings (Sceniak et al. 1999, Polat et al. 1998). A rather surprising result of the experiments presented here, though, is the orientation reversal from orthogonal interference to parallel interference. These results remind on the orientation reversal reported by Ramsden et al. (2001). In their optical imaging and single cell physiology study, area V1 activation to illusory contour stimuli showed a reversed orientation map to activation to real contour stimuli. V2, on the other hand, shows highly overlapping responses to illusory and real contours of the same orientation (von der Heydt & Peterhans 1989, Ramsden et al. 2001). The reversal observed in perceptual real-illusory contour interactions might thus be related to a cortical orientation-reversal in illusory contour processing. However, in a mechanism with orthogonal domain activation in area V1 one might expect low contrast summation effects by orthogonal lines. The results here showed the exact opposite: interference by orthogonal lines at low contrasts. These data are thus not consistent with the orientation-reversal reported by Ramsden et al. (2001).

Comparison of both studies is, however, a very difficult task. Ramsden et al. studied cortical activation to either illusory contours of the abutting line type, or to real contours. Recordings and imaging were conducted in the anaesthetized macaque. The psychophysical experiments conducted in this thesis, on the other hand, employed Kanizsa-figures and investigated perceptual strength of these stimuli under contextual modulation with real contours. Among the various differences between both studies the following are possibly related to the different outcome. First, Kanizsa-figures and abutting line stimuli might use different mechanisms at least in area V1. The results in studies using these different stimuli might thereby not be comparable at all. Second, the comparison between perception in awake humans and processing in anaesthetized macaques can lead to very different results. Humans might use some higher level processes and cognition to solve a given task, which is of course impossible for the unconscious monkey. And third, real line interaction with an illusory contour in a feedforward-feedback system can result in various interactions of real and illusory processes, leading to rather obscuring than enlightening results. To overcome this problem, interaction would have to be tested at different stages of the hypothesized mechanism, thereby testing the development of the processes and their interactions.

One main point in both this and Ramsden's study, however, is the notion that orthogonal domains are involved in illusory contour processing. As the earliest neural response to illusory contour stimuli has been described in parallel domains in area V2 (von der Heydt & Peterhans 1989, Lee & Nguyen 2001), it is safe to suggest that the activation of the orthogonal domain occurs at a later time. In fact, Ramsden et al. (2001) recorded orthogonal activation in area V1, which has been reported by Lee & Nguyen (2001) to signal illusory contours later than area V2. The orthogonal line effects found here thus support a feedback mechanism in illusory contour processing (Roe 2003).

4.4.3 Conclusion

In this chapter, perceptual interaction of real lines with illusory contours was studied. Real lines were found to compete with illusory contours. The interference depends both on real line contrast and orientation. At subthreshold, orthogonal lines interfered, whereas at high contrast predominantly parallel lines interfered with the illusory percept. At no contrast or orientation, facilitation effects were found.

Real lines interact at both sub- and suprathreshold, suggesting that real lines interact at least in part at early stages of visual processing. The orientation dependency of real-illusory contour interactions furthermore supports the hypothesis that these interactions occur in orientation-selective domains. Real-illusory contour interaction, as studied here, might thus reside in areas V1 and/or V2.

The contrast dependency of the effects is consistent with physiological reports about the change in either receptive field size of single neurons [81], or the connectivity between cell pools [?]. Both can result in interference at one contrast level (e.g. subthreshold), but summation at a different contrast level (e.g. suprathreshold).

Also consistent with previous reports [61, ?], interference by suprathreshold parallel lines was observed. This suggests that real line interaction with illusory contours is in part comparable to real-real interaction, which has been described to reside in area V1. This similarity furthermore indicates that masking effects by parallel lines can either occur not only in V1, but also in V2, or that real lines can interfere with illusory contour processes in area V1.

In contrast to the suprathreshold parallel interference, interestingly, real lines orthogonal to the illusory contour were found to interfere at subthreshold contrasts. The orientation-reversal of interference effects indicates that orthogonal domains are involved in illusory contour processing. This interpretation is supported by the physiological orientation-reversal in illusory contour processing reported recently [84]. The sign of the orthogonal line effects, however, is difficult to reconcile with previous studies. This might be due to the fact that real lines were presented for the whole stimulus presentation of 250 msec. In a hypothesized feedforward-feedback mechanism between areas V1 and V2 (Lee & Nguyen 2001, Roe 2003) with an orientation-reversal between these two areas (Ramsden et al. 2001), real-illusory contour interactions are expected to change over time. The experiments conducted here would thereby only show an 'averaged' interaction effect over the complete processing time. Support for this view possibly also lies in the weak effects of real lines on illusory contour perception observed here. Real lines show only general trends in the interaction with illusory contours. This might be due to a change of interaction over time, resulting in an averaged weak effect. Therefore, a follow-up study testing the temporal development of real-illusory contour interaction has to be conducted.

5. INTERACTION BETWEEN REAL AND ILLUSORY CONTOURS OVER TIME

5.1 *Introduction*

Illusory contours are a vital construct of our visual system: objects in our environment may be only partly visible due to poor contrast or obstructed view. Using physical non-existent contours bear thus important information about probable object borders and the structure of a visual scene. Luminance defined contours play a major role in processing the virtual construct, as they provide contextual information inducing the illusory contour process and percept. Understanding the interaction of illusory percept and contextual information leading to that percept is thereby one essential step towards characterizing the mechanism underlying contour perception.

I presented in the previous chapter a new paradigm to test perceptual strength of illusory contours. I could show that real contours interact with illusory contours dependent on real line orientation and contrast. Real lines superimposed or abutting to the illusory contour interfere mostly with the illusory percept, with superimposed (parallel) lines being interfering at high contrast, whereas abutting lines interfere stronger at subthreshold contrasts. Thus, changing contextual stimuli can lead to changes in the illusory contour percept. Which underlying mechanisms might lead to these interactions?

Recent physiological reports showed neural signals to illusory contour stimulation as early as in primary visual cortex (Ramsden et al. 2001, Lee 2001). Signals were, most interestingly, orientation reversed to the real contour signal [84], and later than the V2 signal [58] reported first by Von der Heydt & Peterhans 1989. The psychophysical data presented in the last chapter and the mentioned physiological results suggest a possible feedback mechanism from primate V2 to V1 being involved in illusory contour processing (see also Roe 2003).

Interaction between illusory and real contours has been shown in various studies [77, 114, 69]. Some of these effects can be attributed to primary visual cortex. The suggested early feedback and orientation reversal as part of an illusory contour mechanism should lead to distinct properties which could be measured both psychophysically and physiologically. One major property of such a mechanism would be the change of its dependencies on orientation over time. A feedback mechanism with orientation reversal could lead, as an example, to early interference by one orientation, but possibly even later summational effects of the same oriented stimulus. I test here whether interaction between illusory and real contours is not only dependent on orientation and contrast, but also on timing of their interaction.

5.2 Methods

5.2.1 Apparatus

Experiments were programmed using OpenGL and C/C++ under Linux (Mandrake 9.2) on a pentium computer. Stimuli were displayed on a 17 inch CRT color monitor (Gateway 2000 Vivitron) with refresh rate 75 Hz. The monitor was luminance-calibrated against a Minolta CS-100. Experiments were carried out binocularly in a dark room at a viewing distance of 25 in. Data were analyzed with Mathematica 5 (for details see below).

5.2.2 Stimuli

I presented Kanizsa-type illusory triangles consisting of three black partial disks (0.5cd/m^2) with a diameter of 37 min arc (see Fig.5.1). The right side of the illusory triangle was 2° long with a support ratio of 0.4. Partial disk opening was changed randomly to induce the percept of a curved illusory contour. Opening was changed between $\pm 0-8^\circ$, leading to the percept of an either onward or inward curved contour, as already described in the last chapter.

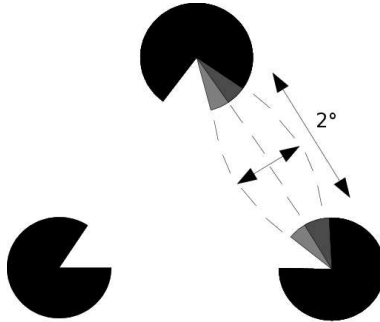


Fig. 5.1: Two of the inducers of a Kanizsa-type illusory triangle were changed randomly (opening $\pm 0-8^\circ$), leading to the percept of the illusory contour tested being curved in- or outwards. The illusory contour's length was 2° .

In part of the experiments, a real contour of 18 arcmin length was present at the position of the middle of the upper half of the tested illusory contour. The real line was either abutting (orthogonal) or superimposed (parallel) relative to the non-bent illusory contour. The position of the real line was chosen to assure least distance changes to the illusory contour between the different bending conditions, as distance has been shown to affect detectability of real components superimposed on illusory contours (McCourt & Paulson 1994).

Real lines interact with illusory contour processing dependent on the perceptual strength of the real lines. Real-illusory contour interaction is different when real lines are displayed at subthreshold, threshold, or suprathreshold contrasts, as shown in the last chapter. Thus, to compare effects of real lines on perceptual strength of the illusory contour, the perceptual strength of the real lines should be equated.

Contrasts were aligned to individual detection thresholds for subjects IK and BD in the threshold measurements. According to the results presented in the last chapter, detection threshold of subject IK was at a contrast of 16%, while threshold of subject BD was at a contrast of 11%. Subthreshold contrasts were categorized as sub1 (IK 3%), sub2 (IK 5%, BD 3%), sub3 (IK 10%, BD 5%), and sub4 (IK 15%, BD 10%). Sub4 is the contrast range closest to detection threshold for both subjects. Above detection thresholds, categories were Supra1 (IK 30%, BD 15%) and Supra2 (BD 30%). Due to the alignment, the categories Sub1 and Supra2 contained each only one data set. Results at these contrasts were therefore not tested in the Mean

Difference Test.

Detection thresholds for subjects YM, AP, and MO, who participated in the testing of the percentage of correct responses at each condition, were not tested. Therefore, results of this experiment are compared at single, unaligned contrasts only. To allow for easier comparison of the over all data, however, single contrasts are assigned in the summary plots to categories of estimated perceptual strength. Assignment of contrasts to the categories is based on the results in the previous detection experiments, that showed that individual detection thresholds for real lines in the experiments were in general at contrasts of about 15%. Perceptual reports of subjects YM, AP, and MO further supported this estimated detection threshold. Subjects reported to not perceive any line at conditions at contrasts of up to 5%. Subjects YM and MO sometimes perceived a real line at a contrast of 10% and more frequently at a contrast of 15%, suggesting that their threshold was at a contrast below 15%. Subject AP reported to not perceive real lines at a contrast of 10% and only rarely at a contrast of 15%, indicating that the detection threshold of this subject was at a contrast above 15%. Therefore, contrasts of 3%, 5%, and 10% were here categorized to be subthreshold, a contrast of 15% was assumed to be close to detection threshold, and the contrast of 95% was categorized to be clearly suprathreshold. Contrasts tested in both experiments and the perceptual ranges

Perceptual Ranges of Contrasts						
	Subthreshold			Threshold	Suprathreshold	
Threshold	Sub 1	Sub 2	Sub 3	Sub 4	Supra 1	Supra 2
BD	-	3%	5%	10%	15%	30%
IK	3%	5%	10%	15%	30%	-
% correct	3%	5%	10%	15%	95%	

Tab. 5.1: Perceptual ranges of real line contrasts used in both experiments. Contrasts in the threshold experiment were aligned to individual detection threshold, contrasts in the % correct experiment were unaligned.

the contrasts were assigned to the perceptual ranges as shown in Tab.5.1. Data were compared in these perceptual ranges. All experiments were conducted at a background luminance of 25.6 cd/m^2 .

5.2.3 Procedure

Subjects were seated at 25 in viewing distance in a dark room. In all experiments, a fixation spot was presented for 500 msec followed by the stimulus, that was shown for 50 msec (see Fig.5.2). A blank of variable duration (between 0 and 200 msec) was presented following the Kanizsa-triangle, followed by either a blank (blank condition), or either the abutting or parallel real contour presentation (non-blank condition). Real line (or blank) frames were 100 msec in duration. The fixation spot remained visible throughout the whole stimulus presentation. After disappearance of the fixation spot, the subject's response was awaited (was the contour curved inward or outward?). No error feedback was given.

Experiments were designed to probe timing of illusory contour processing and its interaction with newly given input (real contours). Delays between presentation of the Kanizsa and each real contour or blank control condition were thus randomly interleaved in a experimental session.

Curvature Discrimination Task

In a 2AFC paradigm with constant stimuli subjects had to indicate via mouse button click, whether they perceived the illusory contour on the right side of the stimulus to be curved inward or outward.

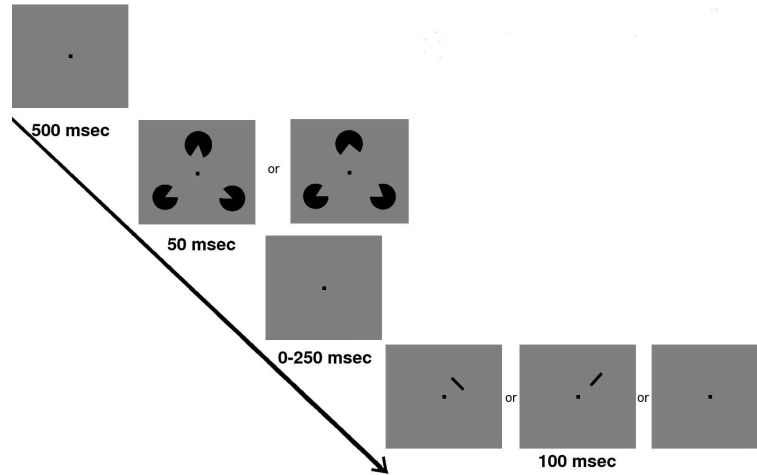


Fig. 5.2: A fixation period of 500 msec was followed by the stimulus (50 msec), whose right side was perceived to be either bent out- or inwards. After a blank of variable duration (0 - 250 msec) and real contour presentation (100 msec), subjects had to decide in a 2AFC paradigm, to what side the illusory contour was bent.

For two subjects (BD and IK), thresholds for the opening of the partial disks needed to produce a reliable percept (i.e. 75% correct responses) of a bent illusory contour were measured. Thresholds are based on at least 300 trials that were collected over several days. Subjects were trained in this task over at least two sessions, before data presented here were collected.

For five more subjects we conducted a shorter experiment. Their thresholds in the blank condition was first estimated by measuring correct/wrong responses to the presentation of an either inward- or outward bent illusory contour of a fixed curvature. Curvature was adjusted in several trials to be perceived correctly in about 70% to 80% of the trials. This “threshold” parameter was then used as fixed illusory contour curvature parameter under different real line orientation, contrast, and timing conditions. The percentage of correct responses is based on at least 60 trials per condition. Typically, 100 trials per condition were collected.

5.2.4 Subjects

Five subjects, between 20 and 28 years old, participated. Three of the subjects were naïve as to the purpose of the experiments. All subjects had normal or corrected to normal acuity. Subjects practiced the experiment for at least three days before the data shown here were collected.

5.2.5 Analysis

If measuring a threshold, psychometric functions were fitted to the subject’s responses to the stimuli. I used Mathematica’s (Wolfram Research) Nonlinear Regress, which finds a least-squares fit to the data for a given model. The model used here for the psychometric function was the Gaussian function. From the fit, the threshold was calculated at 75% correct responses.

Thresholds for both real contour and blank control conditions at each SOA were

compared in paired t-tests. Furthermore, different results in the parallel and orthogonal line conditions were tested for significant differences at each SOA. The same tests were computed with the percentage of correct responses at fixed illusory contour curvature.

5.3 Results

5.3.1 Contrast Dependency of Parallel Line Effects

How do real lines interact with illusory contour processing? As shown in the previous chapter, interaction changes with contrast and orientation of the real line. I therefore tested real-illusory contour interaction at different interaction times (SOA) with real lines of contrasts at subthreshold, threshold and suprathreshold. Here results of the experiments with real lines parallel to the illusory contour are shown. Plotted in Fig.5.3 are the differences between the parallel line condition and blank in the threshold measurement of illusory contour curvature discrimination. Values above zero indicate interference effects by the real lines, whereas values below zero indicate summation effects in the real line condition as compared to blank. Two subjects (BD & IK) took part in this experiment. Results are shown in separate graphs for results at subthreshold, threshold and suprathreshold contrasts. Perceptual ranges of the real line contrasts are based on alignment to the individual detection thresholds, as indicated in Tab.5.1.

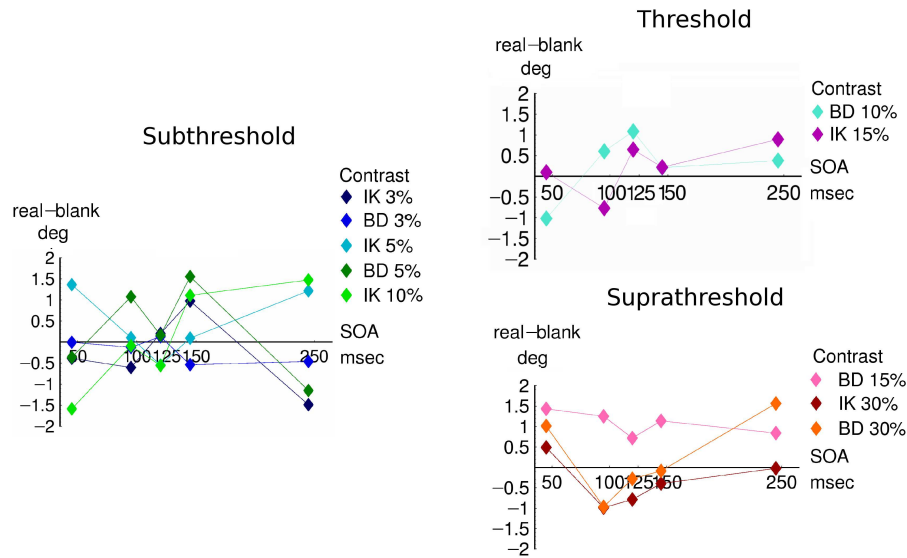


Fig. 5.3: Differences of discrimination thresholds in the parallel line condition from blank in deg over SOA in msec. Individual results of two subjects are shown at aligned subthreshold, threshold, and suprathreshold contrasts. Positive values show interference, negative values summation effects by the real line.

At subthreshold the results appear to be highly inconsistent. At short SOAs (50 & 100 msec) no general trend can be observed. At an SOA of 50 msec subject IK shows both interference (contrast 5%) and summation (contrast 10%), while no effect can be seen for subject BD at that SOA at any subthreshold contrast. At an SOA of 125 msec real lines show no interaction effect for any subject and contrast. perceptually similar contrasts and both subjects. Interactions by real lines can be found again at the SOAs of 150 and 250 msec. At the first SOA, parallel lines appear to increase thresholds, while at an SOA of 250 msec the same is true only for subjects IK (5% and 10%). Tested in a paired t-test parallel real lines at subthreshold show no significant effects on performance in the task.

At threshold interaction effects are variable until an SOA of 125 msec. From that time on parallel lines tend to interfere with both subjects' performance in the task. Trends were found at the SOAs of 125 msec ($p < 0.1$) and 250 msec ($p < 0.1$).

Parallel lines at suprathreshold contrast show very similar pattern of interactions for

both subjects at a contrast of 30%, with early interference (SOA of 50 msec), weak summation at 100 msec, and no effects at 125 and 150 msec. At the longest SOA of 250 msec suprathreshold parallel lines interfere with subject BD's performance, but show no effect on subject IK's results. The contrast of 15% is clearly suprathreshold for subject BD. Parallel lines at this contrast, however, interfere at every SOA with the illusory contour percept. This effect stands in contrast to results at 30%. Effects at suprathreshold were therefore not found to be significant in a paired t-tests.

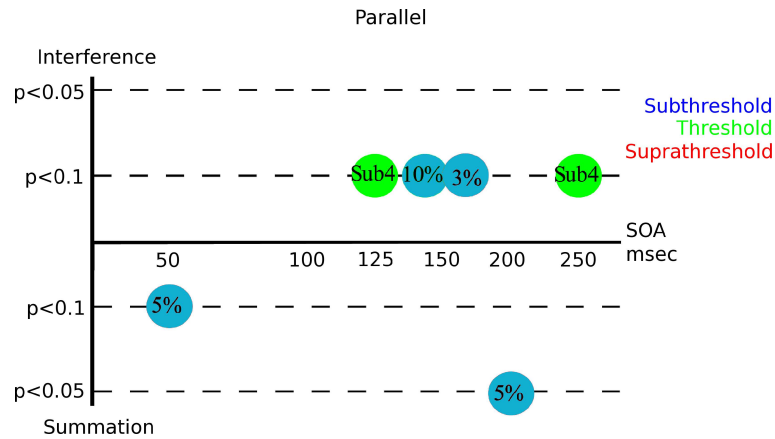


Fig. 5.4: Parallel line effects on illusory contour perception over time in msec of SOA. Results of both experiments are shown as interference or summation effect with their respective significance level. The plot shows results at subthreshold (blue), at threshold (green), and suprathreshold (red).

Parallel line effects were tested against blank in a paired t-test at aligned (threshold measurement, two subjects) or unaligned (% correct tests, four subjects) contrasts (compare Tab.5.1) at each SOA for both measurements separately. Fig.5.4 shows the results at each SOA with the respective significance level.

At subthreshold contrasts, parallel lines tend to help in the task (% correct test) at an SOA of 50 msec ($p < 0.1$). No significant effect could be found at 100 msec. At the SOA of 125 msec and longer, both lines at subthreshold (3%, 10%, % correct test) and at threshold (Sub4, threshold test) tend to interfere with the percept ($p < 0.1$). At 200 msec, however, parallel lines of a contrast of 5% (% correct test) show summation effects on illusory contour discrimination ($p < 0.05$). At suprathreshold contrasts no real line interaction reached significance.

Taken together, lines parallel to the illusory contour tend to interfere from an SOA of 125 msec on. Interestingly, this interference is only found at subthreshold and threshold contrasts. Subthreshold parallel lines furthermore can improve performance both early on (SOA 50 msec) and late (SOA 200 msec).

5.3.2 Contrast Dependency of Orthogonal Line Effects

To test orientation dependent real line interactions with illusory contour perception, real lines of two orientations (parallel and orthogonal to the illusory contour) were tested. Results with orthogonal lines in the threshold measurements are shown in Fig.5.5 as subtractions real-blank. Values above zero thus indicate higher thresholds in the real line condition (i.e. interference), whereas values below zero indicate lower thresholds in the real line condition as compared to blank (summation). Data from the two subjects at single contrasts are presented together at subthreshold, threshold, and suprathreshold contrast ranges, respectively. Contrast ranges are based on alignment to individual detection thresholds (see Tab.5.1).

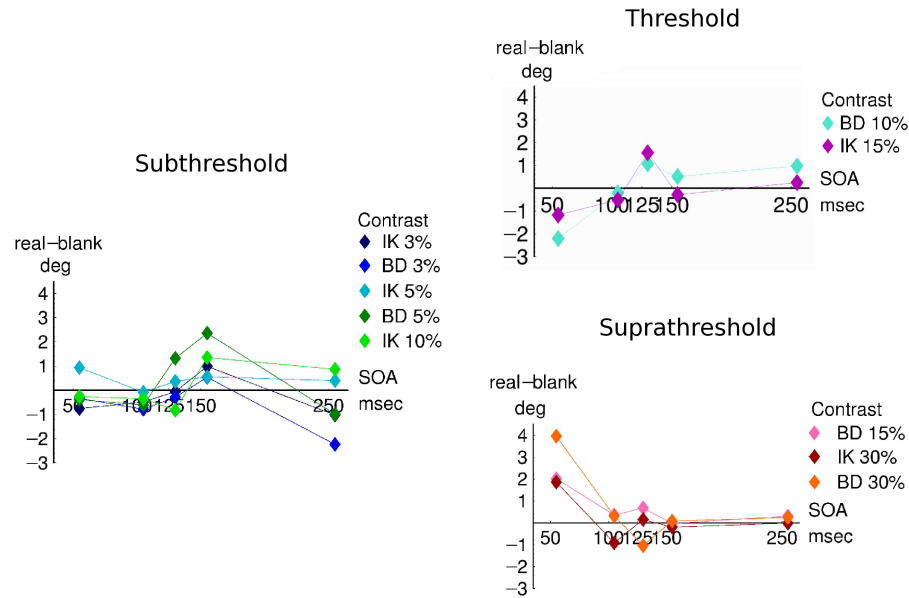


Fig. 5.5: Differences of discrimination thresholds in the orthogonal line condition from blank in deg over SOA in msec. Individual results of two subjects are shown at aligned subthreshold, threshold, and suprathreshold contrasts. Positive values show interference, negative values summation effects by the real line.

In comparison to parallel line interaction effects (Fig.5.3), that were found to be highly variable, results in the orthogonal line conditions appear to be very consistent in the respective perceptual range.

At subthreshold contrasts orthogonal lines do not show any effect on illusory contour perception at SOAs of 50, 100, and 125 msec. Real lines consistently interfere at 150 msec ($p=0.06$). At the longer SOA of 250 msec effects are variable and inconsistent, with summation by lines at the lowest contrast for subject IK (3%), and for subject BD (3% & 5%), but weak interference for higher subthreshold contrasts for subject IK (5% & 10%).

Real lines at threshold help performing the task at the shortest SOA of 50 msec ($p < 0.05$). With longer SOAs the effects reverse to interference at 125 msec ($p < 0.1$). At SOAs of 100, 150, and 250 msec no significant effect can be observed.

Suprathreshold orthogonal lines tend to interfere ($p = 0.1$) at the shortest SOA of 50 msec. At no other time high contrast lines of that orientation interact with the illusory contour percept in the threshold measurements.

Fig.5.6 summarizes the results in the threshold and % correct measurements. The graph shows the significance levels of summation and interference effects by orthogonal real lines that were presented at different times (SOA in msec). Results are shown for single unaligned contrasts (four subjects, % correct tests) and single aligned contrasts (two subjects, threshold tests). Colors indicate the perceptual range of individual contrasts, with blue indicating subthreshold, green indicating threshold, and red indicating suprathreshold contrasts.

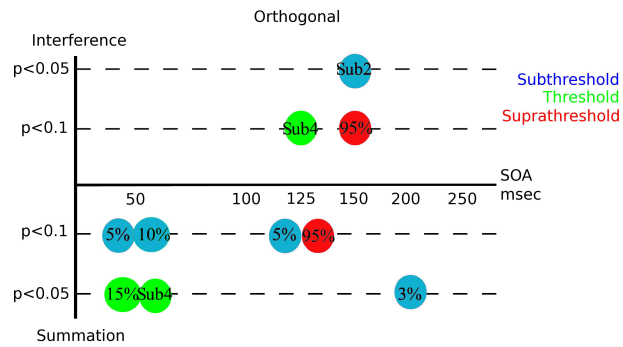


Fig. 5.6: Orthogonal line effects on illusory contour perception over time in msec of SOA. Results of both experiments are shown as interference or summation effect with their respective significance level. The plot shows results at subthreshold (blue), at threshold (green), and suprathreshold (red).

At the shortest SOA (50 msec) orthogonal lines at threshold and below increase the performance of subjects in both threshold and % correct experiments. Lines at threshold show higher significance levels ($p < 0.05$) than lines at subthreshold ($p < 0.1$), suggesting possibly decreasing strength of the interaction with decreasing contrast. Interestingly, lines at the highest contrasts show interference effects at the same time in the threshold measurements.

No significant effect can be found at any contrast and test at the SOA of 100 msec. At 125 msec and 150 msec, a reversal of the effects from summation to interference occurs. First, subthreshold (5%, % correct) and suprathreshold (95%, % correct) tend to improve performance ($p < 0.1$), while real lines at threshold (Sub4, threshold) tend to interfere at the same time (SOA 125 msec). Interference is found 25 msec later (SOA 150 msec) at the highest contrast of 95% in the % correct test ($p < 0.1$) as well as at subthreshold contrasts in the threshold test ($p < 0.05$). In the % correct test subthreshold summation ($p < 0.05$) can be seen at the longest SOA (200 msec). The same trend can be observed in Fig.5.5, where subthreshold orthogonal lines at the lowest contrasts (IK 3%, BD 3% & 5%) appear to improve the subjects performance in the task as compared to blank.

In summary, real-illusory contour interaction changes over time also with orthogonal real lines. First, real lines tend to improve illusory contour perception at an early SOA of 50 msec. At SOAs of 125 and 150 msec, real line effects reverse from being helpful to interfere with the illusory percept. At later interaction times orthogonal real lines at the lowest contrasts might improve performance in the illusory contour curvature discrimination task.

5.3.3 Orientation Dependency of Real-Illusory Interaction

Results presented so far indicate not only contrast and time dependent effects of real-illusory line interaction, but also show orientation specificity of these effects. How substantial are differences between the results in the parallel and the orthogonal condition?

Differences between thresholds in the orthogonal and parallel condition show the orientation dependency of the measured effects (Fig.5.7). Data are plotted over time in msec (SOA). Higher values indicate higher performance in the orthogonal as compared to the parallel line condition.

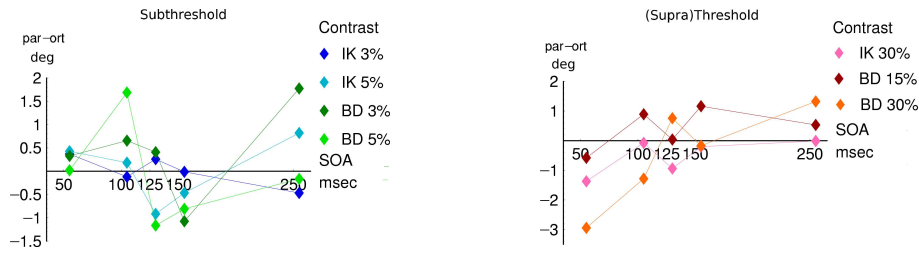


Fig. 5.7: Differences (deg) between thresholds in the orthogonal and parallel conditions. Data are plotted over time (SOA in msec). Results of two subjects are shown at contrasts 3% and 5% (subthreshold) and at contrasts 15% (only BD) and 30% (suprathreshold).

Threshold differences reveal a distinct pattern of orientation specificity, that is different at sub- and suprathreshold contrasts. At subthreshold contrasts, orthogonal lines lead early on (50 & 100 msec) to higher performance than parallel lines. At 125 msec this orthogonal advantage can still be seen for the lowest contrast of 3%. At 5% contrast, however, subjects have lower thresholds in the parallel condition as compared to the orthogonal condition. The orientation dependency at subthreshold is reversed at an SOA of 150 msec relative to the early interaction times of 50 & 100 msec. Here, the performance is in general higher in the parallel than in the orthogonal line condition. At later interaction times no clear trend to an orientation dependency can be seen at subthreshold contrasts.

At threshold and suprathreshold contrasts subjects perform better in the parallel line condition at an early SOA of 50 msec. Orientation dependency is diminished at SOAs of 100 to 150 msec, showing no consistent advantage of one or the other real line condition. At the longer SOA of 250 msec, however, orthogonal lines show a trend to improve performance as compared to parallel line effects.

Alignment of the results to detection threshold, as described in the last chapter, allowed to compare conditions of highest perceptual similarity. Tested in a one-sided Mean Difference Test, aligned parallel and orthogonal results showed a trend to be different ($p < 0.1$) at the shortest SOA (50 msec) at subthreshold contrast ranges (Sub 2 & Sub4). Although the results appear also to be very consistent at the SOA of 150 msec at subthreshold as well as at the SOA of 50 & 250 msec at suprathreshold (see Fig.5.7), none of these effects reached significance.

For comparison, differences in percentage of correct responses between orthogonal and parallel conditions are shown in Fig.5.8. Data of the four subjects were averaged at each contrast separately. If measuring thresholds, higher values equal to lower performance. If measuring the percentage of correct responses, on the other hand, higher values equal to higher performance. To allow direct visual comparison of the data from both experiments, the data from the latter experiment are plotted as subtraction orthogonal - parallel, while the previous graph showed the subtraction parallel - orthogonal. Higher values on the x-axes thus always indicate lower performance in the parallel line condition.

As can be observed in the left graph of Fig.5.8, subthreshold contrasts show weak or no orientation dependency at SOAs 50 to 100 msec. At an SOA of 150 msec, parallel real lines improve the performance in the task as compared to the orthogonal real lines. At the longest SOA (200 msec) no performance differences between the two line orientations can be observed. In the graph on the right side of Fig.5.8 orientation specific effects of real lines at threshold and suprathreshold are shown. At threshold, parallel lines improve performance relative to the orthogonal lines at the shortest SOAs (50 & 100 msec). From an SOA of 125 msec on orientation dependent differences in performance are minimal at the same contrast. At the highest contrast performance differences are found at SOAs of 125 msec, where par-

allel lines relatively improve performance in the task, while at the SOA of 150 msec orthogonal lines lead to higher performance than parallel lines.

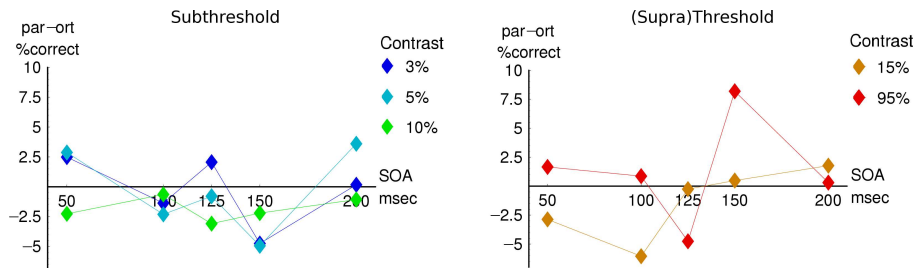


Fig. 5.8: Differences (% correct) between the orthogonal and parallel conditions. Data are plotted over time (SOA in msec). Results of four subjects are averaged at each contrast at subthreshold (3%, 5%, and 10%) and at threshold and suprathreshold (15% and 95%).

Testing these results in a Mean Difference Test shows that parallel and orthogonal effects are different at a contrast of 5% at the SOA of 150 msec (trend, $p < 0.1$). Comparing all subthreshold contrasts (3%, 5%, and 10%) together leads to the same result ($p < 0.1$ at an SOA of 150 msec). At the highest contrast (95%) both conditions also show a trend to be different ($p < 0.1$) at the SOA of 150 msec.

Thus, real line effects on illusory contour perception depend on orientation at interaction times of 50 and 150 msec. Although this dependency was found at the shorter SOA only at subthreshold contrasts in the threshold measurements, the same effect could be seen at the two lowest contrasts in the % correct tests (Fig.5.8, left side). In the % correct tests unaligned contrasts were compared. Thus, higher subthreshold contrast might have been in fact at threshold for some subjects. In the comparison of results at single contrasts subthreshold effects might thereby be obscured by threshold effects in some subjects. At the SOA of 150 msec, orientation dependency has been found at both sub- and suprathreshold contrasts in the % correct test. The same effect is apparent in the threshold measurements (Fig.5.7), but did not reach significance.

In conclusion, real lines interact with illusory contours dependent on time, orientation and contrast. The most consistent effects found here are orthogonal low contrast summation at an SOA of 50 msec, parallel low contrast interference from SOAs of 125 msec on, and a reversal of orthogonal line effects over all contrast ranges from summation to interference at times of 125 msec to 150 msec. The orientation dependency of these results is supported by difference tests of parallel and orthogonal line effects on the subjects performance, showing orientation specificity at SOAs of 50 and 150 msec.

5.3.4 Reliability of the Effects

Comparison of the two Methods

To allow comparison of results obtained by different methods, the similarity of results measured with both methods has to be established first. Results presented so far indicate the comparability of the two methods used. Results in both methods should, however, not only be similar in comparison of several subjects together. How similar are real line effects measured with both experiments in a single subject? To test this one subject conducted both experiments measuring first thresholds of illusory contour curvature discrimination, and second the percentage of correct responses at fixed curvatures of the illusory contour. Results of both experiments are

compared in the following graphs (Fig.5.9). Exemplary only results in the parallel line condition at contrasts of 5% and 15% are shown.

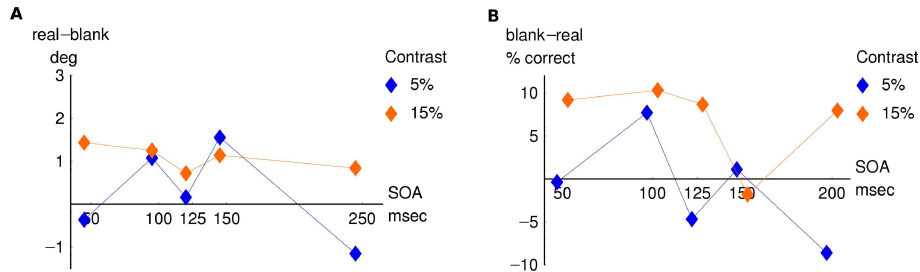


Fig. 5.9: Comparison of results by subject BD obtained by measuring discrimination thresholds in deg (A) and by measuring the percentage of correct responses at a fixed curvature (B). Differences to the blank condition for the parallel line condition at contrasts of 5% (blue) and 15% (orange). Data are plotted over time (SOA in msec). Threshold measurements are shown as subtraction of real-blank, % correct measurements as subtraction of blank-real. Values above zero thereby indicate in both cases interference effects, while values below zero show summation.

The examples shown in Fig.5.9 indicate the general similarity of real line effects on illusory contour perception in the threshold measurements and the % correct measurements. The overall pattern of effects at both contrast of 5% and 15% appear to be comparable. In both tests, the subthreshold parallel line has no or only weak effects on illusory contour perception at the shortest SOA of 50 msec. It interferes with illusory contour perception at an SOA of 100 msec, while the real line effect decreases at the SOA of 125 msec in the threshold tests and even reverses in the % correct test to result in subthreshold summation. At the SOA of 150 msec the effect is again reversed in both tests. In the % correct test, however, interference at that time is very weak. At the longest SOA of 250 msec (threshold test) and 200 msec (% correct test) parallel real lines again enhance the illusory contour percept. At the higher contrast of 15%, which is suprathreshold for this subject, parallel real lines generally interfere with the illusory contour percept in both tests. Only in the % correct test, real lines show a weak summation effect at the SOA of 150 msec. If comparing the results at different contrasts, real lines at suprathreshold lead to poor performance in comparison to real lines at subthreshold contrasts at all SOAs except for the SOA of 150 msec. Here, the subject shows almost identical results with subthreshold and suprathreshold parallel lines. In the threshold test, both lines interfere with the percept while both have no effect on illusory contour perception in the % correct test. This difference indicates a bias towards relatively higher summation or decreased interference in the % correct test than found in the threshold test. Can such a bias be also found in the group results?

Some subthreshold summation results found in the % correct test alone (see Fig.5.4 and Fig.5.6) might be the results of an overestimation of summation effects in this test. On the other hand, summation effects which were not found to be significant in the threshold test can still be seen in the data of single subjects at very low contrasts. For an example, see Fig.5.3: at the lowest contrasts at the SOA of 250 msec, both subjects IK and BD show summation effects. At slightly higher subthreshold contrasts, however, the effect is reversed. The possible bias in the % correct test did therefore probably not produce summation effects unsupported by the results obtained by measuring perceptual thresholds. Thus, both tests are comparable in their general results both at the single subject and the group level.

Consistency of Results at perceptually similar Contrasts

In the previous chapter I reported that interactions of real lines with illusory contours depend on perceptual similarity of real line contrasts. Contrasts can be perceptually similar over a wide range, being either mostly undetected (subthreshold, at contrasts of up to 15%), or easily perceived (suprathreshold, about 15% and above). Contrasts of around 15% might build a separate perceptual category (at threshold). Results presented here were compared either at perceptually similar contrasts at similar physical contrast (“aligned” contrasts in the threshold measurement) or at physically identical contrasts (“unaligned” contrasts in the % correct measurement). If effects are dependent on perceptual similarity rather than on physical contrast, they should, however, be comparable even over a wider range of contrasts. Results might thus reflect different processes at subthreshold, around threshold, and at suprathreshold, as indicated in the previous chapter and as also seen to some extent in the results presented here.

How consistent are the results between different contrasts of high perceptual similarity? To assess this, data at different contrasts are directly compared in the following graphs (Fig.5.10). Results at subthreshold contrasts of 3% (blue), 5% (light blue), and 10% (green) are shown on the left side. Results at threshold (orange) and at suprathreshold (red) are presented on the right side. Plots on the top of the figure (Fig.5.10 A) show data of the parallel line condition, plots on bottom of the figure show results in the orthogonal line condition (Fig.5.10 B).

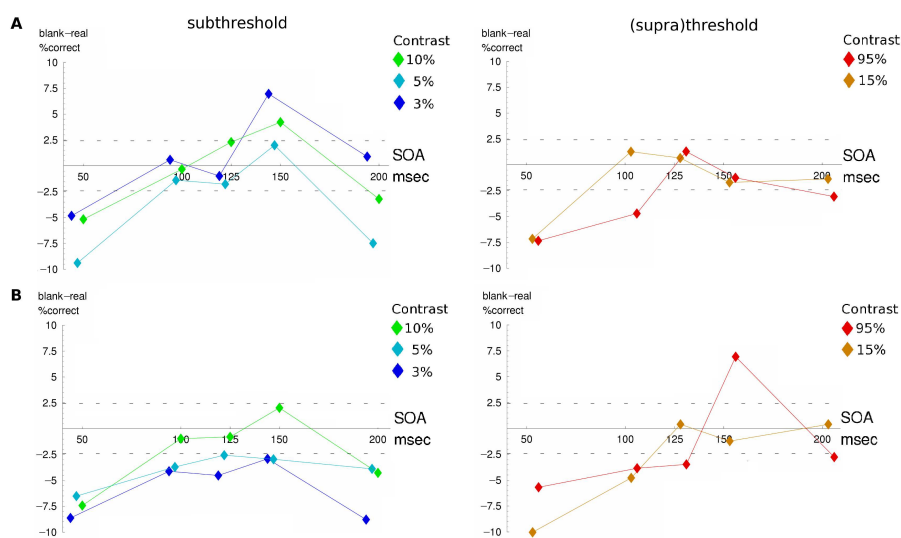


Fig. 5.10: Effects at perceptually similar contrasts averaged over four subjects. Shown are data in the parallel (A) and orthogonal (B) line condition at subthreshold contrasts and contrasts at and above threshold. Results are plotted as real-blank differences in percentage of correct responses. Dashed lines indicate the standard error of the mean of blanks at all SOAs.

Shown are differences of results in the respective real line condition and blank at each SOA. The standard error of the mean of blanks at all SOAs is indicated by the dashed lines.

As can be seen in the graphs on the left side, results at subthreshold show very similar pattern that appear to be mostly shifted along the y-axes with changes in contrast. Orthogonal lines (Fig.5.10 B) appear to be mostly supportive for the illusory percept at the lowest contrast of 3% (blue line). Summation effects decrease with contrast and even change into interference at a contrast of 10% and the SOA of

150 msec. Parallel lines, on the other hand (Fig.5.10 B) show dependent on timing both summation (50 msec) and interference (150 msec) effects at the lowest contrast of 3% (blue). Increasing the contrast to 5% (light blue) shifts the results pattern upwards, leading to summation effects early (50 msec) and late (200 msec), and to a weakening or even loss of the interference. Results at an even higher contrast (10%, green) show a pattern intermediate to the two lowest contrasts, with early summation (50 msec), interference at 150 msec, and weak summation at 200 msec SOA.

In contrast to the similarity of results at subthreshold contrasts, data at threshold (15%, orange) and above (95%, red) differ more from each other (see Fig.5.10 B). Result patterns appear not to be simply shifted along the y-axis with contrast, as seen before in the subthreshold conditions (Fig.5.10 A). Rather the general pattern of interferences and summation over time changes drastically with change in perceptual strength of the real line. Is there further evidence for the importance of the perceptual strength rather than physical contrast of contextual real lines on illusory contour perception?

An increase in the perceptual strength of the real line by higher contrast can be similarly achieved by increasing the length of the real line. Contrast summation leads to an increased effective contrast of the line relative to its background due to contrast summation. Do changes in effective contrast lead to different real line effects on illusory contour perception comparable to the small contrast changes?

Real line effects on discrimination of the illusory contour curvature should be mostly similar over different line lengths at subthreshold. Decreasing line length, however, should lead to lower effective contrast of the real line, thereby substantially diminishing its effects. With increasing line length, on the other hand, line contrast might reach effective contrast levels at detection threshold. Contrasts of different perceptual strength have been shown in the previous sections to lead to different patterns of effects on illusory contour perception. At subthreshold contrasts relatively close to detection threshold a change of the real line effects with increasing line length is thus expected. I tested this in the parallel line condition with real lines of different length, as shown in Fig.5.11.

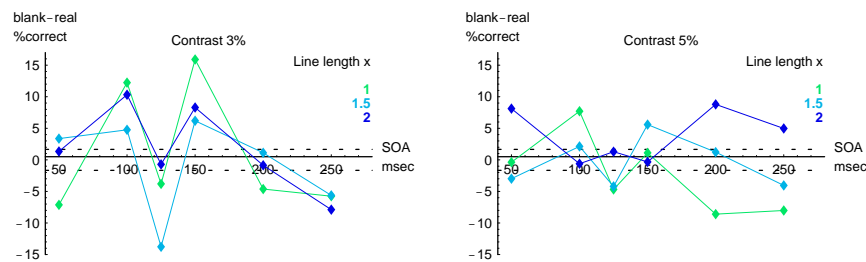


Fig. 5.11: Effects of length of a parallel line in subject BD. Results are plotted as real-blank differences in percentage of correct responses. Dashed lines indicate the standard error of the mean of blanks at all SOAs. Real line effects were tested at two contrasts (3% and 5%). Multiples of the real line length of 18 min of arc (1, 1.5, 2) were tested.

Shown are the results obtained by subject BD in the % correct test. Data are presented as differences of results in the real line condition from blank. Values above zero indicate interference by the real line, values below zero show summation effects. The percentage of correct responses was measured at different real line lengths in multiples (1, 1.5, and 2) of the line length used in all previous experiments (18 min of arc). Tested were real line effects at two subthreshold contrasts (3% and 5%).

In the left graph of Fig.5.11 real line effects at the lowest contrast (3%) are plotted as a function of time (SOA). The general pattern of effects is almost identical at

each line length. At the shortest SOA (50 msec) the shortest parallel lines improve performance in the task, while longer lines show no or weak interference effects. At the SOAs of 100 and 150 msec real lines of all lengths interfere with the percept. At the intermediate SOA of 125 msec, on the other hand, parallel lines enhance illusory contour perception. This effect is diminished at the longest line length. At the SOAs of 200 and 250 msec, finally, parallel lines tend to enhance the percept again, with longer lines showing summation effects only later on. Parallel lines of a contrast of 3% thus show only at some SOAs effects changes consistent with line length changes. In general, the results at different line lengths are virtually identical. At the contrast of 5% (Fig.5.11, right graph), results change more drastically with line length. The shortest real lines (green & light blue) still reveal the same pattern of interference and summation and described previously at the contrast of 3%. Real lines show weak summation effects at the SOAs of 50, 125 and 250 msec. They tend to interfere with the percept at SOAs of 100 and 150 msec. The pattern, however, changes completely with the longest real line (blue). This line interferes at the SOA of 50 msec, has no effect at SOAs of 100, 125, and 150 msec, and interferes again at SOAs of 200 and 150 msec. Thus, the main pattern of real line effects is completely reversed at the identical physical real line contrast (5%) with increased real line length. In comparison to Fig.5.9, in which results from the same subject at sub- and suprathreshold contrasts are shown, the pattern found at the longest line length at a contrast of 5% resembles more closely the effects found at suprathreshold than subthreshold. This suggests that changes in effective contrast due to increased line length affect real-illusory contour interaction comparable to changes in physical real line contrast.

In summary, the results at low contrasts show a very similar pattern of effects over real-illusory interaction time (SOA). The consistency of the results at subthreshold supports the reliability of the effects within perceptually similar contrast ranges. Both changes in physical and in “effective” contrast by increasing or decreasing real line length lead to similar alterations in the real-illusory contour interaction. To some extent real line effects are modulated in amplitude by contrast change. If the real line contrast, however, leads to a different perceptual strength of the real line, real-illusory interactions change accordingly. Thus, the effects found here do not depend so much on physical contrast of the real line, but rather on its perceptual strength.

5.4 *Discussion*

5.4.1 *Induction and Consolidation of Illusory Contour Processing*

The aim of this chapter was to probe the evolution of illusory contour perception with contextual stimuli. Simultaneous presentation of oriented real lines superimposed on illusory contours interferes with illusory contour perception, as was shown in the previous chapter. This interference depends on orientation and contrast of the real line. Real lines interact, however, only directly with the illusory contour processes from about 100 to 125 msec after stimulus onset on, as reported in chapter 3. This timing is consistent with the earliest neuronal activity (V2) related to illusory contour stimulation [78, 109, 58] as well as with psychophysical reports of the temporal development of the illusory contour percept [87, 88, 114, 27].

If only inducing processes are active before 125 msec after stimulus onset, we would expect the interaction of real lines with an illusory contour to change over time. Earlier than 125 msec, real lines would be expected to enhance or interfere with the inducing processes. Later than 125 msec, on the other hand, real lines would interact directly with the illusory contour processes.

In this line of thought, which interactions would be expected with the contextual stimuli presented in our experiment? Real lines orthogonal to the illusory contour activate end-stopped cells that are thought to be part of the processes inducing illusory contours [78]. Early presentation of orthogonal lines would thus be expected to enhance the illusory contour percept, which we found indeed in our results, as can be seen in Fig.5.6. Real lines parallel to the illusory contour, on the other hand, were shown previously (chapter 3) to interfere with the percept comparable to masking of real lines [61]. This interference, however, specifically targets the illusory contour processes and thus starts at about 100-125 msec after stimulus onset. Therefore, late presentation (> 100 msec) of parallel real lines is expected to interfere with illusory contour perception. Our results support this hypothesis with predominantly interfering tendencies by parallel real lines at SOAs of 125 msec and more (Fig.5.4).

Thus, the results presented here support the experiments conducted in chapter 3, again indicating an early induction period and a later period of consolidation of illusory contour processing.

5.4.2 *Evidence for Reverse Oriented Processes*

Contextual stimuli, such as the oriented real lines used here, interact with illusory contour perception. As stated above, real lines interact first with inducing, and only later (at SOAs > 100 msec) with induced illusory processes. Consistent with this, we found enhancement by orthogonal lines (induction phase) and interference by parallel lines (consolidation phase). We observed yet other effects than just these two: orthogonal lines showed a transition from summation to interference at SOAs of 125 to 150 msec. At the SOA of 200 msec, low contrast orthogonal lines again enhanced the illusory contour percept. Parallel lines, on the other hand, showed a trend to enhance the percept at the shortest SOA (50 msec). The same effect also occurred at the SOA of 200 msec. How can we reconcile these results with the existing physiological knowledge?

The earliest neuronal response to illusory contour stimulation has been found in area V2 [78, 109, 58]. An activation of V1 which was delayed relative to the V2 signal was reported recently by Lee & Nguyen 2001, confirming previous reports of illusory contour related activity in the first visual cortical area [26, 96, 84]. The temporal delay of the V1 activation relative to V2 might suggest that feedback from V2 leads to illusory contour responses in V1 [58]. Illusory contour activity in V1 furthermore has been shown to be reverse oriented to real contour activity [84, 96]. If illusory

contour processing involves a feedback system with changing orientation specificity [84, 90], real-illusory contour interaction not only should be orientation dependent, as shown in the last two chapters, but this interaction furthermore should change over time. Real lines of one orientation should interfere early on with the illusory percept, while possibly even enhancing the percept later on.

The data indeed showed this as a general trend: real lines that enhance the percept first, tend to interfere later. The transition from summation to inhibition for orthogonal lines occurs at around 125 - 150 msec, which is consistent with the transition from V2 activation to V1 activation [58]. Similarly, parallel lines interfere in general from the SOA of 125 msec on, while showing no effect or summation trends at earlier interaction times.

In contrast to the parallel lines which reveal consistent effects only in the later phase of illusory contour processing (interference at SOAs > 100 msec), the orthogonal lines show strong effects both early (summation, SOA 50 msec) and later on (interference, SOA 125 msec). This is surprising, as one might instead expect the parallel lines to interact over a wide time range with the illusory contour percept. Low contrast real lines of the same orientation as the illusory contour might enhance neuronal activation by illusory contours without being perceived by themselves, while high contrast parallel lines might interfere by starting up the processing of a real contour percept. Both interactions could act in early and later phases of illusory contour processes, if these activate predominantly parallel orientation domains. We found inconsistent and weak effects by parallel lines that were predominantly interfering even at relatively low contrasts. Orthogonal lines, on the other hand, enhanced and inhibited the illusory contour percept dependent on interaction time. While the earlier interaction effects by orthogonal can be understood by activation of inducing processes, the later effects suggest that orthogonally oriented domains are also involved in the illusory contour consolidation phase. This has already been suggested by Ramsden et al. (2001). They found in an optical imaging study that orientation maps in V2 to real and illusory contour stimulation were highly overlapping, while activation patterns in V1 to illusory contours were reversed relative to patterns of real contour activity. Single cell physiology supported these results, indicating a reverse oriented activation of V1 by illusory contours relative to real contours [84].

Our results thus provide psychophysical evidence for reverse orientated processing of illusory contours. The data presented here furthermore indicate that orientation dependency of these processes changes over time consistent with a transition from an activation of V2 to V1.

5.4.3 A Feedback Model of Illusory Contour Processing

Stimuli of very low contrasts can still be processed in the early visual cortices, although a subject cannot always perceive these stimuli or use their information in a perceptual task. Possible interaction of subthreshold stimuli with higher level processes is thus improbable.

As shown in the last two chapters, real lines can interact with illusory contour perception even at subthreshold contrasts, suggesting that interaction can occur in early processing stages without involvement of higher-level cognition. Interaction was shown to be orientation dependent, suggesting that subthreshold real lines and illusory contours interact in orientation specific cortical areas. The interactions shown here thus might occur in cortical areas V1 or V2.

The experimental data presented in this thesis are consistent with a temporal development of illusory contour processing over two major phases, namely induction and consolidation of the illusory percept. Results furthermore provide support for the reverse oriented activation patterns reported in macaque area V1 by Ramsden

et al. (2001). Following, we describe a possible model of illusory contour processing which reconciles our data with the literature under the assumption that the interactions we found psychophysically are based on processes in areas V1 and V2. The hypothesized processes underlying illusory contour perception are depicted in Fig.5.12.

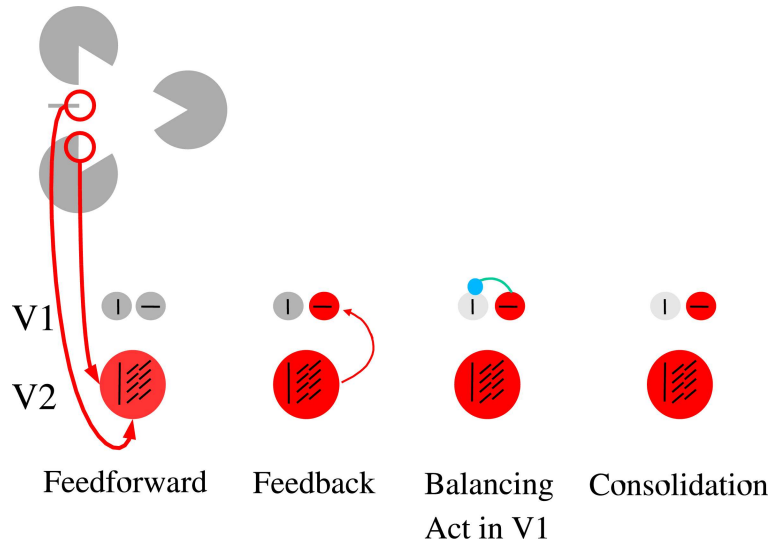


Fig. 5.12: Depiction of the hypothesized processes underlying illusory contour perception. Inducers activate the vertically oriented domain in V2 in a feedforward manner. Feedback to V1 (Lee & Nguyen, 2001) leads to activation of the oppositely oriented domain, which in turn inhibits the vertical domain in V1. Result of this balancing act is the consolidated activation pattern reported by Ramsden et al. (2001).

The first step in this model is the feedforward induction of the illusory contour processes by contextual inducing stimuli, such as abutting lines or partial discs. Induction leads to an activation of V2 domains which are responsive to parallel real and illusory contours [78, 109, 84]. Additional activation of inducing mechanisms can enhance the percept during the induction phase. Lines abutting to the illusory contour activate end-stop cells in V1 that were proposed to be part of the inducing processes [78]. Early presentation of orthogonal lines is thus expected to help in our task. We found, consistent with this, summation effects at the SOA of 50 msec with orthogonal lines at subthreshold and threshold contrasts.

Second, the domains activated in V2 send feedback signals to the orthogonal domains in V1 [58, 84]. During this stage, the induction process might not be terminated yet. Therefore, orthogonal lines can still activate line-end cells, thereby adding information to the inducing processes and thus enhancing the percept, as can be observed in our results at the SOA of 125 msec (Fig.5.6). Additionally, orthogonal lines of low contrast show a trend to enhance the percept at this time, possibly summing with the reversed activation pattern building up in V1.

In the third stage, orthogonal domains in V1 are hypothesized to inhibit parallel domains, thereby increasing the difference between activation patterns in V2 and V1. Parallel lines are now expected to interfere with the illusory percept by reversing the activation pattern in V1, or even by starting up a new real contour process. Accordingly, we found interference by parallel lines from 125 msec on (Fig.5.4). Presenting orthogonal real lines, in contrast, might theoretically still enhance the balance in V1. Adding up activity to orthogonal domains in V1, however, might in turn even lead to feedforward activation of the corresponding domains in V2,

thereby sending the signals for orthogonal real line processing instead of illusory contour enhancement. In agreement with this, the orthogonal summation found previously decreases over time and turns at an SOA of 125 msec into interference at all contrast levels, as can be seen in Fig.5.6.

The last stage consists in the consolidated reverse oriented activation pattern in V1 and V2, as reported by Ramsden et al. (2001). This balance can be enhanced by summation effects by orthogonal line presentation. We found indeed summation by subthreshold orthogonal lines at the SOA of 200 msec.

The major expectations by our model are thus supported by the data presented here. There are, however, some discrepancies between experimental results and hypothesized processes.

First of all, parallel real lines would tend to interfere in our model at any time by either activating a real contour process or by interfering with the balance of reverse oriented activation in V1. We found, however, also summation effects by parallel. While the early parallel summation (SOA 50 msec) was only a very inconsistent trend, the later summation (SOA 200 msec) was observed at some subthreshold contrasts with both test methods, as can be seen in Fig.5.4 and in the individual thresholds in Fig.5.3. These results might also be due to an increase of the receptive field size at low contrast [60, 66]. During the balancing act in V1 (when orthogonal domains inhibit parallel), low contrast activation of parallel might thereby lead to stronger inhibition [81] of that domain by the orthogonal feedback and thereby, counterintuitively, enhance the illusory contour percept.

Another result that appears to be inconsistent with the model is the following. We would expect that higher contrast lines of any orientation interfere by starting up a real line process. We did not find any consistent effect by lines of the highest contrast, though, besides the orthogonal interference at an SOA of 150 msec. High contrast lines might lead to higher level effects, interacting with the subjects' attention and thereby leading to inconsistent results.

In summary, we propose a feedback model of illusory contour processing that consists of four stages, as depicted in Fig.5.12. First, inducing stimuli activate V2 in an initial induction phase. Second, a feedback by V2 to oppositely oriented V1 domains occurs, which, third, in turn inhibit parallelly oriented domains in V1. This cortical balancing act leads to the last stage, which is the consolidated orientation reversed activation pattern in V2 and V1. The data presented here as well as recent literature are consistent with the predictions drawn from this model.

5.4.4 Contextual Effects depend on Perceptual Strength

In this study, we did not systematically test the relationship between contextual effects and individual detection threshold. Yet, our results indicate that the interaction of real lines with illusory contour perception depends strongly on perceptual strength of the contextual stimuli rather than on their physical contrast.

For example, orthogonal real lines of a contrast of 15% enhanced the illusory contour percept at the SOA of 50 msec for subject IK, for whom this contrast was slightly below threshold. The same real line, however, interfered with the percept for subject BD, for whom this contrast was above detection threshold (see Fig.5.5). Comparison of the averaged results of four subjects (Fig.5.10) at perceptually similar contrasts supports this impression. Clearly subthreshold real lines (contrasts of 3%, 5%, and 10%) revealed almost identical patterns of effects on illusory contour perception over time. Here, effects mostly changed in amplitude with increasing contrast. Real lines of suprathreshold contrast (95%), on the other hand, interact very differently with the illusory percept. Simple shifts in amplitude of the effects cannot explain the resulting pattern. The contrast of 15% can be subthreshold for some subjects, but suprathreshold for others. At this intermediate contrast we

observed in the non-aligned average (shown in Fig.5.10) an effect pattern also intermediate to sub- and suprathreshold. On the other hand, individual results at contrasts at detection threshold were found to be distinctly different from both sub- and suprathreshold (see Fig.5.3 and 5.5). These results thus indicate that averages over physically identical, but perceptually different contrasts might reveal only a very crude, or even misleading picture of contextual effects.

We therefore suggest that studies probing contextual effects should align, where possible, the individual results to the perceptual strength of contextual stimuli rather than to their physical contrast.

5.4.5 *Conclusion*

We measured psychphysically the temporal evolution of illusory contour perception by probing the underlying processes with contextual real lines at different interaction times. Real line interaction with the illusory percept changed over time, dependent both on real line contrast and orientation. Real lines of both orientations were found to sometimes help and sometimes interfere with the percept.

Importantly, real-illusory contour interaction depended largely not on the physical contrast of the contextual stimulus, but on its perceptual strength. We therefore suggest that measuring context effects should be conducted either at contrasts that are perceptually very similar for a wide range of observers (i.e. clearly sub- or suprathreshold), or that individual results are aligned to the respective detection thresholds for the contextual stimulus.

We observed real-illusory contour interactions even at subthreshold contrasts, which indicates that the interactions occur at early processing stages that have access both to the low contrast real line as well as to the illusory contour related activity. As the effects were furthermore found to be orientation-dependent, we assume that the real-illusory contour interaction measured here is based on processes in low-level, orientation-selective domains, possibly in areas V1 or V2. We therefore interpret the results as indications for underlying illusory contour processing mechanisms in the early visual areas.

A general transition between summational and interference effects occurred at around 125 msec after stimulus onset. This timing is consistent with the perceptual development of illusory contours [87, 88, 114, 27]. Real line effects before and after this transition are consistent with the major effects described in chapter 3. The effects are interpreted as indication for an early induction phase, where contextual stimulation has not yet fully established the illusory contour process, and a later consolidation phase, where the illusory contour percept is induced. This dissociation of the processes is comparable to the local and global masking of Kanizsa-figures described by Ringach & Shapley (1996). The timing of the transition between induction and consolidation phases is furthermore consistent with the timing of the transition between the first illusory contour related neuronal activity, that has been found in V2 and the possibly feedback-driven activity in V1 [58].

Our data provide psychophysical evidence for a reversal of the orientation-dependency of the real-illusory contour interactions over time. As real lines did not overlap with the inducing stimuli, interference or enhancement of the illusory contour percept by real line presentation was due to the interaction of the real line with the illusory contour and not with the inducers. The results are in agreement with the orientation-reversal to illusory contour stimulation that has been reported by Ramsden et al. (2001) in area V1 as compared to V2.

Based on the cited physiological reports and our psychophysical data, we propose a feedforward-feedback system of illusory contour processing [58, 84, 90]. Shortly after stimulus presentation, a feedforward induction process occurs which leads to illusory contour specific neuronal activity in V2 [78, 109]. Orientation-reversed feed-

back from V2 to V1 [84, 58] activates orthogonal domains, which in turn inhibit parallel domains in V1. The balanced activation of orthogonal and parallel domains in V1 and V2 is the consolidated pattern of illusory contour activation [84].

Our model leads to several predictions. First, orientation-reversed activity in V1 develops over time after the illusory contour-specific activation of V2. Second, the activation of both V1 and V2 is crucial for illusory contour perception. This leads to the third prediction, that enhancement of the balanced activity in V1 will perceptually enhance the illusory contour, while interference with the balance will weaken or destroy the illusory contour percept.

6. CONTEXTUAL MODULATION OF ILLUSORY CONTOUR RESPONSES IN V1?

6.1 *Introduction*

The psychophysical results reported here lead to predictions about the physiological mechanisms underlying illusory contour perception. Based on recent physiological studies [58, 84] I hypothesized a feedforward-feedback model of illusory contour processing in areas V1 and V2. Is there evidence for real-illusory contour interactions in these areas that support this hypothesis?

The interactions shown here are consistent with recent physiological results showing orientation, contrast and timing dependent contextual modulation of neuronal activity in the visual cortex [47, 81, 64, 92, 61]. So far, however, direct interaction between illusory and real contours has not been tested physiologically. To test whether perceptual effects are due to the hypothesized low-level processing mechanisms, it has to be tested, first, whether illusory contour responses in areas V1 and V2 can be modulated by context, and whether illusory contours can provide a context that interacts with real contour processing. Second, it has to be assessed whether the orientation, contrast and timing specificity of these modulations support the proposed model. Third, simultaneous psychophysics and single-cell recordings will have to be conducted to investigate whether the macaque's perceptual modulation is consistent with single cell activity.

In preliminary experiments, I test whether the stimuli used in the psychophysical experiments can be used in physiological experiments. Neural activity to Kanizsa-figure presentation was compared to spontaneous activity as well as to presentation of a control stimulus which did not induce illusory contours. Furthermore, V1 activity to illusory contour and control stimuli with and without contextual modulation was recorded. Single cell responses to real lines were measured in an illusory contour and control stimulus context. If illusory contours do not interact with real line processing in area V1, responses to real lines should be identical in both illusory and control stimulus conditions. If, on the other hand, illusory contour processing interacts with real line processing in area V1, single cell responses to real lines superimposed on illusory contours would be expected differ from responses to real lines in the control stimulus. In the proposed model, single cells engaged in illusory contour processing are expected to show decreased responses to optimally oriented real lines, which is consistent with recent physiological reports [84].

6.2 Methods

6.2.1 Apparatus

Experiments were programmed and executed using OpenGL and C/C++ under Linux (Mandrake 10.0). The stimulus computer presented the stimuli in a pseudo-random order and sent a TTL-pulse to the spike-collecting computer at each stimulus onset.

Stimuli were displayed on a 21 inch CRT color monitor (Barco) with a refresh rate of 75 Hz. The monitor was calibrated against a photometer (Minolta CS-100).

Experiments were carried out binocularly in a dark room, with the main illumination being the grey background of the monitor at a luminance of 22.8 cd/m^2 . The macaque was positioned at and refracted to a viewing distance of 57 inches.

Spikes were collected and offline-sorted using Spike2 (Cambridge Electronic Design), which is a template-based spike sorting system. Data were analyzed with Mathematica 4 (Wolfram Research).

6.2.2 Stimuli

Neuronal activity was measured in a blank condition to stimulation with a moving Kanizsa figure and to a moving rotated control figure without illusory contours. Stimuli were presented either with or without contextual stimulation. Contextual stimuli were lines parallel or abutting to the illusory contour.

Stimuli were presented by a custom-made program using OpenGL, comparable to those used in the psychophysical experiments (see Fig.6.1). Kanizsa-figures were matched to the individual cell's receptive field size such that the illusory contour was three times as long as the RF diameter. The receptive field was centered to the illusory contour, thereby building a gap the size of the receptive field between neuronal RF and inducing stimuli. The support ratio [97] of the Kanizsa-figures was kept constant by the program at the value used in the previous experiments (0.39).

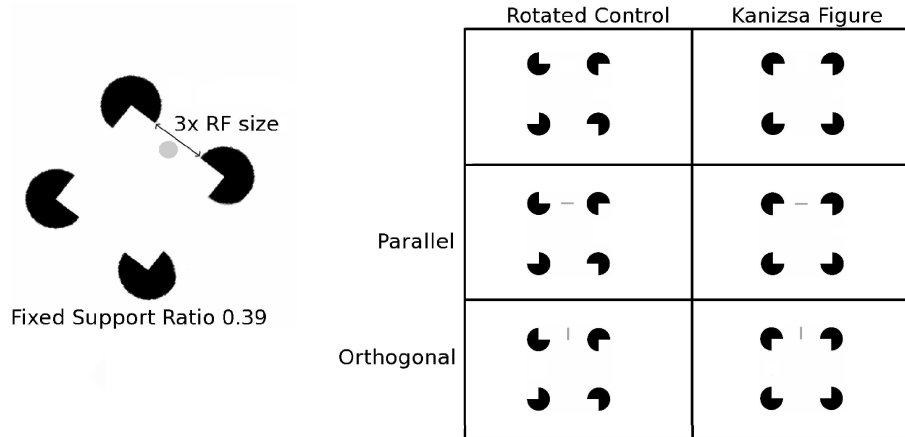


Fig. 6.1: Kanizsa figures or rotated control stimuli were presented with or without contextual real lines, which were parallel or orthogonal to the illusory contour. The illusory contour was adjusted to be 3x as wide as the RF. Support ratio was kept constant at 0.39. The illusory contour was oriented in the cell's preferred orientation and moved orthogonal to this orientation. The length of the moving path was 1° .

Stimuli were adjusted to the receptive field size and orientation preference of each cell. Illusory contours and parallel real lines were oriented optimally for the individual cell, whereas orthogonal real lines were rotated by 90° to the preferred

orientation.

Contextual real lines were presented at the center of the cell's receptive field. Line length was kept constant at 18 min of arc, comparable to the psychophysical settings used in this thesis. Real lines were presented at a luminance contrast of 5%, which is in general perceptually at subthreshold for human subjects (see chapter 4).

In initial trials, I qualitatively compared neural activity to the moving [78], flashing [58], and static stimulation. In the setup used here, moving stimuli were stimulating the cells stronger than flashing or static stimuli. Hence, moving stimuli were used in all following experiments. Stimuli moved across the receptive field along a path orthogonally to the cell's preferred orientation. This way, the optimally oriented illusory contour moved across the receptive field, yielding the strongest responses in previous studies [109, 78]. The stimulus moved over a distance of 1° in 400 msec. Stimulus onset in this experiment is defined as the point in time at which the illusory contour entered the receptive field.

6.2.3 Procedure

Experiments were conducted with an anaesthetized macaque in the laboratory of Prof. Roe (Vanderbilt University). Surgical and experimental procedures conformed to the guidelines of the National Institute of Health and were approved by the Vanderbilt University Animal Care and Use Committee. The tests described here were conducted as a terminal experiment. Surgical procedures were conducted by Prof. Roe and Haidong Lu (Vanderbilt University).

The artificially ventilated macaque monkey was anaesthetized with an i.v. application of thiopental sodium (1-2mg/kg per h), and paralyzed with vecuronium bromide (i.v., 100 μ g/kg per h). To assure a constant level of anaesthesia EEG, end-tidal CO_2 , as well as pulse and heart rate were continuously monitored. In addition, responses to toe pinching were tested regularly.

Eyes were dilated with atropine sulfate and retracted with specula. Refraction was adjusted by means of contact lenses such that the eyes focussed on the monitor. The eyes were furthermore aligned before the experiment. To that end, the receptive fields of a binocular V1 cell were converged with a prism over one eye.

Cortical areas V1 and V2 were exposed by craniotomy and durotomy. The cortex was covered and stabilized with an agarose solution, which was flattened parallelly to the cortical surface to allow optical imaging.

Optical Imaging

To determine the border between areas V1 and V2, a mapping of the functional structures using optical imaging was conducted. Intrinsic optical imaging uses changes in the cortical reflectance to an illumination. As the reflectance is largely due to hemodynamic activity, reflectance changes relate to neuronal activity of the respective cortical domain. The method has a high spatial resolution, allowing to image functional domains such as blobs/interblobs in V1 as well as the stripes in V2 [90]. Example maps obtained with optical imaging are shown in Fig.6.2.

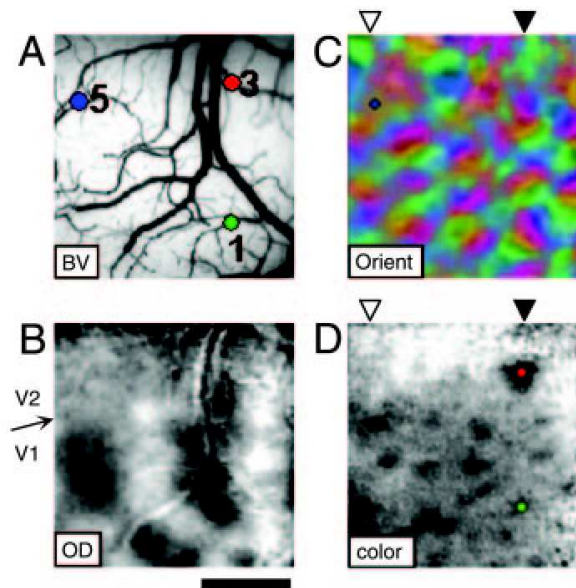


Fig. 6.2: Roe et al. 2005. Exemplary cortical maps of areas V1 and V2 obtained with optical imaging. The blood vessel map (A) helps to identify specific locations on the cortex. The ocular dominance map (B) reveals OD columns in V1 and shows the border between areas V1 and V2 (arrow). Contrasting responses to different orientations (C) allows to target domains of a specific orientation selectivity, while contrasting color with luminance (D) indicates the locations of blobs (V1) and thin stripes (V2).

To map functional structures of visual cortex, oriented stimuli (sinusoidal gratings) were presented either colored (red-green), or with high luminance contrast (black-white). Stimuli were presented monocularly as well as binocularly, allowing to map structures responsive to disparity. Ocular dominance patterns indicated the location of the V1-V2 border. V2 cells are mostly binocular, therefore V2 does not, in contrast to V1, show ocular dominance columns. Colored stimuli revealed the location of blobs in V1 and of thin stripes in V2. The location of thick and pale stripes was revealed by reflectance difference maps between stimuli of different orientation. The cortical map thus allowed to place the recording electrodes in specific functional substructures. To study neural responses to illusory contour stimuli, orientation selective cells in the interblobs in V1 and in the pale and thick stripes in V2 are the most promising targets. The latter two have also been reported to contain cells responsive to illusory contours [80, 84]. Here, area V2 was largely folded into a sulcus. I therefore conducted single cell physiology in area V1 only. Blood vessel maps obtained in the imaging session provided 'landmarks' which were easy to identify. These landmarks allowed targetting of interblob regions in area V1.

Single Cell Physiology

Following the optical imaging, microelectrodes were inserted into the agar pointing towards the cortical location of a interblob regions in area V1. Positioning of the electrode was done by comparing the cortical surface with the vessel map and the overlaid optical imaging map indicating the location of the functional structures. While advancing the electrode with a microdrive into the superficial layer of V1, raw spike activity was amplified with an audio speaker and monitored. Responsiveness of cells at each location was tested with a hand-held projection lamp. Electrodes were advanced until cells were clearly modulated by the visual stimulation produced

by the projection lamp.

The projection lamp was then used to map the receptive field of the cell. The classical receptive field (RF) was defined as the minimum response field. Borders of the RF were determined with a flashing light patch that was moved from all sides towards the RF. Each border was drawn at the position of increased response to the flash, specifically at the nearest edge of the flashing patch. RFs were also determined with the preferred stimulus (e.g. oriented line of a certain length) to ensure precise determination of the RF borders. In doubt the larger RF measurement was taken. Response characteristics of the neuron were tested by presenting various stimuli and qualitatively assessing the firing rate. Cells were tested for responses to light modulation (on/off, color, full field vs. small light patches), line presentation, orientation, length, and position of lines in the receptive field (e.g. end-stopped).

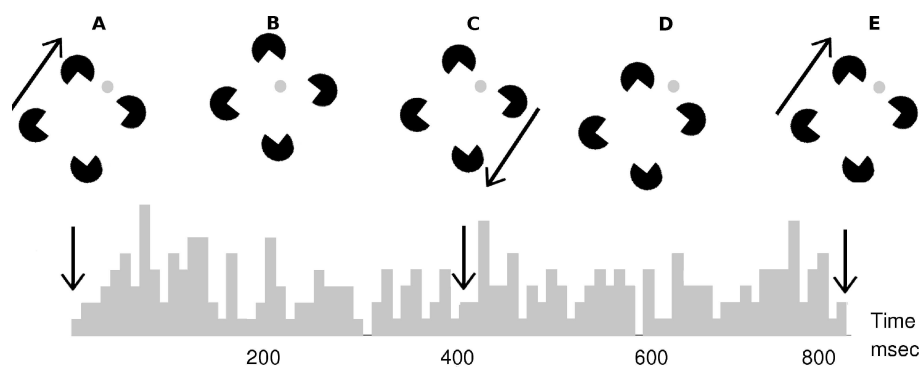


Fig. 6.3: Depiction of the stimulus and its movement across the receptive field of the recorded neuron. Exemplary, the perisstimulus time histogram of a V1-neuron is shown over stimulus presentation time. The illusory contour enters the RF at stimulus onset (0 msec, A) and moves across the RF to a position with the RF lying centrally between the partial discs (B) in the following 200 msec. The stimulus returns during the next 200 msec to again cross the RF border (400 msec, B). In the following 400 msec the stimulus moves further to a position distant from the RF (600 msec, D). It finally returns to reach the stimulus onset position at 800 msec (E). Times at which the illusory contour crosses the RF to either enter or leave it are indicated with arrows.

Stimuli were positioned such that the RF was in the center of the moving path of the stimulus. Recordings were conducted in blocks, with collecting spontaneous activity first and following spike recording Spiking activity was recorded at a temporal resolution of 0.02 msec, with stimulus onset being the time point at which the illusory contour enters the receptive field (see Fig.??).

6.2.4 Analysis

Firing activity of the neurons has been analyzed in two ways. First, spikes were binned in 10 msec bins after stimulus onset. Neural activity at different conditions is then plotted in histograms. Second, raster plots of cell responses to the stimulation were plotted to allow a general comparison between cell activity in different conditions. Here, single spikes are plotted over time in a row representing each stimulus presentation. Following it is described in more detail how the two methods were used here.

Raster Plots

Different stimuli were presented in blocks that were interleaved in pseudo-random order. As recordings took a few minutes, sometimes cells were lost, or their firing

rate changed during the recording. Presentation of firing rate at consecutive stimulus presentations therefore sometimes shows a very uneven activity pattern over trials. After initial low firing rate, the neuron shown in Fig.6.4(A) is very active in the beginning of the recordings (trials 10-24). It then responds less in later trials (25-55), but shows again in the last trials of the session (46-52) the neuron a higher activity, suggesting that its baseline activity is increased in respect to the previous trials. This change in general activity of a cell over time affected every stimulus condition as they were randomly interleaved during the recording session. Presenting neural activity to one stimulus in consecutive trials is not helpful in the comparison of neural activity during stimulus presentation, as the overall activity modulation over trials might obscure the activity modulation during stimulus presentation.

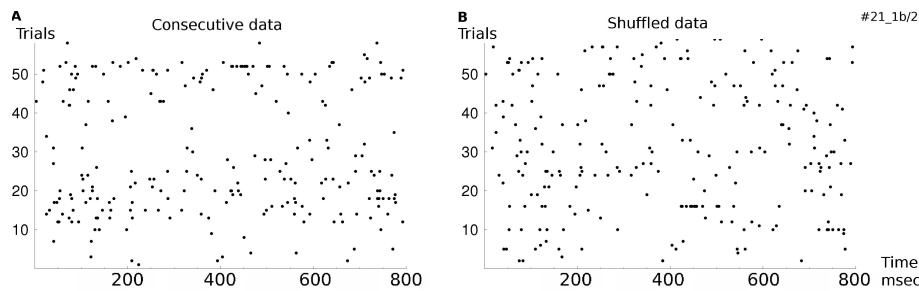


Fig. 6.4: Raster plots of the spiking activity of a V1 cell. (A) shows firing activity over time for consecutive trial numbers. Low numbers on the y-axes indicate trials earlier during the recording than higher numbers. In (B) the same data are presented after randomizing the trial numbers.

Therefore, trials of each condition and cell were shuffled before raster plotting the spiking activity. Shuffled raster plots thus show a general activation by a stimulus during single trials, but do not show the temporal development of the cell's activity over the whole recording session, as can be observed in Fig.6.4(B).

This procedure is especially important because blank stimuli (i.e., the background gray of the monitor) were not interleaved with the other stimulus presentations. Instead, baseline responses were collected in blocks of several seconds before and after the complete set of stimulus presentations. Fluctuations in the overall responsiveness of a cell during the recording session can therefore not be detected, and firing rates to stimulation cannot be corrected. The main point of interest here was, however, to compare neuronal responses to different physically highly similar stimuli. These stimuli were all randomly interleaved and presented for about 40-60 times each in blocks of 5 repetitions. Thus, eventual changes in baseline activity of a neuron during the recording would probably affect few presentations of different stimuli. Consecutive trials collected during a high baseline period of the respective neuron might indicate higher firing rate in comparison to consecutive trials of a different stimulus. This difference can, however, disappear in the shuffled data as trials with higher spontaneous activity are randomly interleaved with trials of lower baseline activity. The shuffling thus allows visual comparison of raw data that are uncorrected for baseline activity.

Binned Firing Rate

Binning neural activity of one cell to a given stimulation gives a general impression of the temporal development of the neuron's average response. Comparison of the firing rate of a cell to one stimulus versus another is possible in histograms showing binned firing rates to both stimuli, as can be seen in Fig.6.5. It is, however, virtually impossible to get an impression of the differences in the population responses

to different stimuli using these graphs.

Therefore, to assess the differential activation of a neuron by two stimuli a modulation index (MI) for each neuron was calculated. This index for each bin i is the ratio between the difference of binned firing rate (F_i) in conditions StimA and StimB and their sum:

$$\frac{F_i(\text{StimA}) - F_i(\text{StimB})}{F_i(\text{StimA}) + F_i(\text{StimB})} \quad (6.1)$$

Consider the MI of Kanizsa figure and rotated control stimulus. An MI of 0 indicates equal firing rates of a neuron to both stimuli, while a MI value of -0.33 results from a two times higher firing rate to the control than to the Kanizsa figure. Averaged MI of all recorded neurons at each bin thus show the differential activation of the population of cells between two conditions over stimulus presentation time. Bin width chosen for this calculation was 50 msec.

The results presented here are preliminary. The low number of cells recorded does not allow to draw final conclusions from these data. To not give the impression of presenting 'strong' data, statistical tests were not conducted or are not presented. Furthermore, due to the low number of neurons, no cell-type specific analysis was conducted. Therefore, results are, for example, averages over neurons with different end-stop behaviour.

6.3 Results

6.3.1 Neural Responses to Illusory Figures and Controls

Are neurons responding differentially to an illusory figure as compared to the rotated stimulus not inducing illusory contours? Exemplary, the firing rate histogram of one cell is shown in Fig.6.5, showing the activity to Kanizsa figure and rotated control stimulus.

Here, neural activity in spikes/sec is plotted over time (msec) in bins of 10 msec width. Gray bars show the neuron's response to the rotated control stimulus, black bars depict activity during Kanizsa-figure presentation. Firing rates to illusory figure presentation shows peaks in firing rate at around 50, 450, and 750 msec after stimulus onset. Peaks in neural activity to the control figure, in contrast, are seen at 300, 600, and 800 msec and appear less pronounced than peaks to illusory figure stimulation.

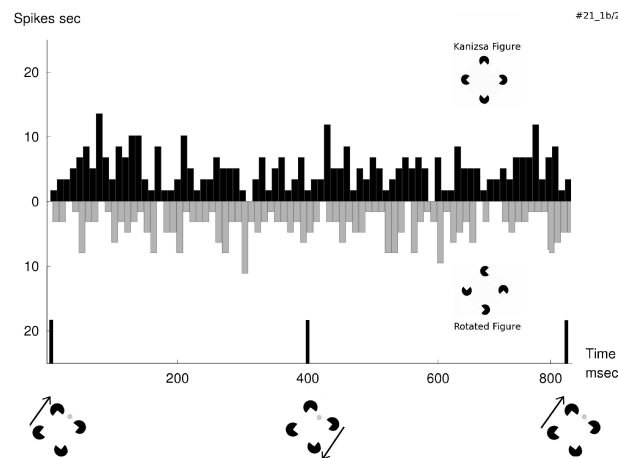


Fig. 6.5: Peristimulus time histogram of a V1 single cell. The firing rate is plotted in spikes/sec in bins of 10 msec width over time after stimulus onset (msec). The stimulus (Kanizsa figure: black, rotated figure: gray) moved back and forth across the RF, as depicted below the timeline.

The timing of peaks in firing rate in the illusory figure stimulation is consistent with the movement of the stimulus. The neuron is most active at around 50-100 msec after the movement of the illusory contour is closest to the receptive field. The last peak of the cell, however, is not supporting this interpretation: the cell is most active shortly before the illusory contour touches its receptive field. Why can that be? The cells' receptive fields were mapped manually. The stimulus was then placed such that the RF was centered in the movement path of the stimulus. The positioning of the stimulus relative to the neuron's RF was therefore not overly precise. Exact timing of passing of the illusory contour through the receptive field of a single neuron is thus questionable. In the exemplary neuron shown here, the stimulus path might have been not centered exactly to the RF, with the path being longer on one side of the neurons RF than on the other side. The latter phase of stimulus movement would thereby effectively be shorter than the earlier phase. This might explain why the single cell presented here shows increased neural activity around 750 msec, which would be before the illusory contour reaches the neuron's receptive field if the stimulus was positioned correctly.

Is the single cell results consistent with the tested population? A very similar picture emerges in the population of 16 visually responsive, oriented single cells. Neural activity generally is higher with illusory contour stimulation than with presentation of the control stimulus, as can be seen in the direct comparison of both. MI values

between Kanizsa figure and rotated figure are plotted over time in Fig.6.6. MI values above 0 indicate higher firing rates with Kanizsa figure than with the control stimulus.

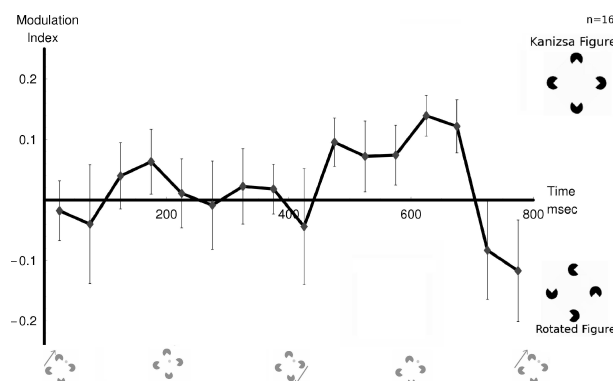


Fig. 6.6: Averaged modulation indices over 16 cells at bins of 50 msec width during stimulus presentation. Values above 0 indicate higher activity to the Kanizsa figure, values below 0 show higher firing to the control stimulus. Error bars show the standard error of the mean.

The population of neurons tested here shows, comparable to the single cell example presented in Fig.6.5, response modulation over stimulus presentation time. Neurons on average do not respond different to Kanizsa figure and rotated figure in the first 400 msec of the stimulus presentation, although a trend to stronger responses to the illusory figure can be observed. The cells clearly prefer the illusory figure in the second half of the stimulus presentation (500-700 msec), followed by increased firing of the population to the control stimulus.

The overall pattern of differential activation by the two stimuli furthermore reveals a trend towards neurons responding preferentially to the control stimulus at 0-100, 400, and 750-800 msec. At these times the illusory contour, or the respective location in the control figure, just entered (0 msec) or left (400 msec) the neuron's receptive field. As only the Kanizsa figure induces an illusory contour which stimulates the neurons, one might expect neural activity to be higher in the Kanizsa-stimulation than in the control stimulation. At the same times, though, both the partial discs in inducing and control stimuli are closest to the RFs of the recorded neurons. The stimuli physically present in the display might activate the neurons even without inducing illusory contours. As both Kanizsa figure and control stimulus contain the partial discs it is expected that neurons respond similar strong to both stimuli at times at which the illusory contour is either not in the receptive field of the neuron or not yet processed. This can indeed be observed at stimulus onset (0-50 msec) and 400 msec later. Not consistent with this interpretation, however, is the higher response of the population to the control than to the Kanizsa figure at 750-800 msec. Here, the illusory contour is still distant from the receptive field, while the physical stimuli are already at their closest point to the receptive field (compare Fig.6.3). The neurons are thus not expected to fire to the illusory contour, but should instead signal the partial discs outside the RF. That this is not the case might indicate that the neural processing of the illusory contour and surface leads to decreased processing of physically present stimulation. The low number of recorded cells, however, does not allow to draw further conclusions from these results.

6.3.2 Baseline Activity versus Illusory Contour Responses

Are the neural activities shown in Fig.6.6 higher than spontaneous activity? To assess this the raster plots of the neural activity of one cell in the blank condition, with Kanizsa-figure stimulation, and with presentation of the rotated control figure are compared in the Fig.6.7.

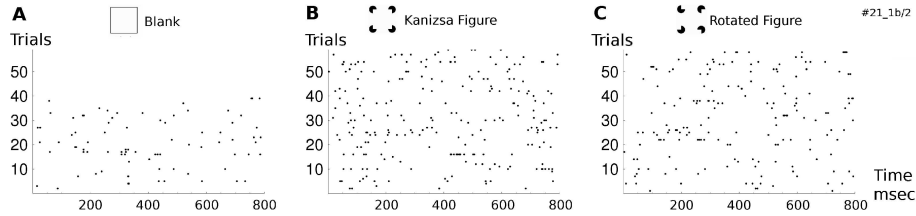


Fig. 6.7: Rasterplots of the spiking activity of one neuron to blank (A), Kanizsa figure (B), and rotated figure (C) presentation. Time in msec is shown on the x-axes, rows show single repetitions of the stimulus presentation.

As can be observed in Fig.6.7, this cell generally responded stronger to the Kanizsa-figure than to both the blank screen or to the control stimulation. Besides the overall higher activity to illusory contour presentation the difference between the three conditions appears to be most pronounced until up to 200 msec after stimulus onset, where a darker band can be seen in the Kanizsa-condition than in the blank or control condition.

How pronounced is the differential activity to Kanizsa figure and control stimuli from blank on the population level? To answer this question, the modulation index (MI) for each neuron for bins of 50 msec width was calculated as described in the method section. MI between e.g. the Kanizsa figure stimulation and blank show higher firing rates to the stimulus with positive MI, and higher firing rates to blank with negative MI. The average of these MI of all cells recorded in this condition is now plotted for each bin in Fig.6.8(A). In Fig.6.8(B) the averaged MI of rotated control figure versus blank is shown. Error bars indicate the standard error of the mean over 16 cells.

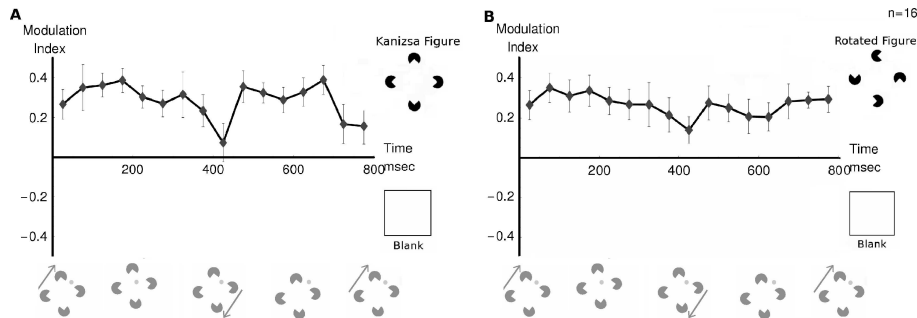


Fig. 6.8: Averaged modulation indices over 16 cells at bins of 50 msec width during stimulus presentation. Values above 0 indicate higher activity to the stimulus (A: Kanizsa figure, B: rotated control), values below 0 show higher firing rates to blank. Error bars show the standard error of the mean.

As can be observed in Fig.6.8 the V1 cells recorded respond much stronger to both stimuli than to the blank screen. No MI reaches values below 0, showing that both visual stimuli lead during the whole stimulus duration to neural activity above spontaneous levels (compare [58, 109, 78]). With illusory figure stimulation, as can be seen in Fig.6.8(A), MI are lowest at 0, 400 and 800 msec after stimulus onset, corresponding to the time at which the illusory contour enters the receptive field.

Values increase while the contour moves across the receptive field and decrease again between 200-400 msec after stimulus onset. Values increase drastically during the second phase of stimulus movement (400-450 msec) and remain stable until about 750 msec after stimulus onset. At this time, the neuron's receptive field lies outside of the surface of the illusory figure. The shape of the averaged MI thus reflects the stimulus movement back and fourth over the receptive field. This modulation is more pronounced with the illusory contour stimulus than with the control stimulus. The latter shows an only slightly decreased firing rate during stimulus onset and at 400 msec, while firing rate remains high at 800 msec after stimulus onset. In comparison to Fig.6.8, where MI over Kanizsa figure versus rotated control are plotted, these results show that the neurons recorded respond to inducing stimuli lying outside of their receptive field. The temporal modulation of neural responses, however, indicates that neurons also respond to the illusory contour as it crosses the receptive field.

6.3.3 Contextual Modulation of Neural Activity

Are illusory contour processes contextually modulated by real lines and vice versa? To test this, real lines were superimposed on the illusory contour or the respective location in the control stimulus. Real lines were either parallel, or orthogonal (abutting) to the illusory contour, and were presented such that they moved directly through the receptive field of the recorded neuron.

The superimposed real lines used here were subthreshold for human observers, but not necessarily for V1 single cells. Differential activity of neurons to figures with real lines of the two orientations would thereby possibly be due to a changed firing rate of the cells in response to real lines in an optimal or a non-optimal orientation. Therefore, it was investigated first, whether neurons responded to stimuli with superimposed real lines different than to stimuli without additional real lines. To that end the MI of firing rates in the Kanizsa figure and figure plus real line were calculated. Averaged values for the 16 neurons are plotted in Fig.6.9, showing the MI for the two line conditions (parallel and orthogonal). Values above 0 indicate higher firing rate to the Kanizsa figure, negative values show higher activity to stimulus presentation with superimposed real line.

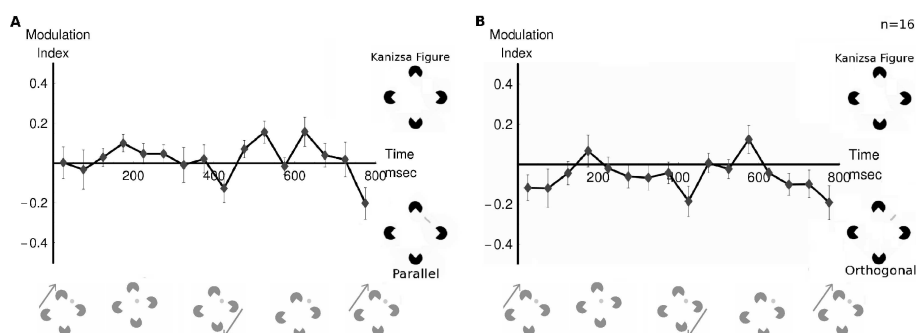


Fig. 6.9: Averaged modulation indices over 16 cells at bins of 50 msec width during stimulus presentation. Values above 0 indicate higher activity to the Kanizsa figure, values below 0 show higher firing to real line conditions of the same figure (A: parallel, B: orthogonal). Error bars show the standard error of the mean. Stimulus movement in respect to RF location is indicated below the plots.

As can be seen in Fig.6.9(A), superimposed parallel real lines show a general trend to decrease neural activity in the Kanizsa figure, while orthogonal lines (B) rather tend to increase spiking activity. Both effects show a temporal modulation consistent with the stimulus movement.

Parallel lines have no effect (0-100 msec) or even increase activity (400 msec, 800 msec) when illusory contour and superimposed parallel line touch the border of the RF and cross it. This indicates that the parallel line is strong enough to activate the neurons, leading to a weak response to the optimally oriented stimulus. Activity decreases in the real line condition relative to the no-line condition as illusory contour and real line move away from the RF. Cells increase their firing activity to the real line condition again as the stimulus moves back towards the RF. This is true both when the RF lies on the stimulus surface and outside of the stimulus. Interestingly, no difference in activity between both stimulus conditions was found at 600 msec, at which time the real and illusory contour are most distant from the RF, with the RF lying outside the stimulus surface. This is inconsistent with the general pattern observed, but might be explained by a lower activity of the neurons to the stimulus in all conditions as it is distant from the RF. In comparison to differential activity in the Kanizsa figure versus blank (Fig.6.8(A)), however, no significant decrease in neural activity is observed at this point. It is thus unclear why stimuli with and without parallel real line show identical spiking activity at 600 msec (Fig.6.9(A)). A very similar temporal development of differential activity between stimulus and real line condition can be observed with the orthogonal real line in Fig.6.9(B). Real lines help when they are close to the RF (0-100 msec, 400 msec, 700-800 msec), with decreasing neural activity as real and illusory contour move away from the RF. Activity relatively to the no-line condition increases again as the contours move closer to the RF and finally cross it.

In summary, real lines of both orientations alter neural activity in the Kanizsa figure display. Modulation of firing activity depends on stimulus position relative to the RF. While parallel and orthogonal lines show a very similar general pattern of effects, parallel lines tend to rather inhibit neural activity, and orthogonal lines tend to increase neural activity in the cells recorded.

It is not clear so far whether the effects described above are due to low contrast stimulation independent on orientation, or to neural activity by oriented real lines, or rather to an interaction between real lines and the illusory contour.

If neuronal activation in different real line conditions is due to neural stimulation by the real lines and not due to real-illusory contour interactions, we would expect that the difference between two real line conditions is identical whether tested with a surrounding Kanizsa figure or a rotated control stimulus. I tested this assumption, as shown in Fig.6.10. MI to different test conditions are averaged over 16 cells. In (A) the MI of parallel to orthogonal line conditions during Kanizsa figure presentation are shown. In (B) the MI of both real line orientations in the control stimulus are plotted.

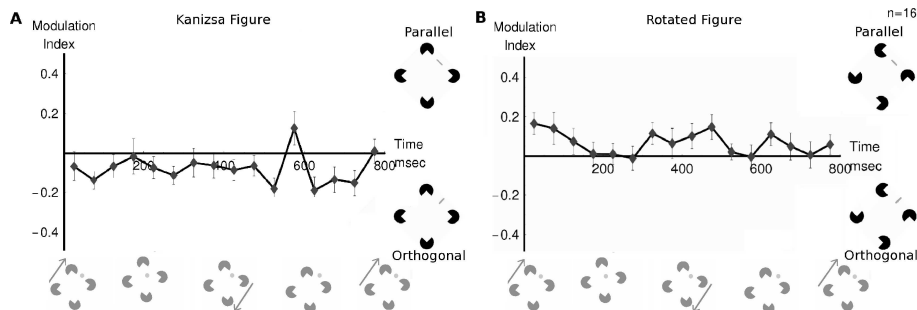


Fig. 6.10: Averaged modulation indices over 16 cells at bins of 50 msec width during stimulus presentation. Values above 0 indicate higher activity to the stimulus (A: Kanizsa figure, B: rotated Control) with superimposed parallel line, values below 0 show higher firing to orthogonal real line conditions of the same figure. Error bars show the standard error of the mean.

In contrast to the expectation, neural responses to the real lines were different in illusory contour and control condition. As can be seen in Fig.6.9, neurons modulate their activity with the movement of the stimulus. This temporal modulation is stronger in the control condition.

Interestingly, the responses to parallel lines (i.e. in the preferred orientation) in respect to orthogonal lines are less pronounced in the illusory figure condition than in the control stimulus. In fact, in the Kanizsa figure condition neurons even respond often stronger to the non-optimal stimulus (orthogonal line) than to the optimal stimulus (parallel line). This orientation reversal shows some temporal modulation with the stimulus movement, but is generally present as a trend during the whole stimulus presentation.

This result is counterintuitive: parallel real lines are oriented optimally for the respective cells. Neurons should therefore, in principle, fire more strongly with superimposed parallel lines. That they do so only in the control stimulus condition indicates that the Kanizsa figure acts as contextual modulation on the neurons responsiveness to its preferred stimulus. The cells respond less to Kanizsa figures with than without parallel lines (Fig.6.9), which additionally indicates that the responses to parallel lines are indeed decreased. This is surprising as one might expect even collinear facilitation (Kapadia et al. 2000) by the Kanizsa figure's inducers, which would lead to an increased neuronal response to parallel lines in the Kanizsa figure as compared to the rotated control stimulus. Furthermore, at the real line contrasts used here (5%) neurons in V1 were found before to show summation effects with high contrast flankers (Polat & Sagi 1998). That the opposite effect is found here suggests that not so much the inducers, but the illusory contour might interfere with V1 signals to real lines of the preferred orientation.

Even more puzzling is the result that not only Kanizsa figures with superimposed orthogonal lines lead to stronger firing relative to the same stimulus with superimposed parallel lines, but that also orthogonal lines sometimes increase the neurons firing rates as compared to illusory contour stimulation alone (Fig.6.9). Orthogonal lines do, in contrast, not increase neural activity when simultaneously presented with the rotated control stimulus, as can be observed in Fig.6.10(B). Taken together, this suggests that orthogonal lines modulated neural responses to illusory contour stimulation in these experiments. This could possibly be mediated by co-activation of illusory contour inducing processes such as end-stopped cells.

6.4 Discussion

6.4.1 Illusory Contour Responses in V1?

The earliest neural responses to illusory contour stimulation have been observed in area V2 (von der Heydt & Peterhans 1989). But also area V1 has repeatedly been reported to show illusory contour responses (Grosf et al. 1991, Ramsden et al. 2001) which are delayed in respect to the V2 activation (Lee & Nguyen 2001). Here, single cell recordings were conducted in area V1 to probe illusory contour processing with contextual stimuli. One major aim of these recordings was to assess whether the stimuli used in the psychophysical experiments of this thesis could also be used for single cell recordings.

Neural responses to optimally oriented, moving Kanizsa-figures were recorded and compared to spontaneous activity (response to blank) as well as to responses to control stimuli. Control figures consisted of partial discs rotated such that they did not induce illusory contours.

The V1 neurons tested responded significantly stronger to the Kanizsa-figure than to a blank screen during the whole stimulus presentation. This comparison is, however, difficult to do as spontaneous activity was not measured before every stimulus presentation. Shifts in baseline activity would thus be undetected (compare Fig.6.4) and might result in apparent differences between blank and stimulus responses, which in fact might be due to a changed overall firing rate of the neurons.

However, the experiment was designed such that a comparison between firing rates to illusory figure and control stimulus could be conducted. To that end the stimuli were presented continuously moving across the receptive field. Stimuli were presented in blocks of 5 complete movements. Blocks of different stimuli were each repeated for 10-15 times in a randomly interleaved manner. As control stimulus and Kanizsa-figure show a very similar contrast pattern, the neural stimulation by luminance contrast only changed with the stimulus movement, but not with stimulus type. Comparison between responses to control and Kanizsa-figure therefore allowed to examine whether neurons were mainly driven by luminance contrast or by the context-induced contour.

Neurons were stimulated comparably strong by both Kanizsa-figures and the control stimulus during the first half of stimulus presentation, indicating that the distance of the partial discs in both stimuli was too small, therefore possibly leading to a contrast response of the neurons rather than to an illusory contour response. In the second half of stimulus presentation, on the other hand, neurons preferentially respond to the Kanizsa-figure. This indicates that the neurons recorded might have been signalling the illusory contour, but were biased in their average direction-sensitivity, thereby preferring the stimulus movement in one versus the other direction. Such a bias, however, was not observed in the initial mapping of the neurons' receptive field properties. Furthermore, the responses difference between Kanizsa-figure and control stimulus is only a trend. Differences were more pronounced in the temporal modulation of spiking activity than in their actual strength when comparing stimulus responses with spontaneous activity (see Fig.6.8). Still, future experiments will have to take the possibility of direction selective preferences into account and compare neural activity to stimuli in the preferred with non-preferred directions.

Taken together, the comparison of neural responses to the Kanizsa-figure with responses to blank and control stimulus cannot rule out the possibility that neurons signalled the high contrast partial discs rather than an illusory contour. Average single cell responses, however, showed a more pronounced temporal modulation with illusory contour stimulation than with the control stimulus, suggesting that neural responses to Kanizsa-figures were not only driven by the high contrast inducers, but at least also modulated by the illusory contour. To allow for a clear distinction

between illusory contour and control stimulus response, further experiments will have to be conducted with inducers being located further away from the receptive fields.

6.4.2 Context leads to Orientation Reversal

Is there evidence for contextual effects which are consistent with the model of feedforward-feedback processing of illusory contours? The model, as depicted in Fig.5.12, would predict that V1 neurons engaged in illusory contour processing show inhibited responses to optimally oriented real lines. Inhibition is proposed to be mediated by orthogonal domains in V1, which are activated by V2-feedback. Consequently, neurons should respond less to optimally oriented real lines superimposed on an illusory contour than to the same lines in a control context. These predictions were tested here by presenting Kanizsa-figures and control stimuli with superimposed real lines. Real lines were either optimally oriented (parallel), or were rotated by 90° to the cell's preferred orientation (orthogonal).

V1 is known to mostly contain orientation-selective neurons (Hubel & Wiesel 1968), which even respond to stimuli of very low contrast. Hence, single cells in V1 are expected to respond stronger to optimally oriented real lines (parallel) than to real lines in the orthogonal orientation. In the control stimulus this was exactly the observed result: neural responses were stronger to parallel real lines than to orthogonal real lines. At no time during stimulus presentation orthogonal lines were preferred over parallel lines, as plotted in Fig.6.10(B).

Firing rates to real lines superimposed on Kanizsa-figures, on the other hand, revealed a different result. In this case, orientation preference was reversed, as can be observed in Fig.6.10(A). Neurons responded in general stronger to non-optimally oriented real lines. The comparison between responses to real lines superimposed on Kanizsa-figure and control stimulus thus indicates that single cells in area V1, which are engaged in illusory contour processing reverse their orientation preference.

These results do not confirm the prediction stated above. Responses to optimal stimuli were not changed or only slightly decreased, while responses to non-optimal stimuli were increased in illusory contour context. How can this orientation reversal observed in single cells be interpreted? Cross-orientation facilitation has been observed by Sillito et al. (1995). They reported that V1 neurons responded stronger to a texture figure when this figure was surrounded by an orthogonally oriented texture. In the stimulus used here an illusory figure was presented and possibly enhanced by cross-orientation facilitation using an abutting line. The observed increased activity to the orthogonal real line might thereby be an indication for an increased response to the illusory figure. Also iso-orientation inhibition has been reported repeatedly [98, 103] and was attributed to feedback by various groups [50, 53, 37, 4]. These studies showed that contextual effects in V1, which were mostly related to figure-ground segregation, relied on information from higher cortical areas. Previous reports of surround suppression as well as of cross-orientation facilitation are thus consistent with the results presented here.

Importantly, previous studies investigated contextual modulation of single cell properties with complex luminance contrast stimuli such as texture figures in a texture surround [53, 37], luminance gratings in center and surround [98, 42, 4], or single lines in the receptive field center with an array of lines in the surround [49, 62, 104]. Here, modulation of single cell activity has been found in an illusory contour context. This supports, first, the idea that area V1 is involved in illusory contour processing [26, 58, 84]. Second, it shows that illusory contour processing can lead to a reversed orientation preference, or to a cross-orientation facilitation in V1 single cells. Third, these results suggest that illusory contour processing might be comparable

to figure-ground segregation in texture or grating stimuli in which cross-orientation facilitation and surround-suppression effects similar to the results presented in this thesis have been reported previously [98, 53, 4, 104].

Of course, contextual interactions in area V1 show in fact a variety of effects besides cross-orientation facilitation and parallel suppression [49, 42]. Which effect can be observed depends on contrast [81, 49], orientation [49, 61, 104], position of context and target relative to the receptive field [49, 62], and on the properties of the individual neuron [42]. The data presented here can thereby only be understood as preliminary results. More extensive receptive field mapping and correlating the data with specific cell properties, such as width of the orientation tuning curve or direction selectivity, will have to be undertaken to get a better estimate of the effects of illusory contour processing on V1 activity.

6.4.3 Conclusion

The psychophysical experiments conducted in this thesis provided evidence for close connection between real and illusory contour processing. Real-illusory contour interaction showed a temporal development dependent on real line orientation which supported the hypothesized feedforward-feedback model proposed in chapter 5. The aim of the single cell recordings conducted here was to assess, first, the feasibility of physiology experiments using stimuli comparable to those employed in the psychophysical studies. Second, I attempted to test two predictions of the hypothesized model: a) real-illusory contour interactions occur in area V1, and b) illusory contour context leads to reversed orientated activity in V1 single cells.

This was tested by measuring V1 single cell responses to illusory contour stimuli with and without superimposed real lines. Real lines were either parallel to the illusory contour (optimally oriented) or abutting to it (non-optimally oriented). Illusory contour responses were furthermore compared to the firing rate to a control stimulus which did not induce illusory contours.

The physiological results obtained in visual area V1 indicate that the stimulus used in the psychophysical experiments can be used, with only minor changes, also for physiological measurements. Single cells responded stronger to the illusory contour figure than to the control stimulus. Responses to control stimuli, however, were still much stronger than spontaneous activity, suggesting that future experiments should be conducted with the partial discs being at greater distance from the receptive field.

Responses to oriented real lines were observed to be modulated by illusory contour presentation as compared to presentation of the control stimulus without illusory contours. Neurons, on average, showed an orientation reversal when engaged in illusory contour processing. The effects observed here appear to be comparable to effects of contextual interaction reported previously by various groups. This indicates that illusory figures might contextually interact with V1 processing similarly to contextual stimuli defined by luminance contrast. It furthermore shows that the stimulus design employed here is in general well suited to measure real-illusory contour interactions. Thus, the results obtained in area V1 encourage further studies of real-illusory contour interaction effects in areas V1 and V2.

7. OUTLOOK

7.1 *Relevance of Real-Illusory Contour Interaction*

The properties of real-illusory contour interaction as reported here can be understood as indication for properties of contour-processing mechanisms. The effects can be side effects of the system which may be only accessible in the artificial world of the psychophysical setup. They might, however, also be useful features of the contour processing system that help extracting objects in a normal, natural scene. The following sections will give some ideas about how to test the real-life importance of the effects reported in this thesis.

Identity of Illusory Contours

The temporal development of real-illusory contour interaction has been shown in this study in Kanizsa-figures alone. These stimuli are in many ways different from other virtual contours types. For example, Kanizsa-figures induced contours, surfaces, brightness, as well as a depth percept. Illusory contours in the Kanizsa-figure thus are embedded in a complex stimulus and possibly even induced by more than the partial disk inducers alone. Are illusory contours which are induced by different stimuli identical to illusory contours in Kanizsa-figures? The physiological studies by von der Heydt & Peterhans (1989) show that both abutting line and Kanizsa-type illusory contours activate the same neurons in area V2. Various psychophysical studies showed the high similarity between illusory contours with different inducers [45, 77, 114]. Based on these reports it can be assumed that illusory contours are processed by the same mechanisms despite different inducing stimuli. The temporal development of real-illusory contour interaction, as reported here, should thus be identical for different types of illusory contours. This can be tested with abutting line stimuli, illusory contours induced by depth information as well as with spontaneous splitting figures.

Additivity of Inducers

If illusory contours induced by different stimuli share a common neural representation and processing pathways, activation from different inducers must feed a common induction process. Are these inputs used in a binary fashion (i.e. on/off), or can different inputs add up to perceptually and neurally enhance an illusory contour? By measuring real effects on perceptual strength of different types of illusory contours alone as well as of illusory contours induced by a combination of inducing stimuli, the additivity of inducing stimuli can be tested. If inducers are additive, the strongest real contour effects would be expected with abutting line patterns, the weakest effects possibly with Kanizsa figures with additional depth information. If there is a dependency on information amount the results might indicate how the different systems (contrast, orientation, depth, etc) work together to extract the best possible explanation for an object in our visual environment.

Illusory Contour Perception in Natural Scenes

To test the relevance of contextual modulation in illusory contour perception in natural life it might be interesting to probe our senses with more complex stimuli such as natural scenes. In natural scenes, object boundaries are mostly defined in various ways, i.e. they are generally induced with different inducers simultaneously. If illusory contours are additive, as hypothesized above, interaction with them should be more difficult as more inducing stimuli lead to the illusory percept. The question is then, whether the natural illusory contour is usually prone to the type of interactions presented here, or whether subtle interactions can change also natural perception. To test this, photographs of illusory contours in nature could be "enhanced" or interfered with by superimposing low contrast real lines or additional inducers. Perceptual strength of the illusory contours can then be assessed by means of, for example, object detection tasks.

7.2 Perceptual Interaction = Physiological Interaction?

Based on the psychophysical results obtained in this thesis a model of the cortical processes underlying illusory contour perception was proposed. To test the validity of this model it is crucial to link perceptual results with physiological data. To that end single cell physiological experiments should be conducted to test the contextual modulation of illusory contour specific neuronal activity. As shown psychophysically, contextual modulations depend on orientation and contrast of the context as well as on timing of the interaction. The feedforward-feedback model predicts a change of modulation in areas V1 and V2 over time. To relate neuronal activity with perception, I will therefore test single cell responses in areas V1 and V2, using stimuli similar to the ones used in the psychophysical experiments conducted here. First assessments of modulation of illusory contour related neuronal activity will be conducted in the anesthetized macaque, as already reported in chapter 6. To measure the relationship between perceptual and physiological context effects in illusory contour processing, however, single cell recordings in the awake, behaving macaque are planned. To allow furthermore the comparison between illusory contour processing with different inducers, stimulation with abutting line type stimuli is also planned.

Temporal Development of Illusory Contour Processing

To investigate the temporal development of illusory contour processing and its interaction with real contour processes, neural activity in areas V1 and V2 will be tested with the backward masking paradigm employed in chapter 5. In the recordings conducted so far the Kanizsa-figure was moved back and forth over the receptive field. This stimulation was found to produce stronger cell responses than static or flashing stimuli. Contextual interactions have been shown, however, to depend on the location of stimulus and context relative to the receptive field [49, 42]. In a moving stimulus these relative locations change continuously, thereby producing different interaction patterns over time that cannot clearly be attributed to the timing of illusory contour processes. Either static or flashing stimuli will therefore also have to be tested. Kanizsa-figures will be presented with and without real contours in optimal or non-optimal orientations. Real lines will be presented at different times before and after stimulus presentation to probe the timing of illusory contour processing.

Neural Activity and Perceptual Strength of Illusory Contours

The aim of this thesis was to relate the perception and physiology of illusory contour processing by probing them with contextual real contours. Real line interaction was thought to modulate physiological processes and thereby to modulate perceptual strength of the illusory contour. A different approach to compare perception and processing is to change the perceptual strength of illusory contours by changing the inducing stimuli. The effect of the illusory contours on real line processing can then be tested physiologically, as already presented in chapter 6. If perceptual and physiological strength of illusory contours are directly related in areas V1/V2, an increase of e.g. the support ratio in a Kanizsa-figure [97] should result in stronger modulation of real contour processing by the illusory contour stimulus. Furthermore, illusory contour stimuli of the same perceptual strength (i.e. identical support ratio in the Kanizsa-figure) should lead to the same effects on real line processing. This should be true even if the inducing stimuli are presented at a greater distance from the receptive field of the recorded neuron.

8. SUMMARY

Illusory contour processes are initiated by real contextual information, the inducers. Changes in the illusory contour percept is based on modification in the inducing or other contextual stimuli. To understand the processes underlying illusory contour perception, it is thereby essential to investigate the context effects on illusory contour perception.

Recent physiological reports showed neural signals to illusory contour stimulation as early as in primary visual cortex. Signals were, most interestingly, orientation reversed to the real contour signal (Ramsden et al. 2001), and appeared later in V1 than in V2 (Lee & Nguyen 2001). These physiological results suggest that a feedback mechanism from primate V2 to V1 is involved in illusory contour processing (Roe 2003).

Real-illusory contour interactions in such a mechanism are expected to have specific properties. First, interactions should be orientation dependent, with context affecting the inducing stimuli during induction of the illusory contour, and affecting the illusory contour during establishment of the illusory percept. Second, even contextual stimuli at subthreshold contrasts should affect illusory contour perception by interacting with processes in the early visual cortices. With increasing contrast, however, effects are expected to change due to different receptive field properties in early processing stages at different contrast levels (Polat et al. 1998, Mareschal 1998). Third, real-illusory contour interaction and its dependency on orientation should change over processing time in the proposed feedback mechanism with orientation reversal in area V1.

In this thesis, the three predictions were tested psychophysically by measuring the perceptual saliency of illusory contours with different contextual stimuli. Based on the results a model of illusory contour processing in areas V1 and V2 is proposed. In preliminary single cell recordings in area V1 it was finally tested whether neural activity to illusory contour stimulation with and without contextual real lines is consistent with an interaction between real and illusory contour processes in that area.

Induction and Consolidation of Illusory Contours

Physiological and psychophysical studies show interaction and overlap between real and illusory processes in the first visual areas (von der Heydt & Peterhans 1989, Westheimer & Li 1996, Ramsden et al. 2001), suggesting a feedforward-feedback mechanism with the illusory contour being developed first in V2, but fed back to V1 (Lee & Nguyen 2001). In such a mechanism real lines would interact early with inducers only, but later predominantly with the illusory contour.

This hypothesis was tested in an orientation discrimination task with an illusory contour tilted around vertical. The illusory contour was induced by oblique abutting lines. Real-illusory contour interaction was probed by means of backward masking with real line patterns identical to the inducers, but not inducing an illusory contour. Mask were presented at orientations either parallel to the inducing lines (ipsi), parallel to the illusory contour (vertical), rotated by 90° in respect to the inducing lines (contra), or rotated by 90° in respect to the illusory contour (horizontal).

Illusory contour stimuli were presented for 100, 125, or 150 msec, followed by the mask for 100 msec. Thresholds for orientation discrimination of the illusory contour were measured in a 2AFC paradigm under masked conditions and compared to an unmasked condition.

As real lines are masked best by parallel real lines (Li et al. 2000), it is expected that masks in the same orientation as the inducing lines interfere with the inducing processes, while masks oriented parallel to the induced contour might rather interfere with the illusory contour itself. Masking of the illusory contour, however, is only expected after completion of the illusory percept. In the hypothesized mechanism only inducing processes would be active early on, indicated by strongest masking with real lines parallel to the inducing stimuli at short presentation times.

The results in this experiment supported the hypothesis. Two major stages of illusory contour processing were indicated by masking effects that changed with presentation time. At the shortest presentation time of 100 msec all line patterns masked with varying strength, suggesting either a fragile state in processing, or an overlap between real and illusory processes. At the longer presentation times of 125 and 150 msec only lines parallel to the illusory contour were masking the illusory contour percept. The evidence presented here thus indicates that abutting line induced illusory contours are processed in two steps. First, they are induced, and second, their neural representation is consolidated. Induction processes are completed at a time of about 125 msec, while consolidation of the illusory contour extends at least over 150 msec. This interpretation is consistent with previous reports about the temporal development of illusory contour perception (Reynolds 1981, Ringach & Shapley 1996, Westheimer & Li 1996, Lee & Nguyen 2001, Guttman & Kellman 2004).

Based on these results, a mechanisms for orientation selective interactions between real and abutting line illusory contours is proposed. Real contours can interfere early on (< 125 msec) with the processes inducing the illusory contour, namely by probably inhibiting end-stopped cells in early visual cortex (von der Heydt & Peterhans 1989). Later on (≥ 125 msec), real contours interfere with the illusory contour, showing parallel line masking effects that might be comparable to masking of real lines as shown in V1 (Macknik & Livingstone 1998, Li et al. 2000). This would indicate that either similar masking effects also occur in V2, or that illusory contours are represented and masked in V1, as suggested by other studies (Lee & Nguyen 2001, Ramsden et al. 2001, Roe 2003).

Contrast dependent Real-Illusory Contour Interaction

Both real and illusory contours provide information about object borders which can be used for scene segmentation. Whether real or illusory contour cues are used, however, can lead to different interpretations of the same scene. How does real and illusory contour information affect each other? Real contours have been reported to both perceptually facilitate (Dresp & Bonnet 1995) and interfere with (Ringach & Shapley 1996, Westheimer & Li 1996) illusory contours. Recent optical imaging and electrophysiological studies (Ramsden et al 2001, Lee & Nguyen 2001) suggested that illusory contours produce a feedback influence from V2 to V1. Interestingly, V1 activation by illusory contours has been found to be orientation-reversed to real contour activation (Ramsden et al. 2001). Based on these results, an orientation dependent competitive interaction between real (feedforward) and illusory (feedback) mechanisms between V1 and V2 has been hypothesized (Roe 2003). This model leads to two predictions: first, interactions between real and illusory contours are expected to be orientation dependent. Second, if these interactions reside in low-level structures such as V1, even real lines of subthreshold contrast should interact with the illusory contour processing. To test these hypothesis psychophysically, the

perceptual strength of an illusory contour in a Kanizsa-triangle was tested in this thesis with and without superimposed real line.

A Kanizsa-triangle was presented for 250 msec. Its perceptual strength was measured without additional real components, with a parallel real line superimposed on the virtual contour, or with an orthogonal real line abutting the illusory contour. Real lines were presented at different subthreshold and suprathreshold contrasts. Two of the inducers of the Kanizsa-figure were varied in their opening, leading to the percept of an illusory contour either curved inward or outward. Subjects indicated the curvature of the illusory contour in a 2AFC paradigm.

Supporting the original hypothesis, real lines in general were found to compete with illusory contour perception. This was found to be true even at subthreshold contrasts, suggesting an involvement of early processing stages. Interference was found to depend on contrast and orientation: at subthreshold, orthogonal lines interfered, whereas at high contrast predominantly parallel lines interfered with the illusory percept. At no contrast or orientation, facilitatory effects were found.

These results support the presence of in part separate real and illusory contour processing mechanisms and suggest that, under some circumstances, real cues can interfere with the processing of illusory cues. Such interference might occur by a relative strengthening of feedforward V1-V2 influences which interfere with the feedback influences prominent during illusory contour processing.

Temporal Development of Real-Illusory Contour Interaction

Our environment is structured by edges defined by contrast or contextual information. These contours build the basis for object and scene perception. The contour processing system has been hypothesized to involve a "cortical balancing act" between feedforward and feedback paths, the latter resulting in a reversal of the orientation tuning map in V1 (Ramsden et al. 2001, Lee et al. 2001, Roe 2003). In the previous chapter, real contours have been shown to influence the perception of illusory contours dependent on their orientation.

Assuming a illusory contour processing system using orientation-reversed feedback, real-illusory contour interactions would be expected to be also dependent on their relative timing. Early parallel real interaction should thereby enhance signals to equal oriented stimuli in V2, thus strengthening the illusory contour, but have the opposite effect later on, adding an ambiguating signal in V1 to the proposed reverse oriented feedback. To test these assumptions, the temporal evolution of illusory contour perception was measured psychophysically by probing the underlying processes with contextual real lines at different interaction times. A 2AFC backward masking paradigm was employed to assess the perceptual strength of Kanizsa-type illusory contours. Real contours parallel or orthogonal to the illusory contour were presented as masking stimulus. Illusory contours were presented for 50 msec followed either by a blank screen, a parallel, or an orthogonal real line. Masks were presented for 100 msec with varying stimulus onset asynchronies (50, 100, 125, 150, and 200 msec) after illusory contour presentation.

Real line interaction with the illusory percept changed over time, dependent both on real line contrast and orientation. Real lines of both orientations were found to sometimes help and sometimes interfere with the percept. Parallel real lines showed a trend to summate with the illusory contour at early interaction times (SOA 50 msec), but more consistently interfered with the percept at later points (SOA 125-150 msec). Orthogonal real lines also showed facilitation effects early on (SOA 50 msec) and a reversal of effects from facilitation at 100 msec SOA to interference at 125 msec SOA.

These data indicate a reversal of the orientation-dependency of the real-illusory contour interactions over time and thus support the hypothesized feedforward-feedback

model of illusory contour processing: a feedforward induction process leads to illusory contour specific neuronal activity in V2 (Peterhans & von der Heydt 1989). Orientation-reversed feedback from V2 to V1 (Ramsden et al. 2001, Lee & Nguyen 2001) activates orthogonal domains, which in turn inhibit parallel domains in V1. The balanced activation of orthogonal and parallel domains in V1 and V2 is the consolidated pattern of illusory contour activation observed with optical imaging (Ramsden et al. 2001).

Modulation of V1 Neural Activity by Real and Illusory Contours

The results so far and the resulting model of illusory contour processing predict that real and illusory contour processes overlap already in area V1. Real-illusory contour interactions would thus be measurable in this area. If parallel domains in area V1 are inhibited during illusory contour processing, as suggested by psychophysical results obtained here and physiological data (Ramsden et al. 2001), then single cell responses in V1 to optimal stimuli should be decreased in an illusory contour context than in a context not inducing illusory contours. I tested these predictions in area V1 of an anaesthetized macaque using single cell physiology.

Neural responses were recorded to illusory contour stimuli with and without superimposed real lines, which were either oriented optimally (parallel) or orthogonal to the optimal orientation (orthogonal) for the respective neuron. 16 single cells were recorded.

The illusory contour stimulus in general elicited stronger responses than both control stimulus or blank. The rotated inducers used as control lead to neural activity clearly beyond spontaneous levels. Thus, the stimulus used might have been displayed too close to the neurons receptive fields, thereby inducing a strong luminance contrast response. To clearly distinguish between luminance contrast and illusory contour activity future recordings might have to be conducted at a greater distance of inducing stimuli and receptive fields. Results indicate, however, that V1 neurons respond different to the illusory contour than to control stimuli, as has already been reported by previous studies (Grosf et al. 1993, Lee & Nguyen 2001, Ramsden et al. 2001).

Testing the contextual effect of illusory contours on neural responses to real lines revealed a stronger indication for illusory contour related modulation of activity in V1. Responses to non-optimally oriented real lines in illusory contour context were increased as compared to responses to the same stimulus in the context of the control stimulus without illusory contours. Single cells were thus observed to reverse their orientation selectivity, or to respond stronger to the illusory contour with an abutting real line. In contrast to the prediction stated above, however, neurons did not show strong inhibition of responses to optimally oriented real lines in illusory contour context. In this experiment I thus observed real-illusory contour interaction in area V1. Results are, however, not consistent with the predictions of the proposed model. Still, the stimulus design employed here appears to be well suited to measure real-illusory contour interactions in visual cortex. To reconcile the psychophysical results with neural activity more recordings will be conducted also in the awake behaving animal. Furthermore, future recordings in areas V1 and V2 will have to take into account that context effects depend on contrast, orientation, and timing of interactions as shown psychophysically in this thesis.

Conclusion

In this thesis I tested illusory contour perception and processing by psychophysically and physiologically measuring real-illusory contour interactions. Using a simultaneous masking paradigm I could show orientation-dependent real line effects

on illusory contour perception changing over time (chapter 3). The psychophysical results of these experiments provide evidence for two stages of illusory contour processing, namely the induction and establishment of the percept. The results are consistent with previous psychophysical studies reporting the temporal development of illusory contour perception (Reynolds 1981, Westheimer & Li 1996, Guttman & Kellman 2004) and local versus global masking of Kanizsa-figures (Ringach & Shapley 1996). Data furthermore showed that real contours can directly interact with illusory contours, and not only with their inducers. This was previously indicated by a study employing Kanizsa-figures (Ringach & Shapley 1996), while it had not yet been shown with stimuli of the abutting line type. The experiments conducted here thus indicate that illusory contours of the abutting line type show a similar to illusory contours in a Kanizsa-figure temporal development. Furthermore, real-illusory contour interaction is similar in both stimuli. It has previously been shown that the underlying processes overlap in area V2 (von der Heydt & Peterhans 1989, Peterhans & von der Heydt 1989). I suggest that only the inducing stage in illusory contour processing differs dependent on the type of inducing stimuli presented. Illusory contours, however, might be processed via common consolidating mechanisms disregarding of their inducers.

Oriented real lines can directly interact with an illusory contour. Real lines can thus be used to probe illusory contour perception to assess the orientation and contrast dependency of real-illusory contour interactions. Perceptual strength of illusory contours in a Kanizsa-figure was measured psychophysically with and without simultaneously presented real lines that were either parallel or abutting to the illusory contour. In general, real lines interfered with the illusory contour percept. Interference was most pronounced with suprathreshold lines parallel to and superimposed on the illusory contour. This has been reported previously (Ringach & Shapley 1996) and was also found with the abutting line stimuli used in chapter 3. Interestingly, also subthreshold lines abutting to the illusory contour were found here to consistently interfere with the percept. These effects by subthreshold lines indicate that early processing stages in visual cortex mediate at least part of the observed real-illusory contour interactions. Summation effects were not observed in contrast to previous reports (Dresp & Bonnet 1995, but compare also McCourt & Paulson 1994). The dependency of real-illusory contour interactions on real line orientation indicates that the interaction occurs in orientation-selective domains (Paradiso et al. 1986, Westheimer & Li 1996). The observed reversal of orientation dependency from high to low contrasts might be related to contrast-dependent changes in receptive field sizes (Polat et al. 1998), which were also demonstrated psychophysically (Mareschal 2002). The results might, however, also be an indication for an orientation reversal in illusory contour processing which was observed in area V1 with optical imaging and single cell physiology (Ramsden et al. 2001).

V1 activity to illusory contour stimulation arises later than illusory contour responses in V2 (Lee & Nguyen 2001) and might thus be due to feedback information from area V2. The orientation reversal observed in area V1 therefore might develop over processing time. To test this hypothesis I probed the temporal development of illusory contour processing with real lines that were displayed at different times after illusory contour presentation (chapter 5). The expectation that real lines interact with the perceptual strength of the illusory contour dependent on timing was supported by the experimental results. Orthogonal lines facilitated the percept early on (50 msec after stimulus onset, SOA), which is consistent with an activation of inducing processes such as end-stopped cells in V1 (von der Heydt & Peterhans 1989). Indicating real line interaction with illusory contour processes rather than with the inducing processes was found at SOAs of 125 msec and more, at which parallel lines in general interfered with the percept, consistent with the parallel real line effects found in earlier experiments in this thesis as well as by Ringach & Shap-

ley (1996). As explained in chapter 3, this parallel interference is probably related to the consolidation phase of illusory contour processing. This interpretation is consistent with the fact that parallel interference with illusory contour perception was measured only after SOAs of 125 msec, at which time the illusory contour induction is completed (Reynolds 1981, Westheimer & Li 1996, Ringach & Shapley 1996, Guttman & Kellman 2004). At the same time illusory contour responses can be recorded in area V1 (Lee & Nguyen 2001), suggesting that V1 activation might be part of the consolidation phase of illusory contour processing. Support for this interpretation comes from another result of the experiments conducted here. Lines abutting to the illusory contour showed a transition from summation to interference at SOAs of 125 to 150 msec. This indicates that orthogonal domains are involved in illusory contour processing even after the induction phase is completed. The timing of this transition is furthermore in agreement with the transition of illusory contour responses from area V2 to V1 (Lee & Nguyen 2001). The data reported here thus are consistent with an orientation reversal in illusory contour processing which develops over time. Based on these results a feedforward-feedback model of illusory contour processing is proposed (Fig.5.12). According to the model, illusory contour processing is initiated by inducing stimulation feedforward from V1 to V2. The parallel real-illusory domains in V2 then send feedback information to orthogonal domains in area V1, which in turn inhibit the parallel domains in that area, resulting in a reverse orientated activation of area V1.

The proposed model leads to a number of predictions about illusory contour processing and its interaction with real lines in cortical areas V1 and V2. One prediction was tested here in single cell recordings in macaque primary visual cortex: if illusory contour processing leads to an inhibition of parallel domains in V1, then V1 responses to parallel real lines should be decreased in illusory contour context as compared to contextual stimuli that do not induce illusory contours. This hypothesis could not be supported by the physiological results. Responses to optimally oriented lines in the context of the control stimulus showed only tendencies to be stronger than to real lines superimposed on an illusory contour. However, single cells engaged in illusory contour processing responded consistently stronger to non-optimally oriented real lines than to both optimal lines in an illusory contour context and non-optimal lines in a control stimulus context. Thus, illusory contours contextually modulate neural activity and response properties of single cells in area V1. This modulation leads to a reversed orientation preference of the neurons, possibly comparable to the reverse oriented activity in V1 found by Ramsden et al. (2001) with abutting line stimuli.

While these data indicate that illusory contour processing can be studied physiologically by probing it with real lines, the recordings conducted so far are only preliminary attempts to assess the feasibility of the experiment. To draw any further conclusions, extensive mapping of single cell receptive fields will have to be conducted as contextual effects have been reported to correlate with stimulus location relative to the receptive field (Kapadia et al. 2000, Jones et al. 2002). Furthermore, the effects reported here will have to be compared to results with different illusory contour stimuli before interpreting them as an indication for distinct properties of illusory contour processing in general.

To summarize: the results presented here suggest that dependent on timing, orientation and contrast of a real line presentation the respective “cortical state”, that is the stage of processing the system is currently engaged in, is either consistent (i.e. supportive) or inconsistent (i.e. interfering) with the illusory contour to be processed. By presenting stimuli that either interfere with the illusory contour process or enhance it, it is thereby possible to probe the underlying processes and characterize their properties. Perceptual real-illusory contour interactions support the

hypothesis that illusory contours are extracted at early processing levels in visual cortex, possibly in areas V1 and V2. The dependency of real-illusory contour interaction on timing and orientation is consistent with a feedforward-feedback model between these two areas. In this model, an orientation reversal occurs in area V1, with domains orthogonal to the illusory contour inhibiting domains parallel to the illusory contour. First physiological experiments indicate that V1 single cell activity is contextually modulated by illusory contours, interestingly leading to reversed orientation preferences of the neurons. To reconcile these results with the perceptual effects of real line interaction with illusory contours, single cell recordings will have to be conducted in the awake behaving animal.

Based on the results reported here, further studies of illusory contour processing and its interaction with real contours will be conducted using psychophysical and physiological methods. Real-illusory contour interactions will be studied in cortical areas V1 and V2 to investigate the contribution of both areas to the illusory contour percept. Experiments will be conducted in humans and the anesthetized as well as in the awake, behaving macaque, thereby allowing to correlate perception and processing of illusory contours.

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Curriculum Vitae

Barbara Dillenburger

Geburtstag: 19.06.1976
Geburtsort: Dillingen/Saar
Familienstand: ledig
Staatsangehörigkeit: deutsch

Ausbildung

1986-1995	Gymnasium in Dillingen/Saar
1995	Abitur (Dillingen/Saar)
1995-2001	Studium der Biologie an der Karl Eberhard Universität Tübingen
2001	Abschluss als Diplom-Biologin mit Hauptfach Tierphysiologie Titel der Diplomarbeit: Bewegungssehen chromatischer isolu- minanter Reize Betreuer: Prof. Wehrhahn (MPI für Biologische Kybernetik)
2002-2005	Dissertation Titel: Perception and Processing of Illusory Contours Betreuer: Prof. Wehrhahn (MPI für Biologische Kybernetik) Prof. Roe (Vanderbilt University)
01/2002-09/2003	MPI für Biologische Kybernetik (Prof. Wehrhahn) Stipendium des Graduierten Kolleg für Kognitive Neurobiolo- gie der Karl Eberhard Universität Tübingen
10/2003-11/2004	Vanderbilt University, Nashville, Tennessee (Prof. Roe) Grant EY11744 der Packard Foundation
12/2004-07/2005	MPI für Biologische Kybernetik Tübingen (Prof. Wehrhahn) Finanziert durch Prof. Wehrhahn und Prof. Logothetis

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