VISUAL COMPLETION IN AN ILLUSORY FIGURE

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ABBREVIATIONS

FoS	Frequency of Seeing
LOC	Lateral Occipital Cortex
MT	Medial Temporal visual area, or V5
SEM	Standard Error of the Mean
V1	Primary or first visual area, or striate cortex
V2	Second visual area

ABSTRACT

The visual systems of humans and animals represent physical reality in a modified way, depending on the specific demands that the species in question has for survival. The ability to perceive visual illusions is found in independently evolved visual systems, from honeybees to humans. In humans, the ability emerges early, at the age of four months. Thus the perception of illusion is likely to reflect visual processes of fundamental importance for object perception in natural vision.

The experiments reported in this thesis employed various modifications of the Kanizsa triangle, a drawn configuration composed of three black disks with missing sectors on a white background. The sectors appear to form the tips of a triangle. The visual system completes the physically "empty" area between the disks, generally called inducers, with giving the perception of an illusory triangle. The illusory triangle consists of an illusory surface bounded by illusory contours; the triangle appears brighter than and to lie above the background. If the sectors are coloured, the colour fills the illusory area, a phenomenon known as 'neon colour spreading'.

We investigated spatial limitations on the perception of Kanizsa-type illusions and how other stimuli and viewing parameters affected these limitations. We also studied complex configurations – thick, bent, mobile and chromatic inducers - to determine whether illusions combining several attributes can be perceived.

The results suggest that the visual system is highly effective in completing a percept. The perception of an illusory figure is spatially scale invariant when perceived at threshold. The processing time and the number of fixations modify the percept, making the perception of the illusion more probable in various viewing conditions. Furthermore, the fact that the illusion can be perceived when only one inducer is physically present at any given moment indicates the potential of single inducers. Apparently, modelling illusory figure perception will require a combination of low-level, local processes and higher-level integrative processes.

Our studies with stimuli combining several attributes relevant to object perception demonstrate that the perception of an illusory figure is flexible and is maintained also when it contains colour and volume and when shown in movement.

All in all, the results confirm the assumed importance of the visual processes related with the perception of illusory figures in everyday viewing. This is indicated by the variety of inducer modifications that can be made without destroying the percept. Furthermore, the illusion can acquire additional attributes from such modifications. Due to individual differences in the perception of illusory figures, universal values for absolute performance are not always meaningful, but stable trends and general relations do exist.

TIIVISTELMÄ (ABSTRACT IN FINNISH)

Näköjärjestelmä tuottaa edustuksen fyysisestä maailmasta muunnellusti, riippuen siitä minkälaisia erityisvaatimuksia kyseisellä lajilla on eloonjäämisen kannalta. Kyky havaita visuaalisia illuusioita on tavattu toisistaan riippumattomasti kehittyneistä visuaalisista järjestelmistä, mehiläisestä ihmiseen asti. Ihminen alkaa havaita illuusioita aikaisin, noin neljän kuukauden ikäisenä. On aiheellista olettaa, että illuusion havaitseminen heijastaa esineiden havaitsemiseen liittyviä visuaalisten prosessien perustapahtumia.

Tutkimukset, joista tässä väitöskirjassa raportoidaan, käyttävät muunneltuja versioita Kanizsan kolmiosta, piirretystä kuviosta, joka koostuu kolmesta mustasta kiekosta valkoisella taustalla. Kustakin kiekosta puuttuvat sektorit on sijoitettu ikään kuin kolmion kärjiksi. Näköjärjestelmä täydentää kiekkojen väliin jäävän fyysisesti ”tyhjän” alueen illusorisen kolmion havainnolla. Havainto koostuu illusorisesta pinnasta, joka rajoittuu illusoriseen ääriviivaan; kolmio näyttää taustaansa kirkkaammalta ja vaikuttaa olevan myös sitä ylempänä. Jos sektorit ovat värilliset, tämä väri leviää myös illusoriselle alueelle; tätä ilmiötä kutsutaan neonvärin leviämiseksi.

Tutkimme illusorisen kuvion havaitsemisen spatiaalisia rajoituksia ja sitä, miten muut ärsyke- ja katseluparametrit saattaisivat vaikuttaa näihin rajoituksiin. Tutkimme myös, voiko monimutkaisista kuvioista – paksuista, taivutetuista, liikkuvista ja värillisistä kiekoista - hahmottua näitä ominaisuuksia yhdistävä illusorinen kuvio.

Tulokset osoittavat, että näköjärjestelmä on erittäin tehokas täydentämään havaintoa. Illusorisen kuvion havaitseminen on skaalainvarianttia kun illuusio havaitaan kynnystasolla. Prosessointiaika ja fiksaatioiden määrä muokkaavat havaintoa ja tekevät myös mahdolliseksi illuusion havaitsemisen monenlaisissa katsomistilanteissa. Illuusion havaitseminen myös näytettäessä kiekkoja yksitellen osoittaa yhden kiekon sisältävän jo yksinään paljon tietoa illuusion havaitsemista varten. Illusorisen kuvion muodostuminen vaatii ilmeisesti sekä matalan tason paikallisia prosesseja että korkean tason integroivia prosesseja.

Tutkimuksemme monimutkaisilla kuvioilla puolestaan osoittavat, että illusorisen kuvion havaitseminen on joustavaa ja havainto säilyy myös silloin, kun siinä on väriä, volyymia ja kun se näytetään liikkeessä.

Kaiken kaikkiaan tulokset vahvistavat oletusta illuusion havaitsemiseen liittyvien visuaalisten prosessien tärkeydestä jokapäiväiselle havaitsemiselle. Tähän viittaa se, kuinka paljon kiekkoja voidaan muunnella illusorisen havainnon katoamatta. Sen lisäksi illuusion havainto voi saada myös lisää ominaisuuksia muuntelun myötä. Koska illusorisen kuvion havaitseminen on yksilöllistä, yleiset arvot eivät ole aina merkityksellisiä, mutta trendejä ja yleisiä syysuhteita on olemassa.

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Helsinki, October 2007
Marja Liinasuo

LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following publications, which are referred to by their Roman numerals I-V.

I Kojo, I., Liinasuo, M., & Rovamo, J. (1993). Spatial and Temporal Properties of Illusory Figures. *Vision Research 33*(7), 897-901.

II Kojo, I., & Liinasuo, M. (1994). Three-dimensional illusory objects produced by rotation in depth. *Perception 23*(8), 905-912.

III Liinasuo, M., Rovamo, J., & Kojo, I. (1997). Effects of Spatial Configuration and Number of Fixations on Kanizsa Triangle Detection. *Investigative Ophthalmology & Visual Science 38*(12), 2554-2565.

IV Liinasuo, M., Kojo, I., Häkkinen, J., & Rovamo, J. (2000). Neon colour spreading in three-dimensional illusory objects in humans. *Neuroscience Letters 281*(2-3), 119-122.

V Liinasuo, M., Kojo, I., Häkkinen, J., & Rovamo, J. (2004). Visual completion of three-dimensional, chromatic, moving stimuli in humans. *Neuroscience Letters 354*(1), 18-21.

1 INTRODUCTION

Vision is the most important sense for humans, helping us to orient and act adequately in the world. It is essential for finding a way in crowded streets, reaching for a coffee mug or detecting embarrassment by facial expression. Correspondingly, about a fourth of the human cerebral cortex is concerned with visual functions. Not surprisingly, vision is the sense that has been most intensively studied and many general principles of brain function have been derived from these studies. Although much is known about determinants of visual perception, brain anatomy and neural responses in the brain, however, the knowledge is still very fragmentary. For instance, many vision-related brain areas that have a name but no identified function and many recognised visual functions exist for which the neural substrates and algorithms are largely unknown.

1.1 Why study illusory figures?

Trying to understand vision is an immense enterprise requiring studies on many levels by many different techniques and many different research strategies. One strategy is to investigate cases where functions appear to fail: the system performs poorly or makes apparent mistakes. Thus visual illusions, in which perception demonstrably differs from an objective account of the physical world, can tell us something fundamental about how the system works. They also serve as a powerful reminder that all vision is based on representations and interpretations of the world.

It is useful to think of illusions as revealing rules of visual processing shaped by biological evolution. The abilities of existing species, based on their physiology and anatomy, must support their survival and reproduction. For most vertebrates, the visual system is important for finding food, shelter, mating partners, and in avoiding enemies. It may be assumed that evolution has hard wired the visual system to make useful assumptions about the world – e.g. assumptions that help in detecting, identifying and reacting adequately and, when needed, quickly to relevant objects in the environment. On one hand, some general assumptions about the continuity of objects and movements in our common world may be shared by all animals with developed vision. On the other hand, many useful assumptions may be different depending on the living environment and the way the animal breeds, what it eats and what its natural enemy looks like.

Assumptions may also be plastic, shaped by experience. Given the variety of creatures that have the ability to see, it is obvious that there cannot be such a thing as a universally true or even optimal visual perception. From this perspective, it is hard to clarify distinctions between illusions and veridical perception. It has been shown that some human "illusions" are shared by very different animals, from monkeys to honeybees (for examples, see Nieder, 2002). Hence, the concept of illusion is a relative one. Even if in a given experimental context it appears as some kind of false perception, the underlying processes may form a common and supposedly vital part of the visual abilities of human beings or even all seeing animals. It has been claimed that no theory of human perception would be acceptable if it could not handle the perception of illusions, nor would any artificial intelligence effort at real-world pattern recognition work without also processing illusory figures (Meyer & Petry, 1987).

On the other hand, illusions exist as a category of phenomena amenable to experimental investigation. In our study, the term "illusion" is used to denote features of a percept that lacks a correlate in the physical stimulus, i.e. something that the visual system creates when building up representations of the world. In this context, the perception of an illusion can really be seen as some kind of false performance, which is interesting in itself because it tells about the functioning of the visual system. At the same time, it is easy to speculate how corresponding phenomena may be useful in natural vision. For example, large portions of objects can be missing in the retinal images of natural scenes because of insufficient local image contrast, due to camouflage or poor viewing conditions (e.g. fog). Reintegration of the object then involves defining the visually missing boundary segments and filling-in surface properties. This thesis on the perception of an illusory figure focuses on this fundamental task faced by the visual brain: computing object structure from fragmentary retinal input, separated in space and sometimes also in time. Based on psychophysical experiments, it addresses the abilities and limitations of the human visual system in composing such percepts and offers some guesses on how this could be performed in the neural domain.

1.2 Approaches to illusory figures

In the beginning of the 20th century the Gestalt school of psychology studied the perception of wholes as qualitatively different from the parts that constitute them. The percepts were not termed illusions but in the Gestalt, too, the visual system adds something that would not be present in an objective description of the physical stimulus. Simple objects such as dots or bending lines are perceived as coherent groups or continuous forms. Generalizations about how the parts are perceived as a whole were summarised as "laws". As the Gestalt school failed to explain why and how such percepts arise, the entire line of research almost vanished. When Kanizsa presented his soon-to-be famous illusion in 1955, the Kanizsa triangle, he first explained the percept as a Gestalt phenomenon, in which the visual system strives to perceive complete, "perfect" wholes instead of incomplete ones. Kanizsa himself abandoned the explanation later and the Gestalt principles are now mentioned only rarely in scientific discourse. No corresponding general framework has emerged after the Gestalt school.

The study of Kanizsa-type illusions, configurations that have some physically real (drawn) objects arranged around an empty space in which the illusory figure appears, was first purely phenomenological. No groups of subjects were used but the percepts were supposed to be so general that it was assumed everybody sees the stimulus in a similar manner. Gradually, the methods became more stringent and statistical treatment gained ground. In psychophysical investigations, the stimulus is parametrically manipulated and the effect on perception is studied by quantitative experimentation. These are the main methods used in our study.

The study of visual illusions is now a very large research field employing all the methods used by visual science in general. The central goal today is usually to identify the neural correlates, ideally mechanisms that underlie the perceptual phenomena. For this, the entire repertoire of electrophysiological and imaging techniques of modern integrative neuroscience is applied. Another approach is to use computational models. As expressed by Marr (1982), these represent a level of understanding that is independent of the particular mechanisms and structures that implement the computations in our heads. They may, however, shed light on the neuronal operations on a more general level.

To summarise, the potential usefulness of the processes manifested in the perception of illusory contours appears quite evident. A deeper understanding of these functions and underlying mechanisms requires a combination of insights from very different types of studies. This thesis is a psychophysical contribution towards this goal.

2 LITERATURE REVIEW

2.1 The illusory nature of visual perception

2.2 Relative veracity

Vision can be examined from many perspectives. One perspective is the veracity of perception. The concept of veracity, the truthfulness of the percept or the equivalence between the percept and the corresponding physical properties of the object, is in many ways a relative one. Veracity can be defined as something coinciding with reality but this coincidence is never total. For instance, our photoreceptor cells mediate only a narrow band of the electromagnetic radiation present in the environment, the range of visible wavelengths being ca. 400 – 700 nm. A fly is surely a different thing for humans and frogs and yet the percept may be "veridical" for both species as related to their needs. We learn expectations about the visual world and suppose that a heavy-looking object is heavy and that sitting people have feet below the table; sometimes these expectations are true and sometimes not. What is perceived cannot be separated from these expectations; and sometimes what we perceive or think that we perceive is not veridical by any reasonable criterion but an "illusion".

A common criterion for phenomena having been categorised as illusory or non-illusory is hard to find. One criterion for distinguishing between a non-illusory percept and an illusory one might be how well the percept helps in orienting in the real world. Such an instrumental criterion cannot provide a strict definition, but is often consistent with common usage. If a perceptual transformation helps us to orient in the world, it is often considered as belonging to normal visual phenomena.

Contours provide important information about the shape of objects, thus being a key cue for the segregation of figures from the background. Detecting and identifying objects is vital for survival. Thus, from the very first stages of visual information processing contour is enhanced. Even the cells of the retina are more strongly excited by the presence of a border (luminance contrast) than by uniform light. Analogous phenomena occur at many levels in the visual system. The general mechanism is lateral antagonism, whereby the response of one "central" cell is suppressed depending on the stimulation of surrounding cells that provide sign-reversed or inhibitory input. At lower levels in the system this simply serves to enhance responses to contrast borders.

2.3 The function of perceiving illusory figures

Contour processing, as described above, is not considered as illusory. Given the important role of contours for vision, it is easy to understand why the visual system should “facilitate” contour perception. For the same reason, it is sometimes meaningful to generate a response signalling a contour when physically there is none. Contours that are (re)constructed do not only exist in scientific experiments (illusory contours in the traditional sense). In the real world, contours of objects may not be properly visible due to poor viewing conditions. Then the “improved” percept may, strictly speaking, be illusory despite corresponding to the real world. In a situation where real contours are only weakly visible, this ability can be important. For example, for preys and predators it may be important in making or breaking camouflage. This point of view appears plausible, as many animals are able to see illusory contours (for a review, see Nieder, 2002).

The ability to perceive illusory figures emerges relatively early in humans. Four month old infants look longer at a stimulus that generates the percept of an illusory square in adults, appearing to move across the computer screen, than similar stimuli but with outward pointing notches to eliminate this possibility (Kavšek & Yonas, 2006). Furthermore, four month old infants show a strong preference for a continuously moving illusory square, looking at it longer than an illusory square that randomly changes position (Kavšek & Yonas, 2006). These results are interpreted as an indication that the infants do perceive the illusory figure (Kavšek & Yonas, 2006). Related with the perception of occluded objects, Craton (1996) found that eight month old infants perceived a static rectangle as unified when occluded by a bar in its centre. Apparently, children perceived its total shape, because they looked at the figure for a longer time if a cross instead of a rectangle was revealed when the bar was removed. Infants of 6.5 months were agnostic regarding its specific form. The earlier appearance of the ability to perceive illusory figures over occluded ones indicates that modal completion developmentally precedes amodal completion. Moreover, it suggests that that the processes related with visual completion are at least equally important in everyday vision as the perception of occluded objects.

Similarities in the processing of illusory and real lines are suggested by several types of evidence. Dresp and Bonnet (1995) showed that illusory contours and subthreshold lines tend to sum their energies in the same way as real lines and subthreshold lines. Classic subthreshold summation means that when a nondetectable (subthreshold) line is added to a target line of the same orientation, the detection of the target line has a lower threshold (Kulikowski & King-Smith, 1973). Similarity between real and illusory contours is supported by the finding that the same cells that get activated by illusory contours also get activated by real contours (von der Heydt, Peterhans & Baumgartner, 1984). Moreover, active processing of an illusory figure and the processing of a real surface with stereoscopic depth occupy the same lateral occipital (LOC) areas (Mendola, Dale, Fischl, Liu & Tootell, 1999).

On the other hand, complete identity of the patterns of neuronal activation due to real and illusory contours would imply the inability to separate them. This is not the case. People tend to be aware that the percept is not based on physical substance (Ware & Kennedy, 1978). This difference is also reflected in some psychophysical results. For instance, although the tilt aftereffect can be induced by both illusory and real lines, it is not symmetrical but the effect is weaker when illusory lines are used for adaptation and real lines serve as test stimuli (Paradiso, Shimojo & Nakayama, 1989).

To summarise, the vividness of illusory perception suggests that it has a role in orienting in the world. The fact that contours and lines are represented explicitly in the visual system, even at locations where no direct physical evidence of them exists, suggests the same (Lee, 2002). Furthermore, the detection of illusory contours in independently evolved visual systems, even in bees (van Hateren, Srinivasan & Wait, 1990), and the early emergence of the ability to perceive the illusory figure (Kavšek & Yonas, 2006) argue that perception of edges in the absence of contrast gradients reflects fundamental visual processes. Hence, it can be claimed (von der Heydt, Heitger & Peterhans, 1993) that no model of visual perception can be operational without taking into account the perception of an illusory contour.

2.4 Attempts at classifying illusions

Many different kinds of phenomena are commonly defined as illusions. To the extent that the mechanisms are more or less unknown, an analytic classification is hard to produce. From a different viewpoint, Gregory (1997) has suggested a classification that pairs visual illusions with language errors. It includes ‘ambiguities’ (e.g. Necker cubes), ‘distortions’ (e.g. Ponzo figures), ‘paradoxes’ (e.g. impossible figures), and ‘fictions’ (e.g. Kanizsa figures). Specifically, Kanizsa figures are supposed to be a result of misleading general rules (cognitive cause) in Gregory’s classification. Evidence exists, however, that the perception of an illusory figure depends also on the way signals are processed at a low level in the brain. Hence, Kanizsa figures could be referred to as Gregory’s class for illusions due to distorted physiological signals in the eyes or the brain.

Alternative classifications have been presented when illusions have been listed on e.g. the Internet, but they lack classification rules. One way to categorize illusions could be according to the relationship between the stimulus and the percept, without accounting for the possible explanation. Then, ‘impossible figures’ are a result of an (usually deliberate) error related for instance to perspective in the drawing, hard to understand at first sight, ‘ambiguous images’ can be interpreted in either of two mutually exclusive ways, resulting in unstable, alternating percepts (such as Rubin’s vase or face or the Necker cube), ‘distortion illusions’ have some attribute perceived in a distorted way (e.g. the Müller-Lyer illusion and other geometrical illusions, as well as illusions in which colour or brightness is perceived erroneously), and in ‘emerging illusions’ the visual system generates something new that does not physically exist in the stimulus (e.g. an illusory contour produced by abutting gratings with a phase shift or an illusory figure such as the Kanizsa triangle or the Ehrenstein figure (Ehrenstein, 1941/1987).

Illusory figures or contours may also be seen in the more general framework of *object perception*. Object perception can be regarded as a process with many stages. No consensus regarding the stages involved exists and the discussion around the topic appears quite fragmented, at least in relation to illusory figures. In the context of perceiving something illusory by nature, special care must be taken to include all factors relevant to formation of the percept. Several candidate frameworks for conceptualizing illusory figure perception in the general context of object perception exist. For instance, ‘visual segmentation’ has been described as a process of parsing the different surfaces of an image, grouping together parts of the same surface that are separated from each other in the image by other, occluding surfaces (Shapley, Rubin & Ringach, 2004). Shapes defined by illusory contours, such as Kanizsa-type illusory figures, are of special interest because they reveal mechanisms that segment figures from the background, but are not confounded with luminance-defined cues (Kanizsa, 1979). The concept of ‘perceptual grouping’ has also been used for the process whereby individual items in the visual image are aggregated into larger structures to integrate, for instance, a contour (Feldman, 2001). This contour can also be illusory, produced for instance by physically separate objects, i.e. inducers. As a concept, ‘figure-ground segregation’ is close to perceptual grouping. It can be used when focusing on the problem of how the illusory figure segregates as a figure in the middle of the inducers that form the background.

The above-mentioned concepts imply some explanation, but have not yet led much further. It seems that they are usually offered as a general framework for studies, but they are not analysed further nor do they as such generate strong predictions. This reflects insufficient knowledge of the processes involved in object perception. A simple and telling concept that is, however, useful both in connection with normal and illusory-figure or illusory-contour perception is ‘visual completion’. In the stimulus/percept-discrepancy based classification of illusions (see above), this concept is related to ‘emerging illusions’. Visual completion implies that something physically nonexistent is perceived based on the information available in the surroundings.

2.5 Visual completion

Visual completion, filling-in and modal completion are closely related concepts that are occasionally used interchangeably.

Filling-in refers in a broad sense to the situation in which some visual attributes (brightness, colour, texture and motion) are perceived in a region where the information is actually missing: the region has been “filled-in”. Hence, filling-in mostly refers to featural (surface) qualities.

The concept of filling-in is easily related to situations where “nothingness” is filled-in with attributes visible in the surrounding field. Examples of such a situation are the blind spot and scotoma. The blind spots of the two eyes do not overlap in the visual field so they cause observable phenomena under monocular viewing conditions. Unlike the blind spot, a scotoma can lie anywhere in the visual field. A scotoma is easily ignored even under monocular viewing, due to filling-in even when in or near the fovea (Zur & Ullman, 2003). In studies, however, that deal with filling-in the centre is not always empty and the role of the surroundings also varies.

Filling-in demonstrably occurs at the level of perception but it must depend on specific neural processes. These processes must differ in some respects between the paradigms where filling-in has been studied. Additionally, the traditional focus on the blind spot may unnecessarily have limited the scope of investigations related to filling-in.

Thus, to maintain a broad perspective and to use a term that can be easily applied to the perception of illusory figures, visual completion is preferred in this study (as also suggested by Pessoa, Thompson and Noë (1998)). Here it includes two types of completion. Boundary completion specifies the shape of the object, and featural completion (which can be used as a limited synonym for filling-in) supports the perceived continuity of the surface. In the context of the perception of a Kanizsa illusion, both types of completion are functional. Illusory contours represent the result of boundary completion whereas an illusory surface (e.g. a surface brighter than the background if black inducers with white background are used) is the result of featural completion.

In principle, the term ‘modal completion’ (introduced into current scientific discourse by Michotte, Thinès & Crabbé, 1964/1991) could also be used instead of ‘visual completion’. Both concepts refer to the same perceptual phenomenon, that is, completion of physically existing gaps by the visual system. ‘Modal completion’, however, is often used as a counterpart of ‘amodal completion’ (Michotte et al., 1964/1991; Kellman & Shipley, 1991) but here, the question of the relation between modal and amodal completion is set aside. Furthermore, the concept ‘modal completion’ could refer to any sense modality. Thus this term will be used here only when modal and amodal completions are discussed together.

Regarding the Kanizsa-type figures we use, two different cases emerge from the point of view of visual completion. The starting point is the central area of the configuration that is completed and the surrounding area that induces the completion. The centre can be completed when (i) the stimulus surrounds the completed area in a fragmented way (Kanizsa square in figure 1 (Kanizsa, 1955/1987)); or when (ii) the stimulus not only surrounds but also is perceived as being part of the completed area (Kanizsa square with neon spreading, figure 2 (Varin, 1971)).

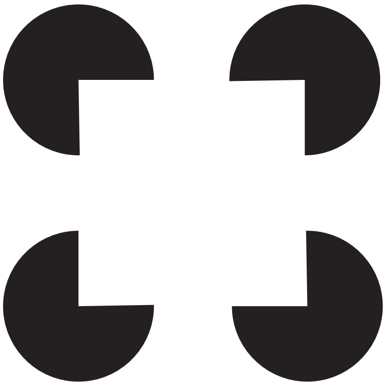

Figure 1. Kanizsa figure, eliciting the perception of an illusory square.

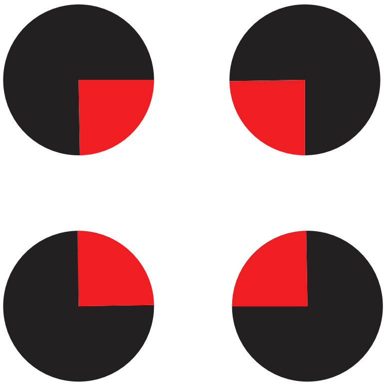

Figure 2. Kanizsa figure with coloured notches, producing a coloured illusory square. The figure is a coloured version of Kanizsa square (Varin, 1971), producing the perception of an illusory square tinged with the colour of the notches.

2.6 Kanizsa illusion

The first version of a configuration with separate objects resulting in the perception of illusory contours and brightness enhancement between them was a pattern consisting of black semicircles opposing each other across a gap, presented by Schumann in 1904. This type of figure, however, did not become a frequently used stimulus in scientific research until Kanizsa presented his triangle (figure 3) in 1955.

The Kanizsa illusion refers to the illusory figure, usually a triangle or square that is perceived between the physically defined circles with cut-out sectors. Although the middle parts of the sides of the illusory configuration are not physically present, they are clearly visible to the observer. Then, not only an illusory contour but also an illusory surface is perceived, as if lying above the inducing disks. Additionally, the illusory surface appears brighter than the background if the background is light and inducers dark, and darker if the background is dark and inducers light.

Kanizsa originally presented his triangle (Kanizsa, 1955/1987) in the spirit of Gestalt. He claimed that the illusory figure constitutes a better form, being more than the sum of the real objects, nowadays called inducers, or sometimes also pacmen. ("Pacman" is a term that refers to a computer game agent from the early 1980s. The shape of a pacman is the same as the cut-off circles Kanizsa originated in illusory figures much earlier.) According to Kanizsa, the illusion is perceived because it is the simplest way in which the fragmented real patterns "improve" their form. Later (Kanizsa, 1979) abandoned the hypothesis of a tendency toward a more regular, simple unit as a cause for the inducers to evoke the perception of an illusory figure, admitting that other types of inducers can also produce the illusion.

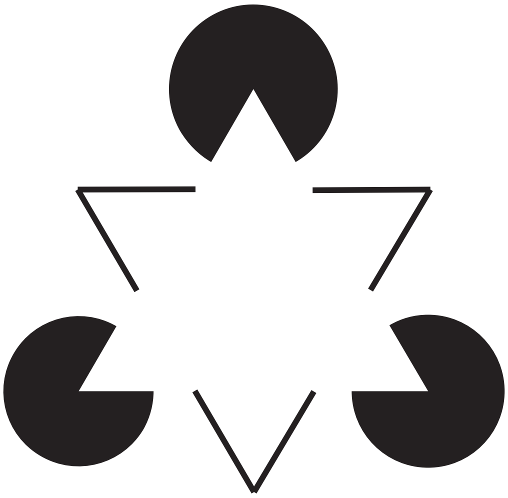

Figure 3. Kanizsa triangle as presented by Gaetano Kanizsa in 1955, the black-disk version; the white-disk version has black and white reversed.

The themes that Kanizsa presented in his original article (1955) are still partly present in today's research. The search for the determinants that affect the emergence of the illusion, i.e. the relation between inducer characteristics and the resulting percept, still pervades psychophysical studies including this thesis. Kanizsa himself found many figural prerequisites for the appearance of an illusion, e.g. that outline inducers do not elicit the perception of an illusory figure and that inducer regularity is not necessary, contrary to what he had originally stated (Kanizsa, 1979). The search for the basic rules that govern the appearance of the illusion has faded to some extent, however, perhaps because no satisfying general account of the determinants of the perception of an illusory figure has been found. In contrast to models that have been developed, the illusory figure formation might not be explicable by a single exclusive theory (Seghier & Vuilleumier, 2006).

After Kanizsa's article, the search for the vital characteristics for the appearance of the illusion was purely phenomenological for a couple of decades, with only the author(s) as viewer(s), as it was supposed that the images are perceived similarly by everybody. Eventually, psychophysical methods became more common and nowadays phenomenal studies are rarely published. Additionally, the functions related to the processing of an illusory figure have been the subject of much mathematical modelling. The emergence of new electrophysiological and imaging techniques has resulted in a large number of studies on cortical correlates and putative mechanisms of the processing.

Another topic that Kanizsa brought up in his article (1955/1987) is about modal and amodal (Michotte, et al., 1964/1991) completion. 'Modal' refers to perceptual qualities of visible parts of a scene, whereas 'amodal' refers to qualities of the hidden regions. Illusory figure perception is a case of modal completion (or 'visual completion'). The percept of (illusory) borders surrounding the (illusory) figure is created modally, by the visual system. Amodal completion is the kind of completion that takes place when something phenomenally continues behind an occluder although we don't see it. For example, we "see" that there is a whole girl standing behind a fence although we only see parts of her. In real life, completion of occluding forms probably does not occur as often as that of occluded forms. On the other hand, in everyday vision, inferred contours may be even more frequent than clear-cut contours. Kanizsa-type illusory figures in which part of the configuration is completed by the visual system can be an exaggeration of the natural situation of contours that vanish at some point, either because they are missing or are

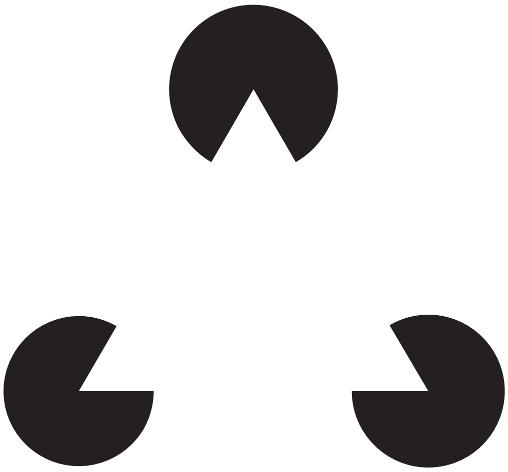

Figure 4. Kanizsa triangle as the stimulus used in present studies.

merged with background structures (von der Heydt, Heitger & Peterhans, 1993). The discussion about similarities between modal and amodal completion continues, in regards to their order of emergence in infant development (Kavšek & Yonas, 2006) or whether both share the same functional background (Ringach & Shapley, 1996).

Usually, a simplified version of the original Kanizsa figure is used in experiments. In our studies, we have used Kanizsa triangles of the basic type shown in Figure 4, but modified according to the questions posed.

2.7 Induction of the illusory figure

The induction of Kanizsa-type illusory figures requires at least two elements (inducers) since the illusion is created between them. The elements must also be properly positioned, with the parts of the separate inducers that define the illusory contour co-aligned, i.e. relatable (Kellman & Shipley, 1991). Additionally, there should be a luminance difference between inducers and background as the Kanizsa-type illusion completely vanishes at equiluminance (Li & Guo, 1995).

The estimate of the induction period for an illusory figure varies between studies depending on their experimental parameters. Reynolds (1981) found that when inducers for a straight-sided or curved-sided Kanizsa triangle are presented for 50 ms, followed by three random-dot circles in the same places as the original inducers after 50 ms, correct categorisation is obtained. Hence, 100 ms processing time is sufficient for the induction of an illusory percept. It has also been suggested that the induction process consists of two phases. In the first, local features such as boundary segments are detected. This lasted about 117 ms in the study of Ringach and Shapley (1996). The second phase, lasting about 140-200 ms could be responsible for integrating local information into a global percept (Ringach & Shapley, 1996). On the other hand, an exposure of 1 s was needed in a study where a mask with outlined circles was presented to limit the processing time of the illusory figure (Gellatly, 1981).

It is not known from earlier studies, however, whether the perception of an illusion could be induced by sequential presentation of inducers and if possible, what induction time is needed. Furthermore, it is not known whether spatial relationships affect the perception of the illusion. Knowing how (and if) the perception of an illusory figure can be induced by sequential presentation can reveal new spatial and temporal attributes of the induction process. The more flexible the induction process is the more useful and common it is likely to be in normal viewing.

2.8 The detectability of an illusory figure with spatial alteration and various viewing strategies

The perception of an illusory figure is suggested to be scale invariant so only the ratio between inducer radiuses (physically defined portion of the illusory figure side) and total pattern side length of a Kanizsa figure determines boundary clarity (Shipley & Kellman, 1992). Scale invariance holds for the ability to discriminate between a “fat” and a “thin” Kanizsa square, produced by different inducer orientations (Ringach & Shapley, 1996). The parameter kept constant in these studies on scale invariance is the ‘relative illusory contour length’ (according to the terminology in study I), i.e. the ratio between the lengths of the illusory part and the whole triangle side. Ringach and Shapley (1996) later coined the term ‘support ratio’ for a corresponding concept (‘relative real contour length’). In the following, the latter term will be used, as it is has gained general acceptance when referring to scale invariance in Kanizsa-type figures.

Some studies do not explicitly refer to scale invariance, but it is implicitly present in the results (e.g. Dresp & Bonnet, 1993). On the other hand, some experiments suggest that illusory contour and apparent depth perception weakens with increasing stimulus magnification (Dumais & Bradley, 1976; Bradley & Dumais, 1984).

In previous studies, the perception of an illusory figure has been investigated with a specific task that may have affected the result. Perception has not been studied by determining thresholds for the illusion to appear, which would seem to represent a comparatively neutral situation with respect to tasks. Neither is it known how extreme stimulus minimisation or magnification affects the perception of an illusory figure.

The effect of fixation is largely unknown in relation to perception of an illusory figure. Visual integration across fixations is highly relevant in normal viewing, so it would be expected to also be important in the processing of an illusory figure. The only study known to us is by Bradley (1987), who reported that steady fixation tends to result in weaker illusory contours than does free viewing.

2.9 Visual completion of three-dimensional moving stimuli

Perception of a real object includes its three-dimensional properties. It is known that three-dimensional illusory figures also exist. By using stereograms, many three-dimensional illusions have been created. For instance, Nakayama and Shimojo (1992) presented a cross that only had added disparity to its horizontal outer edges. When the apparent depth of these edges was above or below the rest of the configuration, the whole horizontal limb was perceived as lying above or below the vertical limb. When a corresponding configuration was shown to alert macaque monkeys, neurons in V2 responded as if receiving depth information in the area that was visually completed (Bakin, Nakayama & Gilbert, 2000). Carman and Welch (1992) demonstrated that illusory squares curved in depth can be produced by stereograms.

Moving illusions have been created e.g. by Vallortigara (1987), who presented two sequences of dots as tips of a rhombus, removing three upper sectors and three lower sectors in turn so that an illusory Kanizsa triangle could be seen as standing on its base or standing on its tip. When these sets were shown 400 ms after each other, a rotating illusory triangle was perceived. When a pattern composed of concentric circles that were interrupted as if by a bar extending from the centre to the periphery was slowly rotated, an illusory bar slanted in depth was perceived (Bressan & Vallortigara, 1991).

Real objects, however, also have thickness that has not been shown with illusory figures. The possibility of creating illusory figures with such attributes would affirm their use in normal viewing.

2.10 Visual completion of chromatic stimuli at various depth planes

When part of the inducers are black and part white, while the background is grey of intermediate luminance, the resulting illusory figure is not enhanced in brightness or darkness. This shows that brightness contrast is not essential for the appearance for illusory figure and that brightness and form must be computed separately (Shapley & Gordon, 1987). In this kind of configuration, the perception of a depth difference between the illusory figure and the background is also absent. If the inducers are forced to a further depth plane from the surrounding area by stereopsis (provoked by the disparity of images received by the two eyes), however, the perception of an illusion is demolished altogether. This has been shown with achromatic (Gregory & Harris, 1974) as well as chromatic (Nakayama, Shimojo & Ramachandran, 1990) illusory figures. These works used stimuli that occupied only two depth planes. It is not known how more complex configurations, with inducers curving over various depth planes, are perceived.

3 AIMS OF THE PRESENT STUDY

The general objective was to learn how visual completion takes place in the context of illusory figure formation. All the studies are based on psychophysical experiments done with various modifications of the Kanizsa triangle.

The studies fall into two main groups. First, we investigated the perception of an illusory figure at a threshold. Specifically, we wanted to learn more about spatial limitations of the perception of an illusion and whether these limitations can be affected by other stimulus parameters. The results of these studies (study I and III) shed light on both the induction process and the spatial and temporal conditions for the appearance of an illusory figure. Second, we studied whether illusory figures combining several induced properties (three-dimensionality, colour and motion) are possible to perceive (studies II, IV, and V). The more complex illusions are possible to perceive the more probable it is that this ability is used in daily perception. Moreover, perception of complex illusions, produced by complex inducers, would indicate that the processing also takes place in higher visual areas.

The aims of the separate studies are as follows:

Study I: To study further the induction process of illusory figures by investigating the appearance of an illusory figure when inducers are also temporally separated.

Study II: To study whether the illusion can be perceived as “thick” (having volume), thus resembling the perception of real objects.

Study III. To study whether scale invariance holds when the perception of an illusory figure is at threshold, how support ratio interacts with exposure duration and multiple fixations, and what are the spatial extremes for illusory figure perception.

Study IV: To study whether it is possible to perceive an illusion when inducers and the induced figure have different depth signs.

Study V: To study chromatic visual completion with three-dimensional moving stimuli.

4 METHODS

4.1 Subjects

All subjects had normal or corrected-to-normal visual acuity. Before the experiments, the subject's understanding of and ability to perceive an illusory figure (including neon spreading and stereo figures if needed: studies IV and V), were ascertained. In study II only some of the subjects had seen a Kanizsa triangle before, however. Five subjects in study IV and nine subjects in study V were excluded from the experiments as they were not able to see an illusory figure with neon spreading. Additionally, in study II one subject had a deviant threshold for the perception of an illusory figure. Because of that, her results were not always included in all statistical analyses.

In study I, the subjects consisted of members of the same vision laboratory, two of them also being authors of the article (three subjects, age range 31-43). In study III (four subjects, age range 25-40), two subjects were also authors of the article whereas the other two were scientists familiar with scientific methods but only a little with visual psychophysics.

The rest of the studies were conducted with subjects other than the authors. In one study (II, five partly different subjects in each experiment, age range 20-55) the subjects were members of the same department, both with and without scientific background, and in two studies (IV and V) the subjects (13 subjects with age range 19-35 and 25 subjects with age range 19-36) were students of psychology without experience in perception studies.

4.2 Psychophysical methods

Psychophysics is the oldest subfield of the science of psychology. It originated in attempts in the 19th century to measure and quantify sensation. Modern psychophysics continues to quantify the relationship between stimulus and sensation, usually for the purpose of probing the processes underlying perception. The "father of psychophysics" Fechner coined the term, 'psycho' referring to mind, and 'physics' to exact measurement. The methods depend on the experimenter's knowledge of two things: the physical stimulus and the response made by a subject to whom it is presented. The stimulus may vary in many dimensions. In vision research the stimulus ultimately consists of light, which can vary in the spatial and temporal distributions of intensity and wavelength (separately in the two eyes), with infinite possibilities for higher-level patterning. The response to the stimulus may be a simple “I see it”, “these two look alike”, etc. given either verbally or by mechanical means (“press button A when you see the percept 1” and so forth, usually with a computer) or more complex including a more qualitative description of what is perceived.

Psychophysics relates perception directly to the characteristics of the stimulus. In the mid-20th century, classical psychophysics was supplemented by the signal detection theory, which is important for understanding detection or discrimination thresholds. In some of our studies, however, the subject was asked to give a description of the percept, a procedure that is often not considered as psychophysical in a strict sense.

The weakest point in psychophysics is related to the subject. The physical characteristics of the stimulus are controlled by the experimenter, but the response is always subjective and prone to mistakes. Usually a large number of trials and statistical methods must be used to obtain reasonably accurate results. The percept varies from trial to trial, due to internal or external noise (noise here meaning any type of random variation). For example, the subject may have a criterion of responding that does not correspond to what it is expected to be, or the criterion may vary during the experiment. That is why in study I we first showed a Kanizsa triangle with inducers presented simultaneously as a criterion before showing the experimental stimulus. In other studies, a criterion would have resembled the experimental stimulus too much (study III) or a firm criterion was hard to define when the stimulus was complex and prolonged viewing was allowed (studies II, IV, and V).

External noise is easier to exclude. The experiments were usually conducted in a separate room with dark walls and no windows, and the visual surroundings of the stimuli (luminance, etc.) were usually computer-controlled. Stimuli used in psychophysics are generally strongly simplified to ensure that the subject responds to the feature relevant to the experiment, a convention that can also be criticized as being unnatural. The procedures used in classical psychophysics have been developed to overcome potential sources of bias. For instance, stimuli are presented in a random order or, if the presentation is sequential, the order in different sessions is counterbalanced to balance out effects of expectations or trends of answering of the subject.

Psychophysics is the only method that reveals the end result of visual processing, the final percept. Much of the vision research is concerned with neural correlates of visual perception. Although psychophysics cannot directly tell anything about neural processes, well-designed experiments may allow even strong inferences. For instance, when it was found that the Kanizsa illusion can be made to appear tilted in depth with stereo pairs, an effect that cannot be based on a monocular image alone, it was possible to conclude that the phenomenon is not (only) of retinal origin, but is formed after binocular interaction has taken place (Blomfield, 1973), i.e. in the cortex.

In the threshold experiments of our studies, subjects indicated the presence or absence of an illusory figure by pressing certain keys on a keyboard. When viewing complex stimuli, subjects were asked to describe their percepts in words. In the following, a more detailed description is given of the psychophysical methods used in the separate studies.

4.2.1 The staircase method and its simplified version used in study I

The method that probes the threshold by allowing the subject to increase the intensity of the stimulus in a stepwise manner until the stimulus is just perceived and to decrease it until the stimulus has just disappeared is called the staircase method. The stimulus intensity is first either well above or well below threshold and as the experiment proceeds, the successive points where the intensity staircase is reversed usually get closer and closer to the final threshold value, both above and below it. Due to several sources of random variation (noise) no fixed threshold occurs, however, but in a certain range of values, the stimulus is sometimes perceived and sometimes not. More systematic behavioural bias is associated with habituation, the subject continues to respond as if seeing the stimulus without this really being the case, and anticipation, the subject anticipates threshold and gives negative responses to stimuli that (s)he would still see if coming fresh to the situation. Any systematic bias is removed, however, when threshold is calculated as the average of a sufficient number of reversal points.

The purpose of study I was to measure the time limit for integration of sequentially presented inducers to generate an illusory figure, and the relation of this critical duration to the spatial parameters of the inducers. Black inducers of a Kanizsa triangle were presented on a white background. The longest duration of the inducer sequence that allowed the perception of an illusory triangle was used as the indicator of the temporal limit for illusory perception (the critical duration). In order to obtain reliable results, we chose the staircase method that balances response biases and is pleasant to use by subjects that are skilful enough. In this study, all subjects were familiar with scientific methods and vision research.

The initial duration of each presentation sequence was always 250 ms for a single inducer, often producing the perception of three separate disks. Hence, each session usually started by decreasing the duration of the inducing-disk presentation. Throughout the session, the duration of stimulus presentation was increased and decreased under the free control of the subject for as many times as was necessary to accurately estimate the threshold for perceiving an illusory triangle instead of three separate disks. The turning points (where the invisible has become visible or vice versa) were not recorded. Only when the subject deemed (s)he had found the threshold, i.e. the longest duration that allowed the perception of an illusory figure, (s)he pressed a response key on a keyboard and the answer was recorded. Thus, the staircase itself was not limited by the program and the accuracy of the judgement depended on the response criterion of each subject. This short version of the staircase method was chosen as it did not put unreasonable demands on the subjects' attention. Furthermore, this choice did not risk the reliability of results, as all subjects were familiar with the perception of an illusory triangle and either highly motivated (authors IK and ML) or experienced (AR) in visual experimentation. The possible bias in answering strategies was diminished by making each subject perform the experiment ten times for each triangle. Furthermore, the response criterion was kept constant by presenting first (on each trial) a stationary Kanizsa triangle for 33 ms as a comparison stimulus followed by a 1-sec interval before the sequential presentation of inducers.

4.2.2 Method of constant stimuli (study III)

The method of constant stimuli, also known as frequency of seeing, approximates the threshold by repeated presentation of stimuli above and below the pre-evaluated threshold in random order. After each single stimulus presentation the subject indicates whether the stimulus was perceived. As the order of presentation of the stimuli in any trial is random, the subject has no way of anticipating the intensity and thus the expectations of the subject about the occurrence of stimulus are constant.

In study III, thresholds for seeing the Kanizsa illusion with simultaneously presented inducing disks were measured as functions of spatial configuration and fixation strategy. The method of constant stimuli yields reliable results only if the number of presentations is sufficient. It is also a simple method for subjects that are less familiar with visual psychophysics, as no expectations develop during a session. In this study, half of the subjects were not accustomed to vision research whereas the others were authors of the article.

As the subject is asked to report when the illusion is perceived and when not, little control exists over the subjective criterion for "seeing". Using both experienced and inexperienced subjects helped in checking the problem of varying criteria. The problem was not a critical one anyway, as the results (as functions of the experimental variables) were similar with all subjects.

4.2.3 Interview (studies II, IV and V)

Verbal description of what is perceived does not belong to classical psychophysics but can be subsumed among psychophysical methods in a broader sense. Such reports are worth using when the stimulus is novel and complex, possibly generating novel, unexpected, or variable percepts. General qualities of the percepts may then be documented best by letting the subject more freely describe his or her impressions of the stimulus.

This is the situation in studies II, IV, and V where the effects of colour (studies IV and V), depth, and motion (studies II and V) on the perception of an illusory figure were investigated. As no prior knowledge was available, we wanted to learn about the qualities of the perception of an illusory figure rather than just about the visibility of the illusion. Hence, we used a semistructured interview with ready-made questions and the opportunity to freely describe the appearance of the configuration.

In studies II, IV, and V we first confirmed the ability of each subject to see an illusory triangle without (studies II, IV, and V) and with colour (studies IV and V). The subjects were also implicitly told what is important in the perception of an illusory figure when it is stationary and two-dimensional so that they were better prepared to describe their percepts when encountering a different, i.e. three-dimensional, version of the illusion. In study II, the task of the subject was to observe and tell what happens to the illusory triangle and to the illusory contours when the inducing elements rotate. Due to the relatively simple stimulus (three-dimensional black-and-white Kanizsa triangle), the small number of subjects (five), and their previous scientific experience (although not in vision research) more detailed questions were not needed.

In studies IV and V, the subjects were asked to freely report their percepts but when necessary, the experimenter enquired about the appearance of the illusory triangle, illusory contours, colour effects, and three-dimensional properties of the configuration. The more detailed questionnaire, compared with the one used in study II, was needed due to the more complex stimulus (chromaticity added) and the inexperience of the subjects (first-year students of psychology without experience of scientific studies).

4.3 Data analysis

The studies included both quantitative and qualitative measures. Correspondingly, parametric and non-parametric (distribution-free) statistical tests or methods have been used. In addition, some results were obtained as qualitative descriptions of what was perceived without any statistical treatment.

Statistical covariance analysis was applied separately to the data obtained from the experiments of study I. Critical duration was the dependent variable, the subjects were random factors and inducing disk size, triangle size, image size, and relative illusory length were quantitative independent variables. Least-squares regression lines with the same slope but different intercepts were fitted to the data with all combined and replotted as a function of relative illusory contour length (the ratio between the lengths of the illusory part of the triangle side and total triangle side). The F-test was used to estimate on the whole the extent to which the independent variables (inducing disk size, triangle size, image size, and relative illusory length) explained the variation in the dependent variable (critical duration).

The data of study III was analysed using generalised linear modelling with a binary response. The support ratio was treated as a continuous covariate, inducer diameter as an exposure variable, and the subject as a confounder. To answer the question whether masking has an effect of its own or whether it only modifies the effects of other explanatory variables in the model, masking was used as an additional variable. Various plots and experimental modelling suggested that linearity is best achieved using the probit transformation for the relative frequency of seeing and a logarithmic scale for the support ratio. The final model was chosen according to the hierarchy principle, terms and interactions were not dropped if a higher order interaction containing them was present. The practical computations were carried out using the SAS procedure GENMOD. The subject MH was excluded from these analyses since a stimuli set different from that of other subjects had been applied. On a logarithmic scale the range of observations became large since small values of the support ratio were included. The effect of stimulus magnification could not be statistically tested, because for all subjects there were too few observations other than 0% or 100%.

Only relevant information was reported from the results of the studies with descriptive information (studies II, IV and V). To additionally test the goodness of fit between the observed and expected frequencies, i.e. the existence of colour spreading in various stimuli (study IV), the chi square test was used.

The non-parametric McNemar sign test was used for testing the binary (yes/no) report of colour spreading for each subject between thin and thick stimuli (study V). Cochran’s Q-test was used as its extension for more than two related samples, i.e., when the same subjects were studied with the same kind of stimuli but some attribute (the rate of rotation of the stimuli) altered.

5 STUDIES

5.1 Study I. Spatial and temporal properties of illusory figures

5.1.1 Procedure and stimuli

Kanizsa triangle inducers were presented sequentially, one at a time. The shorter the duration of the entire sequence, the easier it is to perceive the illusory figure. We determined the critical duration, i.e. the longest duration that still allowed the perception of an illusory figure instead of three separate inducing elements, by the method of adjustment. Each trial began with a fixation point in the middle of the screen that was present throughout the trial. Then, a comparison stimulus of a stationary Kanizsa triangle was presented for 33 ms and after that the sequentially presented Kanizsa triangle inducers. To keep visual processing simple, viewing was always monocular. It took place at a distance of 114 cm with the dominant eye.

The spatial stimulus parameters that were varied in the experiments were (i) inducer size while the distance between the inducers was held constant (Experiment 1), (ii) inducer separation while the inducer size was held constant (Experiment 2), and (iii) magnification of the whole stimulus (Experiment 3).

5.1.2 Results and discussion

Increasing the inducer size increased the critical duration, increasing inducer separation decreased the critical duration, but general spatial scaling had little effect on critical duration (figure 5). Thus the shorter the illusory contour to be induced, relative to the physically defined part in the inducer, the longer the critical duration. It was fairly independent of magnification and thus scale invariant.

The relative lengths within the illusion were expressed as ‘relative illusory contour length’, i.e. the ratio between the illusory part and the total side length, which is a modified synonym of the ‘support ratio’ of Ringach and Shapley (1996). The support ratio in the experiment where the critical duration was found to be approximately magnification-independent was 0.42. It should be kept in mind that only one inducing element was present at any time in these experiments. Our interpretation is that each element causes a neural activation field in space and time. The temporal overlap of the activation fields of the first and last inducer is particularly crucial. As the critical presentation time of each inducer varied from 110 to 420 ms, the minimum persistence of the activation field is presumed to vary between 110 and 420 ms.

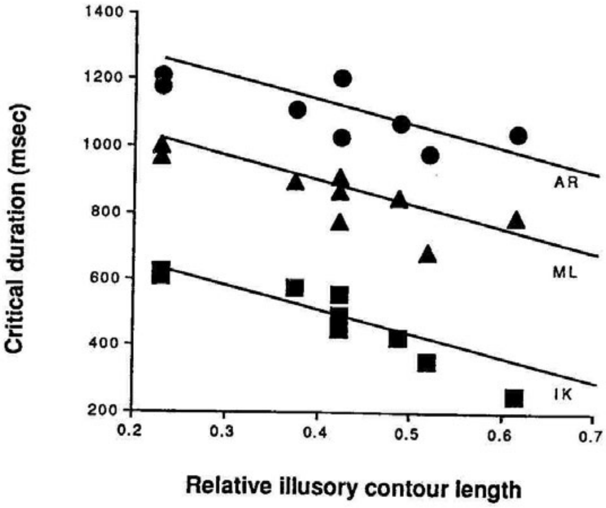

Figure 5. Results from the experiments of study I plotted as a function of relative illusory contour length, i.e. the ratio between the illusory part of the triangle side length and the whole side length (real and illusory). The least-squares regression lines for each subject have the same slope but different intercept.

5.2 Study II. Three-dimensional illusory objects produced by rotation in depth

5.2.1 Procedure and stimuli

The stimuli consisted of three inducing elements forming a Kanizsa triangle. The inducing elements were rotated around the vertical axis of the configurations. In Experiment 1, computer-generated stimuli were (i) thin black inducers, (ii) thick black inducers, (iii) thick grey inducers "illuminated" by a stationary source of light on a display, or (iv) a stereo pair with thin black inducers presented with an opaque sheet between the eyes so that each eye saw only its own stimulus. The rotation rate was always the same and it was counter-clockwise when viewed from above (for examples of the stimuli, see figs. 6a-i). The task of the subject was to observe and verbally express what happens to the illusory triangle and to the illusory contours when the inducing elements rotate.

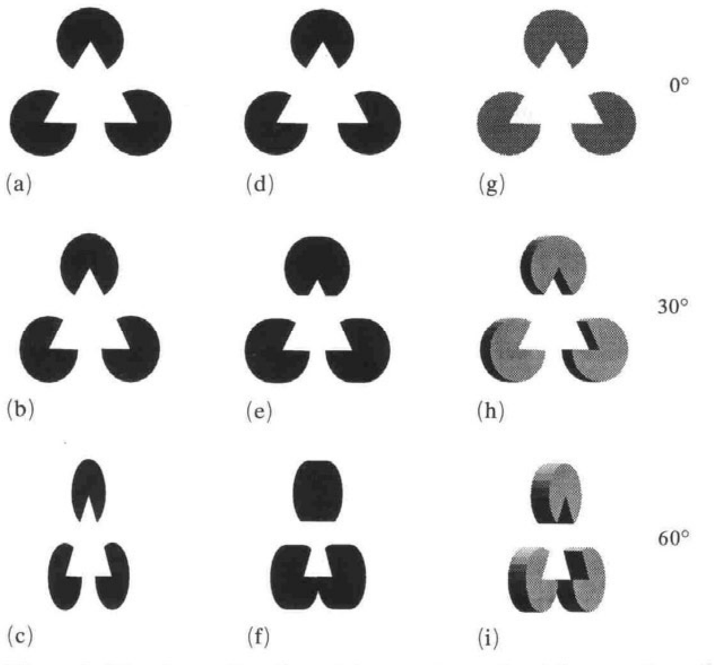

Figure 6. The three stimuli used in the experiment with examples of different angles of rotation. The thickness and "illumination" appear only as the figures rotate (figs. 6b, c, e, f, h and i). The figures on the left (figs. 6a-c) consist of flat black inducers, the figures in the middle (figs. 6d-f) consist of thick black inducers, and the figures on the right (figs. 6g-i) consist of thick grey inducers illuminated by a stationary light source.

In Experiment 2, real inducers, thin and thick, were used as stimuli (figure 7), and the subjects had to rotate the stimulus configuration by means of a vertical bar held between his or her fingers. The rotation was either continuous or stopped at various orientations during which the subject described what happened to the illusory surface and contours.

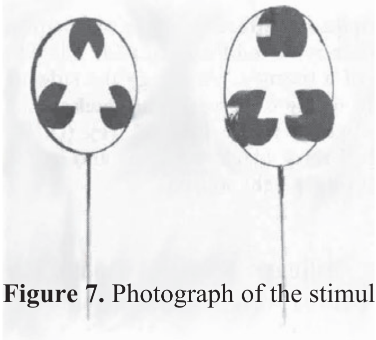

Figure 7. Photograph of the stimuli in the experiment with real inducers, 0.4 and 8 mm thick.

5.2.2 Results and discussion

The computer animation (Experiment 1) made both the inducing elements and the illusory triangle between them three-dimensional. The percepts were similar in a single configuration and when the stimulus consisted of stereo pairs viewed binocularly. With thin black inducers a thin illusory triangle was perceived to rotate within the inducers; however, the illusion could also appear to change its direction of rotation abruptly. The thick black inducers produced a thick illusory triangle, but the percept was less vivid. In this case too, the direction of rotation could appear to change spontaneously. With "illuminated" grey inducers all subjects saw a clear three-dimensional illusory triangle. Moreover, its rotation was in only one direction.

When the thin and thick Kanizsa triangles made of real black inducers (Experiment 2) were seen in different orientations and rotated around the vertical axis of the configuration, they created a three-dimensional illusion as well. With thin inducers, illusory contours were clear and always as thin as the inducers, both when stopped in various orientations and when rotated. For the stimulus with thick inducers, the illusory percept was less strong than with thin inducers with frontal viewing, but rotation emphasised the perception of an illusory triangle that was always as thick as the inducers. To sum up, the visual system is able to complete a moving, three-dimensional configuration although the completion is not always perfect, perhaps due to the high demands on visual analysis and partly conflicting cues. Furthermore, the usual percept of the classical Kanizsa illusion as lying in a plane above the inducers was not present with three-dimensional moving stimuli, in which the illusion was perceived to be located between the inducers.

5.3 Study III. Effects of spatial configuration and number of fixations on Kanizsa triangle detection

5.3.1 Procedure and stimuli

Kanizsa triangle inducers were presented simultaneously and, to keep visual processing simple, they were viewed monocularly with the dominant eye. The method of constant stimuli (frequency of seeing) was used in all the experiments. In most experiments, the exposure duration of 100 ms was used as it should allow the perception of an illusory figure (Reynolds, 1981) and it is short enough to exclude the possibility of eye movements.

Experiment 1 studied the effect of inducer separation by having constant-size inducers with varying separations, viewed at three different viewing distances. The stimulus exposure duration was 100 ms for each stimulus under steady fixation. Support ratios varied from 0.31 to 0.76 for all but one subject who had the range of support ratios from 0.25 to 0.50.

Experiment 2, studying the effects of fixation and exposure duration without masking, was performed with stimuli similar to Experiment 1, with one viewing distance, but with different fixation strategies. In one series, we used 17 ms stimulus exposures under steady fixation, in another 2000 ms under steady fixation, and finally 2000 ms while performing active eye movements.

Experiment 3 studied the effect of post-exposure processing by using the same stimuli, fixation strategies and exposure durations as in Experiments 1 and 2 but with backward masking. All exposure durations (17, 100 and 2000 ms) were followed by a blank period of 50 ms and thereafter the mask for 300 ms. Full black circles superimposed on the inducers served as mask.

Experiment 4 studied the effect of stimulus magnification for stimuli with a support ratio of 0.64. The range of magnification was 140 fold, from a triangle side length from 0.19° to 27°. Exposure duration was 100 ms under steady fixation.

5.3.2 Results and discussion

The frequency of seeing (FoS) the illusion increased with increasing support ratio at all exposure durations under steady fixation (the effect of the support ratio, $\chi^2 = 3415$, df = 1, $p < 0.0001$). The same stimulus was perceived similarly irrespective of varying viewing distance, confirming scale invariance over the tested range. The frequency of seeing the illusory triangle was also affected by exposure duration $\chi^2 = 16.93$, df = 2, $p < 0.0002$), but in somewhat complex manner (Experiment 2). The difference in the results between the 100 and 2000 ms exposures ($p < 0.0001$) was more significant than between the 17 and 2000 ms exposures ($p < 0.0071$). The exposures of 17 and 100 ms produced higher values of FoS than 2000 ms when fixation was steady. The various exposure durations used also produced qualitatively different percepts. At 17 ms there was just a visible trace of the illusion, while 100 ms yielded a subjectively clear perception of an illusory triangle. At 2000 ms the perception of an illusory figure was again more difficult because of strong brightness enhancement around the inducers (Mach bands) and the afterimage of the inducers.

The exposure duration of 2000 ms without steady fixation deviated from all the results obtained with steady fixation by allowing the perception of an illusory figure at the 100% level for all support ratios tested. The negative effect of fixation at 2000 ms exposure was highly significant ($\chi^2 = 1721$, df = 1, $p < 0.0001$).

The effect of masking (Experiment 3) was important as such ($\chi^2 = 6.641$, df = 1, $p < 0.0100$). Its effect, however, was highly variable between subjects (interaction between subject and masking, $\chi^2 = 42.07$, df = 1, $p < 0.0001$) and dependent on exposure duration (interaction between exposure duration and masking, $\chi^2 = 218.0$, df = 2, $p < 0.0001$). Masking shifted the FoS curves (thresholds) toward higher support ratios at short exposures and toward lower support ratios at long exposures. It interacted with exposure duration so that in contrast to the experiment without masking, the duration of 2000 ms produced not the lowest but highest FoS for the illusion at all support ratios with steady fixation. Free viewing at 2000 ms again resulted in 100% perception of an illusory triangle at all support ratios used.

The effect of spatial scale on the thresholds of the perception of an illusory figure was investigated with stimuli having the optimal support ratio of 0.64. When the triangle side length was very short (0.2 deg or less), FoS was 0%. With increasing side length, FoS increased rapidly from 0 to 100%. Thereafter, FoS remained at 100% for all subjects, although the side length increased from 0.625 to 10 deg (increase more than 15-fold). From that point FoS decreased rapidly from 100%, reaching 0% at the longest side lengths studied (at least 27.0 degrees).

The smallest and largest triangle side lengths corresponding to 50% frequency of seeing were 0.368 + 0.033 deg and 17.4 + 2.2 deg (mean ± SEM).

These threshold experiments showed that scale invariance was valid across a large range of areas in the visual field, in agreement with previous supra-threshold (Shipley & Kellman, 1992; Ringach & Shapley, 1996) and threshold experiments (Kojo, Liinasuo & Rovamo, 1993). With the smallest stimuli of optimal support ratio, the failure to see the illusion was due to the visual acuity limit, as subjects had difficulties in seeing the exact form of the cut-out sectors of the inducers, essential for Kanizsa-type illusions. The breakdown of scale invariance for large stimuli, on the other hand, must indicate limits of spatial integration.

Without masking illusory figure perception was clearest with the 100 ms exposure duration, in agreement with brightness enhancement that first increases and then decreases with increasing exposure duration above threshold (Petry & Gannon, 1987). Our results with masking are in agreement with the notion that with 100-ms processing time, the illusion is perceivable (Reynolds, 1981), but more time is needed for improving its visibility (Ringach & Shapley, 1996).

The difference between steady and free fixation is pronounced. With free viewing, the illusion was visible at all support ratios (0.3 to 9.75) tested, both with and without masking when a duration of 2000 ms was used. This is in accordance with the claim that central fixation results in a weaker perception than does viewing with active eye movements (Bradley, 1987). A possible interpretation is that the illusory percept is first created by the first fixation and if more snapshots of the object are gathered by the following fixations, the images are bound together to form a stronger percept of the illusory figure.

5.4 Study IV. Neon colour spreading in three-dimensional illusory objects

5.4.1 Procedure and stimuli

All stimuli consisted of inducers with red sectors that usually elicit the perception of a reddish illusory triangle (neon colour spreading). In two of the sectors, one side was curved to suggest a convexity/concavity of the stereoscopically viewed figure. The stimuli were presented as stereo pairs (figure 8) with a handheld stereoscope that allowed parallel fusion. Three-dimensionally, the tip of the upper sector and the horizontal edges of the lower sectors were always on the same depth level relative to each other. Only the three-dimensional curving and location of the Kanizsa triangle, relative to the surroundings, were varied.

In the first and second stimulus, the tip and the horizontal edges of the lower sectors had null disparity with respect to the contours of the inducers, and should be perceived to be in the same plane. The rest of the red sectors of the first stimulus should appear convex and above the level of the black inducers (figure 8a, the two figures on the right/left for crossed/uncrossed fusion). In the second stimulus, the rest of the sectors should appear concave and further in depth than the black inducers (figure 8a, the two figures on the right/left for crossed/uncrossed fusion).

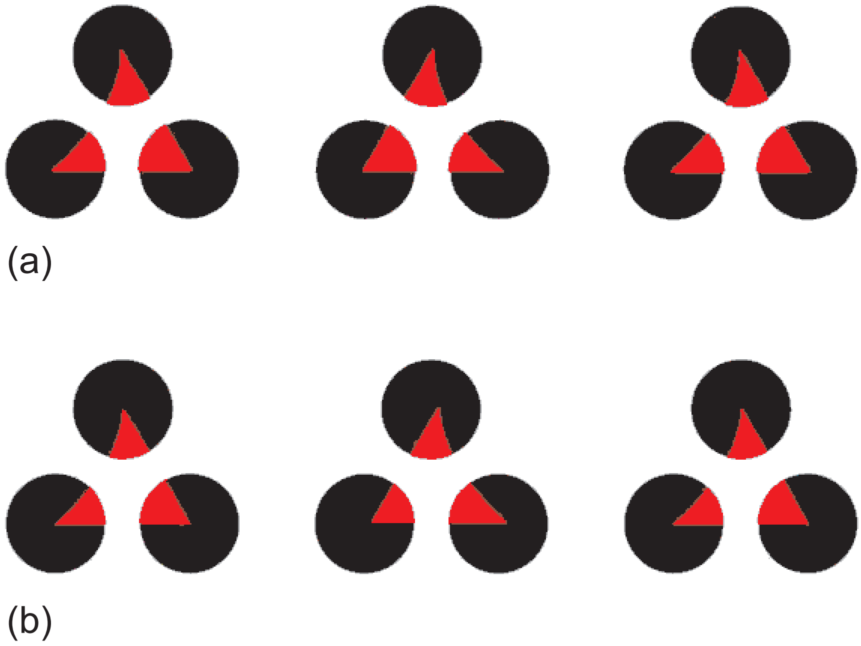

Figure 8. The four stimuli used in the experiments of three-dimensionally curved Kanizsa triangles. Although only parallel fusion was used, stimuli for converging fusion are also provided. The instructions are given for parallel fusion. For converging fusion, the opposite applies. Thus, when instructed to fuse the two leftmost figures, the convergers should fuse the two rightmost figures and vice versa. (a) First stimulus: Fuse the two leftmost figures. Second stimulus: Fuse the two rightmost figures. (b) Third stimulus: Fuse the two leftmost figures. Fourth stimulus: Fuse the two rightmost figures.

In the third stimulus, the tip and horizontal edges of the lower sectors should appear to be further from the observer than the black inducers. The rest of the convex sectors should appear closer than the black inducers and even penetrate the white field bearing the inducers (figure 8b, the two figures on the right/left for crossed/uncrossed fusion).

The fourth stimulus is the reverse of the third. The tip and horizontal edges of the sectors should appear closer to the observer than the black inducers. The rest of the concave sectors should reach into the distance, penetrating the level of the white field so that they are further from the observer than the black inducers (figure 8b, the two figures on the right/left for uncrossed/crossed fusion).

The subjects observed each stereo pair and verbally reported their impressions. After the subject gave a spontaneous response, the experimenter enquired, if necessary, (1) whether the subject saw the illusory triangle, (2) if yes, whether the subject saw contours around the triangle, (3) about the quality of the illusory surface, and (4) about its three-dimensional properties, i.e., were some parts nearer or further away from the observer than others.

5.4.2 Results and discussion

When the tip of the upper sector and the horizontal edges of the lower sectors were further away from the observer than the rest of the configuration (the first and third stimulus), a convex illusory triangle with neon colour spreading was perceived by 12 (first stimulus) and 11 (third stimulus) subjects out of 13. When the abovementioned parts of the sectors were closer to the observer than the rest of the configuration, a concave partly occluded triangle was usually reported, and the neon effect was reported less frequently, by only 2 (second stimulus, $\chi^2 = 121$, $p < 0.001$) and 1 (fourth stimulus, $\chi^2 = 144$, $p < 0.001$) subjects.

Thus, we found that three-dimensional neon spreading can also be produced within steady illusory figures curved in depth. Interestingly, spreading can be induced above the intervening surface even when the inducers are below the surface (stimulus three). This indicates a fairly high degree of complexity of the neural processing.

5.5 Study V. Visual completion of three-dimensional, chromatic, moving stimuli in humans

5.5.1 Procedure and stimuli

Stimuli were either computer-generated or real inducers with red sectors, usually eliciting the percept of an illusory triangle with red tinge (neon spreading). During each trial with stimuli on a display (Experiment 1) or presentation of a real object (Experiment 2), the stimulus was rotated and the subjects reported verbally what they perceived. After the spontaneous response, the experimenter enquired, if necessary, about the appearance of the illusory triangle, illusory contours, colour effects, and three-dimensional properties of the configuration. Viewing time was unlimited.

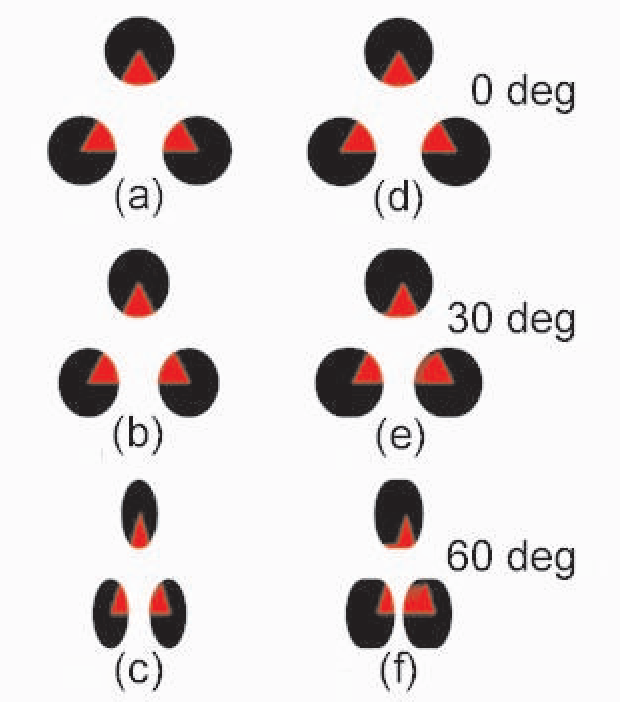

Figure 9. The stimuli used in the experiments with examples of 30 and 60 degrees of angles of rotation. At frontal orientation [(a) and (d)], they look like normal Kanizsa figures with red sectors. In (b-c) and (e-f) are examples of configurations during rotation, orientation as indicated.

In Experiment 1, the rotating stimuli (see figure 9) were three (i) thin or (ii) thick black-and-red disks, presented as rotating on a display. An apparent illuminant below and in front of the screen made the red sectors vary from dark to light during rotation. Both thin and thick configurations were presented at three rotation rates (at 0.25, 0.5, and 1 rotations/s). Thirteen subjects saw the stimuli in random order whereas the other (twelve) subjects saw first thin and then thick stimuli in order of increasing rotation rate.

In Experiment 2, inducers were colour prints that were attached to a circle with a vertical handle. The twelve subjects held, rotated, or moved the object horizontally in front of a white paper and reported what they perceived.

5.5.2 Results and discussion

Study V was an extension of study II that includes chromaticity as a third parameter in addition to thickness and movement. The thicker the triangle and faster the rotation rate, the more difficult it was to perceive colour spreading (Cochran Q-test, $\chi^2 = 13.3$, df = 5, $p < 0.05$) or illusory surface ($\chi^2 = 18{,}06$, df = 5, $p < 0.01$). Irrespective of stimulus thickness, colour spreading was more strongly affected by increasing the rotation rate than illusory surface perception in general (χ^2 -test 11.93, df = 2, $p < 0.01$). Only six subjects out of 25 perceived illusory colour spreading in all rotating stimuli and four of them always saw the illusory triangle as having the same thickness as the inducers.

When the subjects held, rotated, or moved the real flat object horizontally in front of a white paper, eleven subjects out of 12 reported that they perceived illusory colour spreading when the object was held stationary, and all 12 subjects perceived a reddish illusory triangle during both kinds of motion. Possibly, cues for a three-dimensional (illusory) object were more accurate with a real object so that the illusion was best perceived with it.

6 DISCUSSION

6.1 Spatial and temporal integration

In studies I and III we investigated how spatial and temporal parameters of inducer presentation affected the thresholds for perception of the illusory figure. The most striking constancy is the spatial scale invariance, whereby only the support ratio determines visibility (within a certain range). The results can be interpreted partly in terms of spatial and temporal fields of influence of single inducers. They indicate the dependence of the illusory percept on both lower-level, local processes and higher-level, integrative processes.

6.1.1 Scale invariance

With the longest sequential presentation duration of Kanizsa-triangle inducers that still allowed the illusory percept (study I) and with simultaneous inducer presentation at threshold (study III), the perception of an illusory figure was largely insensitive to the stimulus scale and essentially determined by the support ratio, i.e., the ratio between the physically-defined and total side lengths. Scale invariance with 100 ms exposure duration held over a 15-fold range of stimulus size: the triangle side lengths with magnified stimuli that allowed the perception of an illusory figure at 100 % varied between 0.6 and 10 degrees. The limits probably reflect visual acuity for small figures and a general limit of spatial integration for large figures (study III). The finding makes functional sense, as object recognition should be independent of viewing distance and absolute size (Shipley & Kellman, 1992). Scale invariance for illusory figures is consistent with the idea that the process studied is important for natural vision.

Indications of scale invariance have also been found with e.g. Kanizsa figures when the perception is related to a shape discrimination task (Ringach & Shapley, 1996). Deviant results, however, can be found in connection with different tasks. Gerbino and Fantoni (2006) found that visual interpolation is not scale invariant using stimuli that required amodal completion (as opposed to the visual “modal” completion studied here). It has not been verified if visual and amodal completion are based on similar functions. At least in supra-threshold situations visual completion results in an accurate representation whereas amodal completion results in a smoothened representation of a physically nonexistent vertex (Singh, 2004). Secondly, the results of Gerbino and Fantoni (2006) were obtained with supra-threshold stimuli of 300 ms duration, allowing multiple fixations, whereas ours are threshold results with 100 ms stimulus duration, allowing only a single fixation. Indeed, our results with scale invariance are strictly valid only under these conditions. When several fixations were allowed, scale invariance was broken and the illusion was also visible with lower support ratios (study III). This difference alone could be the reason for the failure of scale invariance.

Furthermore, Gerbino and Fantoni (2006) used a narrow range of support ratios, all high (between 0.72 and 0.89) whereas we used support ratios between 0.30 and 0.75. In our experiments, completion always occurred when the support ratio was higher than 0.64 (study III). Also very high support ratios may alter perception. Differences may also depend on their difficult task (vertex extrapolation) as opposed to ours with simple interpolation between straight lines.

6.1.2 The relevance of eye movements

Multiple fixations also allowed the perception of an illusory figure with smaller support ratios compared to the results with steady fixation (study III). When presentation duration was limited to 100 ms, the illusion was always visible only when the support ratio was 0.64 or more. With free viewing for 2000 ms, however, the illusion was always visible over a range of support ratios from 0.31 to 0.76, or (illusory) triangle side lengths from 1.75 to 4.31 degrees. These results indicate highly efficient processes for integrating images across separate fixations and inducer locations. The task to mould a coherent perception of an illusory figure over extended and fragmented space and time would intuitively seem to be even more demanding than the perception of a real, clearly defined object.

Melcher (2001) has published a study on temporal visual integration of object images for recall that shows an analogous capacity. With exposure durations between 250 ms and 2000 ms for a single object, recall for computer-generated, unrelated objects depended only on the total exposure duration, irrespective of whether it was composed of one continuous presentation or several shorter ones.

Our present results appear to be the only ones to date on the ability of the visual system to integrate illusory figures. More extensive studies on the effect of fixation location and temporal binding on illusory figures would shed more light on these issues, usually investigated in the context of more “normal” processes such as reading.

6.1.3 Persistence and processing time

Study I showed that increasing the support ratio increased the critical duration for sequential presentation of the inducers, i.e. made the illusion easier to perceive. By contrast, critical duration was fairly independent of stimulus magnification, but highly dependent on the subject.

Visual persistence may be assumed to play a crucial role when inducers are presented sequentially, as in study I. For a Kanizsa triangle, the first inducer must somehow extend its influence at least over the whole presentation duration of the second inducer, to reach the third inducer.

In study I, the critical duration per sequential inducer varied from 110 to 420 ms depending on the subject and support ratio. If perceptual persistence is vital for temporal integration of sequentially presented inducers, persistence had to be at least 110-420 ms depending on the subject and support ratio. The order of magnitude is roughly the same as the usual estimate of perceptual persistence, 250 ms (Loftus, Johnson, Shimamura, 1985). The highest value 420 ms is clearly larger, which is in qualitative agreement with other studies in which Kanizsa squares have been found to have longer persistence than real figures (square and four complete circles) (Meyer & Ming, 1988). In the experiments of Meyer and Ming (1988), persistence peaked at a 250 ms target duration with about 330 ms persistence for the same Kanizsa square.

In our experiments, persistence seemed to depend on stimulus size (study I): the larger the inducer the longer its persistence. Seeing an illusory triangle when inducers were presented sequentially seemed to be easier, however, than seeing a real triangle when its sides were presented sequentially. We tried to determine the critical duration for the latter type of stimulus, but were unable to produce the perception of a real triangle due to the low frame rate of our display. This means that the critical duration was always less than 150 ms. Evidently the integrative abilities of the visual system are more efficient for configurations that induce the perception of an illusory figure than for fragmented image components.

In study III we also investigated the visibility of an illusory figure with simultaneous presentation of inducers, with and without masking, and with several exposure durations. Then, the visibility of an illusion varied as a function of processing time. Our results showed that the simultaneous inducer presentation of 17 ms (study III) can be long enough for producing an illusory figure when a sufficiently large support ratio is provided. When stimulus processing, however, was restricted by masking, allowing only an additional processing time of 50 ms (delay between stimulus offset and mask presentation), larger support ratios were needed for producing the perception of an illusory figure (study III) than when no masking occurred. This implies that the illusion grows spatially more extensive with increasing processing time. Hence, the perception of an illusory figure requires less physical support when there is enough time for neural processing and vice versa. With a smaller support ratio, a longer exposure duration is needed to render the illusion visible.

This is in rough agreement with results obtained by Ringach and Shapley (1996) and Guttman and Kellman (2004). In the experiments of Ringach and Shapley (1996), the task of the observers was to judge whether the Kanizsa squares of 0.25 support ratio and oriented inducers were “thin” or “fat”. They found that the integration of local (illusory) contours lasted about 117 ms, after which presentation of a local mask (pinwheel) no longer had any effect on performance. Even if our task in study III was simpler and should therefore have required less processing time, most of our subjects were completely unable to perceive the illusion when the support ratio was 0.31 (the smallest support ratio used with them). This may be partly explained by individual differences in the perception of illusory figures, as one subject in study III did perceive the illusion even with a smaller support ratio. Another probably relevant difference between the experiments of Ringach and Shapley and ours is a criterion difference. The demand of positively perceiving an illusion might require a higher criterion, hence higher support ratio, than shape discrimination.

The experiments of Guttman and Kellman (2004) extend the paradigm of Ringach and Shapley (1996) with Kanizsa squares of 0.5 support ratio. Subjects were to judge whether a dot appeared inside or outside the perceived boundary of the illusory or real shape. The authors found that the representation of the illusory contour reached asymptotic precision after about 120 ms of processing. Again, however, the results cannot be directly compared with ours because of the task difference.

Without masking, study III showed that under steady fixation and with very short exposure time (17 ms), the illusion was perceived but poorly. When exposure duration was prolonged (100 ms exposure), the illusion was perceived more clearly. When the exposure lasted too long (2000 ms), however, the illusion was again poorly perceived. This result can be described with an inverted U function. With short exposure, the visual system probably did not have enough time to get a clear representation of the stimulus. As a result, a poorly defined and vague percept was formed. With a long exposure on the other hand, the visual system has ample of time, which, in turn, resulted in disturbing aftereffects and Mach bands. In a natural viewing situation this usually does not occur, due to spontaneously occurring eye movements that take place before aftereffects start to intrude.

6.1.4 The effect of a single inducer

To sum up, studies I and III showed that the appearance of an illusory figure depends on relative inducer size (i.e. support ratio) and the time available for processing. In study I, inducers were shown sequentially and the illusion still emerged. Hence, each inducer must have some potentiality by itself in the process of producing the perception of an illusory figure. Each inducer seems to extend its effect to its surround as a function of its size and the time available for processing. In principle, the larger the inducer the further its influence can reach. How far depends on the time allowed. Supposedly, two types of time exist in the context of the perception of an illusion. Firstly, presentation duration should be long enough so that the inducer is properly coded. Secondly, there should be enough processing time for the inducer to extend its influence as far as possible into the surroundings. There seems to be a trade-off between support ratio and time. When there is not enough time (too short exposure duration or processing time), only illusions with larger support ratios are visible and vice versa: illusions with larger support ratios require less exposure or processing time.

This model agrees with studies by Dresp and Bonnet (1993) and Field, Hayes and Hess (1993). Dresp and Bonnet (1993) measured detection thresholds for a small light spot (i) at various distances from one white inducer on dark background, (ii) between two inducers, or (iii) inside and outside a Kanizsa triangle, finding the same tendency in all three stimulus situations. Threshold was elevated when the target was located close to the potential or actually perceived illusory contour. The detection threshold was lower inside the illusory figure or where the illusory figure would have been if enough inducers had been presented in correct places. In other words, similar effects on thresholds for detecting the probe were observed when only a single inducer was present and no illusory contour could be seen as in the presence of a complete Kanizsa triangle.

Some support for scale invariance can also be found in these results, although not explicitly reported. In the figures of Dresp and Bonnet (1993), it can be seen that roughly, probe threshold elevations diminish with increasing distance between constant-sized inducers, and with the decreasing size of inducers at constant distance. They also studied a detection threshold near complete disks of various sizes, finding greater threshold elevation the larger the disk that is approached.

Field et al. (1993) studied the ability of the visual system to efficiently identify a path of aligned Gabor patches in an array of similar but randomly oriented ones. The study led to the suggestion of an ‘association field’. As the path was identified only when the orientation between consecutive patches differed by no more than ± 60 degrees, information integration across neighbouring filters tuned to similar orientations was suggested. Moreover, paths formed by patches orthogonal to the path direction were hard to identify. As the integration between elements seemed to be related to the continuity of edges or lines rather than a more general segregation process, a low-level origin of the phenomenon was suggested. This tuning resembles the idea of the influence of an inducer presented in this thesis.

Many unanswered questions remain in our model. For instance, the precise interdependences between support ratio, optimal presentation duration, and optimal processing time are not known. What kinds of interactions are there between these variables in generating the percept of an illusory figure? What is the function of the time of presentation and time of processing after presentation for the appearance of an illusory figure? Do various fixation strategies affect the perception of an illusory figure, and if they do, how? How do these attributes vary, if they vary, when measured above and at threshold?

Also the corresponding neural processing is unknown. Present knowledge about cortical processing only allows some rough estimation about the cortical areas involved.

6.1.5 Neural processing

6.1.5.1 About cortical areas involved

The processing of an illusory figure supposedly occupies several areas in the visual system. To start with, the processing of an illusory figure seems to involve both magnocellular and parvocellular input. The parvocellular pathway appears as a natural provider for the processing of the illusion as it carries information about colour and detailed shape information of the inducers. The magnocellular pathway that contains information of rough form, luminance and motion seems to be vital as well as the percept of the illusion vanishes when inducers are presented on an equiluminant background (Li & Guo, 1995).

Similarly, the ventral (“what”) stream, running from V1 to temporal occipital area is involved with object recognition and complex perception of patterns and forms. Undoubtedly, the ventral stream also processes illusory figures along with other object-centred processing. The dorsal (“where”) stream, extending from V1 to parietal cortex, deals with the location of objects, navigation through the world and spatial reasoning. As it seems to participate not only in action organisation but also in space perception (Rizzolatti & Matelli, 2003) (regarding the spatially scattered inducers and also in the enhancement of the percept during fixations) it may have a role in the perception of an illusion.

Considering the separate visual cortical areas involved in the processing of an illusory figure, at least the areas V1, V2, and LOC are supposedly functional. In 1984, von der Heydt, Peterhans and Baumgartner observed neural responses to interrupted line stimuli in monkey V2 but not V1 neurons. The stimuli resembled Kanizsa figures as the ‘illusory contour’ was created in a gap between solid inducers. Accordingly, it was found that V2 exclusively processed a Kanizsa triangle (ffytche & Zeki, 1996). Later, it was found that cells mainly in V2 responded to illusory contours between two separate tabs outside the cells' receptive fields with near depth plane (Bakin, Nakayama & Gilbert, 2000). The cells also responded to a central grating as if contained disparity, even though disparity was present only for the grating's end elements located beyond the cells' receptive field. These results (Bakin, Nakayama & Gilbert, 2000) demonstrate that V2 has an important role in the three-dimensional representation of (illusory) surfaces and contours in space.

A number of studies, however, have also reported neural activity in V1 in response to illusory stimuli. Lee and Ngyen (2001) found (with static Kanizsa squares) that cells in V2 respond first to an illusory figure, but a weaker and significant response in V1 followed. In response to Kanizsa figures, functional imaging studies have also reported neural activity in V1 (Maertens & Pollmann, 2005) or both in V1 and V2 (Seghier, Dojat, Delon-Martin, Rubin, Warnking, Segebarth & Bullier, 2000).

Furthermore, the processing of an illusory figure is not thought to be restricted to the lower visual areas of V1 and V2. A number of functional neuroimaging studies have found sensitivity to illusory figures at higher levels of the visual processing hierarchy, such as lateral occipital cortex (LOC; e.g. Mendola, Dale, Fischl, Liu & Tootell, 1999; Murray, Kersten, Olshausen, Schrater & Woods, 2002). The activation of LOC, however, may be a result of fast but crude region-based segmentation processes, sensitive to any global configuration, with or without illusory contours (Stanley & Rubin, 2003).

The reason for not finding activation in all relevant areas might be the sparse representation of such cells in many visual areas (such as cells performing three-dimensional analysis in V1 (Bakin, Nakayama & Gilbert, 2000)), spatial scale differences between separate hierarchies in the visual processing (Hedgé & Van Essen, 2007) or their possibly brief activation time. Furthermore, the activated area in cortex can be hard to identify as when reaching towards higher cortical areas, the orderliness of the representation of space deteriorates and neurons become increasingly less responsive to simple, meaningless patterns (Smith, 2002).

6.1.5.2 Feedforward and feedback

The processing supposedly requires rapid connections between several cortical areas. This can be performed by horizontal, feedforward and feedback connections.

Two competing types of neural models explaining rapid processing exist, one involving low-level horizontal connections, the other involving feedforward connections. Especially earlier, feedforward and feedback processing was supposed to be too time-consuming but recent research indicates it is possible. For instance, latencies of visual responses of neurons in MT are found to be similar to those in V1, about 50 ms, when several studies are compared with each other (Bullier, 2001). Furthermore, feedforward axons, e.g. from V1 to MT, seem to conduct information in the same time as that needed to transfer information into V2, i.e. around 2 ms (Movshon & Newsome, 1996). Such values show that extremely fast connections between higher and lower visual areas exist.

The idea of feedback is supported by recent results on receptive fields in V1. They show remarkably large surround areas when stimuli are expanding gratings instead of brief high-contrast stimuli, such as classically used for defining the extent of the cell's receptive field (Angelucci & Bullier, 2003). Suppressive effects that are usually considered as due to the surround can extend beyond 13° of visual angle, i.e. significantly further than previously thought. Such an extension supports the hypothesis that feedback connections from higher cortical areas play a major role in centre-surround interactions, while horizontal connections account for the effects in the area classically defined as receptive field centre and the proximal surroundings (Angelucci & Bullier, 2003). Feedback could also be reflected in responses in various visual areas of separate levels in hierarchy as investigating responses in V1, V2, and V4, no hierarchical response preferences could be found (Hedgé & Van Essen, 2007).

6.1.5.3 Scale invariance

Regarding the perception of an illusory figure, several elements occur that indicate the involvement of higher visual areas. One such element is the ability to process large images including scale invariance.

In our study III, the largest inducer diameter that still produced the perception of an illusory figure (in study III) was 6.4 degrees, with a gap to the next inducer of 3.6 degrees. Furthermore, our results showed that the processing of an illusory figure is scale invariant at threshold. Hence, a large configuration elicits the same kind of perception as a smaller one as long as relative sizes of the elements (inducers) of the configuration are the same. These facts indicate that flexible temporal processing with rapid connections over large visual areas is indispensable for the percept to emerge.

Scale invariance extending over large parts of the visual field indicates involvement of visual areas in which receptive fields are large and the processing of large images would be effective, i.e. higher visual areas in the brain (Hegdé & Van Essen, 2007).

Equally important, however, is early involvement of lower visual areas (V1/V2) as the borders of cut-out sectors are to be accurately detected. The orientation of the borders relative to the borders of adjacent inducers determines whether the contours are relatable so that the perception of an illusory figure emerges, and they determine the possible curvedness of illusory contours (Kellman & Shipley, 1991) also three-dimensionally (Kellman, Garrigan, Shipley, Yin & Machado, 2005). As the effect of the border reaches further beyond its own location as a function of time, there should be early cooperation between accurate low-level processing and large visual areas comprising high-level processing. The effect on the surroundings would start from the inducer and stretch further until it reaches its full extent or a mask appears.

Accordingly, it can be supposed that most relevant processing takes place in V1 and V2 (Field et al., 1993; Guttman & Kellman, 2004), modulated by feedback from higher areas (Hess & Field 1999). Firstly, information about the whole configuration is fed forward to generate a representation of the figure, perhaps in MT for global percept formation (Bullier, 2001) or LOC (Murray et al., 2002). When higher areas first perform global processing of the image and then send their feedback to lower ones, the total area of the inducer can affect its surroundings proportionally to inducer size, irrespective of inducer size and with minimal delay (Bullier, 2001). Once represented, feedback from high visual areas determines the area, the activation field (Field et al., 1993) that surrounds each inducer in the low visual areas, V1 and V2. These areas process the details for the production of illusory contours.

Maintaining both aspects simultaneously would seem to require interaction between these levels. This conception is in accordance with the model suggested by Maertens and Pollmann (2007) that emphasises the importance of visual segmentation as a role for high visual areas and representation of crisp illusory contours for the low ones. In the model, these mechanisms interact in order to establish the percept of an illusory figure with sharp illusory contours, in the order from "coarse" to "fine" in terms of the spatial scale of the stimulus, and from higher to lower visual areas in terms of anatomical visual hierarchy. This is in accordance with other current models that tend to support a combination of feedforward and feedback processing (Bullier, 2001; Seghier & Viulleumier, 2006). Essential in such models is early involvement of higher visual areas. It would explain extensive spatial coverage and temporal effectiveness in the processing of an image, both in the context of scale invariance and large images in general.

According to our results, the effect of an inducer on its surroundings should be continuous. The longer the processing is allowed to continue (i.e. the longer the inducers are shown, up to the point when disturbing aftereffects emerge) the further the inducers would stretch their influence over their surroundings. Then, even with a relatively large support ratio, if the presentation duration is very brief, the activation produced by each inducer does not have time enough to reach the adjacent ones, i.e. to produce the percept of an illusory figure. If the activation fields, i.e. neural processing induced by the discs (inducers), have enough time to develop, they get connected with the neighbouring ones and an illusory figure is perceived.

6.1.5.4 Fixation integration and complex image representation

The neurons receiving feedback change from one fixation to another as the locus of the configuration changes on the viewer's retina. This requires very fast processing and some general object representation in higher visual areas as irrespective of these retinal changes, the continuity of the representation of the figure should be maintained. Integration across fixations is especially important with illusory figure as it not only maintains but also enhances its perception (study III). Smaller support ratios can be used and still the perception of the illusion can be maintained, provided that free viewing, i.e., several fixations, is allowed. This enhancement presumes that visual integration is not performed in a visual area with retinotopic organisation. Accordingly, long-lasting representations (contrasted with visually guided action) are suggested to use environmental or object frames of reference instead of retinal coordinates (Creem & Proffitt, 2001).

Cortical areas responsible for such persistent representations are not clearly known. The area V6A in macaque monkey shows body-centred coordinates (Galletti, Fattori, Kutz & Gamberini, 1999) that could also perform visual integration of an illusory figure irrespective of its changing location in the retina. In humans, one specific area suggested to process spatial information, not related with action but perception, is inferior parietal lobule (Creem & Proffitt 2001; Rizzolatti & Matelli, 2003).

The perception of bent, thick, colourful or rotating illusions, induced by complex configurations, and the dependence of the percept on the interpreted transparency of the intervening surface also imply the effect of higher visual areas. The order of processing or the causes and effects are not, however, known. For instance, transparency could be as much a cause as a consequence (Nakayama et al., 1990). Hence, cortical area(s) and processing path(s) responsible for such attributes are probably hard to find.

6.1.5.5 Summary about neural processing

The visual system comprises of a network of functional areas with several hierarchies, where a dynamically varying population of neurons constructs visual representation of visual environment by feedforward and feedback processing. The inducers of illusory form, such as Kanizsa triangle, cues of the existence of the triangle, resulting in bridging the gap between the inducers. While the inducers leave part of the figure without bottom-up evidence of border, without contradicting evidence, such as surface in front of the triangle or closure of inducers to full circles, percept of borders emerge. Thus, illusion of a triangle is the most probable interpretation given the data.

Apparently both high and low areas are essential for illusory figure processing. Higher areas could be responsible for scale invariance, global shape processing, and visual integration across fixations. Processing in higher areas would be followed by activation in and continuous interaction with lower areas, according to input defined by the higher areas. Lower areas would be responsible for the processing of orientation and other fine details that also are vital elements for the formation of an illusory figure. Hence, when the sketch of the figure is formed in higher visual areas, the information could be fed back to lower areas, e.g. V1 and/or V2 that act as ‘active blackboards’ (Bullier, 2001), completing the percept with details, basically according to the principles suggested by Marr as early as 1982.

6.2 Visual completion of complex stimuli

Our studies with illusions including colour (neon-colour spreading), motion, and three-dimensionality (studies II, IV and V) show that the visual system is highly efficient in processing physically separate and qualitatively different attributes and binding them together to produce a coherent perception of an (illusory) object.

6.2.1 Motion

In studies II and V, we used motion with animated objects rotating on a display as well as a hand-held Kanizsa figure that was physically rotated. In all of these stimuli the illusory figure was perceived. Setting the illusion in motion entails varying the appearance of the inducing configuration. In advance it is hard to guess whether this will facilitate or hinder the perception of an illusory figure.

According to the results, the phenomenal alteration of the inducers produced by rotation hardly disturbs the perception of an illusory figure, if enough cues about the shape of the illusory figure are available. Inducers should be carefully made in order not to eliminate the appearance of the illusory figure, however, just like apparently small alterations in configuration can destroy the illusion when presented two-dimensionally.

The fact that the illusion was perceived particularly clearly in the experiment with thick grey, “illuminated” inducers rotating around their vertical axis (study II) shows that these new views revealed by rotation, specifically the thickness of the inducers, did not interrupt the illusory formation. Also, the location of the illusion changed with rotation: usually, the illusion is perceived as lying above the inducers, but during rotation the illusion was set between them. Phenomenally, three conclusions can be drawn. Firstly, illusory figures can contain not only contours and surface but also volume. Secondly, an illusory figure can be accepted as being transparent. If the illusory formation would only be perceived when supposed opaque, the illusory figure would have vanished the moment the further sides of the cut-out sectors were revealed during rotation. Thirdly, although the normally-displayed drawn version of the illusion is perceived in front of the inducers, as if occluding them, this percept is not vital, as during rotation the illusion is attached to the same depth plane as the inducers.

Hence, the usual percept of the illusory surface as lying above the inducers is not an integral part of the appearance of an illusory figure, although its frequent existence easily leads us to conclude so. Similarly, the commonly observed induced brightness (or darkness) in the illusory figure has been found to depend on the convention of using either black inducers on white background or white inducers on black background. When half of the inducers are white and half black, all on a grey background, the illusion is perceived without any surface brightness (or darkness) enhancement (Shapley & Gordon, 1987). Hence, neither brightness enhancement nor the elevation of the illusory figure above the plane of the inducers is a necessary property of the illusion.

In general, it appeared that motion facilitated the perception of an illusory figure. This is in accordance with other studies. Rock and Anson (1979) have shown that self-generated head movement while viewing a stationary Kanizsa triangle supports the emergence of the illusory percept. Enhancement by motion can also be seen at the single-cell response level. To cause neural activation related to a gap between two blocks as if there were an object between the blocks (i.e. a Kanizsa-type illusory object), the inducing indents that correspond to the cut-out sectors in Kanizsa-type inducers can be narrower when presented in motion than when presented stationary (Peterhans & von der Heydt, 1989). These results indicate that motion per se makes the illusion appear more easily, even in configurations where it would not appear if presented as stationary.

The perception of an illusion was least robust when the moving inducers were drawn thick and totally black (study II). The poor visibility of the illusion when thick black inducers were rotated on screen was probably due to lack of proper cues for three-dimensionality as the rotating drawings were like two-dimensional projections of three-dimensional objects, similar to shadows on the wall. The poor visibility of the illusion with real thick inducers could be due to the evident solidity of the inducers, produced by their thickness. Then, there would be no good cue for the visual system of a possible continuation of the outer borders of the inducers (that would result in the formation of an illusory figure), or perhaps the real inducers were just not made accurately enough which abolished the illusory figure.

Rotation as such does not prevent the perception of an illusory figure, as the illusion was especially well visible with the very thin real configuration in motion (study V). Rotation rate, however, did affect the perception when combined with drawn thick inducers: the thicker the configuration and the faster the rotation, the more difficult it was to perceive an illusory surface or neon spreading (study V). This may be related to the longer persistence of an illusory figure compared with a real one (Meyer & Ming, 1988). If long persistence correlates with slow image processing, the perception of an illusory figure may be expected to be more easily disturbed by higher velocities.

The key element in the perception of a moving illusory figure could be the existence of coherent cues for motion and three-dimensionality. Supposing that the perception of illusory contours is better when more cues are offered about the existence of some object between the inducers, one could expect that illusory contours should be better perceived when in motion. Then cues such as the alignment of sector borders of the inducing discs are verified as not being arbitrary, as they retain correct relations also during movement.

Many objects encountered in our everyday life are in motion. During motion, their shape as projected two-dimensionally on the retina is altered and yet we have to be able to deal with them in an appropriate way and to interpret certain types of shape distortion as movement.

The flexibility and continuity in object perception shown in our experiments related with visual (modal) completion are also consistent with the perception of real occluded objects (amodal completion). An object that disappears temporarily behind an occluder and then reappears can be perceived as the same object even if its colour is changed, provided that its motion follows a consistent trajectory (Flombaum & Scholl, 2006). Hence, the importance of object persistence in common life seems to be reflected in the way the visual system readily approves changes in a configuration that is interpreted as an object, without jumping to conclusions of an identity change of that configuration.

The ability of the visual system to also produce the percept of an illusory figure when the configuration is set in motion reflects the importance of perceiving objects and the importance of maintaining their identity also during the virtual transformation of the object's shape due to motion. On the other hand, motion also serves as a means for providing more cues of the entity of the illusory object. If the cues are appropriate and the velocity is not too high, motion can improve the visibility of an illusory figure.

6.2.2 Neon colour and three-dimensionality

In studies IV and V, colour was combined with drawn and real rotating configurations (V) or with pictorially three-dimensional stationary images (IV). The results showed that neon spreading is also fairly visible with three-dimensional illusory figures. Real thick inducers, however, do not tend to produce a thick illusion, even without neon spreading (study II), and when inducers rotate on screen, higher rotation rates result in diminished perception of neon spreading (study V).

In study IV we presented drawn configurations that produced the perception of flat, curved illusory figures with neon spreading when viewed normally. When fused stereoscopically, depth was added to the configurations, which sometimes resulted in the perception of an illusory figure with neon colour spreading.

The three-dimensional percepts were highly uniform among subjects. When the red inducing sectors within black disks bent towards the observer from the level of the white background (level of the paper), a reddish illusory figure bent in a convex manner was perceived, with the exception of only one subject out of 13, who perceived the illusion without colour. When the red sectors bent away from the observer, below or at both sides of the level of the background, no illusion was perceived below the white opaque background by most subjects. Then, only three subjects perceived a reddish concave illusory figure as the white intervening surface (the level of paper) was perceived as transparent. Interestingly, when the upper tips and the horizontal lines of the red sectors were below the white intervening surface and the rest of the sectors stretched through the white surface towards the observer, the illusion with neon spreading appeared to bend above that surface. This is the first time an illusion has been seen to curve in depth and penetrate through the intervening surface. The key elements are supposedly the red sectors that determine by their orientation how the illusory figure will bend.

Apparently, the presence of an additional colour does not significantly burden the formation of an illusory figure produced this way, as neon spreading was usually perceived whenever the illusory figure was perceived. Deviating percepts were related to (i) perceiving the white surface as transparent, resulting in visual (modal) completion (three cases) when others (23 cases) saw it as opaque, resulting in amodal completion; (ii) perceiving the figure below the white surface (two cases), resulting in amodal completion when others perceived the figure as above the surface (13 cases) and hence, visually completed; and (iii) (in one case) perceiving the illusion without neon spreading, although bending above the white surface (like the majority of subjects).

Thus, illusory figures can bend three-dimensionally and capture colour while bending. The disappearance of the illusion in study IV corresponds to its disappearance when behind any surface, resulting in amodal completion of the figure. The key elements determining whether the illusory percept arose were the perceived location of the illusion with respect to the white intervening surface, "paper", and the perceived transparency of that surface. Deviant percepts of the three-dimensional location of the sectors can be explained by subtle deficits in stereo vision. The percept of transparency cannot, however, be explained by these results. Based on experiments where the perception of transparency has been related to different kinds of illusory figures with various depth relations, Nakayama, Shimojo and Ramachandran (1990) have suggested that the perception of transparency is as much a "cause" as an "effect". For instance, from our results it cannot be concluded whether the perception of the illusion was so strong that the surface was perceived to be transparent, or whether the perceived transparency was a cause that allowed the illusory percept to appear.

Hence, the perception of a bending illusory surface with neon spreading in stationary figures depended on whether they are viewed as two-dimensional or fused stereoscopically, what was their three-dimensional location in respect with the surrounding surface ("the level of paper"), and whether the intervening surface was perceived as transparent. It is possible that although the appearance of colour, illusory contours and depth are all represented separately in area V2 (von der Heydt, Peterhans & Baumgartner, 1984; von der Heydt & Peterhans, 1989; Hubel & Livingstone, 1987), the final percept is influenced by higher-order aspects of scene interpretation.

In study V, the coloured sectors producing the perception of neon colour spreading were presented with thin and thick rotating Kanizsa triangles on a computer screen. Colour spreading appeared slightly more frequently with thin inducers. The illusion was sometimes thinner than the inducers, with or without neon spreading. When seen without colour, the illusion comprised brightness enhancement. When the subjects observed a thin hand-held device having the same elements for inducing an illusory figure as in the computer-generated version, however, all subjects perceived the illusion when they moved the device, both with the chromatic (study V) and achromatic (study II) version of the configuration.

It appears that thickness, at least when combined with motion of high velocity and neon spreading, interferes with the perception of an illusory surface in general. It may be that the red sectors appeared too connected with the rest of the inducers, forming single entities with them while thick, which was emphasised while rotating (study V). This could have demolished the possibility of contour continuation between inducers (that would result in the perception of an illusory figure). It is also possible that the configuration is too complicated when so many elements are included as neon spreading seemed to be the first attribute to drop off during fast rotation rate.

On the other hand, as illusion was evident when "illumination" was added to the drawn thick inducers (study II), it is possible that the illusion is perceived as long as inducers are continuously clearly visible, to be able to induce the illusion, and when no conflicting cues contradicting this possibility of (illusory) continuation occurs. Hence, it is also possible that there were not clear enough pictorial cues for the three-dimensional (illusory) continuation of the inducers and that the illusion would have been perceived more often if more pronounced illumination would have been presented on the configuration in this experiment (study V).

7 CONCLUDING REMARKS

The visual system is highly effective in producing the percept of objects. This works well also when the boundaries of an object are not visible although they exist. Optically, such an object seems to be fragmented in space with no contours to unify the parts. If the visual system can “infer” from the parts that they belong to a common object, the object is visually completed. In carefully designed experiments, such completion can be revealed as the perception of illusory figures. The ability to perform this completion apparently reflects important visual functioning as it can be found in many independently evolved visual systems in the animal kingdom (Nieder, 2002).

Our studies show that the formation of illusory figures is highly flexible both temporally and spatially, including the depth dimension. Figures can be rotated (studies II and V) and bent (study IV) and colour can be added (studies IV and V), and still the illusory percept is maintained. Motion seems to enhance the perception of an illusory figure, whereas illusory thickness perception is demanding (studies II and V). Three-dimensionality as such needs not weaken the perception of an illusory figure, though. In study V, an illusory figure was even shown to penetrate through and bend over an intervening surface. Inducers can also be presented sequentially and still allow the perception of an illusory figure, an accomplishment that requires effective spatio-temporal integrative functions of the visual system (study I).

The processing leading to an illusory percept is partly local, depending on spatio-temporal fields of influence set up by each single inducer. The effectiveness of integration depends on several factors that can partly compensate for each other. Such factors are support ratio, stimulus exposure duration (partly related to processing time), and sampling strategies expressed by fixations (studies I and III). For example, an illusory figure can be perceived with a smaller support ratio if longer exposure duration is provided or if several fixations are allowed. There is considerable individual variation (studies I and III; cf. Seghier & Vuilleumier, 2006). Accordingly, universal values, for instance in thresholds related to the perception of illusory figures are not always meaningful, but stable trends and general relations can be readily found.

The importance of single inducers with aligned notches across large visual areas implies that both low and high-level brain areas are involved in the processing of the illusion. However, we are still far from even a reasonably complete understanding of the cortical visual areas and processes underlying the perception of illusory figures.

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