

**From sense to perception:  
representations along pathways  
of sensory information processing**

Tobias Borra

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# **From sense to perception: representations along pathways of sensory information processing**

Van zintuig tot waarneming:  
representaties op het pad van zintuiglijke informatieverwerking

(met een samenvatting in het Nederlands)

Proefschrift

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**Tobias Borra**

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te 's-Gravenhage

Promotor: Prof. dr. F.A.J. Verstraten

Co-promotor: Dr. I.T.C. Hooge

The image displays the first two measures of the Aria in G major, BWV 988 by Johann Sebastian Bach. The score is written for piano in 3/4 time. The key signature is one sharp (F#), and the time signature is 3/4. The first measure features a treble clef with a G4 quarter note, an A4 quarter note, and a B4 quarter note with a fermata. The bass clef has a G3 dotted half note. The second measure continues with a treble clef containing an A4 quarter note, a B4 quarter note, and a G4 half note. The bass clef has an A3 dotted half note. The piece concludes with a double bar line.

*J.S. Bach - BWV 988 Aria*



*Voor Peter*

*24-11-1944*

*27-11-2009*



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# Chapter 1

Introduction



## 1.1 General introduction

As you are reading this thesis, parts of your surrounding world are blocked from view by the pages you are holding in your hand. More specifically, reflected light from objects around you that otherwise would have been projected onto your retina is now cast on the underside of this book. Interestingly, this has no consequence for how you perceive the world that surrounds you. Even though you cannot see parts of your desk, your hands, or the floor, you do not perceive these items as fragmented, they just continue to exist behind this thesis. This seemingly trivial aspect of perceiving and interacting with your surroundings is in fact quite a feat. Apparently our brain is capable of continuing and completing the world around us, even when it is not in direct view.

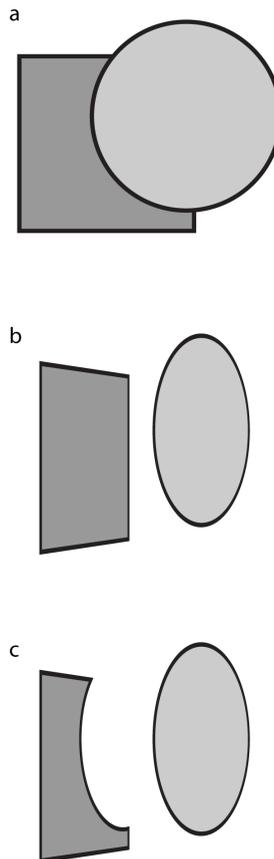
When our senses are only presented with part of an object, we do perceive the whole object; somewhere in our brain a completed representation of this object must exist in order for us to experience it. To illustrate this concept, consider the scene in figure 1a. In this example, one object occludes another object, and multiple interpretations are possible. In figure 1b, a side-view of the most likely interpretation of this scene is depicted; a circle partly occludes a square. An alternative, and equally valid, though less likely, interpretation is shown in figure 1c, where a circle occludes a complex geometrical shape (in essence, a square with an oval cut-out).

That the interpretation shown in figure 1b is the more likely of the two was predicted by Kanizsa (1979), who postulated that the visual system interprets occlusion scenes based on a general principle of good continuation. In essence, the human visual system prefers to continue directions, resulting in a perceived square behind the circle, instead of a square with a circular cut-out. This is reminiscent of basic Gestalt-like principles (Koffka, 1963), and seems to follow a general principle that the visual system completes figures in such a way that it results in the most simple code of the final figure (e.g. Buffart, Leeuwenberg & Restle, 1981; van Lier, van der Helm & Leeuwenberg, 1994).

Since this square is not projected on the retina, somewhere in the visual system a representation must exist that gives rise to this percept of a square. This concept of a representation or idea of an object being active in our brain that is, in a way, independent from what is presented to us through our senses, is reminiscent of Plato's Theory of Forms. Plato suggested that the highest and most fundamental kind of reality is not the world known to us through our senses (eyes, ears etc.), but the world of Ideas or Forms. In other words, even when our sensory information is incomplete or fragmented, as is happening right now as this thesis is blocking parts of your immediate surroundings, our perception of the world is unaffected.

The main focus of this thesis is how information that is presented to our visual and auditory senses influences what we perceive. In chapters 2, 3 and 4, we focus on visual processing of the orientation of objects in our surrounding world. Here, we address questions like: How does the visual system determine the orientation of an object? What strategies

are applied when selecting particular features of an object? How does the visual system determine orientation for objects that are not in direct line of sight? Subsequently, in chapter 5, we investigate how attention modulates auditory processing, how attention can be drawn towards a particular frequency, and what this means for other frequencies that fall in the same perceptual category.

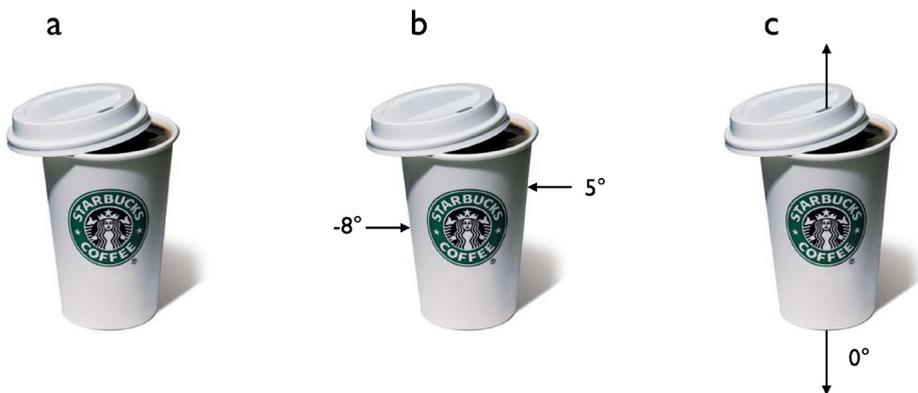


**Figure 1. Object occlusion and scene interpretations.** A) Circle occluding another object. B) Side-view of most likely interpretation of the scene in a), a circle occluding a square. C) Side-view of alternative explanation of the scene in a), where a circle occludes a square-like object with a circular cut-out.

## 1.2 Visual information processing

Consider the following situation: you have just poured yourself a cup of coffee and want to take a sip while you are reading your newspaper. This act can be broken down into a number of key actions, such as grasping the cup, lifting it and bringing it to your mouth, each of which is crucial to accomplish the goal of taking a sip and enjoying your coffee. To successfully grab the cup without spilling its contents over your desk, you need to have access to certain information about the cup, such as its location and orientation relative to the position of your grasping hand. The orientation and position of your hand should then be adjusted to comfortably grab hold of the cup. Needless to say, most, if not all of the processes described above take place without conscious effort: you just grab the cup and take a sip. But how does our visual system accomplish this seemingly trivial process of grabbing a cup and taking a sip as described above?

The cup in figure 2a might elucidate that the process of determining object orientation is not as trivial as it may seem at first glance. Most people will perceive the orientation of the cup in figure 2a as vertical. But which aspects of the cup influence the way in which we perceive its orientation? If we take a look at figure 2b, it is apparent that none of the cup edges are oriented vertically.



**Figure 2. Coffee cup.** Even though the sides of the cup are not vertical (the left side being  $-8^\circ$  and the right side being  $5^\circ$ ) we perceive the orientation of the cup as vertical. In this case the cup contains a vertical axis of elongation, which happens to coincide with the cup's axis of symmetry and axis of inertia. In this example the perceived orientation of the cup can therefore be predicted from the cup's axis of elongation, symmetry and inertia.

Apparently, since all edges are oblique and the perceived cup orientation is vertical, the individual edges of the cup are not a good indicator of the overall orientation in which we perceive the cup. If the individual edges can not directly predict how we perceive the cup's orientation, then what aspect of the cup does?

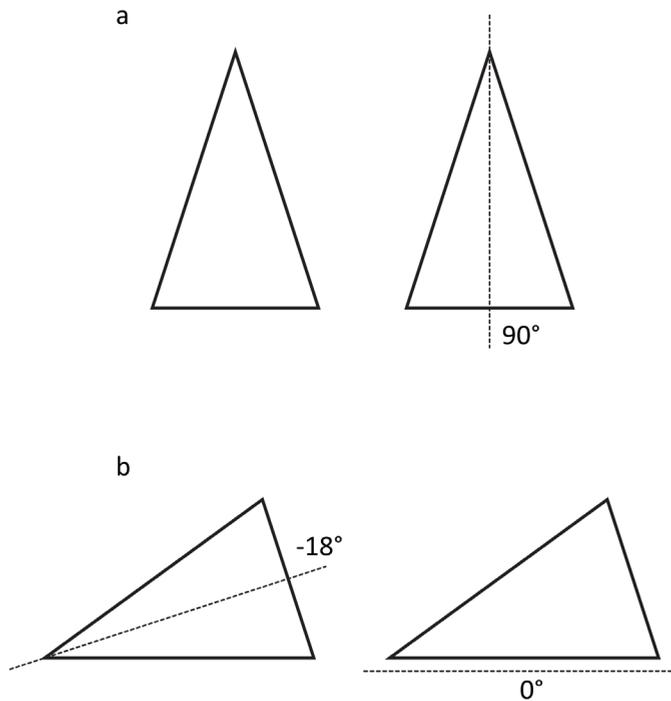
In this case the cup contains a vertical axis of elongation (shown in figure 2c), coinciding with the cup's axis of symmetry. Each of these axes have different definitions. In the example of this coffee cup, they happen to coincide. Since these axes are vertical, and the perceived orientation of the cup is vertical as well, one could make a point that perceived orientation of the cup is determined in this case by the axis of elongation or symmetry.

This implies that the visual system is capable of extracting object features such as axes of symmetry and elongation, and is capable of determining overall object orientation based on the orientation of these axes. This has indeed been found in various studies, showing that perceived object orientation is best predicted from an object axis such as an axis of symmetry, elongation or inertia (Found & Müller, 1997; Boutsen & Marendaz, 2001; DeKuijer, Deregowski & McGeorge, 2004).

Likewise, the perceived orientation of the triangle in figure 3a (vertical) can be directly predicted by the triangles' axis of symmetry, which is vertical. However, when this triangle is rotated 108° counterclockwise, the axis of symmetry does not predict the perceived orientation of the triangle anymore. The axis of symmetry is 18°, but instead, the triangle is perceived to be horizontal, aligned in this case to the base of the triangle. In this particular case, the axis of the triangle does not predict the perceived orientation of the triangle, whereas the base of the triangle does.

Apparently the side of an object also influences its perceived orientation. So why do we not perceive the orientation of the coffee cup in figure 2 as oblique, aligned to one of its sides? And why do we perceive the triangle to be vertical in figure 3a, but when rotated 108° counterclockwise perceive it to be horizontal?

In the following sections a brief introduction will be given into the visual system, its neurophysiological properties concerning orientation processing, and outstanding questions with respect to how the visual system determines object orientation, after which the outline of this thesis will be supplied.



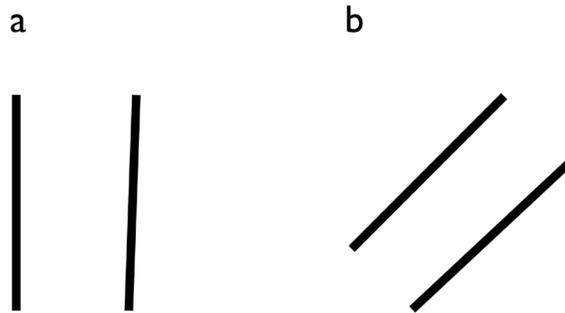
**Figure 3. Triangles.** A) The orientation of the triangle is perceived to be vertical, aligned in this case to the triangle's axis of symmetry. B) When the same triangle is rotated  $108^\circ$  counterclockwise, the perceived orientation of the triangle shifts to horizontal, aligned to the (horizontal) base of the triangle, instead of the axis of symmetry, which is now  $18^\circ$  from horizontal. This example illustrates that besides object axes, object sides can also influence perceived object orientation.

### 1.3 Orientation processing in visual cortex

Light that falls on the photoreceptors, that make up the retinal mosaic, is translated into nerve signals. These signals are sent to early visual areas in the brain through the fibers of the optic nerve. One of the earliest cortical areas to process visual input from the retina is primary visual cortex (V1). Retinal visual input is processed in V1 in a highly retinotopic fashion, which means that there is a precise correspondence between a given location in V1 and the visual field. Each cell in V1 has a unique receptive field; an area on the retina for which that particular cell in V1 is sensitive. An interesting aspect of some cells in V1 is that they

are specialized in processing specific properties of incoming visual information. Hubel and Wiesel (1962) were the first to show that neurons in cat visual cortex are orientation-tuned, meaning that these cells respond primarily to luminance contours with a specific orientation. By using micro-electrodes inserted into the cat visual cortex, they recorded the activity of individual neurons, and determined which visual stimulus produced maximal firing rates for these neurons. Some cells (dubbed 'simple cells') responded not to the presence of light, but to luminance contours in their region of the visual field. More specifically, these simple cells each had a preference for a specific orientation. A simple cell with a higher firing rate for horizontal contours would not fire at all when oblique contours were present in its receptive field and vice versa.

An interesting characteristic of area V1 is that the orientations for which cells are sensitive are unequally distributed, with more cells tuned for horizontal/vertical orientations than for orientations in between (Furmanski & Engel, 2000). The lopsided distribution of cells that prefer horizontal/vertical orientations results in an increased sensitivity of the visual system for horizontal/vertical contours as compared to oblique contours, and is called the oblique effect (Appelle, 1972). This oblique effect not only manifests itself in the human visual system, but has also been found in animals such as rhesus monkeys (Boltz, Harwerth & Smith, 1979), cats (Bonds, 1982), golden hamsters (Emerson, 1980) and pigeons (Donis, 1999). This orientational anisotropy in the visual system is demonstrated by the two line pairs in figure 4. The difference in orientation between the lines in each pair is  $2^\circ$ , but this difference is more easily discernible in the left line pair (4a) than it is in the right line pair (4b). Since one of the lines in figure 4a is vertical, and the visual system has more processing power devoted to the processing of horizontal/vertical orientations, the orientational difference between these two lines is more easily discernible.

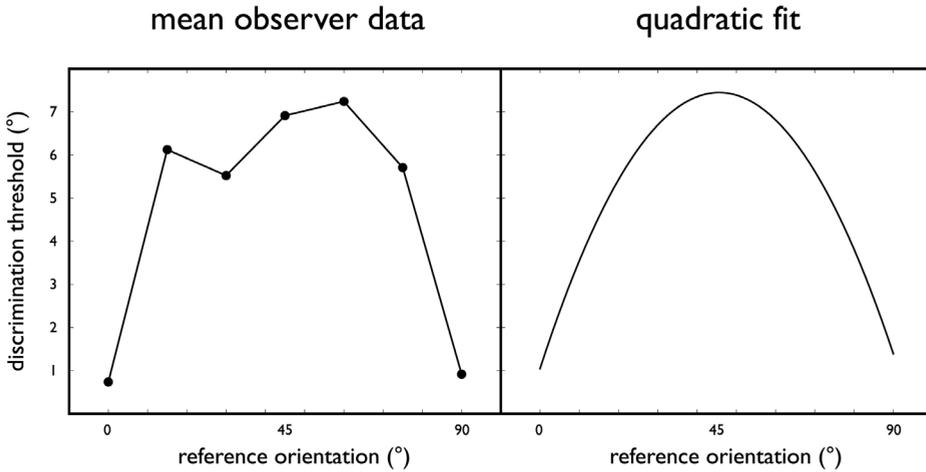


**Figure 4. Illustration of the oblique effect using two line pairs.** The orientational difference between the two lines ( $2^\circ$ ) is identical in A) and B). However, due to the increased sensitivity of the visual system for orientations close to horizontal/vertical, this orientational difference is more easily discernible in the left pair than in the right pair. Simply put, orientational differences between lines are better noticeable when those lines are close to either the horizontal/vertical instead of oblique.

## 1.4 Visual methods

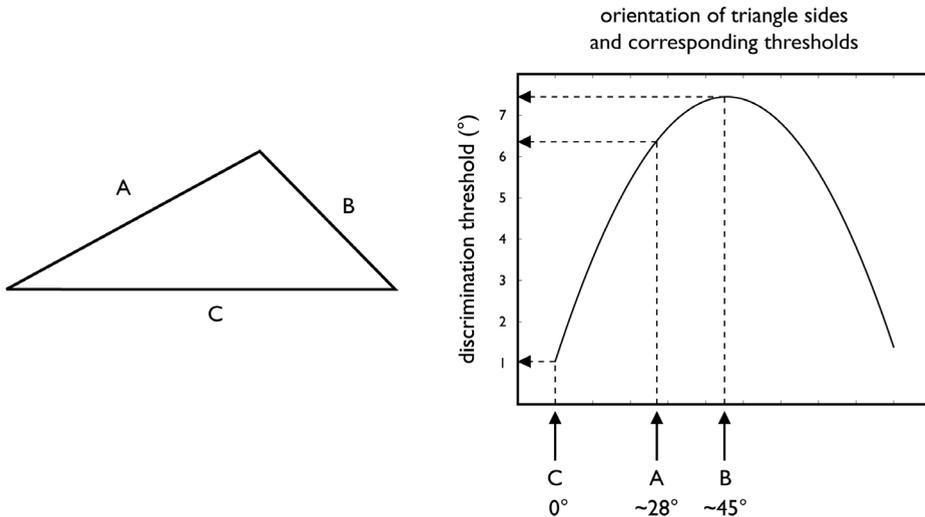
A common way in psychophysics to measure orientation discrimination is to present an observer with a reference stimulus, such as a line, and to ask whether a second separately presented line is rotated clockwise or counterclockwise with respect to the first line. The point at which the observer indicates that the orientation of both lines is identical is called the observers' orientation discrimination threshold. Low orientation discrimination thresholds imply that an observer can detect a very small orientational difference between two stimuli. As demonstrated by the two line pairs in figure 4, orientation discrimination thresholds are lower for orientations close to horizontal/vertical, and higher for oblique orientations. The left panel in figure 5 shows mean orientation discrimination thresholds for four observers, using a line as stimulus, for reference orientations ranging from  $0^\circ$  to  $90^\circ$ . The x axis shows the reference orientation of the line, and the y axis shows the orientation discrimination threshold, i.e. the smallest orientational difference the observer can detect. These data clearly demonstrate the oblique effect: reference orientations near  $0^\circ$  and  $90^\circ$  yield lower discrimination thresholds, whereas oblique reference orientations yield higher thresholds. The curve in the right panel of figure 5 indicates a best fit for these same thresholds. This curve is an approximation of the data points shown in the left panel of figure 5. Since the parabola in the right panel is based on actual observer data, we can use this curve to predict orientation discrimination thresholds for any given line orientation. So instead of

measuring discrimination thresholds for every possible orientation of a line, we can now predict these thresholds by looking at the parabola in figure 5.



**Figure 5. Observer data demonstrating the oblique effect.** Left panel: mean orientation discrimination thresholds plotted for four observers using a line stimulus. Right panel: parabola indicating a quadratic fit.

For one single line this might seem trivial, since we already measured the discrimination thresholds on which the parabola is based. However, consider an object that consists of multiple lines, such as the triangle in the left panel of figure 6. We already posed the following question: which object features (i.e. object axes or sides) influence the orientation with which we perceive that object? Using the parabola from figure 5 we are now one step closer to answering this question. If we assume that the lines of this triangle are processed by the visual system in a similar fashion as single lines, then we can use the parabola from figure 5, which predicts orientation discrimination thresholds for single lines, to predict discrimination thresholds for the three lines making up the triangle in figure 6. Since we can measure the orientation of each of these three lines, we can predict orientation discrimination thresholds for each line individually using the parabola in the right panel of figure 5.



**Figure 6. Orientation discrimination thresholds for each line making up a triangle.** By looking at the orientation of each triangle side we can predict the corresponding threshold for that side. Since side C is horizontal, and the visual system has an increased sensitivity for horizontal/vertical orientations, the predicted threshold for this side would be lower, about 1°. Side A however is  $\sim 28^\circ$  and its predicted threshold would be higher, around 6.5°.

For example, side C is  $0^\circ$ , and would yield lower orientation discrimination thresholds, as shown in the graph of figure 6. Similarly, side A is  $\sim 28^\circ$ , which would yield higher discrimination thresholds, as would side B with an absolute orientation of  $\sim 45^\circ$ . We can now predict orientation discrimination thresholds for each of the lines that make up the triangle in figure 6. However, we are not interested in predicting thresholds for individual lines, we want to know which object side influences the orientation with which we perceive that object. In other words, we want to see if we can predict orientation discrimination thresholds for an entire figure, based on the thresholds we obtain for its individual sides. To determine this, we can measure orientation discrimination thresholds for this triangle for the orientation shown in figure 6. Then we would compare the obtained discrimination threshold for the total triangle with the thresholds for each side individually to see which of the sides best predicts thresholds for the triangle. Consider the example in the next paragraph.

Assume we obtained an orientation discrimination threshold of  $\sim 1^\circ$  for this particular triangle orientation. If we know the threshold for the triangle and the thresholds for the lines that make up the triangle we can see which line-thresholds best predict the threshold of the total triangle. Since the parabola in figure 6 indicates that sides A and B yield higher orientation discrimination thresholds, and in our example we obtained a threshold of  $\sim 1^\circ$  for the triangle, these sides do not predict discrimination thresholds for this particular tri-

angle orientation very well. However, side C yields lower discrimination thresholds. In this example side C would therefore best predict orientation discrimination thresholds for the triangle.

In the current example, we only used the sides to predict thresholds for the triangle. However, if we would make the assumption that orientation discrimination thresholds for object axes are based on the same parabola as shown in figure 5, then we could incorporate object axes in our predictions as well. Following the same line of reasoning as in the example mentioned above, we are then able to determine whether object thresholds are best predicted by either its sides, or its axes.

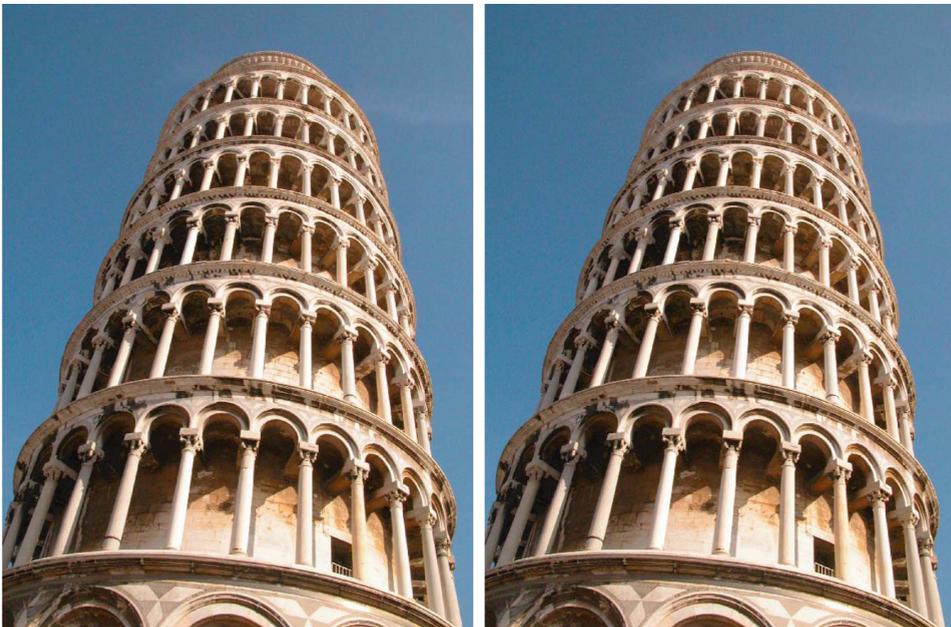
As these examples show, we are able to capitalize on an anisotropy of the visual system (the oblique effect), and use this as a creative tool to establish which object feature (an axis or a side) best predicts orientation discrimination thresholds for a particular object in a specific orientation. By inspecting the obtained threshold for any object orientation, and comparing this with the thresholds for the individual object features, we can deduce which of these object features best predicts overall object orientation.

In chapter 2 we propose a model that incorporates a smart object feature selection strategy, based on a 2D object projection. This model accurately predicts orientation discrimination thresholds for simple geometrical objects in various orientations, based on object features (axes and sides) in a 2D projection. In chapters 3 and 4 we explore a different aspect of orientation perception. Since we have two eyes, each with their own different viewpoint on a particular scene, retinal projections can be different for the left and right eye. Furthermore, as will be outlined below, orientations of retinal projections can differ radically from perceived orientation. In chapter 3 we study how the visual system deals with these retinal disparities when judging object orientation. Furthermore, we distinguish whether object orientation is best predicted from the orientations of retinal projections or from perceived orientation. In chapter 4 we go one step further by using a stimulus that gives rise to a vivid percept, without actually stimulating photoreceptors on the retina. In this chapter we explore how the visual system determines object orientation in the absence of retinal stimulation.

## 1.5 Sensory input versus perception in the visual domain

Based on the previous paragraphs and examples, one might conclude that there is an interdependence between sensory input (in the visual domain: what is projected on the retina), and what is perceived. For example, when a triangle is projected on the retina, one usually has the percept of a triangle and not of a circle or a square. However, there are some exceptions to the correspondence between what is projected on the retina and what is perceived. A vivid example is the leaning tower illusion, first presented by Kingdom, Yoonessi and Gheorghiu (2007). Figure 7 demonstrates this illusion.

Most people will perceive the orientation of the right tower as rotated more clockwise than the orientation of the left tower. However, both pictures are in fact exactly the same. In this particular illusion a discrepancy exists between the orientation projected on the retina and the perceived orientation.

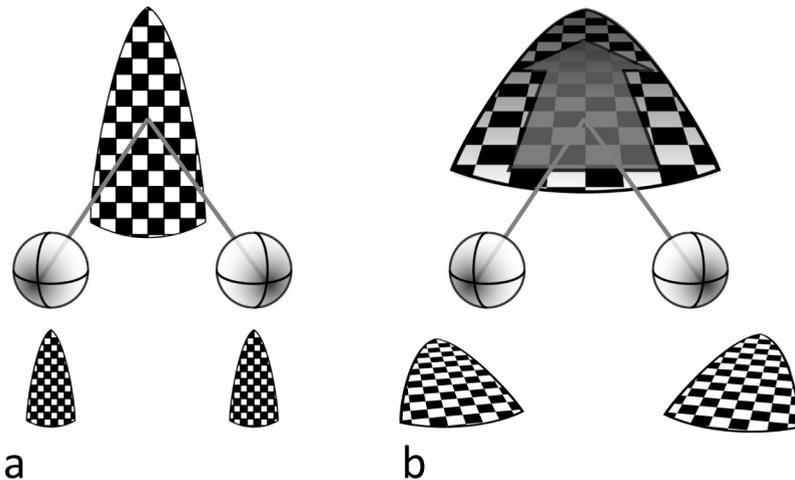


**Figure 7. Leaning tower illusion.** The right tower appears to be rotated more clockwise than the left tower, even though both pictures are in fact exactly the same, and have the exact same orientation. Photo by Adriana Olmos.

This discrepancy between the orientation we perceive and the orientation that is projected on the retina is not unique to the leaning tower illusion. In fact, since we have two eyes that are set apart from each other in the horizontal plane, both eyes view the world from a slightly different perspective. This difference in perspective gives rise to what are

called retinal disparities, small differences between the visual input of the two eyes when looking at the same scene<sup>1</sup>.

Consider the scene depicted in figure 8. In figure 8a, a vertical object is placed directly in front of an observer. Both eyes view this object from a different perspective, but the orientation of this object is vertical from both points of view. Now consider the scene in figure 8b. Here the object is still vertical, but slanted backwards 45°. This backwards slant causes the fronto-parallel orientation of the object to be different for both eyes, rotated more counterclockwise for the left eye, and more clockwise for the right eye. Regardless of this orientational difference, we perceive a vertical object with backwards slant. In this example a discrepancy arises between what we perceive, and what each eye sees, i.e. what is projected onto each retina. Since perceived orientation in this example is vertical, and orientations presented to each eye individually are oblique, it is informative which of these two information sources the visual system uses to determine object orientation. In chapter 3 we exploit this discrepancy, again using the oblique effect as a tool. As oblique orientations lead to higher orientation discrimination thresholds than vertical orientations, we can disentangle which of these two information sources the visual system uses to determine the orientation of a binocularly presented object, slanted backwards in depth.



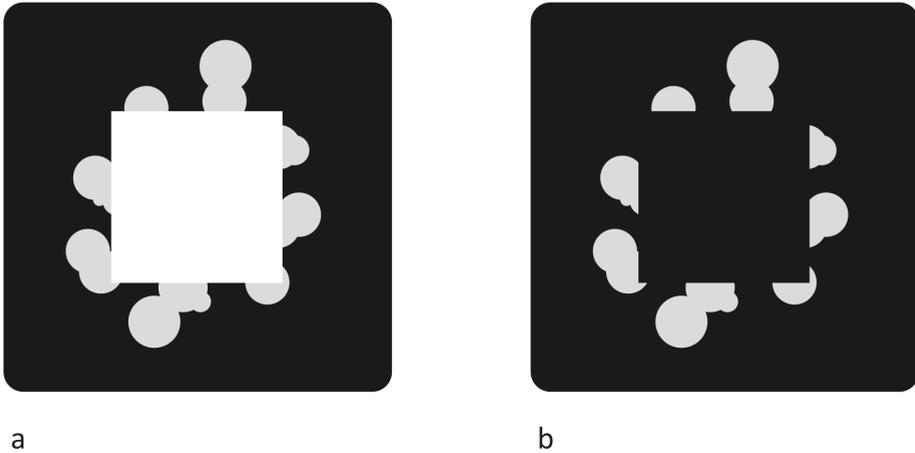
**Figure 8.** A) An object without slant produces orientationally similar retinal projections. (B) An object slanted backwards in depth produces differently orientated retinal projections for each eye.

<sup>1</sup> These differences are apparent when you extend your arm directly in front of you while making a thumbs up sign. When you alternately look at your thumb with your left and right eye, you can see the position of your thumb shift horizontally for each eye.

By creating a stimulus that has different orientations for each eye, and measuring orientation discrimination thresholds for this stimulus, we can answer the question whether orientation discrimination thresholds can be best predicted by retinal projections, or the perceived orientation, i.e. the orientation of the object representation.

In chapter 3 we addressed the issue of retinal disparities, and whether orientation discrimination thresholds can be predicted from retinal projections or from an object representation. In chapter 4 we take this notion one step further. In daily life, objects often occlude each other and only fragments of objects are actually projected onto the retina. The visual system somehow has to fill in information that is not retinally projected, resulting in complete object perception (e.g. Buffart, Leeuwenberg & Restle, 1981; van Lier, van der Helm & Leeuwenberg, 1994; Gold, Murray, Bennett & Sekuler, 2000). For example, consider figure 9. Here, two stimuli are shown that both induce the percept of a square, a white square in figure 9a and a black square in figure 9b. Since the background in both cases is black, the black square does not provide any retinal stimulation for its surface area, whereas the white square does. Regardless, we experience a vivid square percept, even though it is not projected on the retina. To date, no evidence exists to suggest how the visual system determines object orientation for objects that are occluded and how the occluded, invisible, object part influences perceived object orientation.

In chapter 4 we address this issue by using the stimulus shown in figure 9b, consisting of illusory contours. Here, contours of a square are perceived but are not physically present in the stimulus. These illusory contours then give rise to a vivid percept of a square. We can then compare the discrimination thresholds for this stimulus to a stimulus that induces a similar percept, but provides retinal stimulation as well. By measuring orientation discrimination thresholds for both types of stimuli, we can answer the question whether retinal stimulation is actually necessary to explain orientation discrimination thresholds, or if these thresholds can be explained by an object representation instead.



**Figure 9. White and black square on black background.** The squares in A) and B) have identical dimensions, but the square in B) does not provide retinal stimulation. Regardless, a vivid percept of a square arises, even though it is not projected on our retinas.

Summarizing, in chapters 2, 3 and 4, we investigate how the human visual system determines the orientation of an object. Our particular choice of stimuli allows us to make inferences about how our brain actually processes incoming visual information. The stimuli in chapters 3 and 4 give rise to a percept with a different orientation from the retinal projection. We then determine, by making use of an increased sensitivity of the visual system for orientations close to the horizontal/vertical (the oblique effect), which object features the visual system selects to determine object orientation; features of an object as projected on the retina, or features of a completed object representation.

The representation of an object is not unique to the visual domain. For example, when a novel three-dimensional object is haptically explored, this gives rise to a representation of this object as well, activating somatosensory areas in the brain and, interestingly, visual areas as well (James et al., 2002). Similarly, in the auditory domain, a phenomenon exists that suggests that the auditory system can act on auditory object representations as well, octave equivalence, which holds that two tones separated by an octave fall in the same perceptual category, or tone chroma (e.g. Deutsch & Boulanger, 1984; Kallman, 1982). The musical note A4 (440 Hz) falls in the same perceptual category as A5 (880 Hz). Since these two notes are treated as more similar than any other musical interval (i.e. separated by any other interval than an octave), this suggests that auditory attention might be drawn towards a representation of a note (e.g. the tone class A, encompassing amongst others 440 Hz and 880 Hz),

rather than towards one particular frequency. Is there a way in which we can investigate whether our auditory system can act on the representation of a sound as well?

In chapter 5, we address this particular question. Whereas in chapters 2, 3 and 4, we used the oblique effect as a tool to deduce which object features were selected by the visual system, in chapter 5 we will make use of a well-known auditory phenomenon, known as the attention band<sup>2</sup>, to examine how the brain processes auditory information. The auditory system, after being presented with a tone, becomes more sensitive to frequencies similar to that tone, with respect to dissimilar frequencies. This process is thought to be mediated by attention and, as such, can be used to investigate the attentional focus in the frequency domain (e.g. Pashler, 1998).

In the first experiment in chapter 5, and similar to chapter 2, we investigate how attention can be drawn to a cue frequency (e.g. 500 Hz), and what this means for frequencies that fall in the same perceptual category or tone chroma (i.e. frequencies that are octave-related to the cue frequency). In experiment 1, there is a direct relationship between the frequency that is physically presented (e.g. 500 Hz), and the subjective perceptual experience of this frequency, known as pitch. In the second experiment, and similar to chapters 3 and 4, we create a tone where the pitch is different from what is physically present in the sound spectrum. In other words, a pitch of e.g. 500 Hz is perceived, but 500 Hz is not physically present itself. This is called a missing fundamental complex, sometimes referred to as the auditory counterpart of the illusory contour (Pantev, Elbert, Ross, Eulitz & Terhardt, 1996). Finally, in the third experiment, we investigate how imagining a frequency influences sensitivity for similar frequencies. How does thinking of a frequency influence how other, similar frequencies are processed?

## 1.6 Auditory processing and attention

The concept of attention is quite elusive, and is easiest explained by giving an example of a famous phenomenon in the psychological literature; the cocktail party effect. This effect describes the ability to focus one's attention on a single speaker amidst other speakers and background noise. Where this might seem fairly straightforward (you just tune in to the speaker you are interested in) this is in fact quite a complicated process. How are we able to single out only that information that we are interested in? As is implied above, incoming auditory information is passed through an attentional filter. This filter is capable of selecting attended information, and attenuating unattended information. However, when someone

<sup>2</sup> To give an adequate, all-encompassing definition of attention is beyond the scope of this introduction, or thesis for that matter. Some of the phenomena described in this chapter and in chapter 5 are generally assumed to be influenced (modulated) by attentional processes. I have chosen to stay close to the literature and use the term attention and attention band throughout this thesis, without going into detail about what attention specifically is, or neural correlates of attention.

calls out your name, this will very likely break through the attentional filter, and capture your attention regardless.

The example of the cocktail party effect goes to show that auditory processing can be influenced by our attention; we are able to focus on specific aspects of incoming auditory information. This process can be voluntary, where you direct your attention towards a specific speaker, but can be involuntary as well, where your attention is captured when someone calls out your name. In the following sections a brief introduction will be given into the auditory system, its neurophysiological properties concerning the processing of frequencies and pitch, and how the attentional focus can be measured using psychophysics.

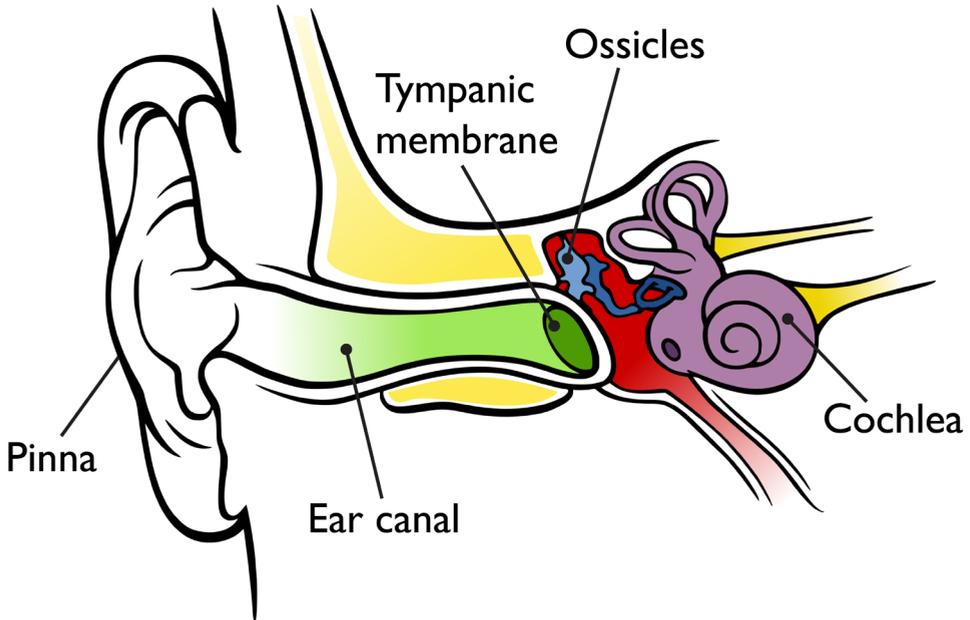
## 1.7 Frequency processing in auditory cortex

From the point in time where someone calls out your name and the moment where you perceive your name being called, a multitude of processes takes place. After your name is called out, sound waves travel through the air, hit the visible part of the ear (called the pinna), which boosts particular frequencies and directs incoming sounds towards the ear canal, and then travel through the ear canal to finally arrive at the tympanic membrane (figure 10). Here, a remarkable amplification process takes place as the vibrations of the tympanic membrane are translated and amplified by the smallest bones in the human body, the ossicles, consisting of the malleus, incus and stapes. Through this amplification process, the pressure at the tympanic membrane is increased, resulting in a mean gain of about 23 dB when the ossicles pass the sound information on to the cochlea (Kurokawa & Goode, 1995). Here, the basilar membrane is set in motion, and the original sound wave is ultimately translated into nerve signals that are passed through to the brain via the auditory nerve. This re-encoded signal travels along several waystations (i.e. the cochlear nucleus, the superior olivary nucleus, the inferior colliculus and the medial geniculate nucleus) to arrive at the auditory cortex; the first region of the cerebral cortex to receive auditory input and consisting of the primary, secondary and tertiary auditory cortex.

Similar to the retinotopic organization of primary visual cortex (a precise correspondence between a given location in V1 and the subjective visual field), primary auditory cortex has a tonotopic organization, meaning that neighboring parts of primary auditory cortex are sensitive to neighboring frequencies (e.g. Wessinger, Buonocore, Kussmaul & Bangun, 1997; Bilecen, Scheffer, Schmid, Tschopp & Seelig, 1998; Langers, Backes & van Dijk, 2007). In other words, that part of the primary auditory cortex that is optimally sensitive to 1000 Hz lies in close proximity to the region sensitive to 1005 Hz.

In everyday life, one hardly encounters tones with only one frequency (e.g. 500 Hz), instead most sounds will consist of multiple frequencies together to form a complex tone. When the string of a guitar is plucked, this will result in a complex tone, consisting of the fundamental frequency ( $f_0$ ) of the string (e.g. a low B:  $\sim 61$  Hz), but also containing harmon-

ics (integer multiples of the fundamental frequency, e.g.  $2x$ ,  $4x$  and  $6x f_0$ ), and partials (non-integer multiples of the fundamental frequency).



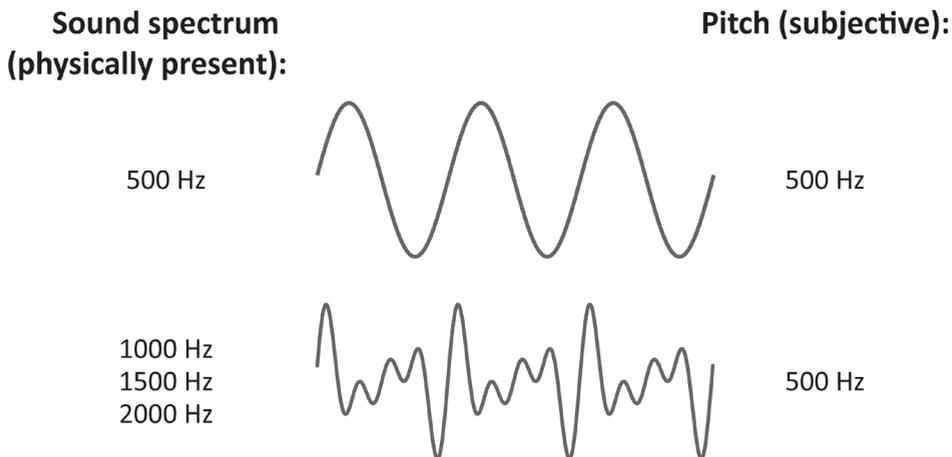
**Figure 10. The human ear.** Sound traveling through the air is collected by the outer ear, the pinna, and directed towards the ear canal (length of the ear canal is exaggerated in this figure). The tympanic membrane then transfers the sound through the ossicles to the cochlea. Figure adapted from Chittka and Brockmann, 2005.

Amongst other things like attack, vibrato and rise/fall time (Klapuri & Davy, 2006), the balance of the fundamental frequency, the harmonics and the partials is what gives each instrument a unique tonal character, or timbre. Even though the tonal quality of each instrument is different, the same note played on a guitar, piano or cello will result in a perceptual aspect of the note that is constant: pitch.

### 1.8 Sensory input versus perception in the auditory domain

Whereas neurons in primary auditory cortex are sensitive to individual frequencies (as in the example above, e.g. for 1000 Hz), neurons in secondary auditory cortex of the marmoset monkey have been shown to be sensitive to pitch, regardless of the specific spectrum of a tone (Bendor & Wang, 2005; Bendor & Wang, 2006). One particularly interesting example of the difference between neurons in primary and secondary auditory cortex is when a missing fundamental complex is played. A missing fundamental complex is a complex tone,

where a pitch is perceived at a fundamental frequency ( $f_0$ ) that is not present in the physical sound spectrum of the complex tone itself. For example, a complex tone consisting of 1000, 1500, and 2000 Hz will give rise to a perceived pitch of 500 Hz (the largest common denominator of the three frequencies).



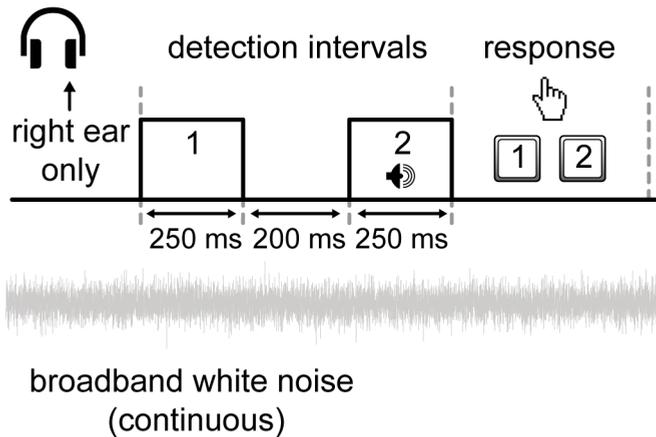
**Figure 11. Simple tone and missing fundamental complex.** Upper part shows a simple tone of 500 Hz, this then leads to perceived tone quality (pitch) of 500 Hz. Lower part shows a complex tone, consisting of 1000, 1500 and 2000 Hz. The largest common denominator of this complex tone is 500 Hz, and this is what determines the pitch of this complex: the missing fundamental.

Neurons in primary auditory cortex that are sensitive to 500 Hz will not fire when this complex tone is presented, simply because their preferred frequency (i.e. 500 Hz) is not present in the complex tone. However, pitch neurons in secondary auditory cortex will become active, since the perceived pitch of the complex tone is 500 Hz. Similar to an illusory contour, where a contour is perceived that is not physically present in the stimulus itself, in a missing fundamental complex, a pitch is perceived that is not physically present. In chapter 5, we will make use of this particular aspect of auditory information processing to study how attention influences processes in the auditory system.

## 1.9 Measuring auditory attention

How does one measure attention? As the example of the cocktail party effect shows, the auditory system is capable of focusing on particular aspects of incoming auditory information, and attenuating unwanted information. The attended information can be a particu-

lar conversation you are eavesdropping on, or the voice of the person you are talking to. One subjective way to measure where attention is, would be to simply ask someone what he or she is focusing on. Obviously, in a controlled experiment, we would like to have an objective measure of the attentional focus. A straightforward method to measure attention involves a target detection task, where a listener is asked to respond whether a target-tone was presented in either interval 1 or interval 2 (figure 12).



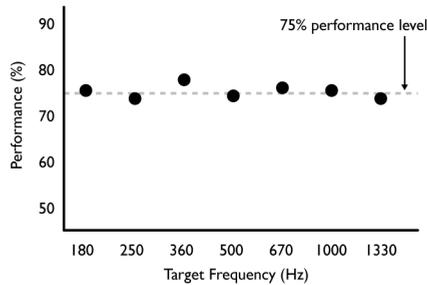
**Figure 12. Target detection paradigm.** A target tone is presented in the presence of continuous broadband white noise in either interval 1 or 2, visually marked on a computer screen with a 1 or a 2. After the two intervals, the observer is asked to respond with a keypress whether the target tone was detected in interval 1 or 2.

Suppose we know exactly at what signal-to-noise ratio<sup>3</sup> we should play a target tone of a particular frequency in order for it to be correctly detected 75% of the time (with chance being 50%). The graph in figure 13 shows simulated ideal detection performance for a particular listener. As shown, for each target frequency, detection performance is roughly 75%.

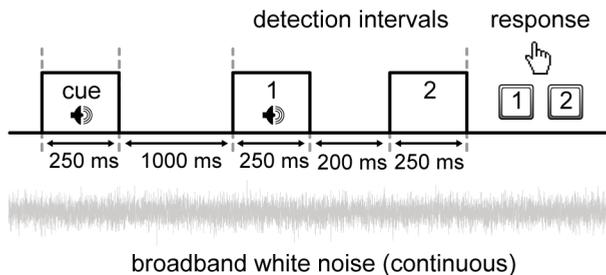
Now, when we slightly alter this experimental paradigm by adding a tone before the detection intervals (the cue tone; figure 14) this dramatically influences target detection performance. Detection performance for targets similar to the cue frequency remains relatively unaffected (even boosted in some cases), but performance for target tones that are different from the cue frequency decreases. This decrease in sensitivity for target tones dissimilar to the cue frequency is thought to be mediated by attention and, to date, is characterized by a bandpass filter (e.g. Dai, Scharf & Buus, 1991). In other words, the location

3 The level of a signal with respect to background noise, expressed in decibels (dB). In this paradigm, the level of a target tone with respect to the broadband white noise. A target tone with a signal-to-noise ratio (SNR) of -20 dB is much harder to be detected than a target tone with a SNR of -5 dB.

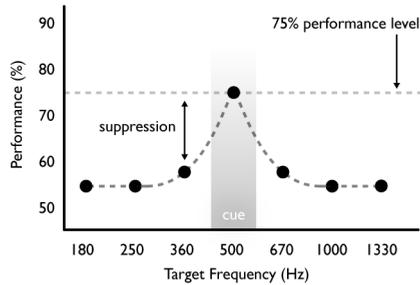
of the performance peak (in figure 15 located at 500 Hz), can be interpreted as the locus of attention, in this case in the frequency domain. Summarizing, auditory sensitivity increases for what is attended and, as a result, detection of a signal becomes easier when this signal is more similar to the attended sound.



**Figure 13. Simulated target detection data.** Simulated target detection data is shown for the paradigm shown in figure 12. For each target frequency, ranging here from 180 to 1330 Hz, the signal-to-noise ratio is set such that correct target detection occurs in approximately 75% of all targets.



**Figure 14. Cued target detection paradigm.** In addition to the experimental paradigm shown in figure 12, a cue tone of 500 Hz is added before the detection intervals. This cue tone is set to a clearly audible level.



**Figure 15. Simulated target detection data for a cued detection paradigm.** Simulated target detection data is shown for the paradigm shown in figure 14. For each target frequency, ranging here from 180 to 1330 Hz, the signal-to-noise ratio is set such that correct target detection occurs in approximately 75% of all targets. By adding a clearly audible cue tone of 500 Hz, detection performance for targets that are dissimilar to this cue tone is suppressed.

This method of deducing where the attentional focus is, is similar to the method described previously in this chapter, where we infer (in hindsight) what object feature is selected by the visual system (horizontal/vertical or oblique) based on overall object orientation discrimination thresholds. If the discrimination threshold for an entire object is low, we infer that the object feature selected was either horizontal or vertical. In the current example of auditory processing, when we find that sensitivity for a particular frequency is higher than for surrounding frequencies (e.g. a sensitivity peak for 500 Hz, but not for 400 or 600 Hz), we infer that this particular frequency must have been attended.



# Chapter 2

The use of optimal object information in  
fronto-parallel orientation discrimination



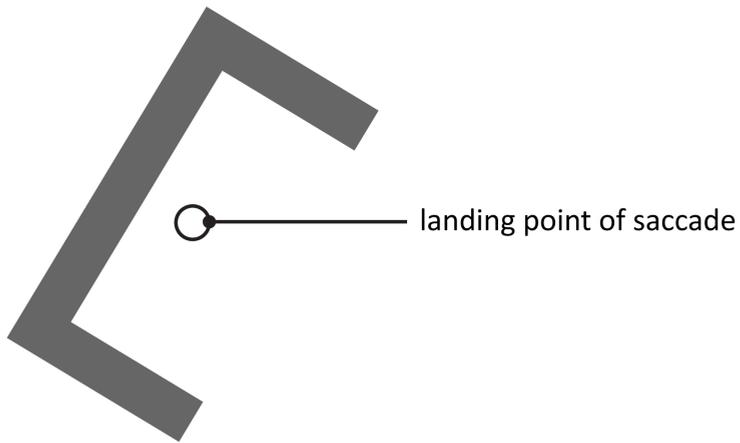
## 2.1 Abstract

When determining an object's orientation an implicit object axis is formed, based on local contour information. Due to the oblique effect (i.e. the more precise perception of horizontal/vertical orientations than oblique orientations), an object's orientation will be perceived more precise if the axis is either horizontal or vertical than when the axis is oblique. In this study we investigated which object axis is used to determine orientation for objects containing multiple axes. We tested human subjects in a series of experiments using the method of adjustment. We found that observers always use object axes allowing for the highest object orientation discrimination, namely the axes lying closest to the horizontal/vertical. This implies that the weight the visual system attaches to axial object information is in accordance with the precision with which this information is perceived.

## 2.2 Introduction

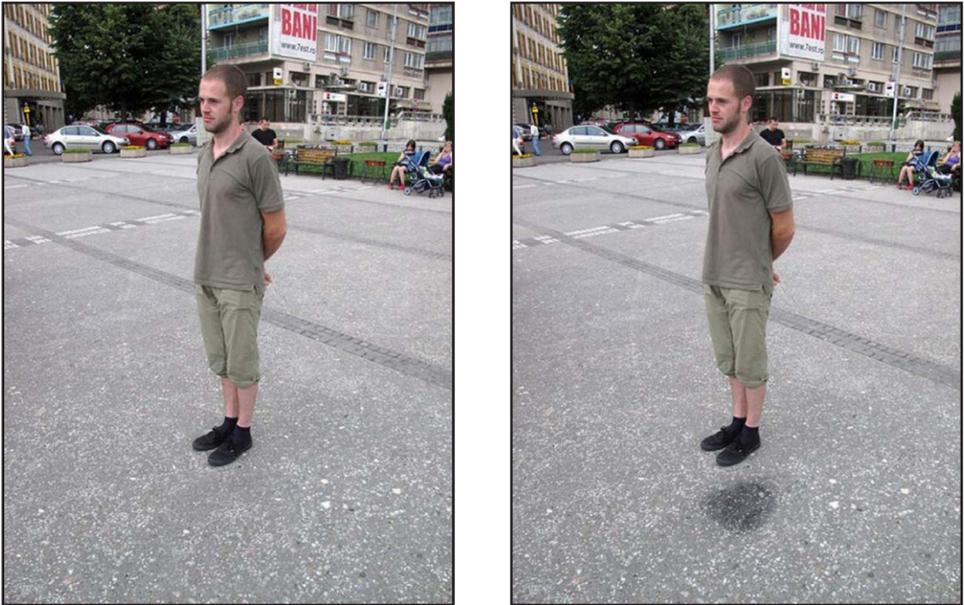
In order to optimally interact with the environment, one needs particular information about any specific object. To grab a book, you must rotate your hand in such a way that facilitates grabbing the book in the specific orientation it is in. Similarly, trying to pick up a small object while the grip aperture of your thumb and forefinger is very wide will probably be less successful than if you were to adjust the distance between your thumb and forefinger to the size of the object you want to pick up. In most cases, elementary object attributes, such as location, shape, color and orientation, are automatically processed by the visual system. No conscious effort has to be made to determine the orientation of the book you are reaching for, or to determine the size of the object you want to pick up. These elementary visual object features need then be integrated into higher order representations up until a point where semantic and contextual properties are attributed (Jeannerod, 1997). Detection and processing of these elementary visual features must occur sufficiently early along the pathways of visual processing in order to be able to select objects and interact with them (Boutsen & Marendaz, 2001), such as grabbing the book, or picking up a small object.

An example of fast detection and processing of object attributes can be found in the literature regarding saccadic localization. Saccades directed to simple two-dimensional target shapes, where the instruction is to look at the target as a whole, land near the center of gravity (COG) of the object (Vishwanath & Kowler, 2003). This happens even when the COG is outside the object itself and thus outside the region of retinal stimulation (figure 1).



**Figure 1. Saccades land on object center of gravity (COG).** Saccades directed towards a target object land near the object's COG, even when the COG is outside the region of retinal stimulation. Adapted from Vishwanath & Kowler, 2003.

This example illustrates that detection and processing of object attributes like mass happens on a time-scale sufficiently short in order to influence an eye-movement towards the object. Another example can be found in a study by Castiello et al. (Castiello, Lusher, Burton, & Disler, 2003), who suggest that object-shadow processing in humans is outside conscious awareness. A vivid demonstration hereof is given in figure 2 where two identical scenes are depicted, left the original scene, and right the scene with an added object "shadow". Even though one is aware of the added shadow, the implications for how the visual system interprets this scene is striking: the right person appears to float above the ground, simply by adding a shadow.



**Figure 2. Automatic processing of object shadow.** An object shadow is automatically processed by the human visual system, resulting in a scene interpretation where the man on the right seems to levitate above the ground, even though both photos are exactly the same, with exception of the added shadow.

### 2.3 Perception of orientation

Even though the orientation of an object is processed automatically and without conscious effort, there are large differences in the sensitivity of the visual system for particular orientations. A wealth of literature exists (e.g. Appelle, 1972; Vogels & Orban, 1985; Gentaz & Hatwell, 1995) that describes an increased sensitivity for orientations along the cardinal axes (i.e. horizontal/vertical orientations) with respect to sensitivity for oblique orientations (anything not horizontal/vertical). This orientation-dependent sensitivity is termed the “oblique effect” and is reflected in an increased precision in perception of horizontal/vertical orientations with respect to oblique orientations. This oblique effect has been confirmed in various behavioral studies in both man (Appelle, 1972), and animals (Bonds, 1982; Emerson, 1980). Interestingly, the oblique effect is not purely visual. For example, Kappers (2002) describes that for a haptic orientation matching task on the horizontal plane, where the orientation of two rods needs to be determined, deviations belonging to oblique reference orientations are significantly larger than for cardinal reference orientations.

Early theories attributed the oblique effect to frequent micro saccades along the Cartesian axes. Damped oscillations of the eye would presumably lead to preferential vibrations

in the horizontal and vertical planes (Higgins & Stultz, 1950). However, these theories were refuted by experimental data, suggesting that these physical factors cannot contribute significantly to the oblique effect (Higgins & Stultz, 1950; Nachmias, 1960). Furthermore, when making eye movements, no difference was found between the accuracy of horizontal/vertical and oblique saccades (Becker & Jürgens, 1990). This implies that the origin of the oblique effect does not lie in physical properties of the eye, nor in its mechanics.

An alternative explanation was suggested by Coppola, Purves, McCoy, and Purves (1998), who report a prevalence of vertical and horizontal orientations in indoor, outdoor, and even entirely natural settings. The authors reason that since visual experience is known to influence the development of visual cortical circuitry, this real world orientation anisotropy might be related to the enhanced ability of humans and other animals to process contours along the cardinal axes. One possible consequence of this outer world orientation anisotropy, and a possible explanation for the oblique effect, would be an increased stimulation of visual circuitry specifically devoted to the processing of vertical and horizontal contours. If this is indeed the case, then this would suggest that the oblique effect has a cortical basis.

More recent research has elaborated on this neuronal explanation. Furmanski and Engel (2000) reported that functional magnetic resonance imaging (fMRI) responses in V1 were reliably greater for cardinally oriented gratings than for oblique gratings, a finding also reported by Yacoub, Harel & Ugurbil (2008). This suggests that one of the earliest cortical areas of visual processing, V1, already displays an oblique effect. That this anisotropic response to orientations is not exclusive to V1, but also occurs outside V1 has been shown in optical image studies. For example Wang, Ding, & Yunokuchi (2003) show that area V2 also displays this same orientational anisotropy. Additionally, Coppola et al. (1998) measured the amount of cortical space activated by differently oriented gratings in the ferret and found that on average 7% more area of the exposed visual cortex was activated by cardinally oriented gratings than by gratings having an oblique orientation. In summary, the above mentioned studies seem to indicate that the oblique effect is based on characteristics of low-level cortical areas, as low as V1 and V2.

These findings raise the question as to how the visual system actually determines the orientation of an entire object. When an object, such as a book, has multiple sides, each with its own orientation, how does the visual system determine overall object orientation? Are the individual features, such as the sides, weighed in a particular way? Or does the visual system have a preference for particular orientations?

## 2.4 Local and global orientation processing

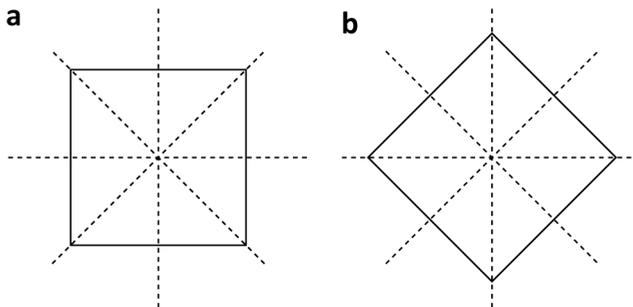
It seems straightforward enough that individual features of an object, e.g. the sides, influence the overall perceived orientation of the object, simply because the object

exists as a function of its sides. Found and Müller (1997) studied this particular aspect of object orientation processing, and found that an implicit object axis is formed, based on local contour information. In other words, based on the sides of an object, a global axis is formed, and the orientation of this global axis determines the orientation with which we perceive this object.

This finding was corroborated in a series of elegant experiments by Boutsen and Marendaz (2001). The authors made use of the fact that, in a visual search task, an oblique object amidst vertical objects is found faster than the reverse, called orientation search asymmetry. Boutsen and Marendaz found that this orientation search asymmetry was not dependent on local contours (the sides of the objects), but instead, dependent on the orientation of a global axis. An object with a global axis that is oblique is found faster amongst objects with a global axis that is vertical than the reverse. Continuing this line of reasoning, one would expect that this global object axis also influences the precision with which we perceive an object's orientation. If the global axis is horizontal/vertical, the object's orientation will be perceived more precisely than when the global axis is oblique.

A further object feature that is based on local contour information and that can be used to determine overall object orientation is apparent in symmetrical objects: the axis of symmetry. De Kuijer, Deregowski, and McGeorge (2004) showed that when using simple flat objects, the orientation of the axis of symmetry had the single highest influence affecting the reproduction of a symmetrical stimulus. To the best of our knowledge, there are no reports on which object information observers use to determine fronto-parallel object orientation.

In this study, our aim is to investigate which object information is used in determining fronto-parallel object orientation. More specifically, we want to determine what criteria the visual system uses to select object features (axes or sides), and, as a result, whether a specific strategy is applied in determining global object orientation. To illustrate this, an object with multiple features, each with its own orientation, is shown in figure 3.



**Figure 3. Square and axes of symmetry.** A) A square in a  $0^\circ$  orientation, with dashed lines indicating the axes of symmetry. B) The same square rotated  $45^\circ$ .

## 2.5 An optimized visual system

The object in figure 3a shows a square with four axes of symmetry, and four sides. In total, these object features have orientations of  $0^\circ$  (two sides, and one axis of symmetry),  $90^\circ$  (two sides, and one axis of symmetry),  $-45^\circ$  (one axis of symmetry) and  $45^\circ$  (one axis of symmetry). Suppose that the visual system “selects” one particular object feature to determine overall object orientation, and assume that this object feature is  $45^\circ$  (in this case this would be one of the axes of symmetry). Since we know that the visual system is more sensitive for orientations along the cardinal axes (horizontal/vertical), and less sensitive for oblique orientations (such as  $45^\circ$ ) it would follow that overall object orientation would be perceived less accurately than when a horizontal/vertical object feature (e.g. one of the sides) would determine overall object orientation. Continuing this line of reasoning, it follows that the precision with which we perceive the orientation of an object reflects the orientation of the object feature that determines overall object orientation. If the selected object feature is oblique, overall object orientation is less precise than when the selected object feature is horizontal/vertical. An object with multiple object features, such as the square shown in figure 3, where features have different orientations, would therefore enable us to study which object feature the visual system has selected. Furthermore, it allows us to inspect whether the visual system applies a specific strategy in selecting object features.

One possible, and optimal, strategy would be to always select that particular object feature for which the visual system is most sensitive. For orientation judgment, this would be a strategy where object features oriented closest to the horizontal/vertical are preferred over obliquely oriented features. This optimized strategy would allow for the highest possible precision in orientation judgment.

An optimization process such as described above closely resembles the findings of Schräter and Kersten (2000), albeit in a different domain. They describe a Bayesian approach to depth cue integration, based on the premise that a fundamental goal of the visual system is to make optimal statistical estimates of scene variables. The authors show that human observers’ decisions are near optimal for certain depth representation and conclude that subjects weight cue information in accordance with their informativeness. If the visual system indeed strives to make optimal decisions based on the available information in a particular scene, then the optimization strategy for orientation judgments we detailed in the previous paragraph would be a plausible strategy of dealing with the orientations of multiple object features. Additionally, Ernst and Bühlhoff (2004) describe the Modality Precision Hypothesis which states that in situations of modality conflicts, discrepancies are always resolved in favor of the more precise or more appropriate modality. Even though this does not directly apply to orientation judgment, where only one modality is present, it strongly hints at a general principle that governs the human sensory system. Incoming (multimodal) information seems to be weighted in such a way that allows for optimal interaction with the environment.

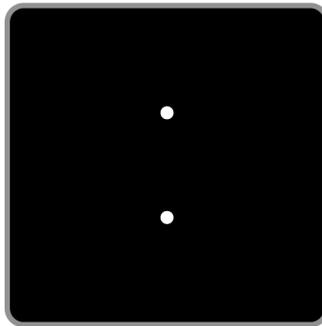
## 2.6 Dot stimuli

To test the validity of our assumption that orientation judgment occurs in an optimal fashion, we designed an orientation adjustment experiment, using objects with multiple object features, each with different orientations. Here, observers are asked to adjust the fronto-parallel orientation of a test stimulus to the orientation of a reference stimulus. The standard deviation of the difference between the adjusted orientation of the test stimulus and that of the reference stimulus is then an indication of the precision with which both stimuli are perceived. Large standard deviations would indicate a low precision in orientation perception, and would therefore be indicative of selection of obliquely oriented object features, whereas small standard deviations would imply that horizontal/vertical object features were selected.

In order to minimize interference between local and global contours, we chose to use dot stimuli, since these contain no global contour information. Li and Westheimer (1997) have shown that thresholds for detecting the angle of rotation for stimuli containing contours without luminance contrast (using a stimulus consisting of two dots) were almost as low as those for an actual vertical line. They dubbed this implicit orientation discrimination. This further supports our choice for using dot stimuli. Experiment 1 was designed to validate our stimulus and ascertain the existence of an oblique effect using a dot stimulus. In Experiments 2 and 3 we used a square and an equilateral triangle stimulus, respectively, both consisting of dots.

## 2.7 Methods

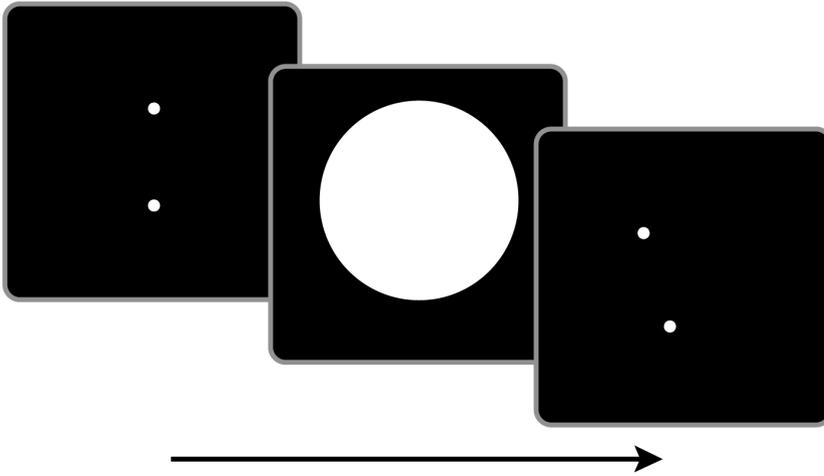
Three observers took part in Experiment 1. All observers were experienced in visual psychophysics experiments but were naïve as to the purpose of this experiment. The age range of the observers was 24–30 years, all had normal or corrected to normal vision. The experiments were performed using an Apple G4 Power Mac computer and an Iiyama Visionmaster Pro 454 CRT screen (vertical refresh rate of 80 Hz and a resolution of 1024 · 768 pixels). Stimuli were presented using Matlab 5.2 using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997). Stimulus displays consisted of two dots, each dot measured 0.53° in diameter and was presented with a luminance of 25.2 cd/m<sup>2</sup>, with a background luminance of 0.0 cd/m<sup>2</sup>. The distance between the two dots was 4°. See Figure 4 for an example of the “two dot line” stimulus.



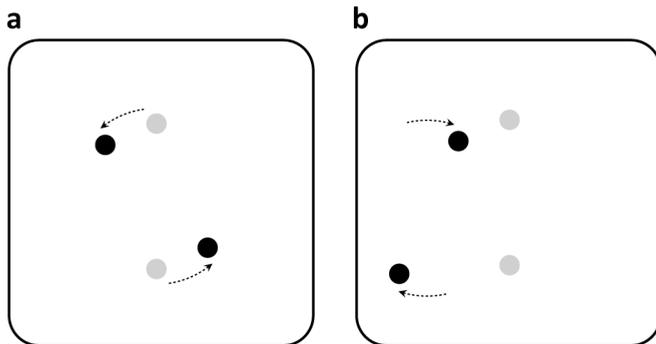
**Figure 4. Dot stimulus.** An example of the two dot line stimulus used in Experiment 1. Each stimulus dot measures  $0.53^\circ$  in diameter, with the distance between dots being  $4^\circ$ .

Observers looked straight ahead, using a chin-rest located 57 cm from the computer screen. The experiment was performed in a dark room. A black cloth with a circular aperture was draped over the monitor to prevent the light of the screen illuminating the edges of the monitor. Each trial started with the presentation of the line stimulus in the center of the screen for 500 ms. This stimulus had an orientation randomly chosen per trial out of 5 standard orientations:  $0^\circ$ ,  $22.5^\circ$ ,  $45^\circ$ ,  $67.5^\circ$ , and  $90^\circ$ . After the initial 500 ms presentation a white circular mask with a diameter of  $8.5^\circ$  was presented for 1500 ms. This was to make sure no information could be derived using the phosphor excitation (afterglow) of the stimulus on the monitor at the time the test stimulus appeared (figure 5). After this 1500 ms interval, the test stimulus appeared. This stimulus was rotated a random amount of degrees with respect to the reference stimulus and randomly chosen per trial to be clockwise or counter-clockwise, within a range of  $10\text{--}20^\circ$  from the orientation of the reference orientation.

Observers were instructed to adjust the orientation of the test stimulus to the reference stimulus by pressing the 5 (counter-clockwise rotation) or the 6 key (clockwise rotation) on the keyboard's numerical keypad. Also, the position of the test stimulus was translated a random number of degrees (with a minimum of  $1.42^\circ$  and a maximum of  $2.14^\circ$ ) for both the x and the y position as compared to the reference stimulus. This stimulus shift was introduced to exclude that observers perform the task using the location shift of one single dot. Figure 6 illustrates this stimulus shift. The reference orientation is shown in grey, with the test stimulus shown in black. In Figure 6a the test stimulus is rotated  $45^\circ$  counter-clockwise, with no stimulus translation. The upper dot of the test stimulus now moves to the left with respect to the upper dot of the reference stimulus. In Figure 6b, we show the stimulus translation. Although the upper dot of the test stimulus is in the exact same position as in 6a, it does not correspond to the same  $45^\circ$  counter-clockwise rotation.



**Figure 5. Stimulus presentation.** A circular mask (with a diameter of  $8.5^\circ$ ) was used to compensate for stimulus afterglow on the monitor due to phosphor excitation.

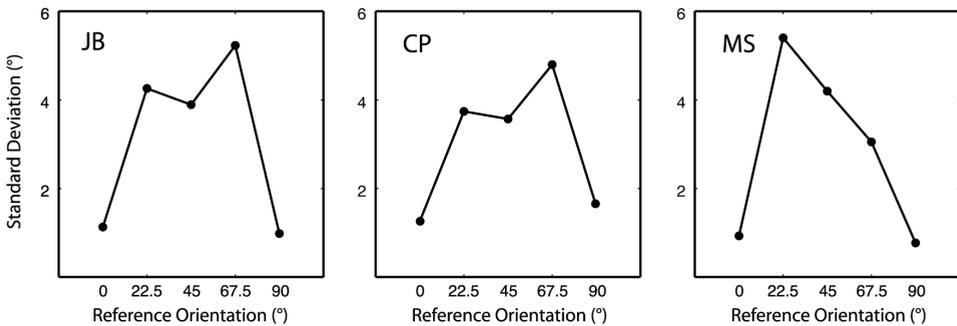


**Figure 6. Stimulus shift.** Reference stimuli are shown in grey, test stimulus is shown in black. A) The test stimulus rotated  $45^\circ$  counter-clockwise but not translated on screen. B) A clockwise rotation of  $45^\circ$  with a translation. This stimulus shift was introduced to force observers to attend overall stimulus orientation instead of attending only to the location of one of the stimulus dots.

Our variable of interest is the standard deviation of the adjustment errors, i.e., the standard deviation of the difference between the observer-adjusted test stimuli and reference stimuli for each condition. When observers were convinced that the test stimulus had the same orientation as the reference stimulus they pressed the space bar to start the next trial. A total of 30 trials was collected for each reference stimulus orientation.

## 2.8 Results experiment 1

Experiment 1 was designed to test for the existence of an oblique effect using dot stimuli. As described earlier, a two dot ‘line’ stimulus was presented in various orientations. The results are shown in figure 7. As expected, the lowest standard deviations of the adjustment errors were found for the cardinal object orientations (i.e.,  $0^\circ$  and  $90^\circ$ ) while the highest standard deviations were found for the oblique object orientations (i.e.,  $22.5^\circ$ ,  $45^\circ$ , and  $67.5^\circ$ ). Standard deviations ranged from  $0.77^\circ$  for the cardinal orientations to  $5.4^\circ$  for the oblique orientations. For each observer both  $0^\circ$  and  $90^\circ$  differed significantly from all oblique orientations (Levene test for equality of variances,  $p < .001$ ). The results from Experiment 1 indicate that there is an oblique effect for dot stimuli. The lowest standard deviations are found for the cardinal object orientations for each observer (i.e. horizontal/vertical orientations), while the highest standard deviations are found for the oblique object orientations. This means that we can proceed with Experiments 2 and 3 where we test whether the human visual system applies the aforementioned strategy of selecting optimal (horizontal and vertical) object information to determine object orientation.



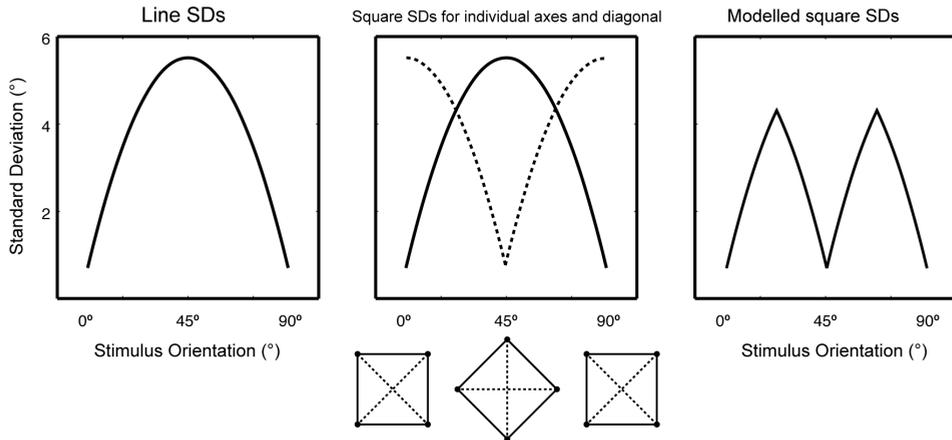
**Figure 7. Results experiment 1.** Individual data for three subjects are shown. SDs are plotted on the y-axis, the x-axis shows the orientation of the reference stimulus.

## 2.9 The model

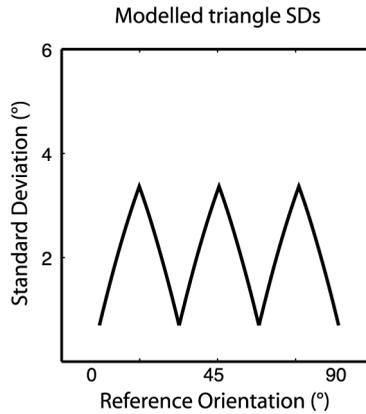
To simulate a strategy that optimally selects object features based on their orientation, and to test our hypothesis of an optimized orientation judgment system, we constructed a model based on the data obtained in experiment 1. Here, a winner takes all strategy is simulated to determine which object feature best predicts global object orientation. We have fitted the data of experiment 1 with a quadratic fit, and used the resulting parabola to model observers’ performance from experiment 1, i.e. for two-dot stimuli. The horizontal and vertical positions of the parabolas’ vertex are determined by the data from Experiment 1. The

horizontal position of the vertex is determined by the reference orientation in Experiment 1 yielding the highest SD (the 45° condition), and the height of the vertex is determined by the SD corresponding to this reference orientation.

For each orientation of a given dot stimulus the model then estimates which combination of stimulus dots or axes of symmetry yields the lowest SD. This lowest SD is then selected by the model to represent the modelled threshold for the global stimulus orientation. Since the lowest SD determines the modelled threshold for a given stimulus orientation, this is termed a winner takes all strategy. Figure 8 shows the modelled threshold for a dot square, based on the threshold data from Experiment 1.



**Figure 8. Modelled thresholds for a square using a winner takes all approach.** The first graph shows SDs for a two dot 'line' stimulus, low SDs when this stimulus is either 0° or 90°, and higher SDs when the stimulus is oblique. The solid line in the second graph shows SDs for the horizontal and vertical axis of symmetry of a square, with low SDs when the orientation of this axis is 0° or 90°, and higher SDs when the orientation of this axis is oblique. The dashed line in the second graph represents SDs for the diagonal of the square. When the square is oriented 45°, SDs for the diagonal are low, and when the square is 0° or 90°, SDs for the diagonal are higher. The final third graph represents the modelled graph for a dot square. For each orientation of the square, SDs are plotted that yield the highest orientation discrimination accuracy, i.e., lowest SDs.



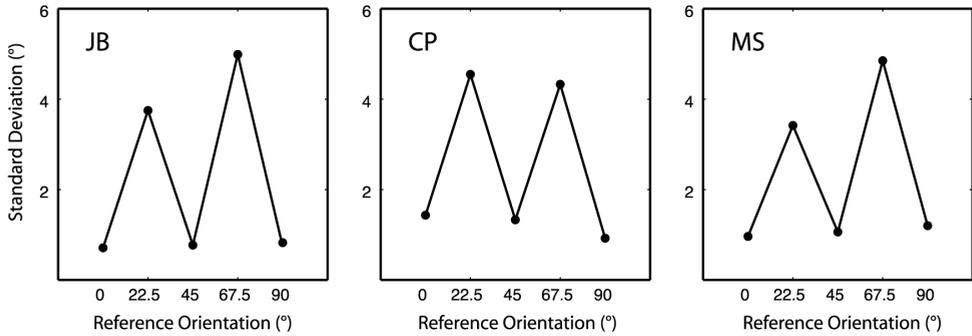
**Figure 9. Modelled triangle SDs using a winner takes all approach.**

Figure 9 shows the model's thresholds for the triangle stimulus, obtained similarly as the modelled threshold curve for the square. We then ran Experiments 2 and 3 to see if the model is an appropriate description of the observer's behavior.

## 2.10 Experiments 2 and 3

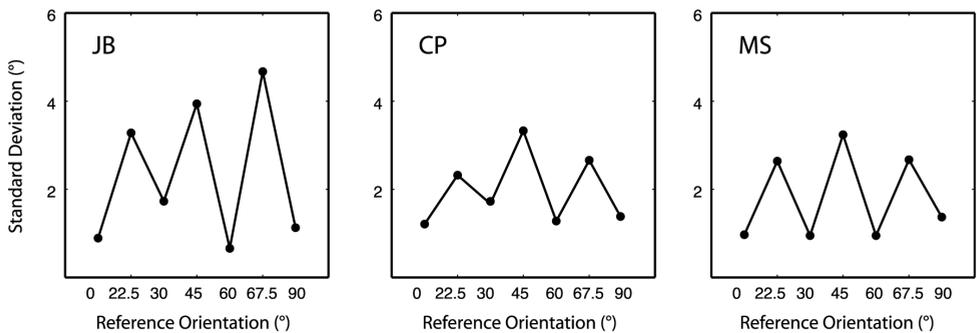
The same conditions from Experiment 1 were applied to both Experiments 2 and 3. Experiments 2 and 3 consisted of a four dot square stimulus and a three dot equilateral triangle stimulus, with sides measuring  $4^\circ$  for both the square and triangle stimulus. We will refer to these stimuli as the square and triangle stimuli, respectively. In each trial the square had an orientation randomly chosen out of 5 standard orientations ( $0^\circ$ ,  $22.5^\circ$ ,  $45^\circ$ ,  $67.5^\circ$ , and  $90^\circ$ ). Similarly, the triangle had an orientation randomly chosen out of 7 standard orientations ( $0^\circ$ ,  $22.5^\circ$ ,  $30^\circ$ ,  $45^\circ$ ,  $60^\circ$ ,  $67.5^\circ$ , and  $90^\circ$ ), in which the  $0^\circ$  orientation had the triangle pointing upwards. Orientations of the square were chosen such that in three of the square orientations the sides, the axes of symmetry, or the diagonals were either horizontal or vertical. For the triangle stimulus four orientations were chosen such that one of the sides and one of the axes of symmetry was aligned with either the horizontal or the vertical. Also, three orientations were chosen such that the sides and the axes of symmetry were oblique. Experiments 2 and 3 were designed to find out whether observers select object information lying closest to the horizontal/vertical in order to determine global object orientation. As described earlier, a 'square' and a 'triangle' stimulus were presented in various orientations. Results for Experiment 2 are shown in Figure 10, lowest SDs were found not only for the  $0^\circ$  and  $90^\circ$  object orientations, but also for the  $45^\circ$  object orientation. SDs range from  $0.71^\circ$  for the  $0^\circ$ ,  $45^\circ$ , and  $90^\circ$  object orientation, to  $4.9^\circ$  for the  $22.5^\circ$  and  $67.5^\circ$  object orientation, a

similar order of magnitude as in Experiment 1. For each observer the SDs for the 0°, 45°, and 90° object orientations (in which at least one of the object axes was horizontal/vertical) were significantly lower than for the oblique object orientations (Levene test for equality of variances,  $p < .01$ ).



**Figure 10. Results for the square stimulus experiment 2.** Individual data for three subjects are shown. SDs are plotted on the y-axis, the x-axis shows the orientation of the reference stimulus. Observers show a significant increase in orientation matching for the 45° reference orientation.

Results for Experiment 3 are shown in Figure 11. SDs range from 0.9° to 4.6°. Although there are individual differences, a pattern similar to that found in Experiment 2 emerges: low SDs for the 0°, 30°, 60°, and 90° object orientations and higher SDs for the 22.5°, 45°, and 67.5° object orientations. For observers JB and MS the SDs for the 0°, 30°, 60°, and 90° object orientations (in which at least one of the object axes was horizontal/vertical) were significantly lower than for the oblique object orientations (Levene test for equality of variances,  $p < .01$ ). For observer CP this was not the case for the 30° object orientation, which did not differ significantly from the SDs for the oblique object orientations.



**Figure 11. Results for the triangle stimulus Experiment 3.** Individual data for three subjects are shown. SDs are plotted on the y-axis, the x-axis shows the orientation of the reference stimulus. Observers show a significant

increase in orientation matching performance for the 30° and 60° reference orientations, with the exception of observer CP for the 30° reference orientation.

The results of Experiments 2 and 3 show that observers are more precise in judging object orientation for orientations in which either the object axis of symmetry or the side is horizontal/vertical. The low SDs when the stimulus' sides are either horizontal or vertical (0° and 90°), and when the axis of symmetry is either horizontal or vertical illustrate that observers indeed apply a strategy that favors information closest to the horizontal/vertical. Observers determine an object's orientation based on object information that allows for the highest orientation precision.

## **2.11 General discussion**

In three experiments we investigated how the human visual system determined global object orientation. More specifically, we studied whether this orientation judgment system behaves in an optimal fashion, as previously reported by Schräter and Kersten (2000) and Ernst and Bühlhoff (2004) for depth cue integration and the modality specificity hypothesis respectively. When multiple object features are present, does the visual system always select object features that allows for the highest precision in an orientation judgment task?

Observers were asked to adjust the fronto-parallel orientation of a test stimulus to a reference stimulus in three experiments. All three experiments involved the method of adjustment, with the variable of interest being the standard deviation of the difference between the adjusted test stimulus and the reference stimulus. We indeed found that the visual system always selects object information that allows for the highest orientation matching precision. That is, axes or sides lying closest to the horizontal/vertical are selected to determine an object's orientation.

In Experiment 1, which was designed to validate our dot stimulus, we found a convincing oblique effect. Standard deviations of the errors for the oblique stimulus orientations were significantly greater than for the horizontal/vertical orientations. This is a replication of an experiment by Westheimer (2003), in which the author showed a convincing oblique effect for virtual line segments, with small circles demarcating the endpoints, indicating that overt oblique line segments (i.e. line segments whose contours are defined by luminance contrast) are not a necessary condition for the oblique effect. The data we obtained in Experiment 1 were then used to construct a winner takes all model. This model was used to predict an ideal observer's performance on our adjustment task for the four dot square stimulus, and the three dot triangle stimulus we used in Experiments 2 and 3.

Observers' performance in Experiments 2 and 3 closely resembled the simulated optimal strategy and showed that observers indeed perform the task using object features oriented closest to the horizontal/vertical. Observers showed high task precision for all ob-

ject orientations in which object features were present that were horizontal/vertical, and showed low precision for all object orientations in which object features were oblique. This strategy of always selecting object information lying closest to the horizontal/vertical might suggest that the visual system has prior knowledge about the sensitivity with which object orientation is perceived, and selects available object features accordingly.

Our findings fit in with results obtained by Schräter and Kersten (2000), and Ernst and Bühlhoff (2004) as described in our Introduction. Their findings suggest a general principle that governs the human sensory system when dealing with situations in which multiple sources of (conflicting) information are present. Our experiments show that in determining object orientation, object information is weighed in accordance with its informativeness. Horizontal/vertical object information yields the highest precision in orientation discrimination, and is thus weighed accordingly. Additionally, our findings reflect a coping mechanism of the visual system to deal with the neuronal orientational sensitivity anisotropies as reported in visual areas as low as V1 and V2.

One caveat of our experiments and the stimuli we used is that two-dimensional stimuli may not necessarily generalize to real world (three-dimensional) objects. The optimization strategy of the visual system we report may therefore not directly translate to real-world, 3D object orientations. However, since observers only manipulated the fronto-parallel orientation of our stimulus, we have no reason to suspect differences between fronto-parallel orientation matching for the stimulus we used and three-dimensional objects.

Our findings of an oblique effect using dot stimuli has a further, neurophysiological implication pertaining to the discussion whether the oblique effect originates solely in V1, or extends to visual areas beyond V1. Research by Merigan, Nealey, and Maunsell (1993) suggests a strong role for V2 in the perceptual grouping of objects. Since the stimuli we used in our experiments are dot stimuli, which have to be grouped in order to be judged orientationally, and grouping of these dot stimuli presumably takes place in V2, the origin of the oblique effect seems to extend beyond V1. The study of Merigan et al. (1993) indicate dramatic reductions in feature grouping of dot stimuli when V2 is lesioned in macaque. Macaques were presented with a task that involved the discrimination of the orientation of two parallel lines of five colinear dots each. Orientation of the parallel lines was either horizontal or vertical, with the number of background masking dots controlled with a one-up one-down staircase. Macaques had to push either the left button for horizontal parallel lines, or the right button for vertical parallel lines. Results indicate a threshold reduction for the number of background masking dots when lesions in V2 are applied. Colinearity detection is therefore disrupted by V2 lesions, indicating the role V2 plays in perceptual grouping. The findings of Merigan et al. (1993) are supported by a study by Woelbern, Eckhorn, Frien, and Bauer (2002). Woelbern et al. (2002) supply more evidence suggesting the role V2 plays in perceptual grouping and figure-ground segregation. In a figure-ground task in which a rhesus monkey had to indicate whether two parallel rows of blobs were present amidst distractor blobs, neuron activity in V2 was recorded. Only in the frequency band (35–90 Hz)

did the authors find a highly significant effect in V2: a short phase-coupling before correct perceptual responses. These are first indications that a short synchronous burst in V2 may support perceptual grouping and figure-ground segregation.

However, the already mentioned study by Furmanski and Engel (2000) shows that fMRI responses only in V1 and not V2 were reliably greater for cardinal oriented gratings than for oblique gratings. This can be reconciled with our current findings by what Neumann & Sepp (1999) term recurrent processing. Neumann and Sepp proposed a computational model for recurrent contour processing between V1 and V2, in which normalized activities of orientation selective contrast cells are fed forward to a next processing stage, forming a context-dependent gain control mechanism. The sensitivity anisotropies of orientation selective cells in the first stage (V1) would therefore propagate to the second stage (V2), without the orientation selective cells in V2 having to display the same orientation anisotropies as the cells in the first stage. In other words, characteristics of V1 neurons are fed forward to visual areas higher in the cortical hierarchy, without neurons in these higher areas having to display these specific characteristics themselves.

Further evidence suggesting the importance of recurrent processing is supplied by a study by Hupé et al. (1998). They studied the role of feedback connections in macaque area MT/V5. When area MT/V5 was inactivated by cooling, a substantial decrease in single neuron activity was found for cell responses to an optimally oriented moving bar in areas V1, V2, and V3. Results from a second experiment, where a moving bar on a stationary background was used, showed that feedback connections from area MT/V5 have a facilitatory effect on the responses of neurons in areas V1, V2, and V3.

So, in sum, we have shown in three experiments that observers always use object features in orientation discrimination that allow for the highest precision in determining object orientation. The weight the visual system attaches to these object features is in accordance with the precision with which this information is perceived.

**Acknowledgments.** This work was supported by the Netherlands Organization for Scientific Research (NWO Pionier).

# Chapter 3

A dichoptic study of the oblique effect



### 3.1 Abstract

The oblique effect is a decreased sensitivity for oblique orientations compared to horizontal/vertical orientations. We investigated whether orientation-matching acuity for binocularly presented stimuli is dependent on orientations of retinal projections or on the perceived orientation of the stimulus. Using a stereoscope, we constructed a stimulus, such that retinal orientations were oblique, while the perceived orientation was vertical. We then used this stimulus to test observers in an orientation-matching task. If orientation matching depends on the orientations of retinal projections, low matching performance would be expected, since retinal projections are oblique. However, if orientation matching depends on perceived orientation (vertical), high matching performance would be expected. We found that observers' performance can only be predicted from the perceived orientation, not the orientations of retinal projections, implying that in binocular viewing the oblique effect occurs after binocular fusion.

### 3.2 Introduction

The way in which we perceive our environment is, to a certain extent, determined by characteristics of the senses that translate outer world information and send this translated signal onwards into the cortex for further processing. For example, we can not see in the infrared or ultraviolet spectrum simply because photoreceptors in our retinæ are not equipped to process light of these wavelengths. Similarly, our hearing is limited to a particular frequency domain (roughly 20-20000 Hz) as a direct result of characteristics of our peripheral auditory system. Additionally, some features of sensory information processing are determined by neuronal characteristics of low-level visual areas, such as V1. Here, more neurons are tuned to horizontal/vertical orientations than to oblique orientations. As a result, the human visual system is much more sensitive to small orientational differences along the cardinal axes (i.e. horizontal/vertical) than along oblique axes, where oblique refers to any orientation that is not horizontal or vertical. This oblique effect has been reported in various behavioural studies in man (e.g. Appelle 1972; Essock 1980; Furmanski and Engel 2000; Vogels and Orban 1986) and in animals (Coppola et al 1998; Emerson 1980). Not only in the visual domain, but in the haptic domain as well (Luyat et al 2001; Essock et al 1992; Kappers 2002). That this orientation anisotropy also arises in the haptic modality, and not just in vision, suggests that the increased sensitivity for horizontal/vertical orientations might be based on a general characteristic of human sensory processing, at least in the visual and haptic domains.

The exact cause of this anisotropy in orientation sensitivity of the human visual system remains a topic of debate. That more neurons prefer orientations along horizontal/vertical axes has been established (e.g. Furmanski and Engel, 2000; Wang, Ding, & Yunokuchi, 2003),

but the reason why our visual system has developed in such a fashion is not clear.

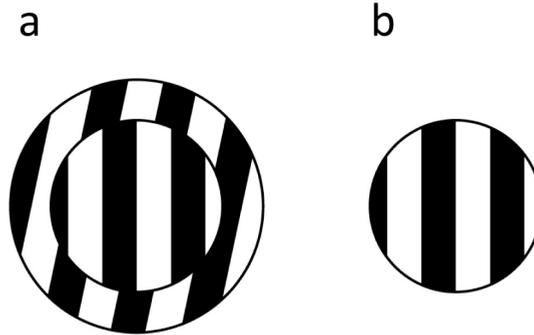
Early theories sought to find the cause of the oblique effects in eye movements, suggesting that mechanical properties of the eye-muscles might be a contributing factor to the oblique effect. However, Higgins and Stultz (1950), showed that preferential vibrations of the eye in the horizontal and vertical planes cannot account for the oblique effect, since the oblique effect persists even during stimulus presentation times under 1 ms, which is too short to make eye movements. A further argument against the role of eye movements as a contributing factor to the oblique effect was put forth by Becker and Jürgens (1990), who found no difference in saccade accuracy along either the oblique or cardinal axes.

Since the structure of the outside world is known to influence cortical circuitry, for example, kittens reared in an environment devoid of any horizontal orientations fail to develop cells that are tuned to horizontal orientations (e.g. Daw & Wyatt, 1976), a plausible explanation for the oblique effect may be found in the distribution of contour orientations in our surroundings. This has indeed been reported by Coppola, Purves, McCoy, and Purves (1998), who found an increased number of vertical and horizontal orientations in indoor, outdoor, and natural settings. This increased stimulation of the visual system by horizontal/vertical contours may very well contribute to the phenomenon that our visual system is much more sensitive to horizontal/vertical contours than to oblique contours. Recent research suggests that these orientational anisotropies are found early along the pathways of visual information processing, as low as primary visual cortex (V1; Furmanski & Engel, 2000).

### 3.3 Perceived versus physical orientation

In most cases, there exists a direct relationship between what is perceived and what is projected on the retina. An object that is projected on the retina with a fronto-parallel orientation of  $45^\circ$  will be perceived as having an orientation of  $45^\circ$ . However, in some special cases, a discrepancy exists between an orientation that is perceived, and the actual orientation of the retinal projection. The relationship between retinal stimulus orientations and perceived orientations was investigated by Meng and Qian (2005). They showed that orientation acuity depends on the perceived orientation of a stimulus axis, rather than on the orientation of retinal projections of the stimulus. One way to induce a difference between a perceived orientation and the orientation of the retinal projection is to make use of an illusion called the simultaneous tilt illusion (STI). In this illusion, an oriented grating is surrounded by a differently oriented grating, as illustrated in figure 1. Although the retinal projection of the inner grating is  $90^\circ$  in both panels, the perceived orientations of the inner grating in figure 1a and the grating in figure 1b differ. Meng and Qian reported that, in accordance with the oblique effect, orientation discrimination is always better when the inner grating is perceived more vertically than obliquely. Their results indicate that, at least in the special case of the simultaneous tilt illusion, orientation discrimination is determined by

perceived, rather than physical, orientation (Meng & Qian, 2005).



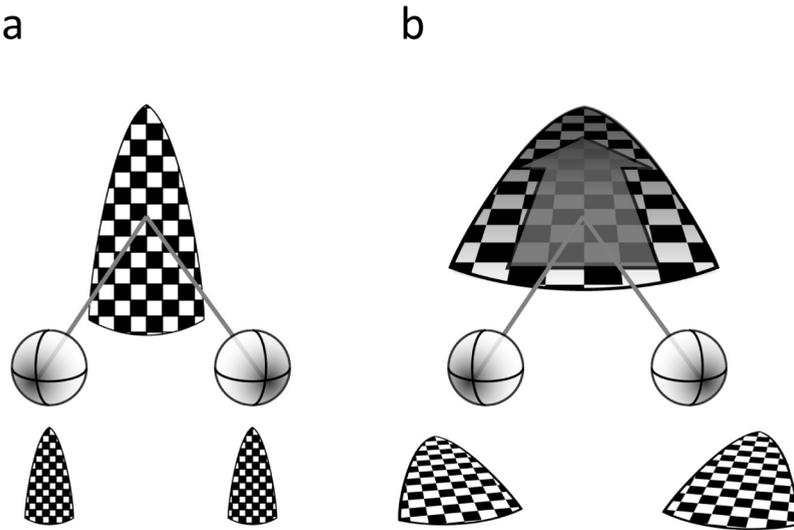
**Figure 1. Simultaneous tilt illusion (STI).** A) Inner-grating orientation is  $90^\circ$ , with an outer-grating of  $107^\circ$ . The perceived orientation of the inner grating shifts away from the outer grating. B) A grating with an orientation of  $90^\circ$ .

A similar conclusion was reported by Adam and Mamassian (2002), who investigated how monocular and binocular adaptation influence the phenomenon known as the tilt aftereffect (TAE). The TAE occurs when looking at a nonvertically oriented stimulus for an extended period of time and subsequently viewing a vertical stimulus, which then appears rotated in the opposite direction. Again, a discrepancy arises between the actual stimulus orientation as it is projected on the retina, and the orientation that is perceived. Adams and Mamassian showed that, for two out of three observers, monocular adaptation to a nonvertically oriented Gabor patch (either  $-3^\circ$  or  $+3^\circ$ ) produced larger TAEs than when the same patches were presented binocularly (with  $-3^\circ$  to the right eye and  $+3^\circ$  to the left eye) and were perceived as having zero tilt. In other words, perceived orientation influences TAEs, regardless of the orientations of retinal projections. One of the questions that arises from the above-mentioned studies is how the visual system handles orientation information projected onto the retina. The mentioned studies seem to point to a preference of the visual system, at least in judging orientation, to act on a perceived orientation, rather than on the orientation of a retinal projection. In the current study we examine this hypothesis by making use of a different and real-life scenario where an orientational discrepancy exists between what is perceived and what is projected.

### 3.4 Orientation discrimination for binocularly viewed objects

When navigating through a three-dimensional world, differences between corresponding image features in the two eyes occur as a result of the horizontal separation of the eyes. These differences are called binocular disparities, and lead to an interesting situation for

vertical objects with slant, as illustrated in figure 2. Slanted vertical objects project with fronto-parallel orientational differences onto each retina. Figure 2a shows a vertically oriented object, without slant, and the projections of this object onto both retinas. The two projections have more or less the same vertical orientation. However, a vertically oriented object slanted backward in depth (figure 2b) and positioned directly in front of an observer will project obliquely in the frontoparallel plane onto both retinas. So for everyday situations, and not induced by controlled lab settings, differences between the orientation of an object's retinal projection and its perceived orientation occur as well.



**Figure 2. Object orientations and their projections onto the retina.** A) A vertical object without slant and the two corresponding retinal projections. B) the same object, slanted backwards  $60^\circ$ . This illustrates an orientation difference in the frontoparallel plane between an object with a vertical orientation and slanted backwards in depth and the corresponding retinal projections. Both projections have oblique orientations, whereas the physical object itself has a vertical orientation.

The object of the current study is to investigate whether orientation acuity for binocularly viewed stimuli is determined by the orientations of retinal projections or by their perceived orientation. We test this hypothesis by making use of the aforementioned oblique effect, the decreased sensitivity for oblique orientations as compared to horizontal/vertical orientation. If the orientation of an object's retinal projection is oblique, and its perceived orientation is vertical, then the orientation acuity for this object will be informative as to which orientation source (perceived vs. retinal orientation) the visual system acts on to determine orientation.

Additionally, the outcome of this experiment will also allow us to localise the oblique

effect for binocular vision, that is whether it occurs before or after binocular fusion. If orientation matching is determined by the orientation of retinal stimulus projections, then the oblique effect has its origin before binocular fusion. But, if orientation acuity is determined by the perceived orientation of the stimulus, then the oblique effect occurs after binocular fusion. In other words, is orientation acuity for binocularly presented stimuli dependent on the orientations of retinal projections, or on the perceived orientation of the stimulus?

### 3.5 Experiment 1

In order to determine whether the visual system acts on retinal or perceived orientation we need to make certain that for our stimuli a difference in performance of orientation matching will arise from the perceived versus the retinal projections. In other words, the difference in sensitivity of the visual system for what is perceived and what is retinally projected must be sufficiently large to be able to be measured. Ideally, a stimulus is required with a difference in retinal orientation versus perceived orientation, either with an oblique perceived orientation and vertical retinal orientations, or oblique retinal orientations and a vertical perceived orientation. As mentioned in section 3.4, when an object is vertical, slanted backwards in depth, and placed directly in front of an observer, its retinal orientations will be oblique, but its perceived orientation will be vertical. We therefore constructed our stimulus so that it projected obliquely on both retinae, resulting in a vertical perceived orientation. To distinguish whether the visual system uses retinal or perceived object orientation, we need to determine thresholds for these stimuli containing no binocular disparity. The reference orientation closest to  $0^\circ$  that produces a significant decrease in orientation-matching performance compared to the  $0^\circ$  condition can then be used to construct our stimulus for experiment 2, simulating an object with a vertical orientation and backward slant. We chose to use dot stimuli instead of line stimuli because it prevents interference of local and global stimulus contours, and enables comparisons with previous studies into the oblique effect with dot stimuli (Borra et al, 2007). Li and Westheimer (1997) have shown that thresholds for detecting the angle of rotation for stimuli containing contours without luminance contrast (using a stimulus consisting of two dots) were almost as low as those for an actual vertical line. They dubbed this implicit orientation discrimination. This lends further support for our choice to use dot stimuli.

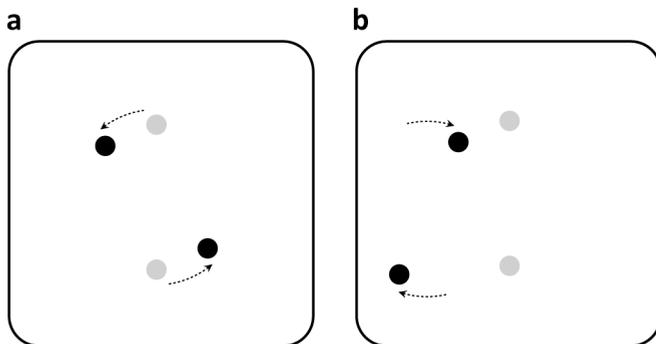
### 3.6 Methods

Three observers took part in experiment 1; two were experienced in visual psychophysics experiments, and one (TB) was an author. The age range of the observers was 25 - 38 years and all had normal or corrected-to-normal vision. The stimuli consisted of two dots,

with each dot measuring 0.53 deg in diameter and having a luminance of 25.2 cd m<sup>2</sup>. The distance between the dot centres was 7°. The stimuli were generated by an Apple Macintosh dual 867 MHz G4 PC with Psychophysics Toolbox extensions (Brainard 1997; Pelli 1997), and displayed on a luminance-linearised 22 inch LaCie Blue Electron monitor at 85 Hz. Dichoptic presentation was achieved by means of a mirror stereoscope. Observers looked straight-ahead using a chin-rest, with a viewing distance of 57 cm to the computer screen. The experiment was performed in a dark room. Each trial started with a reference stimulus simultaneously presented to each eye for 1000 ms. The orientation of this stimulus was randomly chosen out of five orientations: 0°, 4°, 6°, 8°, and 10° (with no binocular disparity).

After 1000 ms, a white circular mask appeared for 1500 ms, followed by the test stimulus. The mask was used in order to cancel phosphor persistence of the reference stimulus on the monitor. The test stimulus was rotated by a random angle clockwise or counterclockwise with respect to the reference stimulus. Observers were instructed to adjust the frontoparallel orientation of the test stimulus to the reference stimulus by pressing the 5 key or the 6 key (counterclockwise and clockwise rotation respectively, with large steps of 1.8°) or the 2 key or the 3 key (small steps of 0.25°). Before starting the actual experiment, observers were asked to adjust the horizontal position of both stimuli to a setting in which binocular fusion was comfortable.

To ensure that dot location was not informative as to the orientation of the test stimulus, a stimulus shift was introduced: the position of the test stimulus was translated by a random distance (from 1.42 deg to 2.14 deg) horizontally and vertically with respect to the reference stimulus. Figure 3 illustrates this stimulus shift.



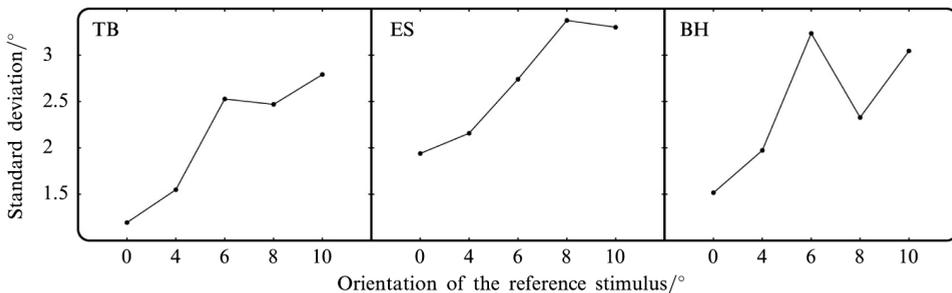
**Figure 3. Test stimulus translation.** Reference stimuli are shown in grey, test stimulus is shown in black. A) the test stimulus is rotated 45° counterclockwise but not translated on screen. Without a shift of the stimulus, the location of the dots is informative with regard to the orientation of the test stimulus. When the upper dot of the (black) test stimulus is shifted to the left, this corresponds to a counterclockwise rotation of the test stimulus. B) The test stimulus is rotated clockwise 45° with a translation. With the introduction of this stimulus shift, the location of the dots is no longer informative with regard to the overall stimulus orientation. In this case a shift of the upper dot of the test stimulus (black) does not correspond to a counterclockwise rotation of the test stimulus.

Since oblique stimulus orientations are adjusted with less precision, this is reflected in the standard deviations of the adjusted test stimuli. Large standard deviations indicate low acuity and small standard deviations indicate high acuity (Borra et al., 2007). The variable of interest, therefore, is the standard deviation of the adjusted test stimuli. Any bias in the adjusted test stimuli would be evident in their mean.

When observers were convinced that the test stimulus had the same orientation as the reference stimulus they pressed the space bar to start the next trial. A total of 50 trials was carried out for each reference-stimulus orientation. The average session typically lasted around 20 min.

### 3.7 Results and discussion experiment 1

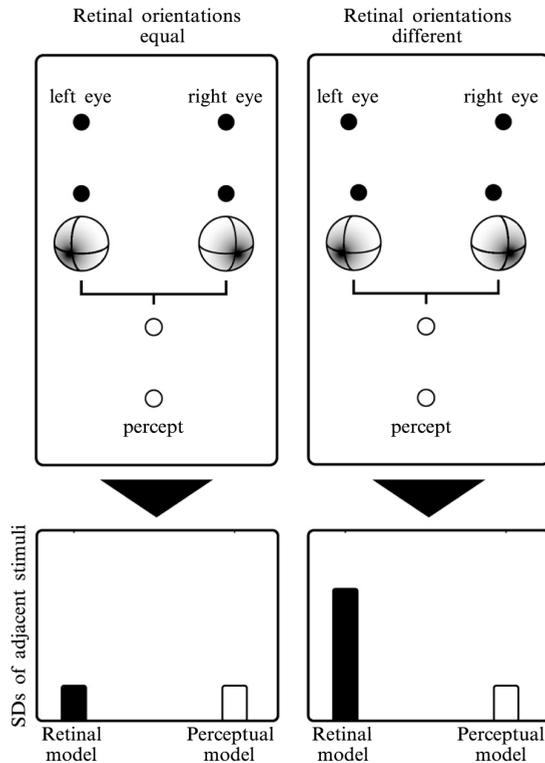
Figure 4 shows the results of experiment 1. A reference orientation as small as  $6^\circ$  produces a significantly higher standard deviation in orientation matching than the  $0^\circ$  reference orientation for each observer (Levene test for equality of variances,  $p < .001$ ). Matching performance for all observers was significantly lower in the  $6^\circ$  condition than in the  $0^\circ$  condition. To err on the side of caution we chose to use the  $8^\circ$  stimulus orientation in experiment 2.



**Figure 4. Results Experiment 1.** Standard deviations (SDs) for the adjustments of the test stimulus are shown as a function of the orientation of the reference stimulus. The three observers show an increase in SDs as the reference orientation shifts away from  $0^\circ$ , indicating low orientation-matching acuity. A significant decrease in matching acuity is found for reference orientations as low as  $6^\circ$ .

Figure 5 shows two predictions for the outcome of experiment 2, one in which binocular orientation matching is determined by the frontoparallel orientation of retinal projections (the retinal model) and one in which matching is based on the perceived frontoparallel orientation (the perceptual model). The retinal model predicts that binocular orientation

matching is determined by retinal projections. Vertical retinal projections lead to low SDs in orientation matching, whereas oblique retinal projections lead to high SDs. The perceptual model predicts that binocular orientation matching is determined by the perceived frontoparallel orientation. If the perceived frontoparallel orientation is vertical, orientation matching results in low SDs, even when the images projected onto the retinae are oblique. Experiment 2 was designed to test which of the two information sources the visual system uses to determine object orientation under binocular viewing conditions: orientations of retinal projections or orientation of the percept. To disentangle these two separate sources, a stimulus was required with oblique retinal projections and a vertical perceived orientation. As shown in figure 2, a vertical object slanted backwards in depth produces the desired stimulus.



**Figure 5. Two models predicting orientation processing.** In the retinal model orientation acuity is determined by the retinal orientation of stimulus projections. In the perceptual model orientation acuity is determined by the perceived orientation of a stimulus. The upper part shows the stimuli as presented to each eye individually, with the frontoparallel orientation of the corresponding percept shown directly below. The left side of the figure shows a condition in which the orientations of retinal stimulus projections are equal for both eyes, and the right

side shows a condition where the orientations of retinal stimulus projections for both eyes are different. Orientation acuity predictions for the two conditions are shown at the bottom.

Since oblique object orientations result in higher SDs (reflecting lower orientation acuity) and horizontal/vertical object orientations result in lower SDs (reflecting higher orientation acuity), the results of this experiment will tell us if the orientation used to determine object orientation (perceptual or retinal) was oblique or vertical. Table 1 shows the conditions used in experiment 2. The first three conditions give the baseline for matching acuity, and contain no differences between perceived orientations and the orientations of retinal projections. Condition 4 is crucial in this experiment, since perceived orientation is vertical, whereas the orientation of the retinal projections is oblique. If the perceived orientation is used SDs will be low, reflecting high orientation acuity. However, if the orientations of the retinal projections determine orientation acuity (oblique for condition 4), then this will result in high SDs (low orientation acuity). Conditions 5 and 6 contain perceived orientations that are identical to conditions 2 and 3, while retinal projections are  $-16^\circ$  and  $0^\circ$  (condition 5) and  $0^\circ$  and  $16^\circ$  (condition 6). The experimental setup and the task for experiment 2 was the same as for experiment 1, with the conditions used shown in table 1. A binocularly viewed dot stimulus was presented to the observer, with the stimulus in each trial having an orientation randomly chosen out of the six conditions shown in table 1.

**Table 1.** Conditions for experiment 2.

	Condition/ $^\circ$ orientation					
	1	2	3	4	5	6
Eye						
left eye	0	-8	8	-8	-16	0
right eye	0	-8	8	8	0	16
Perceived frontoparallel orientation	0	-8	8	0	-8	8

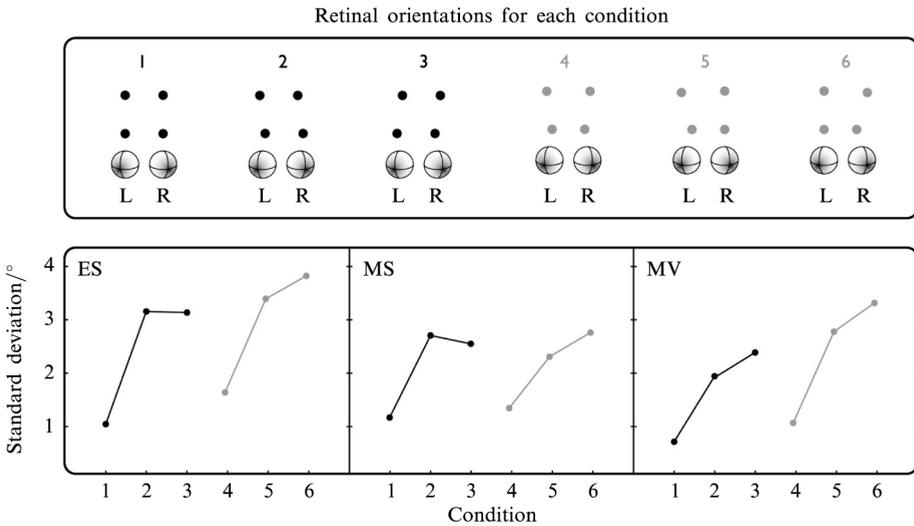
**Table 1.** Conditions for experiment 2.

### 3.8 Results and discussion experiment 2

The results are shown in figure 6. A reference orientation of  $0^\circ$  and no difference between perceived orientation and retinal projections (condition 1) produces low SDs, indicating high matching acuity. As expected, reference orientations of  $-8^\circ$  and  $+8^\circ$  produce higher SDs, indicative of lower matching acuity. This is a standard oblique effect: a decrease in matching acuity when the orientation of the reference stimulus shifts away from  $0^\circ$ . Refer-

ence orientations as small as 8° produce a significant oblique effect with dot stimuli.

For conditions 4, 5, and 6, in which the perceived frontoparallel orientations are identical to conditions 1, 2, and 3, respectively, the same pattern emerges: lower SDs for condition 4, in which the perceived frontoparallel orientation is vertical but orientations of retinal projections are oblique, and higher SDs for conditions 5 and 6, in which both the perceived orientations and the orientations of retinal projections are oblique. This is a clear indication that for these three conditions, the perceived orientation predicts matching acuity. Matching acuity for conditions 4, 5, and 6 correlates with perceived frontoparallel stimulus orientation, rather than with the orientations of retinal projections. The orientation of the combined percept of left-eye and right-eye images is more accurately adjusted to a reference orientation than can be predicted from the orientations of individual left-eye and right-eye projections. The means of the adjustment distributions, which would indicate observers' matching biases, did not show any systematic deviations across observers. Furthermore, with the exception of observer ES, no significant difference in matching acuity arises between conditions 1 and 4. This indicates that matching acuity for a perceived vertical frontoparallel orientation (condition 4) is similar to matching acuity for a vertical retinal projection (condition 1).



**Figure 6. Experiment 2.** Retinal orientations for various conditions and the results of experiment 2. L = left eye; R = right eye.

### 3.9 General discussion

In two straightforward experiments, we investigated whether orientation judgment for binocularly presented stimuli is based on perceived or retinal orientations and, additionally, whether the oblique effect arises before or after binocular fusion.

The first experiment revealed that frontoparallel stimulus orientations as small as  $8^\circ$  are sufficient for an oblique effect to arise. Orientation acuity significantly decreases for stimuli with an orientation of  $8^\circ$  compared to vertical stimuli ( $0^\circ$ ). In experiment 2 we constructed a binocular stimulus with oblique retinal projections (based on the results from experiment 1), and a vertical percept. This difference between perceived orientation (vertical) and the orientations of retinal projections (oblique) allows us to determine whether the oblique effect arises before or after binocular fusion. If the oblique effect arises before binocular fusion, orientation acuity would be expected to be low, since the orientations of retinal projections are oblique. On the other hand, if the oblique effect arises after binocular fusion, then orientation acuity would be expected to be high, since the orientation of the percept is vertical. The results show that the oblique effect arises after binocular fusion, since matching acuity can only be predicted from the orientation of the percept, not from the orientations of retinal projections. The findings reported here are indicative of how frontoparallel orientations of binocularly presented stimuli are processed by the visual system, and how this relates to information projected onto the two retinas. Our findings are in accordance with previous studies by Meng and Qian (2005), and Adams and Mamassian (2001), who report that in cases where differences arise between perceived and retinal orientations, the visual system acts on the perceived orientation.

Implications of the current study for the physiological localisation of the oblique effect seem straightforward: for binocular orientation perception the oblique effect must occur after binocular fusion. Numerous studies have reported visual areas as low as V1 as the location of the oblique effect (Chapman and Bonhoeffer 1998; Coppola et al 1998; Furmanski and Engel 2000; Li et al 2003). Our finding that the oblique effect must occur after binocular fusion (under binocular viewing conditions) does not exclude V1 from being the point of origin of the oblique effect, since V1 is the first locus in the brain at which information from the two eyes converges, and encoding of binocular disparity is thought to begin in this region (Anzai et al 1997).

As mentioned above, the binocular stimulus used in experiment 2 has a perceived orientation that is different from the orientation of its retinal projections. Additionally, the stimulus also has a perceived interdot distance that is different from its frontoparallel interdot distance. Owing to the different left-eye and right-eye stimulus orientations, the stimulus is slanted backwards in depth, thereby substantially increasing the perceived interdot distance in 3-D space, while maintaining the original frontoparallel interdot distance from experiment 1. Numerous studies have shown that an increase in stimulus size in the frontoparallel plane increases orientation acuity (Essock 1990; Orban et al 1984). Since match-

ing acuity is determined by perceived stimulus orientation, it is conceivable that perceived stimulus size could also influence matching acuity to a certain extent. However, results of experiment 2 show that this is not the case. Even though perceived stimulus size is increased, matching acuity is not influenced by this size increase. Although perceived orientation influences matching acuity, perceived size does not seem to play a significant role in orientation matching.

Acknowledgments. This work was supported by the Netherlands Organization for Scientific Research (NWO Pionier).

# Chapter 4

Orientation perception of occluded objects  
is based on perceptually completed objects



## 4.1 Abstract

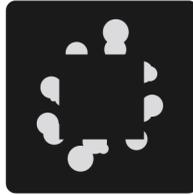
When we look at a scene, parts of objects may be occluded and only fragments of objects are represented on the retina. Yet, our perceptual experience is that of whole objects in their environment. Clearly, the visual system fills-in information; it integrates the visible and the occluded parts. Representing an object is important, but as humans often act upon objects, it is as important to represent the orientation of the objects. It is still unknown how the visual system determines the orientation of an object that only has a fragmented representation on the retina. Does it use information derived from visible local edges or does it use the perceptually completed object representation? We report an answer making use of the well known oblique effect, in which observers are better at judging vertical and horizontal orientations as compared to oblique ones. We used an orientation discrimination task with subjective contours (Kanizsa figure) that evokes the percept of a square but provides no direct retinal information for its orientation. The orientation discrimination thresholds that we found are predicted from a perceptually completed object representation and not from the directly available local contours.

## 4.2 Introduction

The natural world is full of objects and clearly our visual system is good at determining their location as well as their orientation. Processing elementary object attributes such as size, mass, and orientation occurs in an automatic fashion (Castiello, Lusher, Burton, & Disler, 2003), that is, without requiring conscious effort on the part of the observer. However, this seemingly trivial process is not as simple as it may seem. This is especially true when parts of objects are occluded by other objects, resulting in objects that are only partly represented at the retinal level.

Perceiving the unity of moving objects that are partly occluded is already apparent in four-month-old infants (Kellman & Spelke, 1983; Johnson & Aslin, 1996), and the ability to extrapolate the form of stationary, partially occluded objects is apparent in infants as young as 8 months old (Craton, 1996). Extrapolation of form is crucial to interact with objects that are partially hidden from view, as is evident when navigating through a three-dimensional world where objects are occluded by other objects. But how does the visual system process these hidden object parts? One mechanism by which the visual system keeps track of objects that are not in direct line of sight is selective attention. Increased activity in posterior parietal cortex has been linked to maintaining a spatial position of attentional focus (Serences & Yantis, 2007), which may be a mediating factor in keeping a spatially updated representation of an object that moves in and out of view (Shuwairi, Curtis & Johnson, 2007). Intriguingly, neuronal activity in posterior parietal cortex is actually increased during a period when a moving object is occluded (Assad & Maunsell, 1995). This posterior parietal cortex seems to

be part of an extended intricate neural network, uniquely involved in tracking objects when they are not in direct line of sight (Shuwairi, Curtis & Johnson, 2007). A similar situation arises when objects are only constructed at a higher level of visual information processing as is the case for subjective contour objects like the Kanizsa figure shown in figure 1 (e.g. Gold, Murray, Bennett & Sekuler, 2000). Here, a contour is perceived that is not projected on the retina. This contour does not exist in the outer world and arises as a result of the visual system filling in the gap between distinct edges (e.g. Ullman, 1976).



**Figure 1. Kanizsa square.** Even though nothing is projected on the retina, a vivid percept of a black square arises.

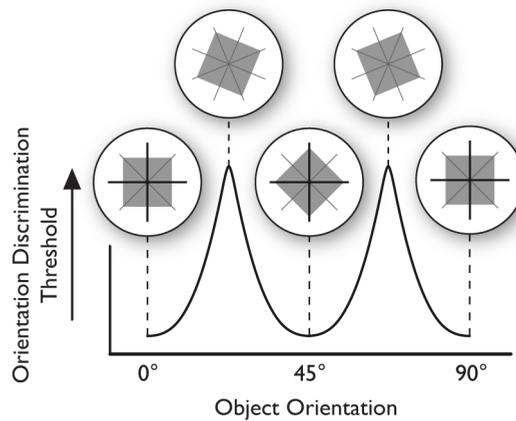
Studies done in alert monkeys show that orientation selective neurons in visual area V2 respond to a subjective contour in the same fashion as if it were a real contour, i.e. defined by luminance contrast (e.g. Von der Heydt, Peterhans & Baumgartner, 1984). A neural mechanism by which the visual system processes these subjective contours possibly involves feedforward signals from low-level visual areas and feedback signals from higher stages in the cortical hierarchy, integrating local features into subjective contours, resulting in perceived continuous forms (Seghier & Vuilleumier, 2006). In the current study, we examine how the visual system processes orientation information for figures consisting of subjective contours.

Recently, we designed a parsimonious paradigm to show that features of an object, such as axes and sides, can predict the accuracy with which the orientation of the entire object is determined (Borra, Hooge & Verstraten, 2007). Interestingly, these features can be luminance-defined (e.g. sides of objects), but can be axes within the object itself as well, i.e. not defined by luminance contrast and therefore not projected on the retina. This is in line with previous work done by Boutsen and Marendaz (2001), who report that orientation search asymmetry (a faster detection of an oblique object among vertical objects than the reverse) is not dependent on local contours (the sides of the objects), but instead, dependent on the orientation of a global axis.

We found that the visual system applies a specific strategy in selecting these object features, by always selecting object features that are oriented closest to the horizontal/vertical (figure 2). This strategy seems to follow from the observation that the visual system is much more sensitive for horizontal/vertical orientations than for oblique orientations. This

phenomenon is called the oblique effect (Appelle, 1972), and has been reported in both man and animal (e.g. Bonds, 1982; Emerson, 1980), and for the visual and haptic domains (e.g. Kappers, 2002). This anisotropy in orientational sensitivity has been linked to neurons in low-level visual areas, such as V1, where an increased number of neurons has a preferred orientation that lies close to the horizontal/vertical (Furmanski & Engel, 2000; Wang, Ding, & Yunokuchi, 2003; Yacoub, Harel & Ugurbil, 2008).

The preference of the visual system to select object features oriented along the horizontal/vertical axes reflects an optimization strategy. By always selecting those object features for which the visual system is most sensitive (i.e. horizontal/vertical orientations), the visual system optimizes object orientation processing. This optimization process resembles how the visual system integrates depth cues, where cue information is weighted in accordance with how informative these cues are (Schräter & Kersten, 2004). Similarly, Ernst and Bühlhoff (2004) describe a principle where conflicts in modality are resolved in favor of the more precise modality, the Modality Precision Hypothesis, suggesting that optimization processes such as those described above are general principles of human sensory information processing.

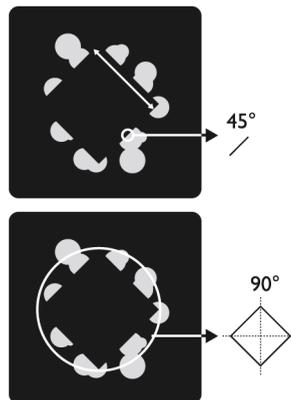


**Figure 2. Optimized object orientation determination.** An optimal strategy in selecting object features (sides/axes) is shown, allowing for the highest orientation discrimination precision. For each square orientation, features are selected that are closest to horizontal/vertical (shown in bold in the squares). This explains the trough in thresholds at the 45° square orientation, since the square contains horizontal/vertical axes of symmetry, and the visual system is more sensitive for horizontal/vertical information (the oblique effect).

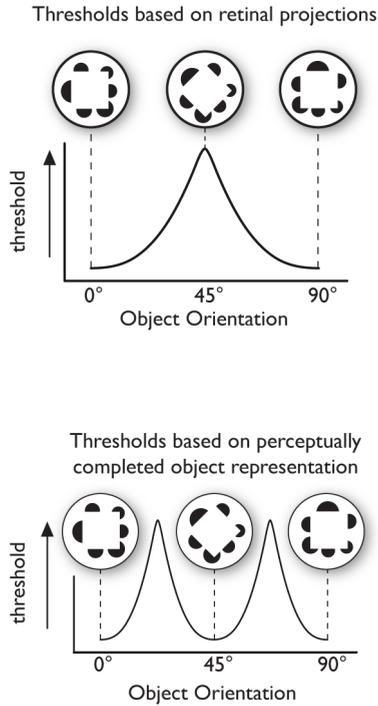
We wanted to find out whether the visual system uses the same optimization strategy in determining an objects' orientation for real objects, defined by luminance contrast, and subjective objects. In other words, is an object's perceived orientation determined by information available at the retinal level, or at a higher level of information processing: the

object's representation. How to measure this? Previously, we showed that object axes, that are not present in the retinal projection, can influence perceived object orientation (Borra et al., 2007), indicating that determining global orientation of an object occurs at a level where an object representation arises. If this same mechanism applies to Kanizsa-like objects, that consist of subjective contours, then one would expect that features of the perceptually completed object, and not of the retinal projection, influence global object orientation. This is illustrated in figure 3, where a Kanizsa square is shown. Local contours of the square, defined by luminance contrast, are all  $45^\circ$  oriented away from horizontal/vertical. If the visual system has access to only these local obliquely oriented contours, then one would expect low precision in an object orientation discrimination task, simply because the visual system is less sensitive to oblique orientations. Alternatively, if the visual system has access to an object representation, including associated object features (axes and sides) then, based on our previous work, one would expect the visual system to apply an optimization strategy by selecting the object features oriented closest to the horizontal/vertical. These different predictions are illustrated in figure 4.

In the current study, we use the oblique effect as a tool to investigate what object information is available to the visual system, and what strategy is applied in selecting object features.



**Figure 3. Local versus global contours in a Kanizsa square.** Local contours are all oriented  $45^\circ$  away from the horizontal/vertical (upper panel). Sides and axes of symmetry of a perceptually completed square are oriented either  $45^\circ$  or  $0^\circ/90^\circ$ .



**Figure 4. Orientation discrimination thresholds for Kanizsa squares.** Orientation discrimination thresholds based on either the orientation of retinal projections (upper panel), or on a perceptually completed object representation (lower panel).

### 4.3 Methods

#### Participants

Four experienced - but naive as to the purpose - observers (28 to 42 years old) took part in conditions 1 and 2.

#### Stimuli

In condition 1 we used a square (luminance  $\sim 25$  cd.m<sup>-2</sup>) with sides measuring 6.5° of visual angle on a dark background ( $\sim 2$  cd.m<sup>-2</sup>), with all edges clearly visible (figure 6, upper panel). For condition 2, the stimulus was only partly represented on the retina: an identical square, but presented equiluminant to the background ( $\sim 2$  cd.m<sup>-2</sup>), positioned on top of randomly arranged circles ( $\sim 25$  cd.m<sup>-2</sup>; diameter varying from .5° to 2°, figure 5, lower

panel).



**Figure 5. Stimuli.** Upper panel shows a real square with sides of  $6.5^\circ$  of visual angle, the bottom panel shows a Kanizsa square with the same dimensions, i.e. an illusory, subjective square where the sides are not defined by luminance contrast.

#### Procedure

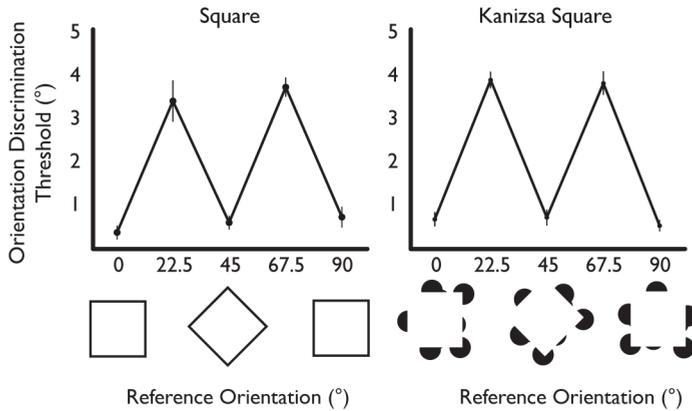
On each trial a reference stimulus was presented for 500 ms, randomly chosen out of 5 reference orientations ( $0^\circ$ ,  $22.5^\circ$ ,  $45^\circ$ ,  $67.5^\circ$  or  $90^\circ$ ), followed by a circular mask (diameter =  $20^\circ$ ; presentation time = 750 ms; luminance  $\sim 25$  cd.m<sup>-2</sup>). This was followed by a randomly rotated test stimulus, randomly displaced for both the x and y position, (where  $3^\circ \leq \text{displacement} \leq 5^\circ$ ). The observers' task was to respond whether the test stimulus was rotated clockwise (numerical keypad #6) or counterclockwise (#5) with respect to the reference stimulus. The amount of rotational difference between the test and reference was controlled by a Quest procedure for each reference orientation. A black cloth masked the edges of the display, in an otherwise dark room.

## 4.4 Results and Discussion

Orientation discrimination thresholds for the Real Square and the Kanizsa Square are shown in figure 6. Each data point represents 40 trials for each observer. The patterns of discrimination thresholds for the two stimuli are basically identical: lower thresholds for reference orientations of  $0^\circ$ ,  $45^\circ$  and  $90^\circ$ , and higher thresholds for  $22.5^\circ$  and  $67.5^\circ$ .

The lower thresholds for both the  $45^\circ$  Real Square and  $45^\circ$  Kanizsa Square orientation indicate that the visual system selects horizontal/vertical object features to determine object orientation. Interestingly, horizontal/vertical object features are not present in the retinal projection of the modified Kanizsa square, as all contours are oriented  $45^\circ$  away

from the horizontal/vertical (figure 3). The perceptually completed square, however, does contain horizontal/vertical features: the axes of symmetry. So, the thresholds we obtained provide a strong indication that the visual system determines object orientation based on features of a perceptually completed object representation.



**Figure 6. Results.** Mean orientation discrimination thresholds for both the Real square and the Kanizsa square.

Current physiological measures seem to indicate that the oblique effect possibly originates at the level of visual area V1. Furmanski and Engel (2000) reported populations of neurons in human visual cortex that display asymmetries in their preferred orientations, with more neurons tuned to horizontal/vertical orientations (see also Yacoub, Harel & Ugurbil, 2008). Additionally, Wang, Ding, & Yunokuchi (2003) show that area V2 also displays this same orientational anisotropy. So far, no such asymmetry, which might reflect the oblique effect, was found in higher, extra-striate, areas. If correct, then this implies that our results, which are based on axes that arise from completed objects, can only be explained through feedback from higher areas, because the object representation supplying the axes is only present at levels beyond V1. This finding is consistent with a rapidly growing body of research on feedback mechanisms in the human brain (e.g. Zipser, Lamme & Schiller, 1996; Lee, Mumford, Romero & Lamme, 1998; Juan & Walsh, 2003). This is, however, a topic for future research. In sum, using a classic visual effect we show how the visual system reconstructs and uses information to determine the orientation of occluded objects in the absence of direct retinal stimulation.

**Acknowledgments.** This work was supported by the Netherlands Organization for Scientific Research (NWO Pionier).



# Chapter 5

An octave effect in auditory attention



## 5.1 Abstract

After hearing a tone, the human auditory system becomes more sensitive to similar frequencies than to other tones. Current auditory models explain this by a simple bandpass attention filter. Here we demonstrate in three psychophysical experiments that auditory attention is much more sophisticated, as it contains multiple pass-bands around octave-related frequencies above and below the cued tone. Intriguingly, this octave effect not only occurs for physically presented tones, but persists for the missing fundamental in complex tones and even for imagined tones. Our results suggest neural interactions combining octave-related frequencies, likely to be located in non-primary cortical areas. We speculate that this connectivity scheme evolved from exposure to natural vibrations containing octave-related spectral peaks, e.g. as produced by the vocal cords.

## 5.2 Introduction

In the previous chapters, we suggested that human visual system acts on object representations, rather than on information represented at the retinal level. In the current chapter, we investigate whether the auditory system can act on object representations as well. Whereas we made use of an anisotropy in orientational sensitivity in the visual system (the oblique effect) in chapters 2, 3 and 4, in chapter 5 we exploit a characteristic of the auditory system. After being presented with a tone, attention is automatically drawn towards the tone frequency, and sensitivity is increased for this frequency, known as the attention band (e.g. Dai, Scharf & Buus, 1991). In the current chapter we make use of this aspect of auditory information processing to infer how attention operates in the auditory domain.

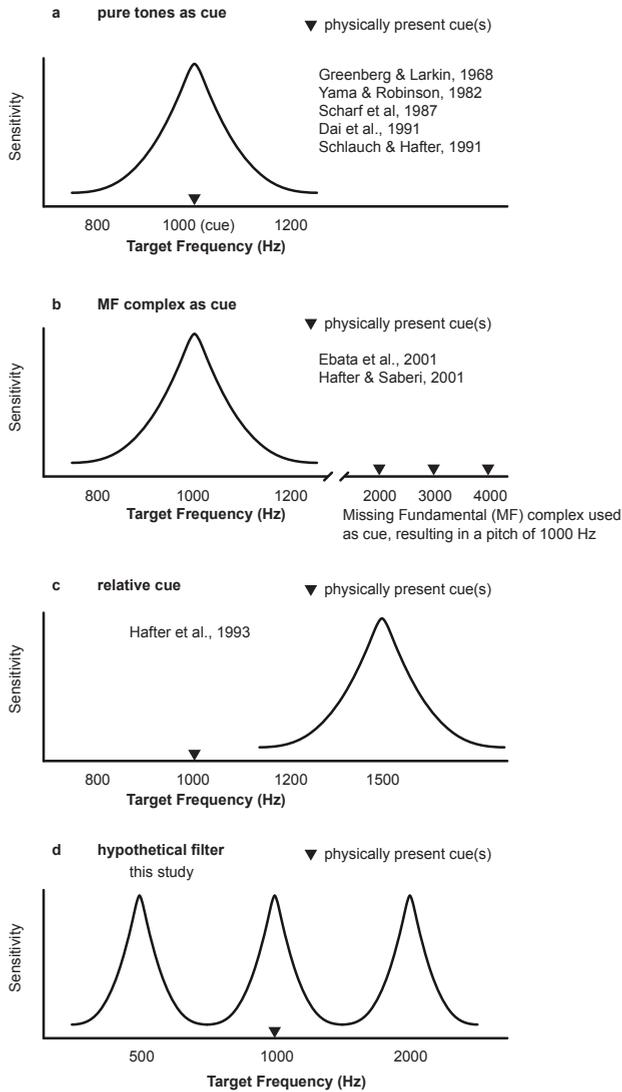
When listeners are exposed to an audible cue tone, sensitivity is highest for tones around the same frequency, and diminishes as a function of distance in frequency to the cue-tone (Greenberg & Larkin, 1968; Dai, Scharf & Buus, 1991; Ison, Virag, Allen & Hammond, 2002; Scharf, Quigley, Aoki, Peachey & Reeves, 1987; Yama & Robinson, 1982). This process is thought to be mediated by attention (Pashler, 1998) and, to date, is characterized by a bandpass filter (Figure 1A). The shape of this attention filter resembles the shape of the peripheral auditory filter (Greenberg & Larkin, 1968; Dai et al., 1991; Ison et al., 2002; Scharf et al., 1987; Yama & Robinson, 1982; Tan, Robertson & Hammond, 2008; Schlauch & Hafter, 1991).

Attention to a tone can be triggered by various cues. For example, as illustrated in Figure 1A, several studies applied a pure tone to assess frequency sensitivity (Greenberg & Larkin, 1968; Dai et al., 1991; Ison et al., 2002; Scharf et al., 1987; Yama & Robinson, 1982; Tan, Robertson & Hammond, 2008; Schlauch & Hafter, 1991; Yost & Shofner, 2009). Subjects can also be cued with harmonic tone complexes, producing a pitch determined by a so-called missing fundamental (MF; Moore, 1993; Ebata, Miyazono, Kumamaru, Chisaki & Usagawa,

2001; Hafter & Saberi, 2001). In this case, a frequency is perceived that is not physically present. Cueing with an MF complex heightens sensitivity for targets with the same perceived pitch (Figure 1B). The target may be a pure tone (Ebata et al., 2001) or another MF complex (Hafter & Saberi, 2001). In the abovementioned studies attention was involuntary, meaning that attention was drawn towards a certain frequency without the subject being aware of this process. Hafter et al. (Hafter, Schlauch & Tang, 1993) showed that voluntarily directing attention to a frequency relative to a cue frequency (e.g. 1.5 times the cue frequency) also heightens sensitivity for the attended frequency (Figure 1C). In summary, auditory sensitivity increases not for what is physically presented, but for what is attended, voluntary or involuntary, and detection of a signal becomes easier when this signal is more similar to the attended sound, in particular when the pitches are similar.

Interestingly, a number of studies have pointed out that two tones differing by an octave are perceived as more similar than when they are separated by any other musical interval (Deutsch & Boulanger, 1984; Kallman, 1982), not only in humans, but in other species as well (Blackwell & Schlossberg, 1943; Wright, Rivera, Hulse, Shyan & Neiworth, 2000). The ability to discriminate between simple frequency ratios (such as the octave) is apparent in infants, well before their first birthday (Schellenberg, 1996), suggesting an innate rather than a cultural predisposition for octave-related sensitivity. This perceived similarity of octave-separated tones may therefore be a plausible explanation for the universal occurrence of the octave in western and non-western music. This notion is further supported by statistical properties of human speech, which, interestingly, show distinct spectral peaks at octave-related distances (Schwartz, Howe & Purves, 2003). Since the shape of the attention filter has generally been studied only over a narrow range of frequencies, typically less than one octave (Greenberg & Larkin, 1968; Dai et al., 1991; Ison et al., 2002; Scharf et al., 1987; Yama & Robinson, 1982), figure 1a, it is not clear whether this octave equivalence would also apply to auditory attention. If so, we predict that cueing on a particular frequency will heighten sensitivity not only for the attended frequency, but for octave-related frequencies as well (figure 1d).

To test this prediction, the current study examined how attention in the auditory domain operates over a broad range of frequencies (4 octaves) and, by extension, whether sensitivity is also heightened for octave-related frequencies to the attended frequency. We performed three experiments with different cue conditions: physically present cue frequencies (experiment 1), cue frequencies that are perceived, but not present (missing fundamentals; experiment 2), and imagined cue frequencies (experiment 3).



**Figure 1. Attention filters.** A) Classic attention filter. Sensitivity is highest for a cue frequency and diminishes as a function of distance in frequency to the cue frequency. B) Attention filter using a missing fundamental complex (MF) as a cue. Sensitivity is highest for the perceived frequency, i.e. the missing fundamental, in contrast with the actual physically presented frequencies comprising the MF complex. C) Relative cueing. Attention can be directed towards a frequency related to the cue, in this case a frequency 1.5 times the cue frequency (cue: 1000 Hz, attended frequency: 1500 Hz), resulting in increased sensitivity at the attended frequency. D) Hypothetical attention filter, with sensitivity being highest for frequencies that are octave related to the cue.

### 5.3 Methods

#### All experiments

Detection performance was measured using a two-alternative forced choice (2AFC) design. Target tones appeared in one of two 250-ms intervals, separated by 200 ms and indicated on screen with 1 or 2. Gaussian white noise was present during the whole experiment (except for the training tasks for experiment 3), set by the subject to a comfortable level, ranging from 80 to 90 dB SPL. Audio was generated by a Power Mac G5 computer (sample rate: 50 kHz) and presented through a Texas Instruments TAS3004 sound card and a Philips SBC HP 910 headphone to the right ear. Cue and target tone stimuli had a duration of 250 ms with 8 ms onset and offset ramps. Sound levels of tones and noise were measured with a Bruel & Kjaer 2260 Investigator and artificial ear 4153; harmonics or subharmonics with levels greater than 37 dB below the level of the fundamental of the tone were not detected. Subjects responded with a keypress of 1 or 2 in which interval they detected the target tone, without feedback. Experiments were self-paced, with the next trial beginning 1000 ms after each response. Cue tones were presented at a signal/noise ratio of -7 dB: clearly audible. Experiments were written in Matlab 7.2, using the Psychophysics Toolbox extensions (Brainard, 1997). Data were acquired in 5 sessions for each experiment. Experiments were carried out in a sound-attenuated, darkened room, with each experiment run on a separate day for every subject. All subjects reported normal hearing.

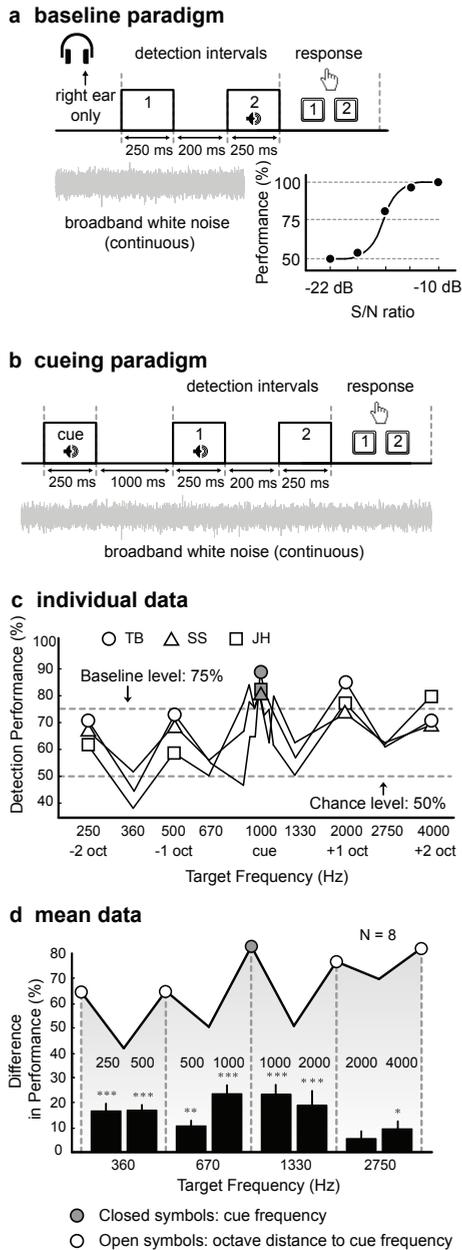
### 5.4 Experiment 1: Physically present cue tone

#### Methods Experiment 1

Cue tones (1000 Hz) were presented 1250 ms before detection interval 1. Target frequencies were chosen from the following 15 frequencies: 250, 360, 500, 670, 880, 920, 960, 1000, 1040, 1080, 1120, 1330, 2000, 2750 and 4000 Hz. 50 trials were collected per target frequency.

#### Results experiment 1

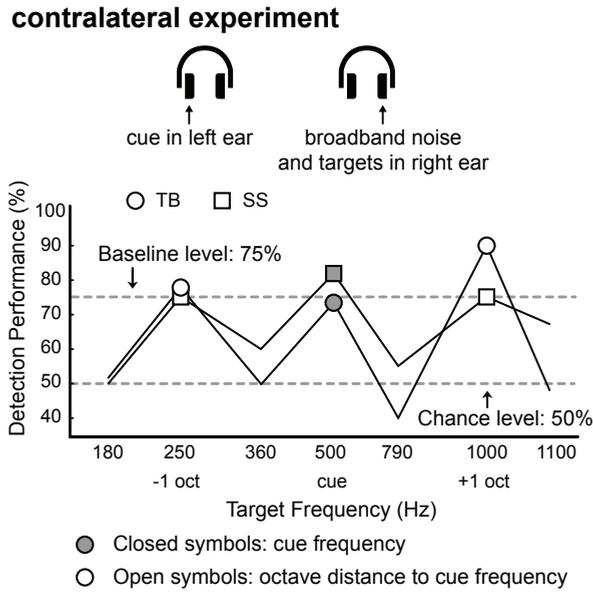
To establish a baseline for detection performance without a cue tone, eight subjects performed a two-alternative forced-choice paradigm (2AFC; figure 2a), for frequencies ranging from 250 to 4000 Hz, at various signal-to-noise ratios (SNRs). To determine for each frequency the SNR at which performance was 75% correct, we fitted a sigmoid function to the data of each subject (figure 2a). Next, we tested detection performance for the same 8 subjects using a pure cue tone of 1000 Hz and a range of target frequencies in background noise, set to 75% performance SNR (figure 2b). Detection performance was best near the cue frequency, and as expected (Greenberg & Larkin, 1968; Dai et al., 1991; Ison et al., 2002; Scharf et al., 1987; Yama & Robinson, 1982; Tan, Robertson & Hammond, 2008; Schlauch



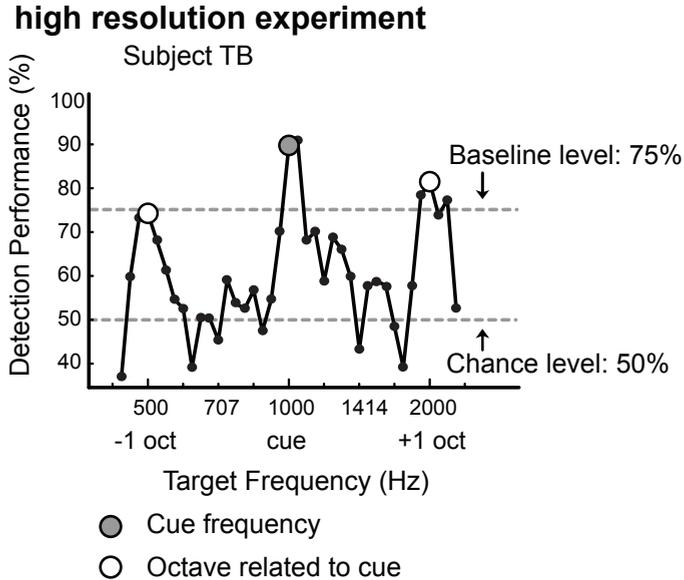
**Figure 2. Paradigm and results experiment 1.** A) A 75%-performance signal-to-noise ratio (SNR) was determined for 250, 500, 1000, 2000 and 4000 Hz by fitting a sigmoid function to detection performance as a function of SNR. By linear interpolation of a neighboring pair of these baseline SNRs, baseline SNRs for other target frequencies were determined. B) Cueing paradigm. An audible cue tone precedes a two-alternative forced-choice detection

task. C) and D) Individual and mean data, showing higher performance for targets identical to the cue tone (1000 Hz) and octave-related target tones than for other target tones. Bars in (d) represent peak-trough differences with the peak frequency indicated above bar and trough frequency below bar. Error bar represents standard error of the mean. Data was collapsed across subjects providing a single proportion correct per target frequency (MacMillan & Creelman, 1991) (\*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ).

& Hafter, 1991), gradually decreased as a function of distance to the cue frequency (figure 2c). However, note the appearance of distinct peaks at exactly one and two octaves above and below the cue (i.e. at 250, 500, 2000 and 4000 Hz, respectively). For example, detection performance for targets of 250 and 500 Hz is 10-15% better with respect to the surrounding frequencies ( $p < 0.001$ , Z test for proportions), while performance for 1000 Hz targets increased by 23% with respect to 670 and 1330 Hz ( $p < 0.001$ ; Z test for proportions; figure 2d). The peak – trough differences (bars in figure 2d) were smaller at 250, 500, 2000 and 4000 Hz than at 1000 Hz (significant for 500-670 Hz, 2000-2750 Hz and 4000-2750 Hz,  $p < 0.05$ , paired t test). To summarize, we observed enhanced mean detection performance for all subjects (figure 2d), not only for targets at the cue frequency, but interestingly, also at octaves above and below the cue frequency. In order to exclude a possible role of the most peripheral and monaural stages along the auditory pathway (cochlea and the cochlear nucleus) underlying this octave effect, we repeated the experiment, but presented the cue tone to the left ear, i.e. contralateral to the ear in which the targets and broadband noise were presented. This produced the same data pattern: higher performance for the cue frequency and at octave distances to the cue (figure 3). We also repeated experiment 1 at a higher spectral resolution by applying an increased number of target frequencies (15 frequencies per octave; figure 4), which again confirmed the octave effect.



**Figure 3. Contralateral experiment.** To exclude a possible role of the most peripheral and monaural stages along the auditory pathway (cochlea and the cochlear nucleus) in the octave effect, we repeated experiment 1 and changed the cue location to the left ear, i.e. contralateral to the ear in which the targets and broadband noise were presented, and set the cue tone to 500 Hz. Detection performance is shown for 2 subjects. The same pattern emerges as reported in experiment 1: local performance peaks located at 500 Hz (the cue frequency), at 250 Hz (-1 octave of the cue frequency) and at 1000 Hz (+1 octave of the cue frequency). A total of 50 trials were collected for each target frequency per subject.



**Figure 4. High resolution experiment.** Fifteen target frequencies per octave in a 6 hour experiment with one subject, and 100 trials per datapoint. Performance data shows the same pattern as found in experiment 1: detection performance peaks at the cue frequency (1000 Hz) and at octave-related distances to the cue frequency.

One consequence of our results is that, whereas the attention filter was previously reported to resemble a bandpass filter (Greenberg & Larkin, 1968; Dai et al., 1991; Ison et al., 2002; Scharf et al., 1987; Yama & Robinson, 1982; Tan, Robertson & Hammond, 2008; Schlauch & Hafter, 1991; Ebata et al., 2001; Hafter & Saberi, 2001; Hafter et al., 1993), a more accurate description would be a filter consisting of multiple pass bands, centered at the cue frequency and at octaves above and below the cue. Our results thus appear to imply neural interconnections for octave-related frequencies in the human auditory system.

## 5.5 Experiment 2: Missing fundamentals as cue tone

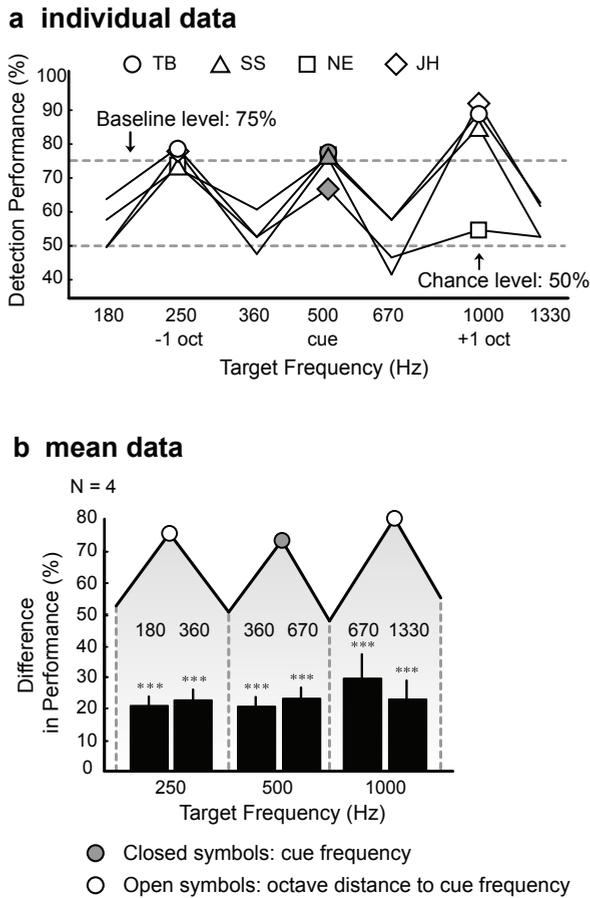
### Methods Experiment 2

Cue tones (a missing fundamental complex consisting of four tones with frequencies of 1500, 2500, 3000 and 3500 Hz) with a fundamental frequency (pitch,  $f_0$ ) of 500 Hz, were presented 1250 ms before detection interval 1. Target frequencies were chosen from the following 7 frequencies: 180, 250, 360, 500, 670, 1000 and 1330 Hz. 100 trials were collected per target frequency.

## Results Experiment 2

To shed more light on the potential neural origin of the octave effect, we performed two further experiments to verify whether the octave effect generalizes to cue frequencies that are perceived, yet are not physically present. To that end, the second experiment used MF tone complexes (Moore, 1993; Ebata et al., 2001; Hafter & Saberi, 2001). In these harmonic complexes listeners perceive a clear pitch at an MF frequency ( $f_0$ ) that is not present in the physical sound spectrum.

Four subjects performed a detection task, in which the cue was an MF complex (consisting of four tones with frequencies of 1500, 2500, 3000 and 3500 Hz) with an  $f_0$  of 500 Hz. We took care that the tone complex did not contain any acoustic energy at the lower, nor at the first two higher octaves of  $f_0$ . Seven pure-tone targets were used, with frequencies ranging from 180 to 1330 Hz. All four subjects convincingly showed increased local performance, both for targets of 500 Hz (i.e.  $f_0$ ) and for targets at 250 Hz, i.e. one octave below  $f_0$  (figure 5a). Three out of four subjects also showed increased performance for 1000 Hz, which is one octave above  $f_0$ . Mean detection performance for targets with frequencies identical to  $f_0$  and an octave above and below  $f_0$  increased by approximately 20% with respect to the surrounding target frequencies (figure 5b). The octave effect is therefore not restricted to the physically presented frequency, but extends to perceived frequencies as well.



**Figure 5. Results experiment 2.** The paradigm shown in figure 1b is applied, with a missing fundamental complex with an  $f_0$  of 500 Hz as cue tone (consisting of 1500, 2500, 3000 and 3500 Hz, note the omitted octaves of 500 Hz). A) Individual data. B) Mean data. A higher detection performance was obtained for targets identical to  $f_0$ , and at octave-related distances to the  $f_0$ , than for other targets. Bars represent peak-trough differences with the peak frequency indicated above bar and trough frequency below bar. Error bar represents standard error of mean (\*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ).

### 5.6 Experiment 3: Imagined frequencies as cue tones

#### Methods experiment 3

Cue tones (1000 Hz) were presented 3500 ms before detection interval 1. Subjects were instructed to imagine a “perfect fourth” interval above 1000 Hz (i.e. 1335 Hz). Target frequencies were chosen from the following 11 frequencies: 500, 584, 667.5, 830, 1000,

1130, 1335, 1667, 2000, 2335 and 2670 Hz. 50 trials were collected per target frequency.

### Results experiment 3

We next investigated the attention filter when subjects were instructed to imagine a particular frequency. While it is known that imagining a tone improves target detection for targets at and around the imagined tone (Haftor et al., 1993), it is unclear if this also holds for targets at octave-related distances to the imagined tone.

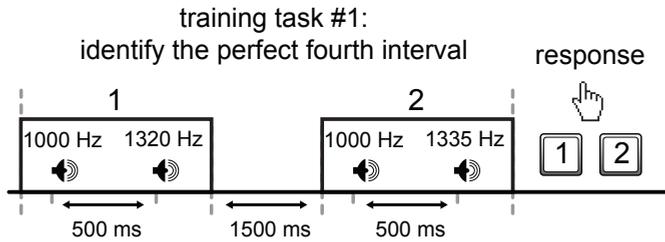
Four subjects were trained to correctly identify a perfect fourth presented above 1000 Hz (2AFC, training task 1, figure 6a), and to indicate whether a musical interval was smaller or larger than a perfect fourth (training task 2, figure 6b). Performance ranged from 75% to 91% on the first task, and from 89% to 97% on the second training task.

For the actual experiment, all four subjects were presented with a tone of 1000 Hz and instructed to imagine the well-known musical interval known as a perfect fourth (identical to the interval between the first two tones of "O Christmas Tree" above 1000 Hz. The imagined cue thus equaled 1335 Hz (figure 7a). Target frequencies ranged from 500 to 2670 Hz. figure 7b shows performance peaks at the physical cue of 1000 Hz and at corresponding octave distances (500 and 2000 Hz), and, crucially, also at the imagined cue (1335 Hz) and its octave-related frequencies (667.5 and 2670 Hz). The peak-trough differences at both cues and low-frequency octave distances were significant (ranging from 9 to 24%).

Two important points emerge from these data. First, the octave effect also holds for an imagined frequency. Second, both physical and imagined cue lead to enhanced detection. Thus, even though attention was presumably drawn towards the imagined tone, attention towards the physical cue frequency (as in experiment 1) was not overruled.

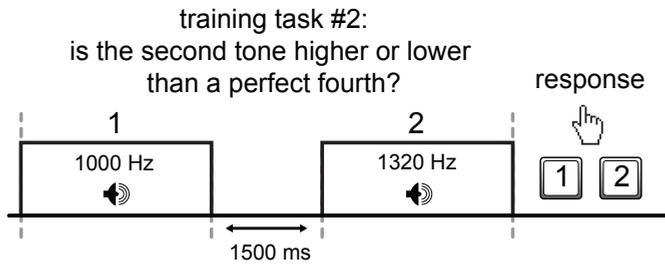
**a training task 1**

🔊 : 250 ms



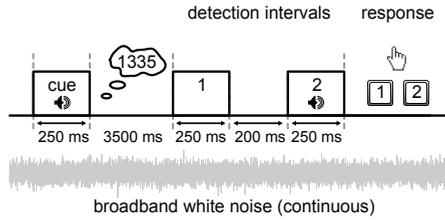
**b training task 2**

🔊 : 250 ms

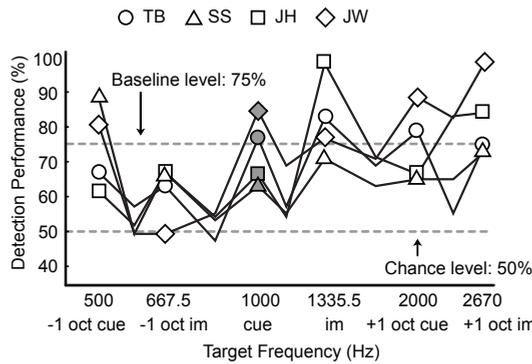


**Figure 6. Training for experiment 3.** Training tasks to imagine a perfect fourth above 1000 Hz for experiment 3. A) Training task 1, subjects are instructed in a 2AFC task to identify which of two intervals contains a perfect fourth musical interval (1000 Hz – 1335 Hz), in this example interval 2. Possible frequencies corresponding to a non-perfect fourth interval relative to 1000 Hz are 1296, 1309, 1322, 1348, 1361 and 1374 Hz. Performance ranged from 75% to 91%. B) Training task 2, subjects are asked to respond whether the second of two tones is higher or lower than a perfect fourth, possible values of the second tone are equal to those in training task 1, i.e. ranging from 1296 to 1374 Hz in 13 Hz increments and excluding the perfect fourth (1335 Hz). Performance ranged from 89% to 97% for training task 2. A total number of 300 trials was collected per subject for each training task.

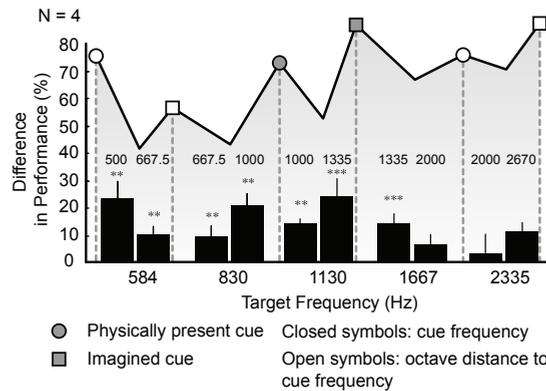
### a imagined cueing paradigm



### b individual data



### c mean data



**Figure 7. Paradigm and results experiment 3.** A) Trained subjects are instructed to imagine a perfect fourth above a presented tone of 1000 Hz, i.e. 1335 Hz. This is followed by a two-alternative forced-choice detection task. B) Individual data. C) Mean data. Detection performance for targets identical to the imagined tone (1335 Hz), and an octave below is significantly increased. Performance for targets identical to the 1000 Hz physical cue tone and an octave below is increased. Bars in (C) represent peak-trough differences with the peak frequency indicated above bar and trough frequency below bar. Error bar represents standard error of mean (\*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ ).

## 5.7 General Discussion

We found relative performance enhancement for target tones that differed by multiples of an octave with respect to the cue tone. This holds true for physically presented cue frequencies (experiment 1), cue frequencies at the missing fundamental (experiment 2), and even for imagined cue frequencies (experiment 3). These findings challenge the current views of the auditory attention filter, so far assumed to resemble a single pass band centered at the cue frequency (Greenberg & Larkin, 1968; Dai et al., 1991; Ison et al., 2002; Scharf et al., 1987; Yama & Robinson, 1982; Tan, Robertson & Hammond, 2008; Schlauch & Hafter, 1991; Ebata et al., 2001; Hafter & Saberi, 2001; Hafter et al., 1993).

Apart from the range of frequencies tested (four octaves versus about one octave) our study differed from previous studies (Greenberg & Larkin, 1968; Dai et al., 1991; Ison et al., 2002; Scharf et al., 1987; Yama & Robinson, 1982; Tan, Robertson & Hammond, 2008; Schlauch & Hafter, 1991; Ebata et al., 2001; Hafter & Saberi, 2001; Hafter et al., 1993) in the following important aspect. In our experiments the target frequency was equal to the cue frequency in only 7% - 14% of the trials (equiprobable) whereas previous studies used a high proportion of a target-cue match (e.g. 75%). This is a relevant difference, as off-cue targets are more suppressed in a high-proportion condition than in a low-proportion condition, as demonstrated by Tan et al. (2008) who compared low (20%) and high (75%) proportions of a target-cue match. In other words, the higher the probability that a target frequency is identical to a cue frequency, the more other target frequencies, possibly including those at octave distances, will be suppressed, resulting in decreased detection performance. This could be the reason that increased sensitivity at octave distances from the cue has not been reported in previous studies, including those applying targets around an octave distance (Schlauch & Hafter, 1991; Yost & Shofner, 2009).

What are possible cortical mechanisms that account for the classic attention filter, and can they be reconciled with the octave effect? A candidate mechanism for the classic attention filter (i.e. a relative increase in performance for targets identical to the cue tone) is rapid plasticity. Recordings from ferrets trained to attend to a tone showed a rapid form of plasticity in the spectrotemporal receptive fields of single neurons in primary auditory cortex (Fritz, Shamma, Elhilali & Klein, 2003; Fritz, David, Radtke-Schuller, Yin & Shamma, 2010). These changes were facilitative and consistent with enhanced performance during a tone-detection task, and were hypothesized to arise from connections between frontal cortex and primary auditory cortex. However, as this rapid type of plasticity seems to be restricted to the attended frequency, and not to extend to neighboring (octave-related) frequencies, it does not seem to account for the octave effect.

A further candidate mechanism for the octave effect could reside in tuning to multiple, harmonically related frequencies as observed in a subpopulation of mammalian primary auditory cortex neurons (Kadia & Wang, 2003; Brosch, Schulz & Scheich, 1999). However,

so far only few studies have described this multi-frequency tuning, and in those studies harmonic relations between the tuning peaks have not been consistently reported (Kadia & Wang, 2003; Brosch, Schulz & Scheich, 1999; Sutter & Schreiner, 1991; Noreña, Gourévitch, Pienkowski & Eggermont, 2008; Pienkowski & Eggermont, 2010). Interestingly, the response for a neuron with a characteristic frequency of 1000 Hz is facilitated when a 500 Hz tone is presented either synchronously (Kadia & Wang, 2003) or within an interval of 400 ms (Brosch et al., 1999). Since the interval to the target in our experiments was considerably longer (1000 or 1450 ms), it seems unlikely that this facilitation in primary auditory cortex would underlie the octave effect.

We suggest that involvement of secondary auditory cortex in the octave effect is more likely for the following reasons. First, the effect also arises for the missing fundamental. It therefore seems plausible that pitch neurons play a role, which are located anterolateral to the primary auditory cortex (Bendor & Wang, 2005). Second, an imagined tone causes the same octave effect, and fMRI studies have indicated that imagining a frequency predominantly activates secondary auditory areas (Halpern & Zatorre, 1999; Halpern, Zatorre, Bouffard & Johnson, 2004), rather than primary auditory cortex.

One consequence of our results is that attention in the auditory domain is not drawn to an absolute stimulus property such as the frequency of the tone, but rather to a more general perceptual class of the tone, called tone chroma (corresponding to the pitch class of the note, ranging in western music from A to G). It is plausible that the octave effect reflects neural connectivity at octave-related frequencies. From an ecological perspective, such connectivity might have evolved from exposure to environmental sounds (e.g. speech, animal vocalizations, and vibrations such as in strings), which contain multiple harmonics such as octaves, which correspond to the 2nd, 4th, 8th etc. harmonic. This notion is supported by statistical properties of human speech, which, interestingly, show distinct spectral peaks at octave-related distances (Schwartz et al., 2003). Connectivity at octave-related distances has been implicated by harmonic template models (Cohen, Grossberg & Wyse, 1995; Shamma & Klein, 2000; Duifhuis & Willems, 1982; Goldstein, 1973; Terhardt, 1974). The ability to discriminate between simple frequency ratios (such as the octave) is apparent in infants well before their first birthday (Schellenberg, 1996), suggesting an innate rather than a cultural predisposition for octave-related sensitivity. This sensitivity is also reflected in the phenomenon of octave equivalence, which dictates that in subjective rating tasks two tones differing by one octave are perceived as more similar than tones differing by any other musical interval (Deutsch & Boulanger, 1984; Kallman, 1982; Humphreys, 1939; Pedersen, 1975), reported in both humans and animals (Blackwell & Schlossberg, 1943; Wright et al., 2000). Our results may thus be interpreted as behavioral evidence for a mechanism in the auditory system, possibly mediated by attention, that processes tones based on their chroma, rather than on their absolute frequency. Importantly, the octave effect might explain why both western and non-western music is based on a universal interval: the octave.

### Acknowledgements

We acknowledge S.A. Shamma for comments and W. Pestman for assistance with the statistical tests.

# Chapter 6

General discussion and concluding remarks



In this thesis, I presented four studies in which we investigated how the human sensory system acts on representations of sensory information. This is most apparent in the visual domain where, in determining object orientation, objects consisting of subjective contours are processed by the visual system as if they were real objects. Additionally, in the auditory domain, we show that the auditory system, when presented with a single frequency, automatically activates a cortical network of frequencies that fall in the same perceptual category. The activation of this category or chroma, encompassing octave-related tones, then determines performance in a tone-detection experiment, as described in chapter 5.

In the introduction I referred to Plato's Theory of Forms, stating that Ideas or Forms are the most fundamental kind of reality. That the human sensory system acts on a representation rather than on elementary sensory input, seems to be hinted at by Plato in the *Phaedo*, where Socrates talks to Simmias about the failing of the senses:

*“Is the truth of them (the reality or true nature of everything) ever perceived through the bodily organs? Or rather, is not the nearest approach to the knowledge of their several natures made by him who so orders his intellectual vision as to have the most exact conception of the essence of each thing he considers?”*

Indeed, in light of our current findings, Plato's distinction between Sensibles (what is presented to us through our senses) and Forms, and the fact that the latter is seen as the more real of the two, is remarkably visionary.

In chapters 2 and 3, and by making use of an anisotropy in orientational sensitivity (the oblique effect), we investigated how the human visual system determines object orientation. We capitalized on this orientational anisotropy of the visual system in a number of experiments to gain insight in how the visual system determines object orientation, and which object features best predict object orientation discrimination thresholds. We showed that the visual system applies an optimized strategy in selecting object features to determine global object orientation. This optimization strategy in selecting object features that allow for the highest orientation sensitivity fits in with previous work (Schräter & Kersten, 2004; Ernst & Bühlhoff, 2004), suggesting that the human sensory system is governed by a general principle of weighting available sensory input in an optimized fashion.

Subsequently, in chapter 4, we investigated how the visual system determines the orientation of an object that is not represented at the retinal level. Using Kanizsa-like square stimuli, and again making use of the oblique effect, we showed that the human visual system determines object orientation based on an object representation, and not on object features present in the retinal projection. That is, it selects features of an object representation in an optimized way, by always selecting features oriented closest to the horizontal/vertical.

The results of chapters 2, 3 and 4 seem to point to a general principle of the human

sensory system, where sensory information allowing for optimal interaction with the environment (e.g. an orientation determination task) is preferred over other information. This principle holds for objects that are fully represented at the retinal level, but for objects that are represented at higher cortical areas as well, e.g. the Kanizsa-like square stimuli we used in chapter 4. This latter finding implies that the visual system acts on a completed representation of an object, not on what is projected on the retina. An interesting phenomenon in the auditory domain, known as octave equivalence (e.g. Deutsch & Boulanger, 1984; Kallman, 1982), seems to suggest that auditory attention can be drawn towards a representation of an auditory object as well. Musical notes that are octave-related (e.g. an A4 note of 440 Hz and an A5 note of 880 Hz) fall in the same perceptual category, known as tone chroma. This might imply that auditory attention is drawn towards a representation of a note, e.g. towards the note A, encompassing all notes that fall in this chroma. In chapter 5, we investigated attentional mechanisms in auditory processing. The auditory system, after being presented with a tone, becomes more sensitive to frequencies similar to that tone, with respect to dissimilar frequencies, a phenomenon known as the attention band (e.g. Dai, Scharf & Buus, 1991). We used this particular aspect of auditory processing to infer how attention operates in the auditory domain. In experiment 1 we found that attention is drawn not only to a cue frequency but to other, octave-related, frequencies that fall in the same perceptual category as well. We then constructed an auditory stimulus that resembles the illusory contours used in chapter 4. In a missing fundamental complex, a pitch is perceived that is not physically present. We then determined that the octave-effect arises as a function of perceptual properties of a tone, rather than the physical sound spectrum. In the third and final experiment we asked observers to imagine a frequency. Here, we showed that by merely thinking of a frequency, attention is drawn not only to the imagined frequency, but again, to octave-related frequencies as well. We discussed a possible mechanism that might give rise to this octave-effect, that reflects neural connectivity at octave-related frequencies. Such a connectivity scheme might well have evolved as a result to being exposed to environmental sounds that contain octaves of a fundamental frequency. Interestingly, spectral characteristics of human speech indeed show an overrepresentation of octave-related frequencies (Schwartz & Purves, 2003). We suggested that our results are behavioral evidence for an auditory, attentionally modulated mechanism that processes tones based on their perceptual category, rather than on absolute properties, such as frequency content.

Summarizing, the chapters in this thesis point to a preference of the human sensory system to act on representations of objects, both in the visual and auditory domain. In everyday life, we rarely, if at all, act on just one particular aspect of an object. For example, when picking up a large box, the brain needs to have an indication of, amongst others, occluded parts of the box in order to grip the sides, the weight, to judge how much force should be exerted on the box, and the center of mass, to pick the box up at a point where it will not topple over immediately. This collection of object features, that are all part of an internal representation of the box, allows for a diverse range of interactions with the box.

When judging the orientation of an object, our visual system reconstructs this object, and selects features of this representation that allows for the highest precision in orientation perception (chapters 2, 3 and 4). Similarly, in the auditory system, upon hearing or thinking of a tone, a cortical network is activated that represents frequencies that fall in the same perceptual category. This representation of an auditory object thereby encompasses octave-related frequencies to the presented or imagined tone (chapter 5).

This raises the question how a representation of an object, visual or auditory, is constructed in the brain, and how our findings fit in with current theories. A number of studies suggest that synchronized firing of distributed cortical networks might be a mediating factor in establishing a representation of visual objects (e.g. Milner, 1974; von der Malsburg and Schneider, 1986; von der Malsburg, 1995; Gray and Singer, 1989). This has been reported in humans (for a review see Courtney & Ungerleider, 1997), and in animals (Gray et al., 1989; Kreiter and Singer, 1996). Additionally, representations of illusory contours have also been linked with synchronized burst of activity, and potentially, feedback mechanisms in the visual system (e.g. Zipser, Lamme & Schiller, 1996; Lee, Mumford, Romero & Lamme, 1998; Juan & Walsh, 2003). Our findings seem to be consistent with this feedback model, since illusory object features such as axes (and used by the visual system to determine object orientation) are not present in lower level visual areas, such as area V1.

Currently, the validity of analogies between visual and auditory object processing is still under debate (e.g. Griffiths & Warren, 2004). One particular aspect hereof, that an object percept arises both in the visual and auditory domain, and that we act on this representation, seems to be a unifying principle of the way in which the brain processes sensory information.

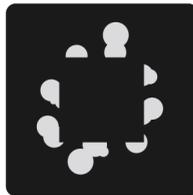
We act on what we *perceive*, not on what we sense.



Nederlandse samenvatting



In deze dissertatie bespreek ik in een aantal studies hoe het menselijk sensorisch systeem zintuiglijke informatie verwerkt. In hoofdstukken 2, 3 en 4 bespreek ik het visuele domein, en in hoofdstuk 5 het auditieve domein. In zowel de visuele als de auditieve modaliteit lijkt het sensorisch systeem te handelen op basis van een representatie van een object opgebouwd op basis van de informatie die onze zintuigen aangeboden krijgen. Dit gegeven is te makkelijk te illustreren aan de hand van een voorbeeld uit het visuele domein. Wanneer een pen half onder een boek of een velletje papier ligt, dan zal het beeld van deze pen op onze retina onvolledig zijn. Met andere woorden, alleen het zichtbare gedeelte van de pen wordt op de retina geprojecteerd. Desondanks nemen wij toch een intacte pen waar, en blijkbaar wordt ergens in ons visuele systeem een pen gereconstrueerd die mede bepaalt hoe en wat wij waarnemen. In hoofdstuk 4 onderzoeken wij hoe het visuele systeem de oriëntatie van objecten bepaalt wanneer de objecten niet in zijn geheel op de retina gerepresenteerd zijn, zoals in het hierboven gegeven voorbeeld van de pen, aan de hand van zogenaamde *Kanizsa objecten* (figuur 1), die deels bestaan uit contouren die niet op de retina gerepresenteerd zijn. Deze Kanizsa objecten worden door het visuele systeem behandeld als een echt object, waarbij de contouren wel op de retina gerepresenteerd zijn.



**Figuur 1. Kanizsa vierkant.** De zijkanten van het zwarte vierkant worden maar ten dele op de retina geprojecteerd, desondanks wordt toch een zwart vierkant waargenomen.

In het auditieve domein treedt hetzelfde fenomeen op. Na het horen van een bepaalde frequentie wordt in het auditieve systeem een netwerk geactiveerd van frequenties die in dezelfde perceptuele categorie vallen. Deze activatie van octaaf-gerelateerde frequenties bepaalt vervolgens hoe het auditieve systeem frequenties detecteert.

In hoofdstukken 2, 3 en 4, hebben we gebruik gemaakt van het feit dat het visuele systeem gevoeliger is voor oriëntaties rond de horizontaal/verticaal dan voor schuine oriëntaties, het zogenaamde *oblique effect*. Deze anisotropie in oriëntatiegevoeligheid van het visuele systeem uit zich in hogere oriëntatie discriminatie drempels voor schuine oriëntaties, vergeleken met horizontale/verticale oriëntaties. De hoogte van deze drempels kunnen derhalve gezien worden als een indicatie voor de *waargenomen* oriëntatie van een bepaald object. Immers, als dit object schuin wordt waargenomen zal deze drempel hoger liggen, omdat het visuele systeem minder gevoelig is voor schuine oriëntaties, en wanneer

dit object horizontaal/verticaal wordt waargenomen zal deze drempel lager liggen. We hebben experimenteel onderzocht hoe het visuele systeem de oriëntatie van objecten bepaalt, en welke object-eigenschappen (zijanten en assen) het best de waargenomen oriëntatie voorspellen. De resultaten lieten zien dat het visuele systeem een voorkeur heeft voor het selecteren van die object-eigenschappen die het meest precies worden waargenomen. Met andere woorden, het visuele systeem past een optimalisatie-strategie toe wanneer het objecteigenschappen selecteert. Deze optimalisatiestrategie lijkt een algemeen principe te zijn, dat over meerdere modaliteiten optreedt (Schräter & Kersten, 2004; Ernst & Bühlhoff, 2004).

In hoofdstuk 4 onderzochten we hoe het visuele systeem de oriëntatie bepaalt van objecten die niet volledig gerepresenteerd zijn op retinaal niveau. Door gebruik te maken van Kanizsa stimuli, die deels bestaan uit subjectieve contouren, hebben we aangetoond dat het visuele systeem de oriëntatie van een object bepaalt op basis van eigenschappen van een object-representatie, niet op basis van eigenschappen van de retinale projectie. De eigenschappen van deze object-representatie worden vervolgens op een optimale manier geselecteerd, waarbij het visuele systeem een voorkeur heeft voor eigenschappen die qua oriëntatie het dichtst bij de horizontaal/verticaal liggen.

De resultaten van hoofdstukken 2, 3 en 4 lijken te wijzen op een algemeen principe van het menselijk sensorisch systeem, waarbij een strategie wordt toegepast die ons in staat stelt optimaal met de omgeving om te gaan. Dit principe gaat op voor objecten die volledig op retinaal niveau gerepresenteerd zijn (hoofdstukken 2 en 3), maar ook voor objecten die bestaan uit subjectieve contouren en derhalve niet volledig op de retina geprojecteerd worden (hoofdstuk 4). Dit laatste gegeven impliceert dat het visuele systeem handelt op basis van een object *representatie* en niet exclusief op basis van wat op de retina wordt geprojecteerd.

Het feit dat ons sensorisch systeem handelt op basis van een representatie, en niet per sé op basis van wat aangeboden wordt aan onze zintuigen, is iets dat ook in het auditieve domein optreedt. Dit is te illustreren aan de hand van het fenomeen octaaf-equivalentie (e.g. Deutsch & Boulanger, 1984; Kallman, 1982), waarbij twee tonen die octaaf-gerelateerd zijn als equivalent worden beschouwd en perceptueel identiek zijn. Wanneer in een melodie een noot wordt vervangen door een octaaf-gerelateerde noot (bijvoorbeeld een A4 van 440 Hz, vervangen door een A5 van 880 Hz), dan blijft de melodie volledig intact, zolang de vervangen noot tot dezelfde perceptuele categorie behoort, in dit geval de categorie (of chroma) 'A'. Dit impliceert dat het auditieve systeem in dit geval handelt op basis van de categorie of representatie waartoe een noot behoort, en niet op basis van de frequentie-inhoud van een noot. Een noot van 440 Hz heeft een andere frequentie-inhoud dan een noot van 880 Hz, maar aangezien beide noten behoren tot de categorie 'A', zijn deze noten inwisselbaar, zonder een melodie geweld aan te doen.

De consequenties van dit fenomeen voor onze waarneming hebben we onderzocht in hoofdstuk 5 door, net als in de voorgaande visuele hoofdstukken, gebruik te maken van

een bepaalde karakteristiek van het sensorisch systeem. Na blootstelling aan een bepaalde frequentie wordt het auditieve systeem namelijk gevoeliger voor frequenties die hieraan identiek zijn. Dit gegeven staat in de literatuur bekend als de *attention band* (e.g. Dai, Scharf & Buus, 1991). Wij maken gebruik van het bestaan van de attention band om te onderzoeken hoe gevoeligheid van het auditieve systeem, na blootstelling aan een frequentie, voor octaaf-gerelateerde frequenties beïnvloedt wordt. In experiment 1 rapporteren we dat gevoeligheid van het auditieve systeem niet alleen hoger is voor identieke frequenties (de klassieke attention band), maar ook voor octaaf gerelateerde frequenties. Met andere woorden, na blootstelling aan een frequentie wordt het auditieve systeem gevoeliger voor frequenties die in dezelfde perceptuele categorie vallen: het *octaaf effect*.

Dit werd gevolgd door een tweede experiment, waarbij we een auditief equivalent van de Kanizsa figuren uit hoofdstuk 4 gebruikten. Vergelijkbaar met een Kanizsa figuur, waarbij een vorm wordt waargenomen die niet op de retina geprojecteerd wordt, wordt bij een *missing fundamental complex* een frequentie waargenomen die fysiek niet aanwezig is. Door gebruik te maken van deze stimulus bepaalden we dat het door ons gerapporteerde *octaaf effect* optreedt als functie van perceptuele eigenschappen van een toon, en niet op basis van het spectrum van die toon. In ons derde experiment stelden we vast dat het octaaf effect ook optreedt wanneer proefpersonen een toon inbeelden. Als proefpersonen aan een toon denken dan verhoogt dit niet alleen gevoeligheid voor de ingebeelde toon, maar ook voor tonen die op octaafafstanden liggen van deze toon.

Een mogelijke oorzaak van het octaaf effect zou kunnen liggen in verbindingen in auditieve cortex waarbij frequenties die op octaafafstanden liggen met elkaar verbonden zijn. Deze neurale connectiviteit zou een gevolg kunnen zijn van blootstelling aan geluiden in onze omgeving waarin octaaf-verhoudingen voorkomen. Opvallend genoeg zijn deze octaaf-verhoudingen inderdaad gevonden in menselijke spraak (Schwartz & Purves, 2003). We suggereren dat het octaaf effect een gedragsmatige aanwijzing is voor een auditief, door aandacht moduleerbaar mechanisme, dat tonen verwerkt op basis van hun perceptuele categorie, en niet op basis van de frequentie inhoud per sé.

De resultaten gepresenteerd in deze dissertatie duiden op een algemeen principe van het menselijk sensorisch systeem dat handelt op basis van object *representaties*, zowel in het visuele als in het auditieve domein.

We handelen op basis van wat we waarnemen, niet op basis van wat onze zintuigen aangeboden krijgen.



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## Publications



## Publications

Borra, T., Hooge, I.T.C. & Verstraten, F.A.J. The use of optimal object information in fronto-parallel orientation discrimination. *Vision research* **47**, 3307-3314 (2007).

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## Abstracts and Conference Proceedings

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T



# Curriculum Vitae



Tobias Borra was born in 's-Gravenhage, the Netherlands on October 3, 1978. Here, he attended high school Gymnasium Haganum, where he graduated in 1997. He went on to study Cognitive Neuroscience at Leiden University and carried out a six-month research internship at the faculty of Aerospace Engineering at Delft Technical University.

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