Illusions of filled extent: psychophysics and neuroimaging methods

Volume 1 of 1

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Abstract

The aim of this thesis is to shed light on the Oppel-Kundt, vertical-horizontal and Helmholtz's squares illusions. Eleven psychophysics experiments and one final fMRI study were conducted in order to inform current literature regarding these illusions. Experiments 1-5 investigated the effect of the number, size and position of vertical lines on the Oppel-Kundt illusion. Whereas five vertical lines allow for veridical size judgment of a horizontal line, a relatively constant and significant Oppel-Kundt 5% effect is observed with eight to twelve vertical lines. Evidence from these experiments also demonstrates that when one vertical line crosses a horizontal, 'bisection' decreases the perceived size of the horizontal by 7-13%. However, no reduction in the perceived size of the horizontal line in an inverted 'T' configuration is observed, challenging the 'bisection' component of the vertical-horizontal illusion as described by Mamassian & de Montalembert (2010). Experiments 6-7 showed that the increase in the perceived size of a horizontal line in an Oppel-Kundt figure can only be partly explained in terms of repulsion between adjacent lines. Specifically, whereas the size of the Oppel-Kundt illusion is 5%, displacement of adjacent lines can only account for 0.5%. Experiments 8-11 assess Mamassian and de Montalembert' s (2010) simple model of the vertical-horizontal illusion and propose the new ABC model consisting of three components; anisotropy, abutting and bisection which were found to affect the perceived size of lines by +7%, +9% and -7% respectively. Finally, an fMRI study was carried out to investigate whether activity in V1 can be linked to perceptual experience. Results generated revealed a significant effect in V1 associated with physical differences between visual stimuli rather than perceived differences. We concluded that intrinsic processing in V1 is not responsible for inducing illusion-related activity and it is likely that feedback from other areas dominates results of other studies. The findings of this thesis have important implications on theories of visual illusions and processing of illusory-related percepts in the brain.

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Acknowledgments

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Author's declaration

This thesis comprises the candidate's own original work and has not, whether in the same or different form, been submitted to this or any other University for a degree. Selected aspects of the research described in this thesis have been presented elsewhere.

Mikellidou, K. & Thompson, P. (2012). Simple line-length estimation not so simple. *Journal of Vision, 12*(9), 320.

Mikellidou, K. & Thompson, P. (2011). Bisection and dissection of horizontal lines: the long and the short of the Oppel-Kundt illusion. *Journal of Vision, 11*, 1184.

Mikellidou, K. & Thompson, P. (2010). The vertical-horizontal and the Oppel-Kundt illusions: how our visual perception changes. *Perception, 40*, 116.

Chapter 1 – Illusions of filled extent: A review

This chapter provides a background on how the human visual system processes information in the visual world in relation to visual illusions.Specifically it provides a description of previous research on the Oppel-Kundt, vertical-horizontal and the Helmholtz's squares illusions. Finally, it critically discusses how neuroimaging methods have been used in the study of visual illusions and provides an overview of the following chapters.

1.1 Introduction

We often equate the functioning of the eye to that of a camera, in that a lens system focuses the image of a visual scene on its light-sensitive retina. However, as illusions of visual perception demonstrate, the representation of visual scenes is not always accurate. This occurs because our visual system makes various assumptions about the world around us in order to provide us with essential visual information. When experiencing visual illusions, stimulus information is gathered by the eye and processed in the brain to give a percept that does not match its physical characteristics. However, some of these phenomena seem rational if we take for granted that the ultimate aim of our visual system is to create a representation of what is out there taking into account factors such as shading and distance away from the observer. Consequently visual illusions can become a useful tool for examining the way our visual system operates to construct our visual scene.

The reason why Illusions of filled extent such as the Oppel-Kundt and the Irradiation illusion ignite the interest of researchers is the fact that they affect the perceived size of objects in everyday life settings (Long & Murtagh, 1984). In the Irradiation illusion, described by Helmholtz (1867), the human perceptual system appears to perceive a bright object in a dark background larger than a dark object of the same physical size on a bright background (Figure 1.1). Since such illusions affect the perceived size of objects, they are very often the reason behind several kinds of human behaviour in the area of architecture and clothing (Thompson & Mikellidou, 2011).

Figure 1.1 The Irradiation illusion; the two circles are identical in size but the one on the left looks bigger compared to the one on the right.

1.2 Illusions of filled extent

The focus of this account will be on illusions of filled extent and how these affect the perception of size. Illusions of filled extent to be discussed in subsequent experiments in this thesis, will focus on two-dimensional stimuli which undergo a perceptual distortion in one of the two dimensions due to the presence of one or more additional lines. Consider an example first introduced by Helmholtz; the stimulus where the acute angle is divided (see Figure 1.2 Stimuli used by Rentschler et al. (1981); divided acute angles (right) look larger than undivided ones (left).Figure 1.2 below), is perceived as larger than the stimulus where the angle is undivided (left). This overestimation of perceived angular size was found to be dependent on the size of the angle between adjacent lines (Rentschler et al., 1981). A complete explanation for such overestimation of angular extent is offered by Blakemore et al. (1970). Researchers claimed that initially, each of the two lines sets up a profile of neural activity among orientation detectors in the visual cortex. The superposition of excitation set up by one line and inhibition set up by the other makes the two look displaced from one another in orientation, thus making an acute angle look larger than it actually is (and obtuse angles smaller). This model which relies on the hypothesis of inhibition between orientation-detectors is also supported by results obtained from single-unit recordings in the cat's visual cortex (Blakemore & Tobin 1972; Hess et al. 1975).

a

b

c

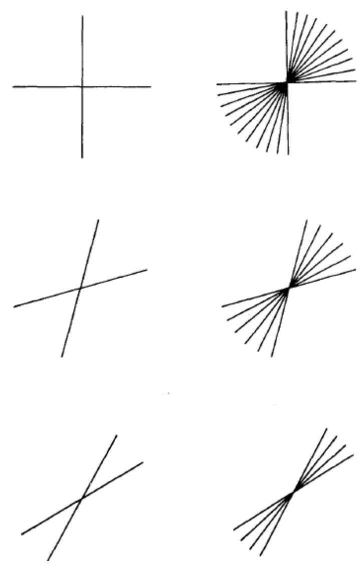


Figure 1.2 Stimuli used by Rentschler et al. (1981); divided acute angles (right) look larger than undivided ones (left).

Although an explanation depending on interactions between adjacent lines is sufficient to explain illusions of filled angular extent, it is unable to give a comprehensive account for the mechanism underlying illusions of filled lateral extent such as the Botti, the Oppel-Kundt and the Helmholtz's squares illusions.

In a classic Botti figure (see Figure 1.3), a filled extent is overestimated when compared with an unfilled extent of the same physical size and the illusion becomes most prominent when the total number of lines is nine (Rentschler et al., 1981; Piaget & Osterrieth, 1953). This illusion was found to be independent of the width as well as the height of the pattern, so Rentschler et al. (1981) concluded that it is independent of the retinal gap size between components of the figure. The only difference between the Botti illusion and the Oppel-Kundt illusion mentioned in due course, is the length of the vertical lines which is greater in the former.

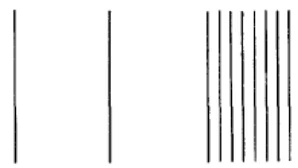


Figure 1.3 The Botti illusion by Rentschler et al. (1981); divided space (right) look wider than undivided space (left).

1.3 The Oppel-Kundt illusion

The focus of our research will be on two illusions of filled extent: the Oppel-Kundt and the Helmholtz's illusions. In the Oppel-Kundt illusion, a graduated division with regularly-spaced vertical lines of a given dimension is perceived as larger than another one which is 'unfilled' (see Figure 1.4 below). More specifically, the area filled with parallel lines appears larger in size in the direction orthogonal to those lines, compared to the unfilled area of equal size.

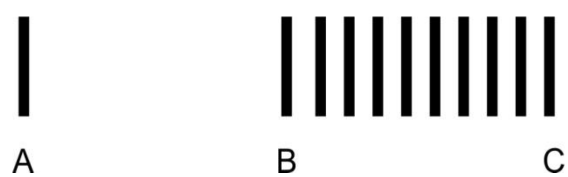


Figure 1.4 The Oppel-Kundt illusion, where AB=BC, but BC looks wider than AB.

The Oppel-Kundt illusion is very well-documented and has been described by many researchers in various ways. Oppel (1855) was the first researcher to report that dividing a stripe into its subparts affected its perceived size and Kundt (1863) investigated how the length of such divided segment is overestimated. Some other researchers reported a so-called ‘effect of partition’ occurring when the perceived size of a segment increased with the addition of a number of dividing lines (Hering, 1861; Delboeuf, 1865; Ebbinghaus, 1908 *as cited in* Giora & Gori, 2010). What is now referred to as the ‘Oppel-Kundt illusion’ has also been found in dynamic touch for a haptically filled space (Sanders & Kappers, 2009).

Although it is one of the most famous illusions of filled extent, the conditions under which it becomes most prominent still remain unknown. The number of dividing lines present in the filled part of an Oppel-Kundt stimulus appears to be a fundamental factor to the size of the illusion. Robinson (1972) suggested that the greater the number of dividing lines, the greater the size of the illusion, but Coren and Girgus (1978) specified that this increase happens only up to a critical point; beyond that, the perceived size gradually decreases. Piaget & Osterrieth (1953) and Oyama (1960) have argued that both a very small and a very large number of dividing lines moderate the effect, with seven to nine lines increasing the illusory percept to its maximum.

On the contrary, Coren & Girgus (1978) by manipulating the retinal size of the Oppel-Kundt stimulus, while keeping the number of dividing lines constant, found that the combination of the spacing between the lines and their width (i.e. the duty cycle) and not the number of lines is what determines the size of the effect. Additionally, it has been reported that the illusion is more prominent with small compared to large stimuli (Obonai, 1954; Long & Murtagh, 1984).

Giora and Gori (2010) investigated how textural characteristics affect the perceived size of two-dimensional patterns. Stimuli consisted of checkerboard patterns and Giora and Gori manipulated the number and arrangement of squares, as well as the fundamental spatial frequency (Figure 1.5). Results generated showed that the illusory percept increased as the fundamental spatial frequency increased, but decreased as the number of squares increased; indicating an independent processing of the two. Additionally, the illusory percept reduced both when the squares were arranged in an irregular manner and when they were indistinguishable from one another.

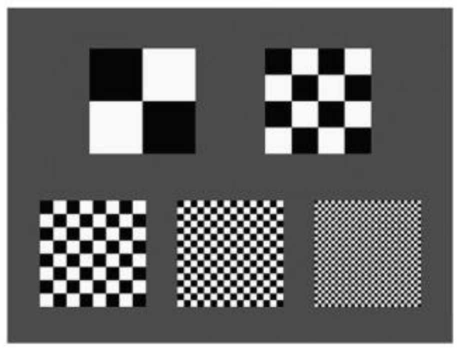


Figure 1.5 Checkerboard patterns used as stimuli by Giora and Goria (2010).

Results generated by Giora and Gori (2010) support a hypothesis put forward by Bulatov et al. (1997) that visual illusions of filled extent can be understood in terms of spatial filtering processes. Specifically, Bulatov et al. (1997) described quantitatively the illusion as a function of two factors; the length of the standard ('unfilled') half and the number of dividing lines in the 'filled' half of the figure. Moreover, they proposed a 'filter model' based on the properties of retino-cortical pathways, the distribution of simple and complex cells and their spatial organization. The filters' parameters varied accordingly depending on the eccentricity of the visual field and the model was able to predict accurately the magnitude of the illusion under varying conditions.

A general explanation for geometrical illusions has been put forward by Ganz (1966) who proposed a lateral inhibition model able to accurately predict changes in the perceived location of the illusory stimulus, as a function of the retinal distance between adjacent contours. As far as the Oppel-Kundt illusion is concerned, Craven and Watt (1989) claimed that the average contour density, determined by the number of zero-crossings in a range of spatial scales (Watt, 1990), is responsible for the phenomenon. Moreover, when the illusion was measured after adaptation of the subject to parallel lines no aftereffect was found leading to the conclusion that the illusory percept is not a product of an uninterrupted spatial calibration mechanism (Craven, 1995).

1.4 The Helmholtz's squares illusion

Another example of an illusion of filled extent is the Helmholtz's illusion (1867), where a square filled with horizontal lines would look taller than a square filled with vertical lines and square filled with vertical lines would look wider than the one filled with horizontal ones (see Figure 1.6). This observation was made by Hermann von Helmholtz in 1867 and the Helmholtz's squares were his demonstration of the illusion. Similarly to the Oppel-Kundt illusion, the perceptual distortion occurs only in one dimension making the Helmholtz's squares appear as rectangles instead.

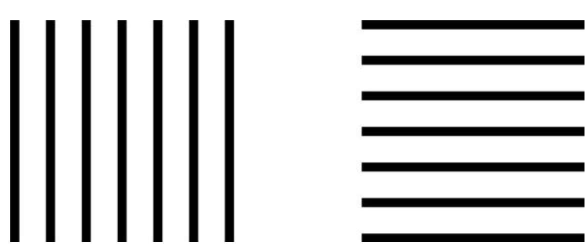


Figure 1.6 The original Helmholtz's squares; the vertically-striped square (left) looks wider whereas the horizontally-striped square look taller (right).

Although Helmholtz was the father of this illusion, he did not provide any empirical evidence supporting his observation. Even at present, the literature available on the Helmholtz's illusion is just as limited as the empirical evidence supporting it. Yoshioka et al. (2004) measured the apparent size of a square patch filled with horizontal or vertical lines and in accordance with Helmholtz's original theory, subjects perceived the horizontal square as being taller than the vertical square and the vertical square being wider than the horizontal. Moreover, Imai (1982) reported that a horizontally striped square was perceived 14.0% taller than its actual size and a vertically striped square 4.06% wider than its actual size. Noteworthy is the asymmetry of the effect which increases in the vertical dimension.

The effect of the duty cycle of the stimulus on the size of the Helmholtz's squares illusion was investigated by Thompson and Mikellidou (2011). The duty cycle is described as the fraction of each cycle which is white; thus a duty cycle of 0.9 will have a narrow dark bar that occupies 10% of each cycle of the pattern. Results generated showed that when two patterns have the same height, the horizontally-striped pattern was perceived as 4.1 – 10.1% taller, depending on duty cycle. On the other hand, a vertically-striped square was perceived as 1.3 – 6.5% wider, depending on the duty cycle, when compared to a vertically-striped pattern of the same width. These results confirmed and quantified the Helmholtz's square illusion and showed that the illusory percept is greater with smaller duty cycles (i.e. narrow black lines on a white background). Similarly to Imai (1982), the effect is greater in the vertical dimension.

The Helmholtz's squares illusion has been also investigated using real 3D vertically oriented cylinders (Thompson & Mikellidou, 2011). Results generated showed that the perceived width of cylinders with horizontal stripes was close to veridical but observers systematically overestimated the diameter of vertically-striped cylinders. Moreover, in accordance with Long and Murtagh (1984) and Obonai (1954) who found that the

Oppel-Kundt illusion diminished with larger stimuli, this illusory percept gradually decreased as the size of the cylinders increased. These results proved that the illusion persists on real 3D cylinders with vertical stripes, contradicting previous suggestions by Taya and Miura (2007) that the addition of 3D cues such as shading and vertical stripes, makes cylinders appear narrower.

The asymmetry of the Helmholtz's square effect which favours the vertical dimension is an indication that another illusion may be present. Noteworthy is an observation, made in a personal communication by Wolfgang Metzler to Zanforlin (1967); when asked to make a vertical pile of coins so that its height is equal to the coins' diameter, a subject will typically make the pile about 30% too short. This coin illusion is a result of two effects - the Helmholtz illusion and the vertical-horizontal illusion. The horizontal orientation of the coins will make the pile appear taller than it really is because of the Helmholtz illusion, and the vertical-horizontal illusion, in which a vertical line appears to look longer than an identical horizontal will reinforce this overestimation of the vertical. This justifies why observers will make a pile of coins too short when asked to match the height of the coins to the width of a single coin. Interestingly, if this task is repeated with the direction of the coins shifted through 90 degrees, the size of the effect is still present but markedly reduced because the two illusions work antagonistically. This suggests that the Helmholtz illusion is larger than the vertical-horizontal illusion.

The asymmetry between the vertical and horizontal component, when the two are of equal length, in an inverted 'T' configuration was first report by Fick in 1851 (as cited in Avery & Day, 1969). In such a configuration, the vertical component appears approximately 10% longer than the horizontal and the effect is commonly referred to as the 'vertical-horizontal' illusion. Figure 1.7 below illustrates the overestimation of perceived line length as a function of its orientation as initially shown by Shipley et al. (1949) and confirmed later on by other researchers (Pollock & Chapanis, 1952;

Cormack & Cormack, 1974; Craven, 1993). From this it can be seen that the greatest size overestimation occurs with lines oriented at approximately 70°.

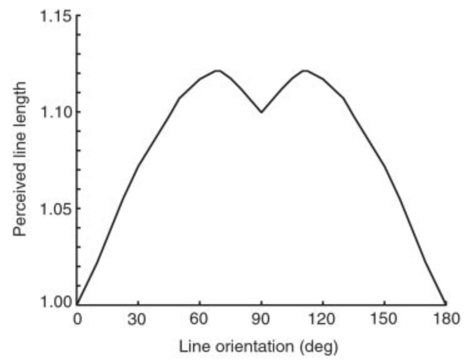


Figure 1.7 Variations in the apparent length of a stimulus as a function of its retinal image orientation.

One of the first attempts to explain the mechanism underlying the vertical-horizontal illusion was made by Wundt (1859 as cited in Künnapas, 1955), who supported the notion that this is a result of specific eye movements. This tendency of an observer to overestimate a vertical line compared with a horizontal one of equal length was also indirectly reported by Helmholtz (1867) using his striped squares.

Künnapas (1955) carried out a study using four different orientations of a 'T' configuration (see Figure 1.8). Künnapas believed that the overestimation of a vertical line compared to a horizontal of the same physical size, in a 'T' configuration, could not account for the whole effect so he carried out an investigation to identify a second component. He hypothesized that the second component of the 'vertical-horizontal' illusion is the overestimation of the dividing line, which is independent of orientation. Results confirmed that in addition to the overestimation a vertical line compared to the horizontal one (component A) i.e. the vertical bias, there is a second component in the vertical-horizontal illusion which is the overestimation of the dividing line (component B). Moreover, asymmetry of bisection of the divided line was found to attenuate the illusory percept, with the phenomenon being stronger when the dividing line was positioned at the midpoint of the divided line and weaker with ‘L’ configurations where only the first component existed. These results were also confirmed by Wolfe et al. (2005).

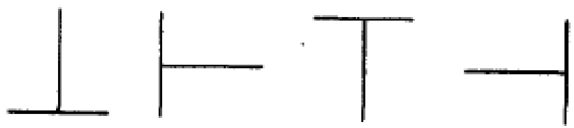


Figure 1.8 Stimuli used by Künnapas (1955).

Three main differences were found between the two components: (i) component A affects only the vertical dimension whereas the latter is independent of dimension, (ii) unlike the component A; component B has a maximum at the midpoint and two minima at the two end positions and finally (iii) component B is stronger than the first one, depending on the distance of the dividing line from the midpoint. Künnapas (1955) also quantified the size of the illusion in a single mathematical equation using Figure 1.9 which illustrates the variables in the formula for the overestimation of the dividing line.

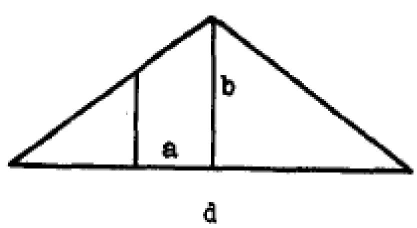


Figure 1.9 This was used by Künnapas (1955) to calculate the magnitude of the illusion.

The equation is:

$$x = b\,(1-(2a/d)) + c,$$

where *x*=the magnitude of the illusion, *a* = the distance of the bisection from the midpoint, *b*=the maximal magnitude of the illusion in the midpoint position, *d*=the whole length of the divided line and *c= t*he classical overestimation of the vertical line. The validity of the equation was confirmed by a comparison between predicted results using the equation and experimental data.

Expanding on the relevance of symmetry of bisection in line length perception, Charras and Lupianez (2009) compared perception of symmetrically bisected lines to that of asymmetrically bisected lines. As previously mentioned, research by Künnapas (1955) and Wolfe et al. (2005) showed that when a horizontal line is bisected by a vertical one, the overestimation of the size of the vertical decreases as the amount of symmetry decreases. These studies investigated only 'T' and an 'L' but not '+' configurations and provided evidence illustrating the underestimation of symmetrically bisected lines. In addition to these, Charras and Lupianez (2009) showed that the perceived sum of parts of assymetrically bisected lines is longer than that of symmetrically bisected ones. Charras and Lupianez (2009) manipulated line orientation and type of bisection and results showed no overestimation of the vertical line in a '+' configuration. Charras and Lupianez argued that when both lines are bisected, the vertical bias is cancelled out implying that neither of the two components of the vertical-horizontal illusion is functioning in a '+' configuration, leading to veridical size perception.

Mamassian and de Montalembert (2010) proposed a simple model to describe quantitatively the overestimation of the vertical segment compared to the horizontal in the vertical-horizontal illusion. This was the most comprehensive study of the vertical-horizontal illusion which aimed at distinguishing and then quantifying the contributing factors, as it investigated 'T', 'L' and '+' configurations. The method of constant stimuli was used with stimuli consisting of two segments, one blue and one red, one horizontal and one vertical touching at one point. Results showed two independent components which were in agreement with previous studies (Künnapas, 1955; Charras & Lupianez, 2009) and quantified them as well: (i) an anisotropy bias of an average of 6% causing an overestimation of the vertical segment relative to the horizontal one and (ii) a bisection bias of an average 16% causing an underestimation of the bisected line relative to the bisecting line.

Mamassian and de Montalembert (2010) showed that a late-noise model described experimental data best, where the participants' uncertainty of stimulus size played a role near the decision stage, rather than directly on measurements of stimulus size. This study confirmed that the bisection component results in the *underestimation* of the bisected line instead of an *overestimation* of the bisecting line. However, contradicting previous evidence by Charras and Lupianez (2010) the '+' configuration generated a similar psychometric function to the 'L' configuration, causing an overestimation of the vertical line due to the anisotropy component. The only difference between the two configurations was that for the '+', size judgments were more difficult to carry out.

There are two hypotheses in the literature which attempt to describe the mechanism underlying the first component of the vertical-horizontal illusion, the vertical bias. The first hypothesis is linked to depth interpretation of two-dimensional images by our visual system (Girgus and Coren 1975; Gregory, 1963, 1970; Woodworth, 1938). The size-constancy mechanisms would produce the vertical line length overestimation, resulting from the misapplication of size-constancy scaling. During depth cue processing of two-dimensional images an assumption is made that the vertical line, but not the horizontal, is further away from the observer. To account for this hypothetical depth illusion, we tend to overestimate vertical lines compared to horizontal ones. As the number of pictorial cues available increases i.e. in natural scenes, the vertical bias increases (Yang et al., 1999; von Collani, 1985).

The second hypothesis is related to the intrinsic properties of our visual system and more specifically visual field anisotropy (Künnapas, 1955b, 1957a, b, 1958). As the visual field has a horizontally aligned elliptic shape, vertical lines are closer to the visual field boundaries than horizontal ones and are consequently perceived longer. Several studies suggesting that the visual field's shape has an impact on the vertical bias, reported that the vertical overestimation is significantly reduced under monocular viewing condition, in comparison to binocular viewing (Künnapas, 1957a, b; Prinzmetal & Gettleman, 1993). It has recently been proposed that both hypotheses can be valid independently (Williams & Enns, 1996) but that neither of the two could account for the amount of the vertical overestimation in some two-line configurations (Wolfe et al., 2005).

Interestingly, Howe and Purves (2002) have suggested a relationship between the size of lines in our visual world and their perceived size, as a function of their orientation. More specifically, they build a database of natural images using a laser range scanner to reveal that the ratios of the actual length of real lines to their length on the retina, when classified by their respective orientations on the retina, matched extremely well subjective line length estimation as a function of angle relative to the observer. For instance, horizontal lines on the retinal image would most likely arise from relatively short physical sources, whereas lines at about 70 degrees relative to the observer would typically arise from relatively longer physical sources, in terms of size.

1.5 Neuroimaging and Illusory Percepts

During the past two decades, the increasing use of neuroimaging methods such as fMRI and MEG has been integrated into the study of visual perception and consequently illusory perception. The focus of interest in visual illusion studies employing neuroimaging methods is to determine whether the resulting non-veridical visual perception can be matched to analogous patterns of brain activity in areas involved in visual processing. In the human brain, the visual cortex which is located in the occipital lobe at the back of the brain is the area responsible for the early processing of visual information. It includes the primary visual cortex which is also known as V1 or striate cortex (anatomically equivalent to Brodmann area 17) and extrastriate visual areas such V2 (Brodmann area 18), V3, V4 and V5 (Brodmann area 18).

The idea that perceived and physical position representation occurs in distinct areas of the visual cortex is based on the fact that these two are often dissociated (Fischer, Spotswood & Whitney, 2011). As a result, it can be hypothesised that some areas in the visual cortex might have percept-based and others retina-based coordinate representation. Many factors have been found to be responsible for this dissociation, such as object motion (DeValois & DeValois, 1991), attention shifts (Suzuki & Cavanagh, 1997) and adaptation (Whitaker, McGraw & Levi, 1997).

Conventionally, it has been hypothesised that activity in early visual processing areas corresponds to physical input from the retina, whereas activity in higher-order areas reflects our conscious perception of the visual world (Sterzer & Rees, 2006). The first study which employed functional neuroimaging and more specifically electroencephalography (EEG) to study the relationship between illusory figures and the waveform of visual evoked potentials (VEPs) was carried out by Sugawara and Morotomi (1991). Eight different visual stimuli were used, four of which induced subjective figures and contours in terms of squares and discs, whereas the remaining four although having identical physical dimensions did not induce any illusory percepts. An increase in VEPs amplitude in the occipital lobe was evident for stimuli inducing subjective figures in all eight human subjects with Sugawara and Morotomi suggesting that illusory percept processing takes place in higher visual areas.

Following this, Hirsch et al. (1995) used functional Magnetic Resonance Imaging (fMRI) to study the haemodynamic brain response to illusory contours using six visual stimuli; three consisting of pacmen figures creating an illusory square, two misaligned sets of pacmen figures and a control square (see Figure 1.10). Results from four subjects demonstrated that the existence of illusory contours generated distinct fMRI responses predominantly in higher visual areas and more specifically Brodmann's area 18 in the right hemisphere. This area of activation was located near the vertical meridian projection between V1 and V2, showing a possible implication of V1. According to Hirsch et al. these results do not rule out the possible contribution of multiple areas or other regions not included in their analysis and are consistent with a bottom-up approach to illusory contour perception.

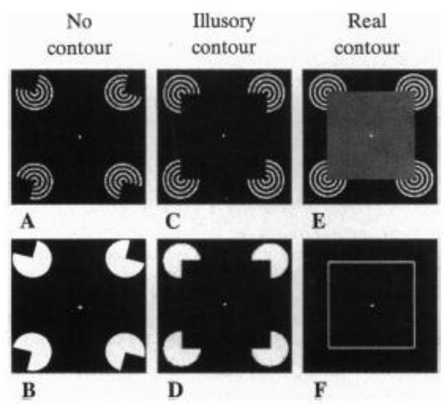


Figure 1.10 Stimuli used by Hirsch et al. (1995)

More recently, Fischer et al. (2011) reported that activity in higher level areas generates a precise representation of perceived and not physical position of a stimulus. The comparison of the physical and perceived object position coding was carried out in five functionally localised higher visual areas; the lateral occipital cortex (LO), the posterior fusiform gyrus (pFs), the fusiform face area (FFA), the parahippocampal place area (PPA) and the motion selective middle temporal (MT) region.

Interestingly, in a follow-up analysis Fischer et al. (2011) measured physical and perceived position discrimination in area V1, which was functionally defined using a standard retinotopic localiser. Although activity observed in V1 was tightly associated to the physical position of stimuli, some unique information on perceived position was also evident. This result is consistent with an fMRI study carried out by Murray et al. (2006) showing that the cortical area activated in the primary visual cortex (V1) by an object in the visual field varies according to perceived angular size. Figure 1.11 illustrates the stimuli used in the study, with a hallway and walls as background and checkerboard spheres always having a constant physical size (6.5˚). Participants were asked to adjust the size of the front sphere to match the angular size of the back sphere, so that if the two were positioned in the same location on the screen they would be identical. Results showed that a distant object appearing to occupy a larger portion of the visual field activated a larger part of V1 compared to an object of identical angular size which appears to be nearer and thus smaller.

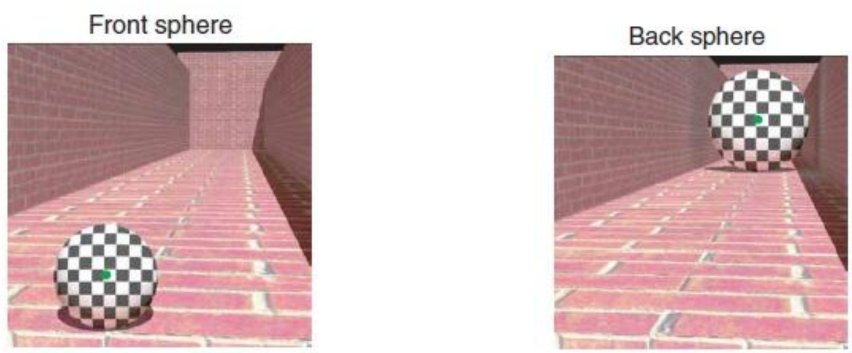


Figure 1.11 Stimuli used by Murray et al. (2006)

According to Sterzer and Rees (2006), the finding by Murray et al. (2006) is a challenge to the traditional notion that V1 contains a retina-based representation of the visual world. Concurrently it provides a link for the first time between the spatial extent of our perception and the spatial distribution of activity in V1. Despite the fact that this is not the first time that activity in V1 has been associated with conscious perception (Tong et al., 2003), this finding challenges the well-accepted notion that V1 contains a retina-based representation of the visual world. Furthermore, it provides evidence that the topographic map in V1 can be dynamically changed in accordance with the perceived size of an object. This dynamic change was also shown by Fang et al. (2008) who compared the size of two 3D rings at close and far apparent depths in a 3D scene. The former was found to occupy a more eccentric portion of the visual field, relative to the close ring and this effect was significantly reduced when the focus of attention was narrowed with a demanding central fixation task. This reduction in activity was taken as evidence of feedback projections from higher visual areas, processing 3D depth cues, to lower visual areas.

Additionally, Sperandio, Chouinard and Goodale (2012) carried out an fMRI study to observe activity in V1 induced by an afterimage projected on a screen placed at various distances. The retinal size of the stimulus was kept constant, while the perceived size in accordance with Emmert's law varied as a function of the distance away from the observer. Results showed that as the size of the afterimage increased, activation in V1 became more eccentric playing an important role in size constancy. Noteworthy is the fact that this activation was not present in visual areas V2 or V3.

Although results generated by Murray et al. (2006) and Sperandio et al. (2012) suggest that V1 is not strictly retinotopic, Fischer et al. (2011) emphasize that in their study object representation in V1 was more accurately predicted by retinal rather than percept-based coordinates. Nonetheless, findings which suggest that a percept-based representation of the visual world exists in V1 (Murray et al., 2006; Sperandio et al., 2012) challenge the previously well-accepted notion that this earliest visual area simply contains a retina-based representation of our visual world.

In addition to illusory contour perception in humans, there is evidence from electrophysiological studies on the role of V1 and V2 from other mammals. For example, von der Heydt and Peterhans (1989) showed that in area V2 44% of neurons were found to signal the orientation of illusory contours in abutting gratings and 32% of neurons responded to Kanizsa-type figures. In cats, information about illusory contours was represented in 42% of V1 neurons and 60% of V2 neurons (Sheth et al., 1996). Ramsden et al. (2001) generated evidence using optical imaging and single-unit recording showing that orientation of illusory contours induced a negative signal in V1 and a positive in V2; a unique combination of neural representation which could be used to identify illusory compared to real contours.

However, the use of fMRI has been questioned as results generated by some studies have suggested that neural activity in V1 is not correlated with visual perception. More specifically, Whitney et al. (2003) used stationary patterns of either inward or outward motion giving rise to an apparent inward or outward movement. Consequently, stimuli illustrating outward movement would appear to occupy a greater part of the visual field when compared to the stimulus illustrating inward movement. Results generated showed that perceived location of an object was consistent with the direction of motion. However, the pattern of activity in V1 was observed in the opposite direction of motion, with an increase in the fMRI signal in eccentric V1 for the inward-moving stimuli and in foveal V1 for outward-moving stimuli. Therefore, Whitney et al. claim that by changing the direction of motion of a stimulus the relationship between perceived location and representations in V1 can be changed.

This claim was investigated further by Liu et al. (2006) who replicated the basic findings generated by Whitney et al. (2003). In contrast, additional experiments did not show significant flexibility of the cortical visual field map and changes in perceived position were found to be irrelevant to this effect. Interestingly, fMRI differences seem to be driven by an increased motion signal arising due to the trailing edge of the stimuli being used and by changes in motion direction. According to Murray et al. (2006), it is possible that this large motion signal might have concealed the minor changes in the distribution of activity arising from the illusory percept making it implausible to measure with fMRI.

Recently morphological variations across individuals were also taken into account in an fMRI study of two common visual illusions, the Ebbinghaus and Ponzo illusions (Figure 1.12), by Schwarzkopf, Song and Rees (2011). In these two illusions, additional information in the sense of surrounding circles in the Ebbinghaus illusion and depth information in the Ponzo illusion, makes two objects of identical size being perceptually different. In contrast to previous studies, instead of correlating V1 neural activity with the size of the illusion, a retinotopic map for each individual was constructed during an irrelevant task and subsequently this was used to predict perceptual differences on object size in each of the two illusions.

Figure 1.12 The Ebbinghaus and Ponzo illusions.

1.6 Thesis Overview

The ultimate aim of the experiments carried out in this Thesis is to shed light on how we localise contours and how we estimate distance in a single dimension. These processes are also relevant when carrying out area estimations in two-dimensional and volume estimations in three-dimensional visual scenes. Understanding length, area and volume estimations has important practical implications on interior design, architecture and fashion (Thompson & Mikellidou, 2011).

Following discussion of background literature in the present chapter, each experimental chapter (i.e. Chapters 3, 4, 5 and 6) will introduce and discuss research questions in relation to relevant literature prior presenting results.

1.6.1 Chapter 2

Chapter 2 provides a description of the methods used to carry out all psychophysics experiments described in Chapters 3, 4 5 and 6 as well as technical details regarding the equipment used.

1.6.2 Chapter 3

This chapter reports a series of five psychophysics experiments on the Oppel-Kundt illusion by varying the position, size and number of vertical lines on a horizontal line. The aim is to identify the ideal combination which will generate the greatest illusory percept and discuss results in relation to possible reasons behind the existence of this illusion.

1.6.3 Chapter 4

The aim of Chapter 4 is to determine whether adjacent vertical lines in an Oppel-Kundt stimulus displace one another in such a way to increase the perceived length of the stimulus as a whole. Two psychophysics experiments are reported which compare the position of either the ultimate or penultimate 'tick' in an Oppel-Kundt figure to a comparison 'tick' located below the stimulus.

1.6.4 Chapter 5

The aim of Chapter 5 is to investigate a discrepancy between results generated in Chapter 3 and evidence from Mamassian and de Montalembert (2010) describing quantitatively the overestimation of the vertical segment compared to the horizontal in the vertical-horizontal illusion. This chapter reports a series of four psychophysics experiments comparing lines of same and different orientations within different shapes and discusses results in relation to the new proposed ABC model; a more comprehensive quantitative explanation of the vertical-horizontal illusion.

1.6.5 Chapter 6

The aim of Chapter 6 is to investigate whether a perceptual effect, as observed in a psychophysics experiment using the Helmholtz's squares illusion can be compared and matched to analogous brain activation patterns using functional Magnetic Resonance Imaging. Neuroimaging results from eight subjects will be presented and main effects will be calculated and critically discussed.

1.6.6 Chapter 7

Chapter 7 provides a summary and evaluation of all results presented throughout the thesis. It highlights the thesis' contribution to scientific knowledge and discusses future research ideas arising from present findings.

Chapter 2 - Methodology

The aim of this Chapter is to describe the methodology used throughout this thesis in order to quantify perceptual judgments. The method of constant stimuli will be discussed and evaluated, technical information regarding the equipment used will be given, participant information will be provided, analysis of results for subsequent experiments will be described and results from pilot studies will be presented.

2.1 Psychometric functions

Theodor Fechner was a German physicist who published a book proposing different psychophysical methods such as the methods of limits, adjustment and constant stimuli to quantify perceptual judgments (Sekuler & Blake, 2002). These are still widely used and their aim is to measure a physical stimulus threshold in order to quantify sensitivity of perceptual systems. In the present thesis the method of constant stimuli will be used throughout in order to construct psychometric functions and determine mean Points of Subjective Equality (PSE). A PSE represents the point at which two stimuli are indistinguishable and perceived as identical under certain conditions.

In psychophysics, the primary aim is to quantify how a stimulus dimension, for example length, is dependent upon another dimension. In order to do that, the proportion of times a variable stimulus (L2) is judged as longer than a standard (L1) is plotted along different points of the variable length dimension in a curve called a psychometric function. An example of a perfect psychometric function is illustrated in Figure 2.1 and the PSE is represented by a constant clear-cut point, when the length of L2 is identical to that of L1. More specifically, the probability of L2>L1 when L2 is 'shorter' is always zero, whereas when L2 is 'longer' this probability is always one.

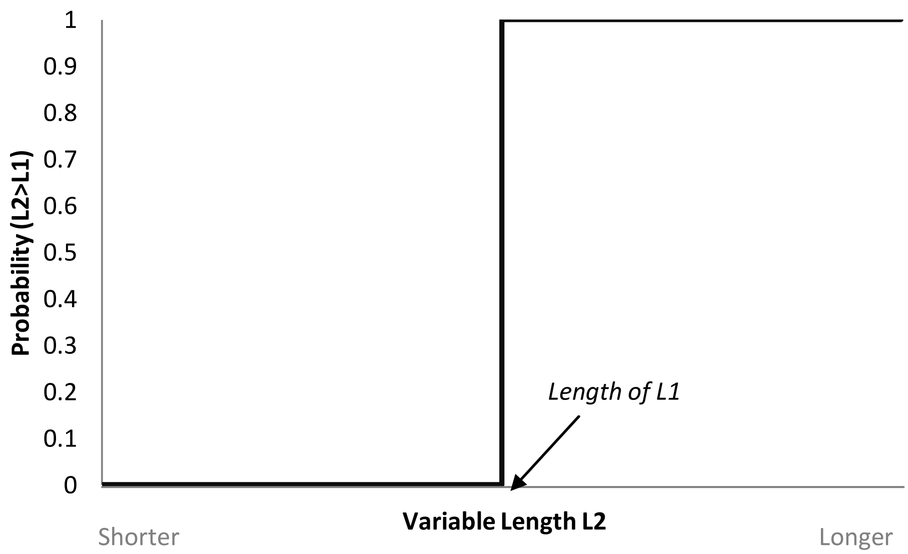


Figure 2.1 The ideal psychometric function showing probability of judging stimulus L2 to be longer than L1, while varying the length of L2 from shorter to longer.

However, in real life perceptual judgments are always affected by uncertainty leading to errors. Consequently, the PSE cannot be considered a clear-cut point where two stimuli are perceived as identical. Any experimental attempts to calculate PSEs have shown that psychometric functions closely resemble the red sigmoid curve illustrated in Figure 2.2, instead of the perfect one shown in black in the same figure. The shape of the perfect black sigmoid curve is combined with the distribution of error varying around the PSE arising due to uncertainty as shown by a green bell-shaped curve. This combination gives rise to the red sigmoid curve. The PSE is determined at the point where the grey dotted line crosses the red sigmoid curve, at P (L2>L1) = 0.5. The logic behind defining the PSE at P (L2>L1) = 0.5 lies on the fact that when the length of the two stimuli is perceptually identical, it will be equally likely to choose either one as the 'longer'.

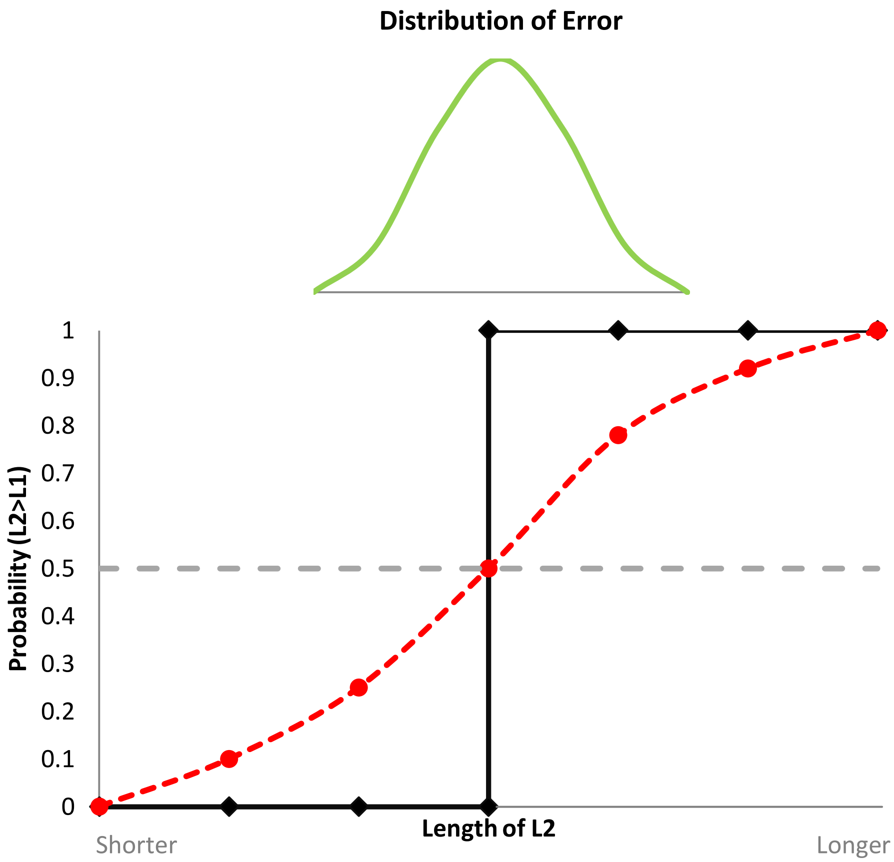


Figure 2.2 An illustration of a realistic psychometric function created by the combination of a perfect psychometric function and the distribution of error around the PSE. The probability of judging L2 to be longer than L1 is plotted against L2 length.

2.2 The method of constant stimuli

The method of constant stimuli is used throughout this thesis because of its precision and the fact that it is a standardized method, less affected by individual biases compared to other methods. As the task involved a forced choice decision of the subject, 'Is line A longer than line B?' we can see that there is a correct decision to the task. Although feedback could have been given to participants regarding their decision, this would have helped them adjust their predictions accordingly and fail to reveal their perception. If feedback had been given throughout experiments, results would provide an indication of their learning skills while failing to reveal the size of the illusion under investigation.

Seven different *variable* stimulus sizes in the region of the presumed PSE were chosen. These are presented repeatedly and randomly throughout each experiment, each one of them compared to a *standard* stimulus. The *variable* stimuli are identical in all aspects except the dimension under investigation (i.e. length) and participants are usually asked to indicate the 'longer' stimulus using a response box. For each stimulus size, the number of times each stimulus is classified as 'longer' is counted and data are then plotted with stimulus size along the abscissa (x-axis) and the probability of the variable stimulus perceived longer than the standard is plotted along the ordinate (y-axis).

In each subsequent experiment in the thesis, three or four types of standard stimuli are used with a different configuration or orientation of line elements that comprise the stimulus. A separate psychometric function will be constructed for each standard stimulus while one of its elements (i.e. horizontal or vertical line) will be compared to a simple line of variable size. The size of the standard stimulus will always remain the same.

In psychophysics, the shape of a psychometric function can be altered in two ways as shown in Figure 2.3 below. The graph on the left illustrates a shallower psychometric function (blue) compared to the original (red) due to an increased amount of error. Throughout the thesis, any participants generating similar psychometric functions with a standard deviation larger by three times or more than the group standard deviation will be excluded from further analysis as this will be taken as an indication of poor discrimination abilities. The second case is shown by the graph on the right indicating a shift of the psychometric function while maintaining its sigmoid shape, which can be seen when a participant perceives two physically identical stimuli as different due to illusory percept as it will be shown in subsequent experiments.

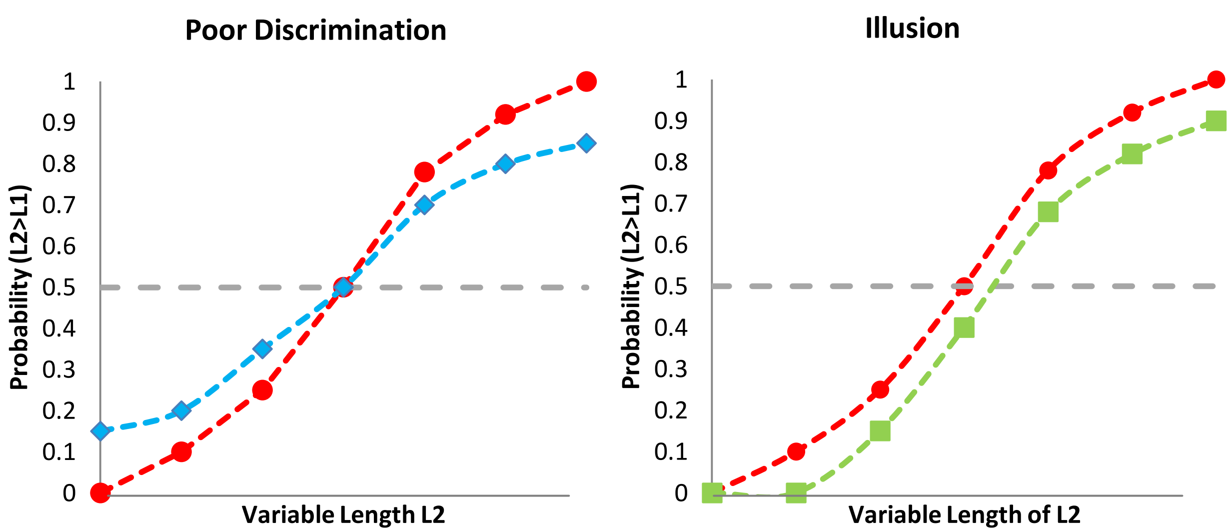


Figure 2.3 On the left a psychometric function with increased amount of error (blue) and on the right a shift in a psychometric function due to illusory percept (right-green). The probability of judging stimulus L2 to be longer than L1 is plotted against the variable L2 length.

2.3 Screen calibration

Three different screens were used to display stimuli throughout the thesis, which were γ-corrected. More specifically, for Experiments 1 - 11 included in Chapters 3, 4 and 5 a Clinton Monoray CRT was used with a P4, fast decaying yellow-green phosphor. The screen's resolution was 1024 x 768 pixels and the frame rate was 60Hz.

Squares of six different sizes, from 50 pixels to 300 pixels in steps of 50 pixels, were drawn on the screen and a measurement of their size in centimetres was recorded. Figure 2.4 below illustrates measurements in the vertical and horizontal axis for the six different squares. The equation generated for each of one of the two lines of best fit were used to calculate the desirable size of stimuli in each one of the experiments in Chapter 3, 4 and 5 and R^2 values were used to determine the accuracy of each equation.

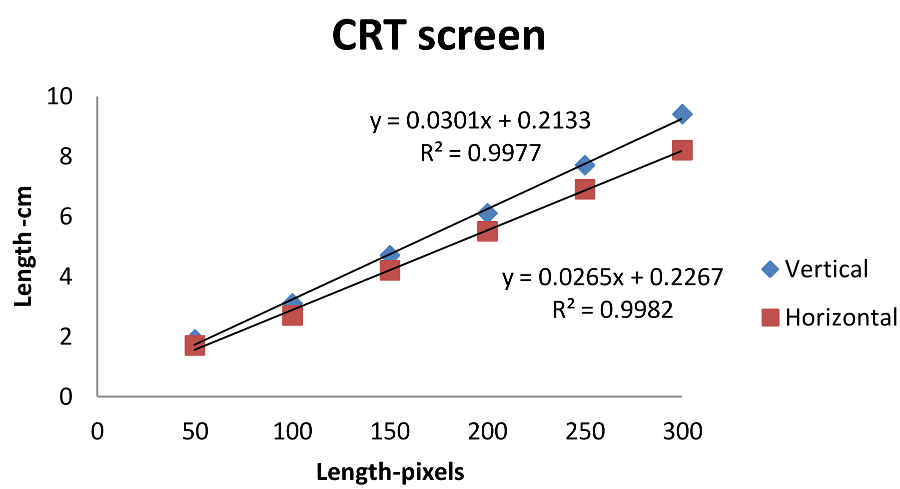


Figure 2.4 CRT screen calibration procedure for Experiments 1-11.

The exact same procedure was followed for both screens used for Experiment 12 carried out in Chapter 6 and Figure 2.5 and Figure 2.6 below illustrate lines of best fit and R^2 values. In the first part of Chapter 6, a Mitsubishi Diamond Plus 91 screen was used to display stimuli. The screen's resolution was 1024 x 768 pixels and the frame rate was 60 Hz.

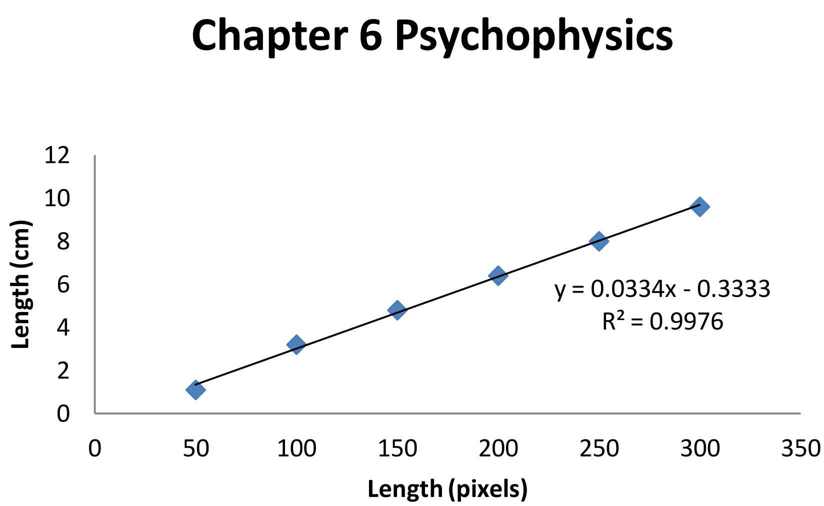


Figure 2.5 Screen calibration procedure for behavioural experiment in Chapter 6. Measurements are the same for the vertical and horizontal axis.

In the neuroimaging part of Chapter 6, a Dukane 8942 ImagePro 4500 lumens LCD projector was used to project stimuli on a custom in-bore acrylic projection screen subtending 45 x 30 degrees of visual angle while participants were lying in the Magnetic Resonance Imaging scanner.

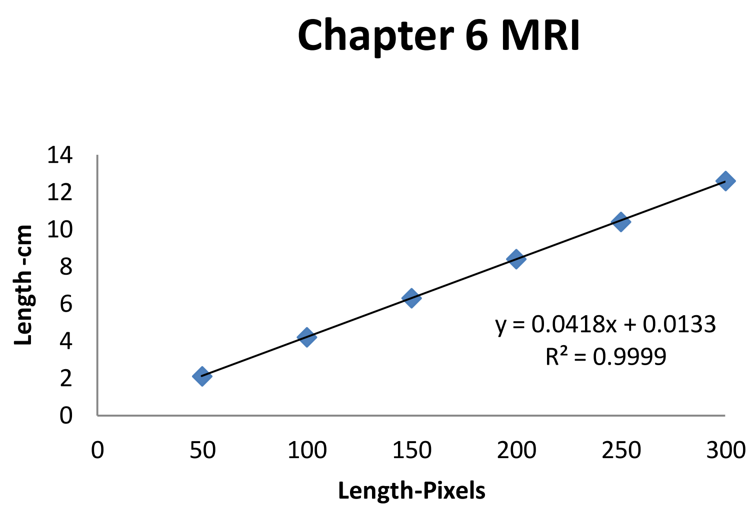


Figure 2.6 Screen calibration procedure for neuroimaging experiment in Chapter 5. Measurements are equal for the vertical and horizontal axis.

All three screens were connected to a ViSaGe Visual Stimulus Generator and calibrated stimuli were presented with precision timing and luminance for each experiment. The ViSaGe was used alongside to a CB6 response box which participants used to make their responses. The CRS Toolbox for MATLAB software was used for programming the ViSaGe.

2.4 Participants

Participants involved in experiments described in this thesis were undergraduate and postgraduate students at the University of York. They were recruited using the online Psychology Electronic Experiment Booking System (PEEBS) of the Department of Psychology, University of York and advertising was carried out through a university-wide email list of students interested to participate in research. Participants signed a consent form and were informed that they could withdraw from the experiment they were carrying out at any point, without giving a reason. First and second year undergraduate Psychology students were carrying out experiments as part of their course requirement and other students were rewarded with a small payment subsidized by the Department of Psychology, University of York. Some participants carried out more than one experiment.

2.5 Analysis of Results

In subsequent pilot studies and experiments psychometric functions (cumulative Gaussians) were fitted through the data for each participant by the method of least squares and the point of subjective equality (PSE) determined. For each experiment, the mean PSE for all participants was calculated and graphs summarizing results from all participants include 95% confidence intervals which are plotted as error bars for each experimental condition. In each experiment in Chapters 3, 4 and 5 repeated measures analysis of variance was carried out to determine presence of main effects and significance of differences between experimental conditions.

2.6 Pilot studies

We carried out two pilot studies in order to determine the appropriate stimulus size range to be used in future experiments and the amount of length change from a variable stimulus to another sufficient to produce a just noticeable difference (jnd) in perception. Each variable stimulus should yield a slightly different response compared to the immediately shorter or longer stimulus in the range. Also, we wanted to determine whether performance, using the method of constant stimuli was satisfactory to generate meaningful results. The task required participants to compare a standard horizontal line with two ‘ticks’ at either end against one of seven comparator stimuli composing of another horizontal line with two ‘ticks’ at either end, varying in size from slightly smaller to slightly longer than the standard and indicate the longer one (see Figure 2.7 below). The deviations from the standard width were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the variable stimulus ranging between 5.2° to 7.0°. The size of the end ‘ticks’ was 0.61°. . The luminance of the stimuli was approximately 20cd/m^2 and the background approaching 0cd/m^2, so the contrast approached 1.00.

Figure 2.7 Stimuli used in Pilot Study 1 and Pilot Study 2.

2.6.1 Pilot study 1

Six participants with normal or corrected to normal vision completed the pilot study. As in all experiments in this thesis a chin rest was used to ensure that they were exactly 57cm away from the screen. The experiment was fully counterbalanced, so that for each of the seven stimulus sizes, on half the trials the variable stimulus was presented on the left part of the screen and for the other half it was presented on the right part of the screen in order to avoid biases to the left or the right side. Also, we randomly added some ‘jittering’ either towards the left or the right so that participants’ responses for a specific trial would not be affected by previous trials. The same counterbalancing and jittering procedures were performed throughout the thesis. Results generated are illustrated in Figure 2.8 below.

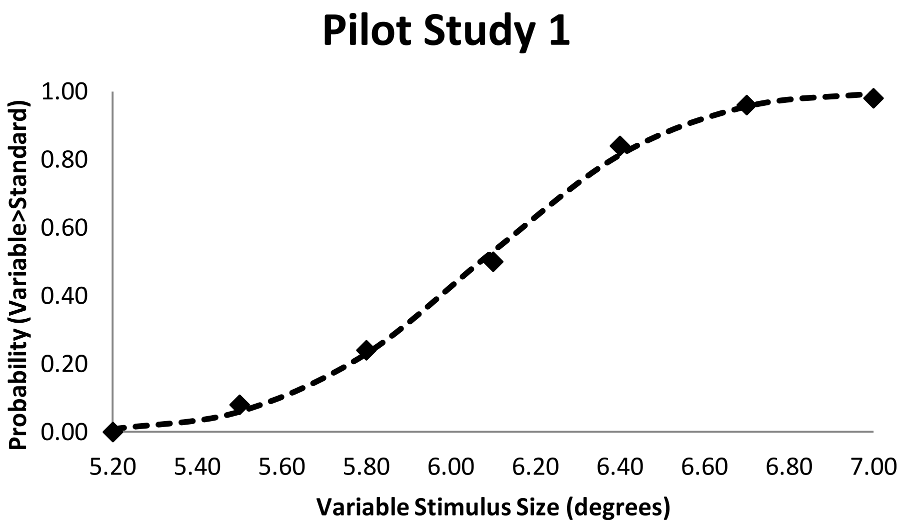


Figure 2.8 Results from Pilot Study 1 (N=6).

2.6.2 Pilot study 2

A single participant with normal vision completed Pilot study 2 with a narrower range of variable stimulus values, smaller separation steps and more stimulus sizes. This was fully counterbalanced in the same way as Pilot study 1 and results are shown in Figure 2.9 below.

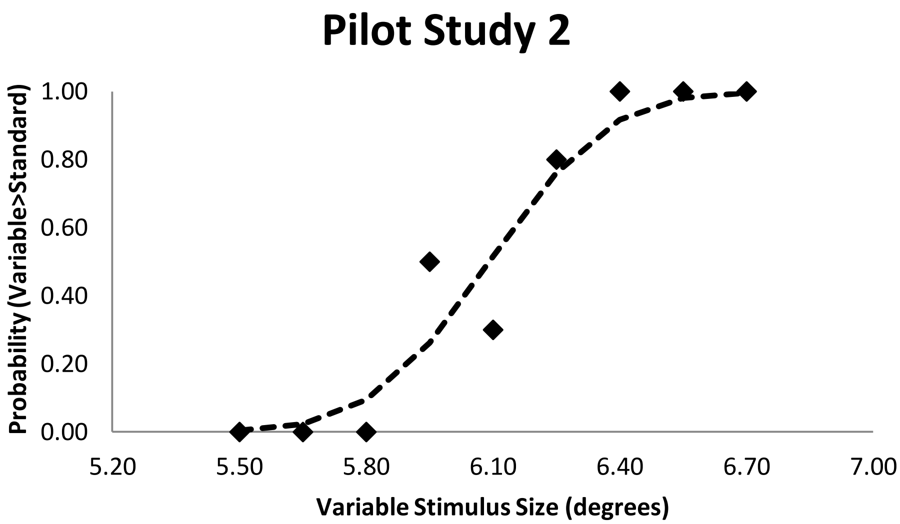


Figure 2.9 Results from Pilot Study 2 (N=1).

In general, the psychometric functions generated by both Pilot studies have a clear sigmoid shape starting from zero and reaching 100% and they show that a range of approximately two degrees encapsulates the complete psychometric function. However, in Pilot study 2 responses for the three shorter as well as the three longer sizes were identical. Specifically, each one of these six sizes failed to yield a slightly different response compared to the previous or next stimulus size.

Consequently, in subsequent experiments we decided to use the wider range of values used in Pilot Study 1, as this would allow for any shifts either to the left or the right due to the presence of an illusion without losing valuable information towards the top or the bottom of the curve. A difference of 0.3 degrees as used in Pilot Study 1 was sufficient to differentiate between adjacent variable stimulus sizes and the method of constant stimuli proves appropriate to produce meaningful results.

Chapter 3 - The Oppel-Kundt illusion

The aim of this Chapter is to investigate the effect of the number, size and position of vertical lines on a horizontal line on the size of the Oppel-Kundt illusion. Additionally, an inverted 'T' configuration will be used to assess the bisection component of the vertical-horizontal illusion, as described by Mamassian and de Montalembert (2010) which will lay the foundation for subsequent experiments in Chapter 5.

3.1 Introduction

As previously mentioned in Chapter 1, in the Oppel-Kundt illusion, a graduated division with regularly-spaced vertical lines of a given dimension is perceived as larger than another one which is 'unfilled' (Figure 3.1). More specifically, the area filled with parallel lines appears larger in size in the direction orthogonal to those lines, compared to the unfilled area of equal size. Oppel (1855) was the first researcher to observe and report that dividing a stripe into its subparts affected its perceived size. Moreover, Kundt (1863) investigated this effect using a straight horizontal line with thick vertical points on either end and some vertical divisions on one side. After 1000 observations were made by different observers using the method of adjustment he concluded that when trying to divide the whole line into two equal parts the one with the divisions was always made smaller. He assigned this overestimation of the 'divided' part to the shape of the eye.

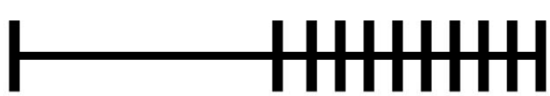


Figure 3.1 Stimulus used by Kundt (1863); the divided part (right) looks wider than the undivided part (left).

In the present chapter we will investigate how changing the number of dividing lines affects the size of the Oppel-Kundt illusion. Whereas Piaget and Osterrieth (1953) demonstrated that the maximum effect arises when 9 to 14 lines are present, Obonai (1933) generated slightly different results suggesting that the maximum effect is found between 7 and 13 lines. Moreover, Coren and Girgus (1978) specified that this increase happens only up to a critical point and beyond that, the perceived size gradually decreases. Additionally, Coren & Girgus argued that the combination of spacing between the lines and their width (i.e. the duty cycle) is the determinant for the size of the effect and not the number of lines. They confirmed this by manipulating the retinal size of the Oppel-Kundt stimulus, while keeping the number of dividing lines constant. In addition, Piaget & Osterrieth (1953) and Oyama (1960) have argued that both a very small and a very large number of dividing lines moderate the effect, with seven to nine lines increasing the illusory percept to its maximum.

Interestingly, according to Helmholtz (1867) the perceived size of a regularly divided space or line is increased compared to an undivided one, because the existence of such divisions confirms the fact that they fit within that space or line. If these divisions were absent we would be unable to mentally estimate how many of them would fit within that space or line. This suggestion is in accordance with an explanation put forward by Ganz (1966) who proposed a lateral inhibition model able to accurately predict changes in the perceived location of the illusory stimulus, as a function of the retinal distance between adjacent contours. As far as the Oppel-Kundt illusion is concerned, Craven and Watt (1989) claimed that the average contour density, determined by the number of zero-crossings in a range of spatial scales (Watt, 1990), is responsible for the phenomenon. Moreover, when the illusion was measured after adaptation of the subject to parallel lines no aftereffect was found leading to the conclusion that the illusory percept is not a product of an uninterrupted spatial calibration mechanism (Craven, 1995).

The stimuli to be used in the experiments described in the present chapter range between 4.7° and 7.5° in size because it has been reported that the Oppel-Kundt illusion is bigger with small compared to large stimuli (Obonai, 1954; Long & Murtagh, 1984). Furthermore, we are only going to investigate the Oppel-Kundt illusion with regularly-spaced divisions because according to Piaget and Osterrieth (1953) the effect of the illusion diminishes with irregularly-spaced divisions.

In addition to the Oppel-Kundt illusion, experiments in the present chapter will investigate amongst others, the exceptional case of a single vertical line abutting (i.e. touching) or crossing a horizontal in various figures, including an inverted ‘T’ configuration. This has been referred to as the vertical-horizontal illusion. According to Finger and Spelt (1947), Titchener (1901, 1925) first reported the importance of bisection in the underestimation of the horizontal line when compared to the vertical, in an inverted ‘T’ configuration. Consequently, Finger and Spelt (1947) investigated this assertion by using four types of figures; an ‘L’ shape with the two lines slightly separated in two different orientations, an inverted ‘T’ and finally a horizontal ‘T’. They used the method of adjustment and asked 72 participants to match the length of the variable line in the figure which could either be the horizontal or the vertical, to its perpendicular line acting as the standard. Results generated showed that the perceptual judgment for the inverted and horizontal ‘T’ was affected not only by the orientation of the two lines as it was previously claimed but by the bisection of the vertical as well. Consequently, Finger and Spelt were the first experimenters to show experimentally that in an inverted ‘T’ configuration ‘...the perceived shortness of the horizontal line is in addition a distinct function of its bisection by the vertical...’ (p. 249).

A study which aimed at distinguishing and then quantifying the contributing factors of the vertical-horizontal illusion was recently carried out by Mamassian and de Montalembert (2010) who used ‘T’, ‘L’ and ‘+’ configurations. Results showed two independent components which were in agreement with previous studies (Künnapas, 1955; Charras & Lupianez, 2009) and quantified them as well: (i) an anisotropy bias of an average of 6% causing an overestimation of the vertical segment relative to the horizontal one and (ii) a bisection bias of an average 16% causing an underestimation of the bisected line relative to the bisecting line.

Mamassian and de Montalembert (2010) found that a late-noise model described experimental data best, where the participants’ uncertainty of stimulus size plays a role near the decision stage, instead of during the stimulus size estimation process. This study confirmed that the bisection component results in the *underestimation* of the bisected line instead of an *overestimation* of the bisecting line. Researchers deduced this because according to the proposed model, the bisection component generates a reduced sensitivity for the ‘+’ figure compared to the ‘L’ figure as indicated by a not-so steep psychometric function. Figure 3.2 below illustrates results generated by Mamassian and de Montalembert (2010) and as it can be seen the two curves are almost identical (L-curve in red, +-curve in pink). However, they have failed to confirm this assertion experimentally by comparing the horizontal segment of each of the two stimuli to another simple horizontal line. In the present chapter, comparisons between an the horizontal segment of an inverted ‘T’ configuration and an independent horizontal line are to be carried out in order to determine the existence and validity of Mamassian and de Montalembert’s (2010) bisection component.

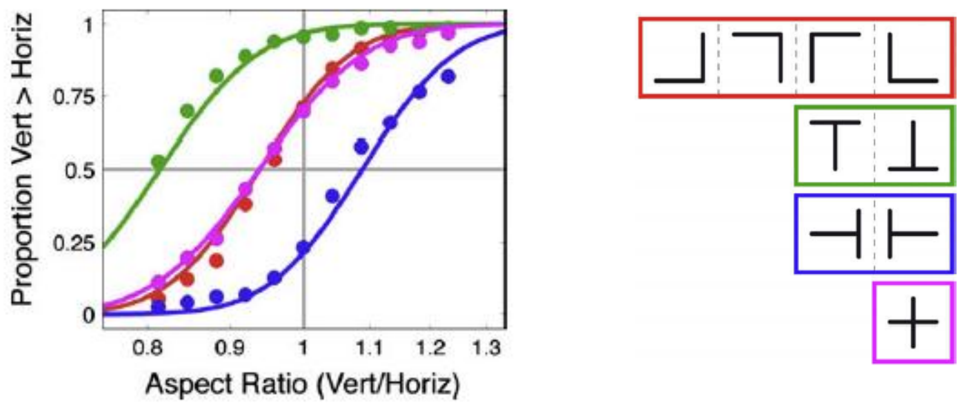


Figure 3.2 Results generated by Mamassian and de Montalembert (2010, Fig.2) showing the proportion of times the vertical line was perceived as longer than the horizontal within a single stimulus for the four classes of stimuli (N=24).

In contrast to Mamassian and de Montalembert (2010), Charras and Lupianez (2009) argued that because both lines in a ‘+’ configuration are bisected, the vertical bias is cancelled out implying that none of the two components of the vertical-horizontal illusion are functioning, leading to veridical size perception. More specifically, their study investigated the role of bisection and anisotropy in line length perception using ‘T’, ‘+’, horizontal ‘T’ and ‘L’ figures.

3.2 Experiment 1

3.2.1 Rationale

The aim of this experiment is to investigate the 'bisection' component of the vertical-horizontal illusion, as described by Mamassian and de Montalembert (2010) in conjunction with the Oppel-Kundt illusion by the method of constant stimuli, with observers comparing the apparent length of two horizontal lines. We manipulated the number of vertical lines regularly-spaced and abutting on the standard stimulus with 0, 1, 5 and 9 vertical lines and each one of these four standard stimuli were compared against a variable stimulus, a horizontal line with no vertical lines.

3.2.2 Method

Four conditions were interleaved; in the control (no vertical lines) a standard horizontal line 6.1° long with two 'ticks' at either end was compared with one of seven comparator stimuli composing of another horizontal line with two 'ticks' at either end, varying in size from slightly smaller to slightly longer than the standard. The deviations from the standard length were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the variable stimulus ranging between 5.2° to 7.0°.For the other three conditions, 1, 5 or 9 vertical lines were positioned on the standard horizontal line in a regular manner and their length was equal to that of the standard horizontal i.e. 6.1°. The size of the two end 'ticks' was 0.61°. Figure 3.3 below illustrates the stimuli used in this experiment.

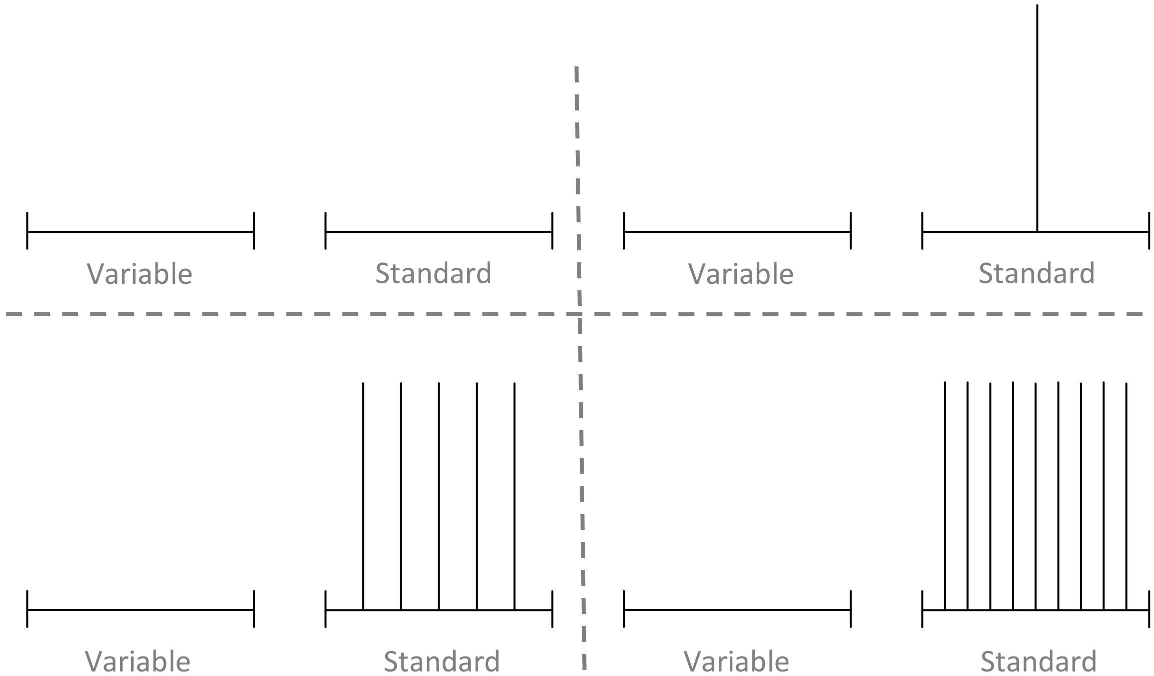


Figure 3.3 Stimuli used in Experiment 1. The variable stimulus was always a horizontal line with two 'ticks' at either end. The control condition is shown in the upper left window.

Each of eleven naïve observers (ten female) undertook 336 trials; eight pairs of stimuli each presented six times for seven variable stimulus sizes. Participants were asked to indicate the longer horizontal line using a response box and the control condition was used to evaluate whether or not participants were able to carry out the task. Stimuli were positioned one next to the other and presented simultaneously for 1000ms. The luminance of the stimuli was approximately 20cd/m² and the background 0cd/m², so the contrast is close to 1.00. The timeline for this experiment is shown in Figure 3.4 below.

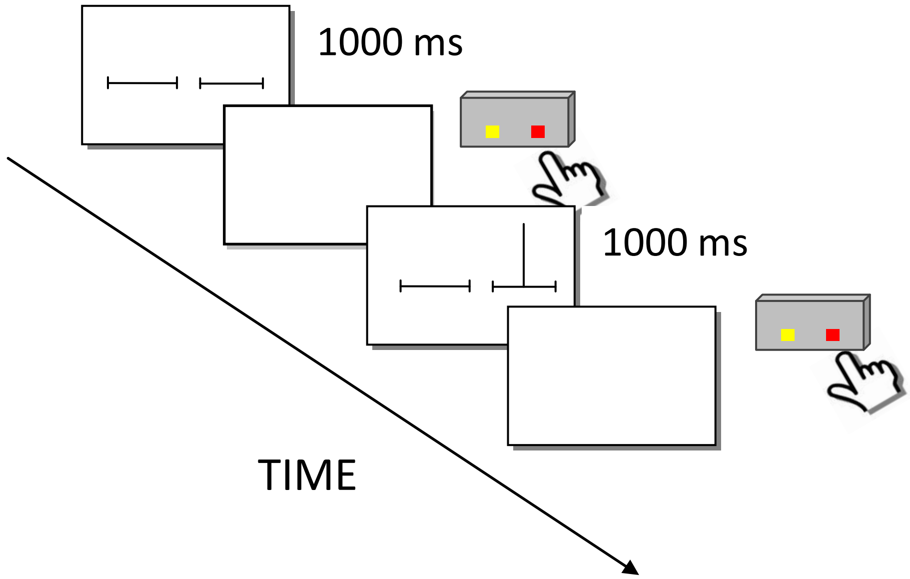


Figure 3.4 Timeline of Experiment 1 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

3.2.3 Results

Comparisons between a horizontal line and the four conditions were made so that psychometric functions could be determined and PSEs calculated for eleven participants. Figure 3.5 depicts the psychometric functions generated for a single participant for all four conditions. As in all subsequent graphs in the thesis, the PSE for each curve lies at the crossing point between itself and the grey dotted line and 95% confidence intervals were calculated and displayed for each condition. The functions for the control condition and five vertical lines are shown in orange and blue colour respectively, with a mean PSE 6.03° for the former and 6.11° for the latter. The function for a single vertical (green) is almost identical to the blue function generating a mean PSE of 6.13°. Also, there is a slight increase in the apparent size of the simple horizontal line when 9 verticals are present, illustrated by a right shift compared to the control condition, giving a mean PSE of 6.25°, shown in purple colour.

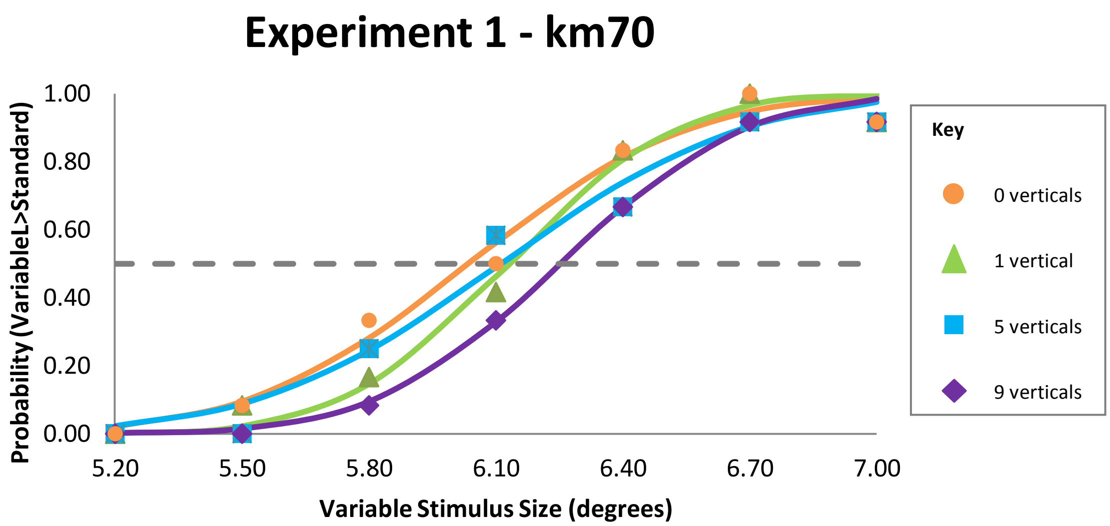


Figure 3.5 Psychometric functions for a single participant from Experiment 1.

Results for all participants are illustrated in Figure 3.6 showing that in an inverted 'T' configuration where the vertical line is equal in length to the horizontal, there is no significant change in the perceived length of the horizontal line. An absence of a significant difference in the perceived size of a horizontal line when five abut it is evident, whereas the perceived length of a horizontal line is significantly increased when nine lines are present.

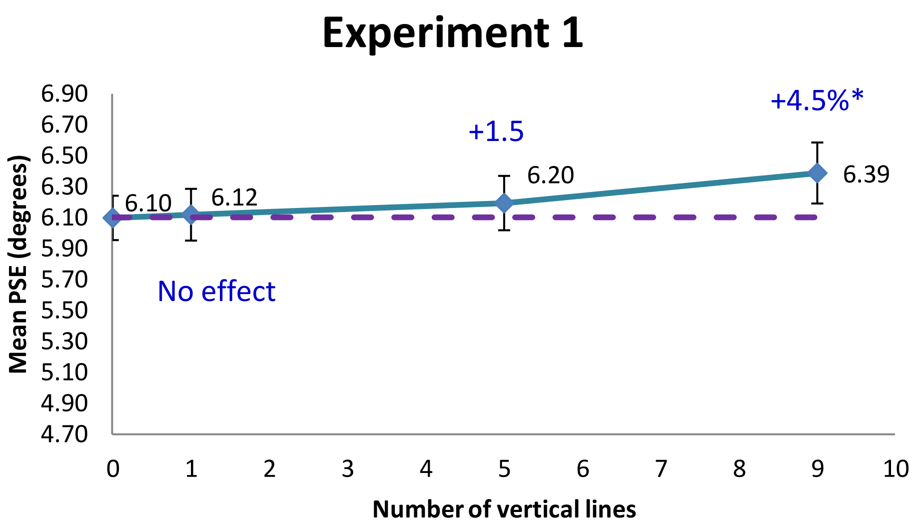


Figure 3.6 Results from Experiment 1, showing a significant overestimation of the perceived size of a horizontal line with 9 vertical lines abutting by approximately 4.5% (N=11). Error bars show 95% confidence intervals.

The results show that the perceived size of the horizontal segment in our stimuli was significantly affected by the number of vertical lines abutting it, V = 0.74, F (3, 30) = 8.20, $p<.05$. *A* z-test showed a significant increase in the perceived size of a horizontal line compared to the actual physical size of the stimulus, when 9 lines were present ($p<.01$).

3.2.4 Discussion

In the present experiment the general trend of the results suggests no significant differences in the apparent size of a horizontal line when one or five vertical lines of the same size abut it. More specifically, when a single vertical line, the same size as the horizontal one, abutted the latter we failed to observe any illusory percept induced by the 'bisection' component of the vertical-horizontal illusion as Mamassian and de Montalembert (2010) would predict. This might be due to the fact that the vertical line does not actually *cross* the horizontal, but only *abuts* it.

The absence of a bisection illusion is rather surprising following from the work of Mamassian and de Montalembert (2010) who would predict a 16% reduction in the apparent size of the horizontal segment of an inverted-T configuration induced by their ‘bisection’ component. A possible reason for this might be the presence of the end ‘ticks’ which might be acting as terminators, therefore allowing the viewer to make veridical size judgments by looking at the lower part of the stimulus where perception is not interrupted by any ‘divisions’.

Furthermore, results generated revealed a significant increase in the perceived size of a horizontal line when nine vertical lines abut it, illustrating the classic Oppel-Kundt illusion. This result is in accordance with Piaget and Osterrieth (1953) and Obonai (1933), who suggested a maximum Oppel-Kundt effect around nine vertical lines.

3.3 Experiment 2

3.3.1 Rationale

The aim of this experiment is to determine whether the end 'ticks' present in all stimuli in our previous experiment, affected the 'bisection' component as described by Mamassian and de Montalembert (2010) and the Oppel-Kundt illusion. Similarly, we manipulated the number of vertical lines regularly-spaced on the standard stimulus with 0, 1, 5 and 9 vertical lines and each one of these four standard stimuli were compared against a variable stimulus.

3.3.2 Method

This experiment is a replication of the previous one with two modifications. Firstly, the end 'ticks' from all stimuli are removed and secondly, the presentation time of the stimuli is reduced from one second to 750 milliseconds. A decreased duration not only was found to be sufficient for participants to make their judgment, but it allowed for more repetitions to be carried out within the same amount of time. Each of ten naïve observers (seven female) undertook 1400 trials; eight pairs of stimuli each presented 25 times for seven variable stimulus sizes. Participants were asked to indicate the longer horizontal line using a response box and the control condition was used to evaluate whether or not they were able to carry out the task. All other experimental details were identical to those in Experiment 1. The stimuli are shown in Figure 3.7 below and the timeline for the experiment is shown in Figure 3.8.

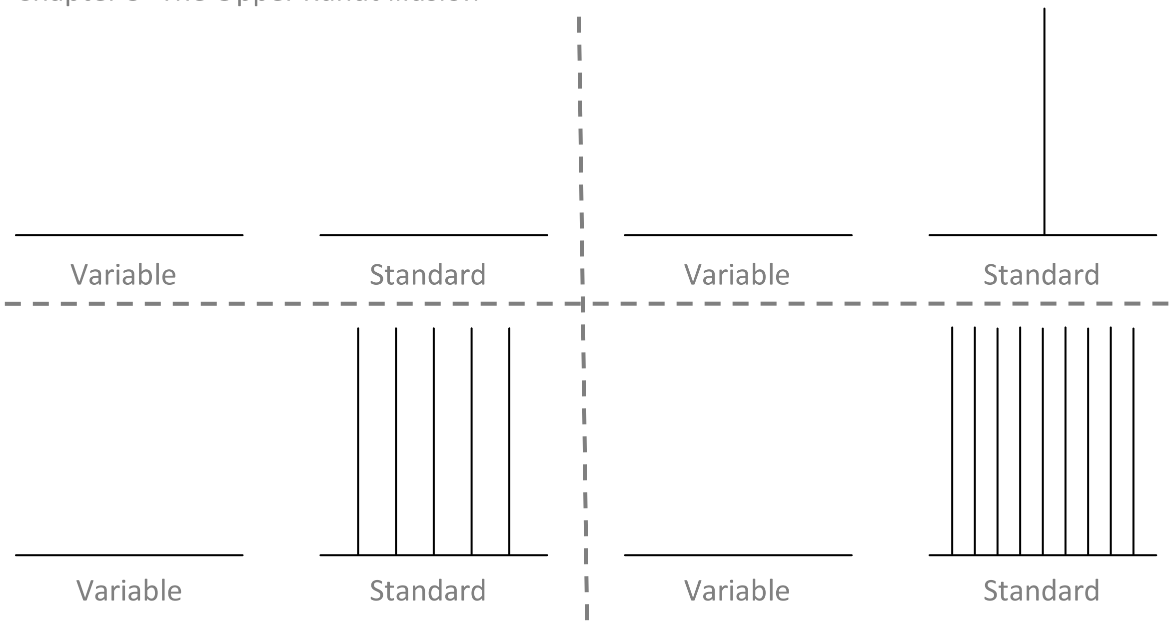


Figure 3.7 Stimuli used in Experiment 2. The variable stimulus was always a simple horizontal line. The control condition is shown in the upper left window.

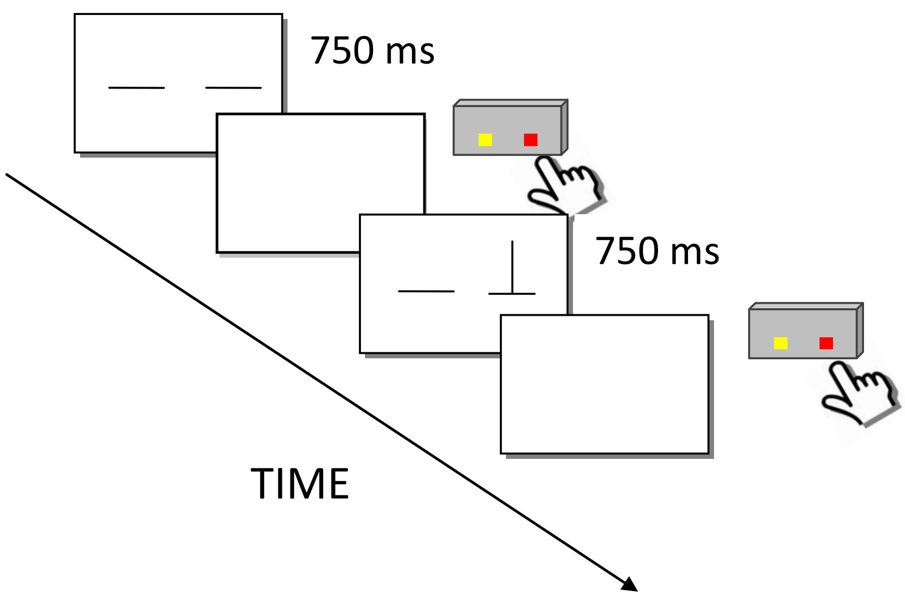


Figure 3.8 Timeline of Experiment 2 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

3.3.3 Results

Comparisons between a horizontal line and the four conditions were made so that psychometric functions could be determined and PSEs calculated for ten participants.

In Figure 3.9 the graphs illustrate the psychometric functions generated for two participants for all four conditions. For both participants, the mean PSE for the control condition is 6.1°. When comparing the two participants, km52 indicates an increased perceived size of the horizontal line as the number of verticals abutting increase and this is evident from the progressive shift of the psychometric functions from the left to the right. On the contrary, jb99 experiences a decrease in the perceived size of the horizontal lines when a single vertical abuts it, whereas the psychometric function for five verticals is very similar to the one for the control condition. Finally, the psychometric function illustrating performance for nine verticals is shifted to the right.

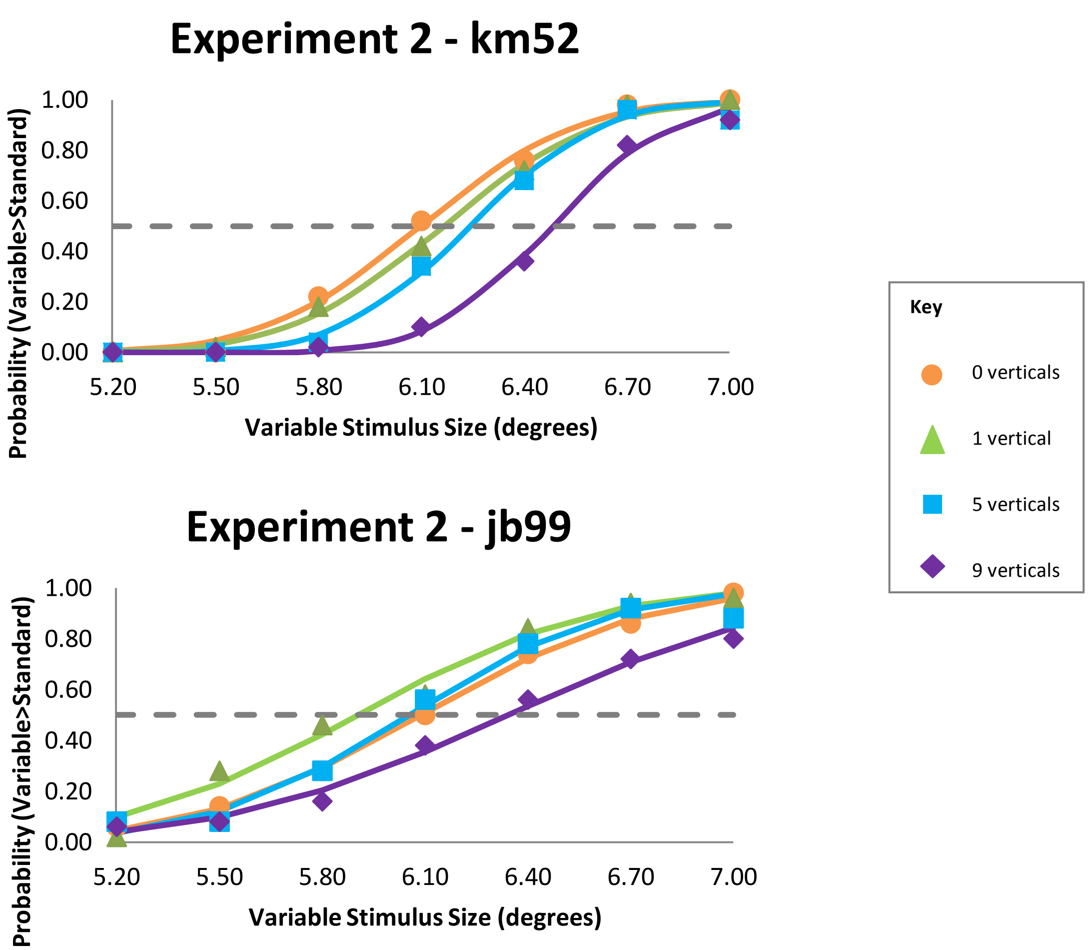


Figure 3.9 Psychometric functions for two participants from Experiment 2.

Results for all participants are illustrated in Figure 3.10 showing that even in the absence of end 'ticks' there is no significant decrease in the apparent size of a horizontal line when a single vertical abuts it at the midpoint. An absence of a significant difference in the perceived size of a horizontal line when five lines abut it and a significant increase of the perceived length of a horizontal line are evident.

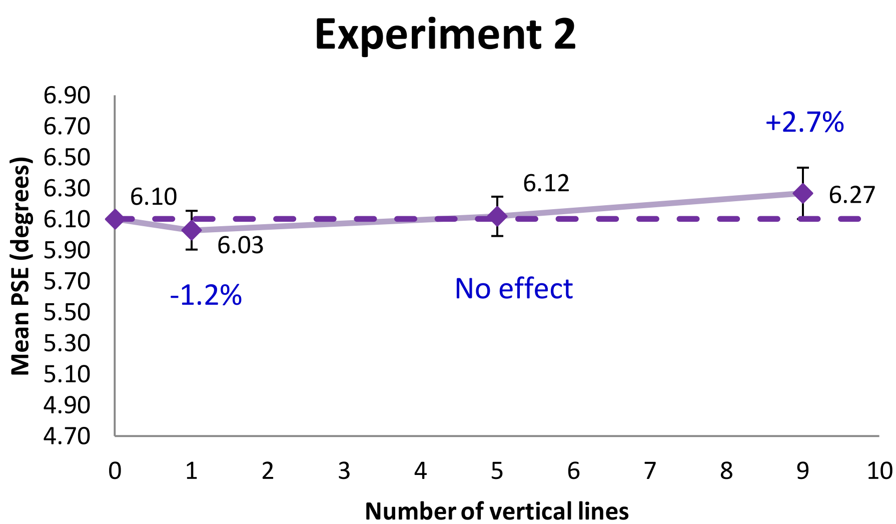


Figure 3.10 Results from Experiment 2, showing a significant overestimation of the perceived size of a horizontal line with 9 vertical lines abutting it by approximately 2.7% (N=10). Error bars show 95% confidence intervals; error bar on zero vertical condition is smaller than symbol.

Results show that the perceived size of the horizontal segment in our stimuli was significantly affected by the number of vertical lines abutting it, $V = 0.74$, $F(3, 27) = 4.04$, $p < .05$. *A* z-test showed a significant increase in the perceived size of a horizontal line compared to the actual physical size of the stimulus when 9 lines were present ($p<.05$).

3.3.4 Discussion

Results generated suggest there is a marginally significant effect of the number of lines abutting a horizontal line on its apparent size. When a single vertical line, the same size as the horizontal one, abutted the latter we observed no ‘bisection’ illusion as described by Mamassian and de Montalembert (2010). Consequently, taking into consideration results from both Experiment 1 and Experiment 2, the presence or absence of end ‘ticks’ does not affect the bisection illusion. We suggest that the absence of the bisection illusion in these two experiments arises from the fact that the vertical line does not *cross* the horizontal but only abuts it.

Furthermore, the Oppel-Kundt illusion was not evident with five vertical lines, a result consistent with Experiment 1. Although the illusion is evident with nine vertical lines the effect is reduced to 2.7% compared to 4.5% from Experiment 1. We speculate that this is due to the absence of the end ‘ticks’ which are usually present in a classic Oppel-Kundt figure.

3.4 Experiment 3

3.4.1 Rationale

The aim of this experiment is to investigate how the size and the position of the vertical ‘divisions’ on a horizontal line affect ‘bisection’ component as described by Mamassian and de Montalembert (2010) and the Oppel-Kundt illusion by the method of constant stimuli, with observers comparing the apparent length of two horizontal lines. There are two fundamental differences compared to previous experiments; (a) the size of the vertical lines is reduced and (b) the vertical lines no longer abut the horizontal, but cross it instead. Similarly to the previous two experiments, we manipulated the number of vertical lines regularly-spaced on the standard stimulus with 0, 1, 5 and 9 vertical lines and each one of these four standard stimuli were compared against a variable stimulus.

3.4.2 Method

Four conditions were interleaved; in the control condition (no vertical lines) a standard horizontal line with two ‘ticks’ at either end was compared with one of seven comparator stimuli composing of another horizontal line with two ‘ticks’ at either end, varying in size from slightly smaller to slightly longer than the standard. The deviations from the standard width were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the variable stimulus ranging between 5.2° to 7.0°. For the other three conditions, one, five or nine vertical ‘ticks’ were crossing the standard horizontal line in a regular manner and their length was identical to that of the end ‘ticks’ i.e. 0.61°. Figure 3.11 below illustrates the stimuli used in this experiment.

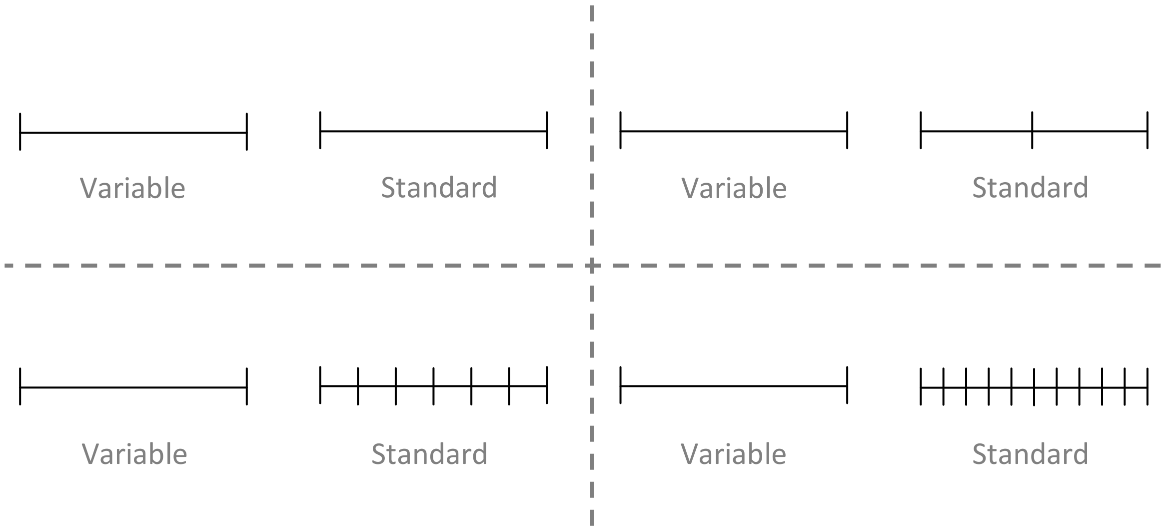


Figure 3.11 Stimuli used in Experiment 3. The variable stimulus was always a horizontal line with two 'ticks' at either end. The control condition is shown in the upper left window.

Each of eleven naïve observers (ten female) undertook 336 trials; eight pairs of stimuli each presented six times for seven variable stimulus sizes. Participants were asked to indicate the longer horizontal line using a response box and the control condition was used to evaluate whether or not participants were able to carry out the task. Stimuli were positioned one next to the other and presented simultaneously for 1000ms. The luminance of the stimuli approached 0cd/m² whereas the background luminance was 20cd/m², so the contrast is approaching 1.00. The timeline for the experiment is shown in Figure 3.12 below.

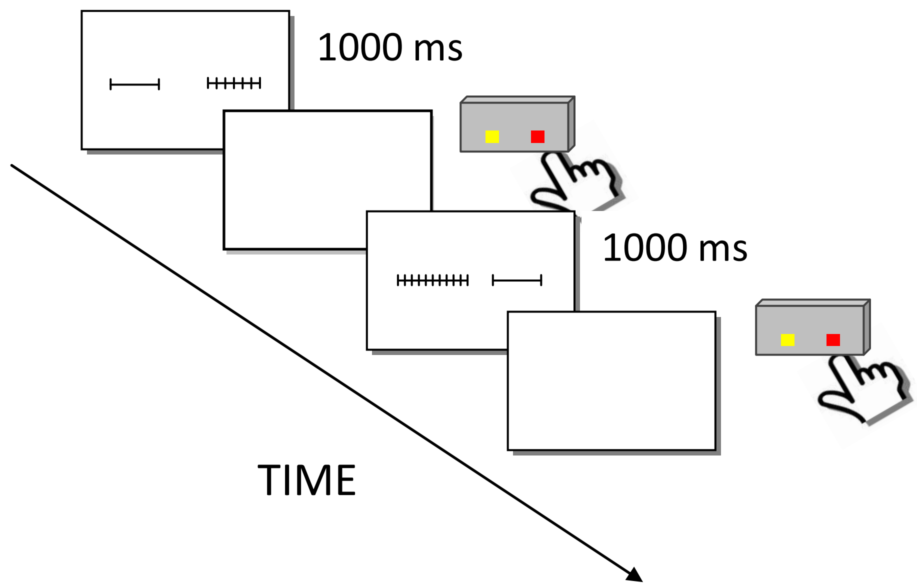


Figure 3.12 Timeline of Experiment 3 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

3.4.3 Results

Comparisons between a horizontal line and the four conditions were made so that psychometric functions could be determined and PSEs calculated for eleven participants. Figure 3.13 depicts the psychometric functions generated for a single participant for all four conditions. The orange curve represents the control condition and the mean PSE for this is 6.08° confirming that the participant is able to match two horizontal lines presented side by side. The green curve represents the condition when a single 'tick's bisects a horizontal line and the mean PSE is 5.95°, showing that bisected horizontal line has to be slightly smaller than the unbisected one, for the two to be perceived identical. The blue curve represents the condition when a five 'ticks' are equally spaced along the length of a horizontal line and the mean PSE is 6.31°, showing that for this specific participant the former has to be slightly longer than the latter, for the two to be perceived identical. The same illusory percept is observed with nine 'ticks' generating a mean PSE of 6.35°.

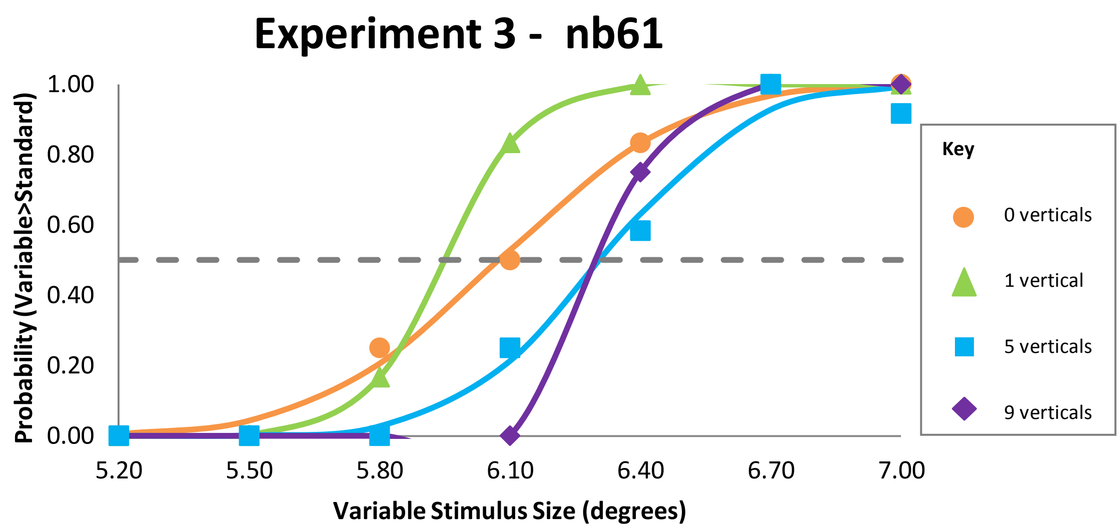


Figure 3.13 Psychometric functions for a single participant from Experiment 3.

Results for all participants are illustrated in Figure 3.14 showing participants could match the size of two simple horizontal lines. Additionally, the perceived length of a bisected horizontal line was found to be approximately 6% smaller than that of an unbisected line of the same size. When five 'ticks' were equally spaced along the length of a horizontal, there was no significant difference in its perceived size, but when the number of 'ticks' was increased to nine, there was a 5% significant increase in the perceived size of the horizontal line.

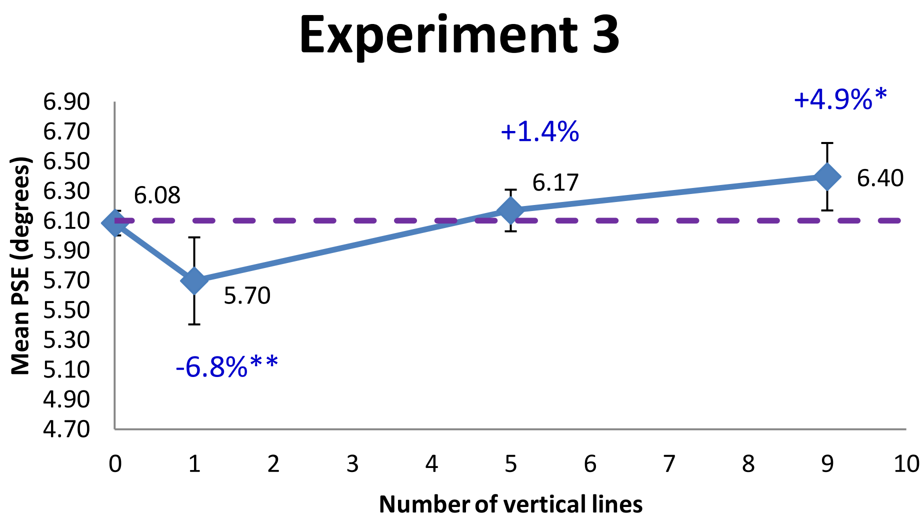


Figure 3.14 Results from Experiment 3, showing a significant underestimation of the perceived size of a horizontal line with a single 'tick's by 6.8% and a significant overestimation of the perceived size of a horizontal line with 9 'ticks' by 4.9% (N=11). Error bars show 95% confidence intervals.

The results show that the perceived size of the horizontal segment in our stimuli was significantly affected by the number of vertical lines crossing it, V = 0.65, F (3, 30) = 10.23, p < *.05. A* z-test revealed a significant decrease in the perceived size of a horizontal line compared to the actual physical size of the stimulus, when a single 'tick' was present (p<*.01*). Another z-test revealed a significant increase in the perceived size of a horizontal line compared to the actual physical size of the stimulus when 9 'ticks' were present (p<*.01*).

3.4.4 Discussion

The aim of this experiment was to investigate how the size and the position of the vertical 'divisions' on a horizontal line affect the bisection component as described by Mamassian and de Montalembert (2010) and the Oppel-Kundt illusion. From results generated it is evident that the altered size and position of the vertical 'ticks' affect the magnitude of these two illusions.

In the present experiment we have generated evidence of a bisection illusion, illustrating that the presence of a single ‘tick’ dividing the horizontal line into two, reduces the perceived size of the latter by 6.8%. Following the absence of a bisection illusion in Experiment 1 and Experiment 2, when comparing the horizontal line (with and without end ‘ticks’ respectively) of an inverted ‘T’ to another horizontal line (with and without end ‘ticks’ respectively) we have suggested that such an illusory percept might only exist when a vertical segment *crosses* the horizontal and indeed this is what we have proved in the present experiment.

In the previous two experiments when a vertical line was *abutting* a horizontal, participants were essentially comparing two identical lines simply ignoring the presence of a vertical line and comparing only the lower parts of the two horizontal lines where perception was uninterrupted, achieving veridical judgments. Additionally, their task was easier in Experiment 1 due to the presence of the end ‘ticks’ acting as terminators. However, in the present experiment the position of the vertical ‘ticks’ made it impossible for participants to employ a strategy similar to the one we suggested they might have used in Experiment 1 and Experiment 2.

Consistent with the previous two experiments we failed to find an Oppel-Kundt illusion when five ‘divisions’ were crossing a horizontal line. This confirms that size perception of a horizontal line is near-veridical when five lines are present, irrespective of size or position. Finally, the Oppel-Kundt illusion was only evident with nine vertical ‘ticks’ crossing a horizontal, increasing significantly its perceived size by 4.9%, a result consistent with past literature (Piaget & Osterrieth, 1953; Oyama, 1960).

3.5 Experiment 4

3.5.1 Rationale

The aim of this experiment is to determine whether merging the standard and variable stimuli into one to resemble the original Oppel-Kundt stimulus would increase the illusory percept. As in the previous experiments, we manipulated the number of vertical 'ticks' regularly-spaced on the standard component of the stimulus with 0, 1, 5 and 9 'ticks' and each one of these was compared against the variable component of the stimulus.

3.5.2 Method

Four conditions were interleaved; in the control (no 'ticks') a standard horizontal line with two 'ticks' at either end was merged with and compared against one of seven comparator stimuli composing of another horizontal line with two 'ticks' at either end, varying in size from slightly smaller to slightly longer than the standard. The deviations from the standard width were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the variable stimulus ranging between 5.2° to 7.0°. This merging resulted in a single horizontal line with three 'ticks'; one at the midpoint, one on the left end and another one on the right. For the other three conditions, one, five or nine vertical 'ticks' were positioned on the standard horizontal line in a regular manner and their length was identical to that of the end 'ticks' i.e. 0.61°. Figure 3.15 below illustrates the stimuli used in this experiment.

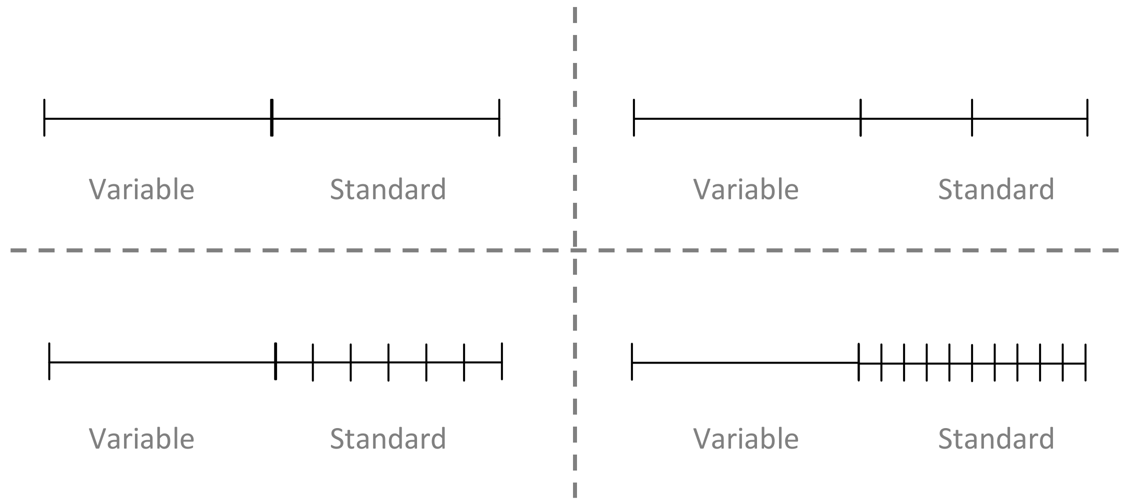


Figure 3.15 Stimuli used in Experiment 4. The variable part of the stimulus contained no vertical 'ticks'. The control condition is shown in the upper left window.

Each of six female naïve observers undertook 336 trials; eight pairs of stimuli each presented six times for seven variable stimulus sizes. Participants were asked to indicate the longer component of the stimulus (i.e. left or right) using a response box and the control condition was used to evaluate whether or not participants were able to carry out the task. Stimuli were positioned one next to the other and presented simultaneously for 1000ms. The luminance of the stimuli approached 0cd/m² whereas the background luminance was 20cd/m², so the contrast is approaching 1.00. The timeline for the experiment is shown in Figure 3.16 below.

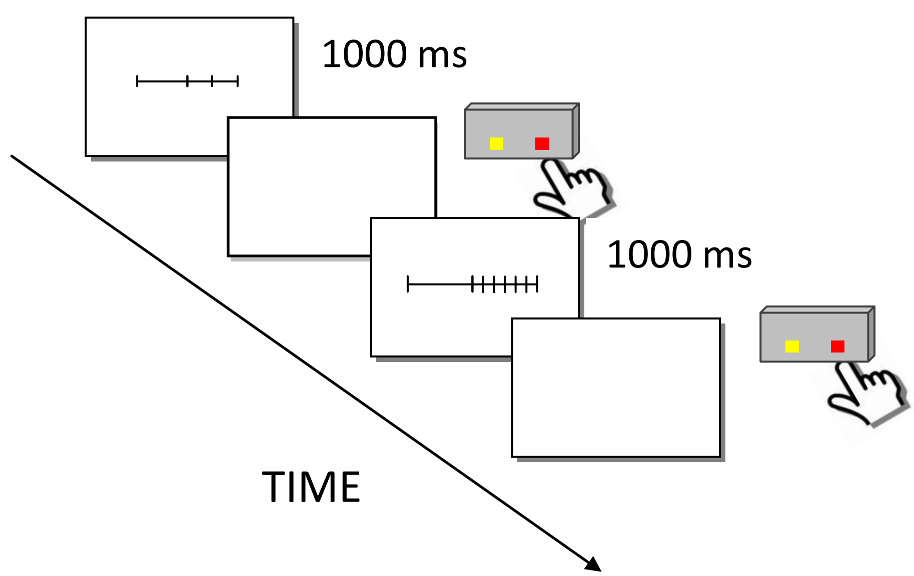


Figure 3.16 Timeline of Experiment 4 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

3.5.3 Results

Comparisons between the simple horizontal component of the stimulus and the four conditions were made so that psychometric functions could be determined and PSEs for nine participants calculated. Figure 3.17 depicts the psychometric functions generated for a single participant for all four conditions. The orange curve represents the control condition and the mean PSE for this is 6.10° confirming that the participant is able to match two horizontal lines presented side by side. The green curve represents the condition when a single 'tick' bisects a horizontal line and the mean PSE is 5.93°, showing that bisected horizontal line has to be smaller than the unbisected one, for the two to be perceived identical. Moreover, the blue curve represents the condition when a five 'ticks' are present and the mean PSE is 6.40°. An increase in perceived size of the horizontal is observed with nine 'ticks' generating a mean PSE of 6.51°.

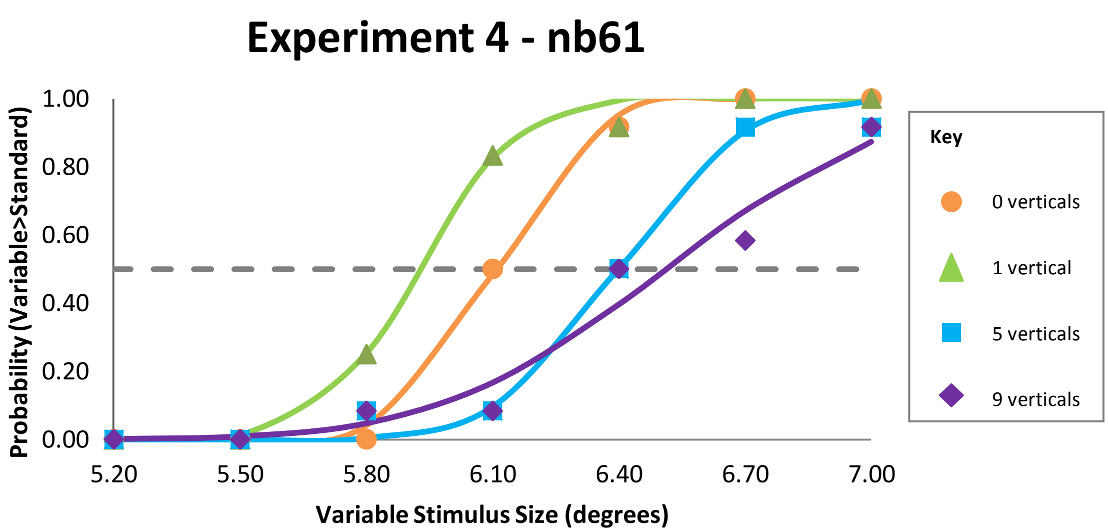


Figure 3.17 Psychometric functions for a single participant from Experiment 4.

Results for all participants are illustrated in Figure 3.18 showing that participants could match the size of the two simple horizontal components in the control condition. Additionally, the perceived length of a bisected horizontal line was found to be 9.0%

significantly smaller than that of an unbisected line of the same size. When five or nine 'ticks' were equally spaced along the length of a horizontal, there was a 5.4% and 6.6% increase respectively in its perceived size.

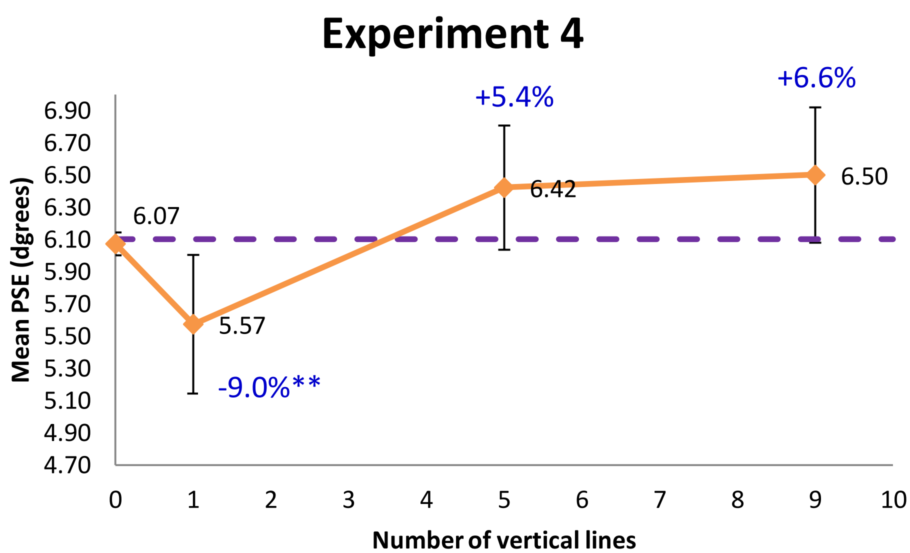


Figure 3.18 Results from Experiment 4, showing a significant underestimation of the perceived size of a horizontal line with a single 'tick's by ~9% and a significant overestimation of the perceived size of a horizontal line with 9 'ticks' by ~7% (N=6). Error bars show 95% confidence intervals.

Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(5)$ = 15.37, *p* < .05 therefore multivariate tests are reported *ε* = .54*.* A repeated-measures ANOVA revealed that the perceived size of the 'divided' part of the stimulus was significantly affected by the number of vertical lines abutting it, *V* = 0.95, F (1.61, 9.63) = 14.0, *p < .05*. *A* z-test revealed a significant decrease in the perceived size of a horizontal line compared to the actual physical size of the stimulus, when a single 'tick' was present (*p<.01*). Another z-test revealed a significant increase in the perceived size of a horizontal line compared to the actual physical size of the stimulus, when 9 'ticks' were present (*p<.05*).

3.5.4 Discussion

The aim of this experiment was to investigate whether the size of the bisection illusion, as well as the Oppel-Kundt illusion that we found in Experiment 3 would be altered if we merged the two stimuli into a single one. Results generated showed that the size of the two illusions is indeed affected by this factor.

In the present experiment the pattern of results is identical to that in Experiment 3. The control condition acts as a confirmation that participants are able to match accurately the two components of our stimulus. Moreover, the bisection illusion present when a single 'tick' bisects one component of the stimulus was found to reduce its apparent size by approximately 9%. Consequently, since the bisection illusion effect in Experiment 3 was only found to be 7% we deduce that the merging of two stimuli into a single one makes the illusion more prominent.

Moreover, although a 5.4% increase in the perceived size of the horizontal line was found when five vertical divisions were crossing it, consistently with the previous three experiments and as a z-test and the 95% confidence intervals indicate this was not found to be significant.

Finally, the Oppel-Kundt illusion was only evident with nine vertical 'ticks' crossing a horizontal, increasing significantly its perceived size by 6.6%, a result consistent with previous experiments in this chapter as well as past literature (Piaget & Osterrieth, 1953; Oyama, 1960).

3.6 Experiment 5

3.6.1 Rationale

As previously mentioned in the Introduction, Piaget and Osterrieth (1953) demonstrated that the maximum effect arises when 9 to 14 lines are present, whereas Obonai (1933) suggested that the maximum effect is found between 7 and 13 lines. The aim of this experiment is to observe how the prominence of the Oppel-Kundt illusion is affected around and beyond nine 'ticks'. Similarly to Experiment 4, we manipulated the number of vertical lines regularly-spaced on the standard component of the stimulus with 0, 1, 8, 10 and 12 vertical 'ticks' and each one of these were compared against the variable component of the stimulus.

3.6.2 Method

This experiment is a replication of the previous one with three modifications. Firstly, five instead of four conditions were interleaved; in the control (no 'ticks') a standard horizontal line with two 'ticks' at either end was merged with and compared against one of seven comparator stimuli composing of another horizontal line with two 'ticks' at either end, varying in size from slightly smaller to slightly longer than the standard. This merging resulted in a single horizontal line with three 'ticks'; one at the midpoint, one on the left end and another one on the right. For the other four conditions, one, eight, ten or twelve vertical lines were positioned on the standard horizontal line in a regular manner and their length was identical to that of the end 'ticks' i.e. 0.61°.

Secondly, the range of the variable component values was wider. This was done in order to capture both ends for the psychometric function for all types of stimuli and generate a more accurate mean PSE for each individual case. Deviations from the standard width were -1.4, -0.9, -0.5, 0, 0.5, 0.9, 1.4 degrees, with the length of the variable stimulus ranging between 4.7° to 7.5°. Figure 3.19 below illustrates the stimuli used in this experiment.

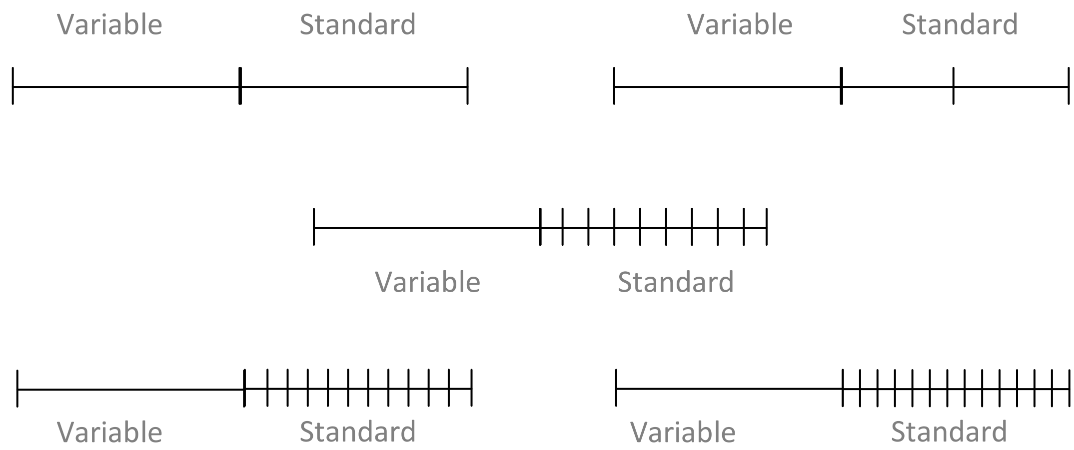


Figure 3.19 Stimuli used in Experiment 5. The variable part of the stimulus contained no vertical 'ticks'. The control condition is shown in the upper left window.

Thirdly, the presentation time of the stimuli is reduced from one second to 750 milliseconds a duration which was found not only to be sufficient for participants to make their judgments, but it also allowed for more repetitions to be carried out within the same amount of time. Each of eight naïve observers (4 female) undertook 1750 trials; ten pairs of stimuli each presented 25 times for seven variable stimulus sizes. Participants were asked to indicate the longer horizontal component using a response box and the control condition was used to evaluate whether or not they were able to carry out the task. The luminance of the stimuli was approximately 20cd/m² whereas the background luminance approached 0cd/m², so the contrast is approaching 1.00. The timeline for the experiment is shown in Figure 3.20.

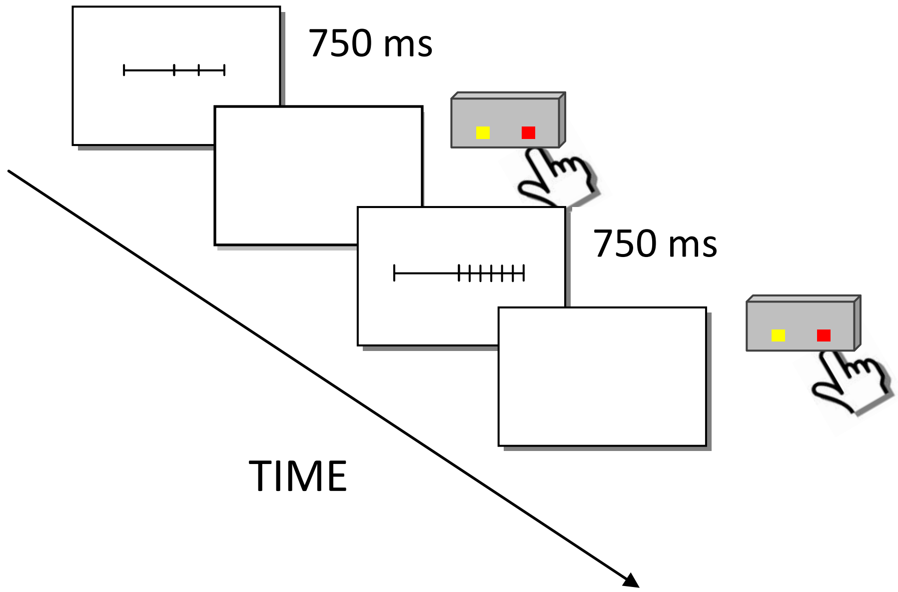


Figure 3.20 Timeline of Experiment 5 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

3.6.3 Results

Comparisons between the simple horizontal component of the stimulus and the four conditions were made so that psychometric functions could be determined and PSEs for eight participants. Figure 3.21 depicts the psychometric functions generated for a single participant for all four conditions. The orange curve represents the control condition and the mean PSE for this is 6.11° confirming that the participant is able to match two horizontal lines presented side by side. The green curve represents the condition when a single 'tick' bisects a horizontal line and the mean PSE is 5.75°, showing that bisected horizontal line has to be smaller than the unbisected one, for the two to be perceived identical. Moreover, the grey curve represents the condition when a eight 'ticks' are present and the mean PSE is 6.33°, showing that former has to be longer than the latter, for the two to be perceived identical. The same illusory percept is observed with ten and twelve 'ticks' generating a mean PSE of 6.39° and 6.27° respectively.

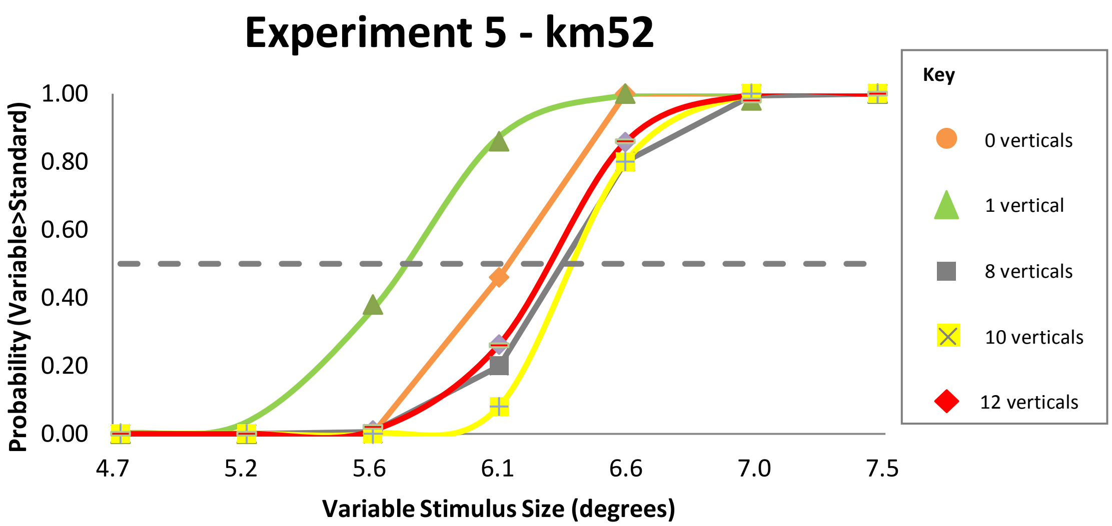


Figure 3.21 Psychometric functions for a single participant from Experiment 5.

Results for all participants illustrated in Figure 3.22 show that participants could match the size of the two simple horizontal components in the control condition. Additionally, the perceived length of a bisected horizontal line was found to be approximately 13% smaller than that of an unbisected line of the same size, an effect even larger than that found in Experiment 4. When eight, ten or twelve 'ticks' were equally spaced along the length of a horizontal, there was a 4.8%, 5.2% and 5.1% increase in its perceived size respectively.

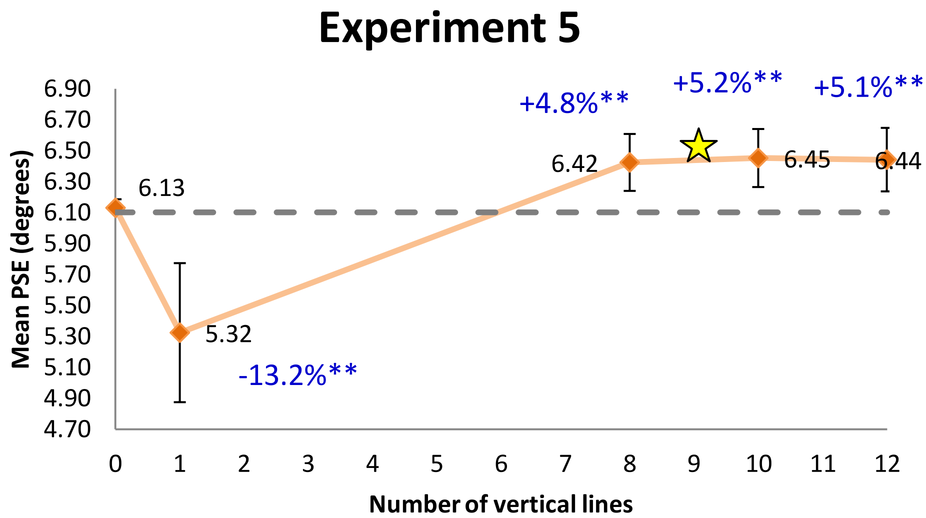


Figure 3.22 Results from Experiment 5, showing a significant underestimation of the perceived size of a horizontal line with a single 'tick' by ~13% and a significant overestimation of the perceived size of a horizontal line with 8, 10 and 12 'ticks' by ~5% (N=8). Error bars show 95% confidence intervals. The star indicates the mean PSE generated for nine vertical 'ticks' from Experiment 4 which was 6.42°, revealing a fairly constant Oppel-Kundt effect for 8-12 'ticks'.

Mauchly's test indicated that the assumption of sphericity had been violated, χ^2 (9) = 57.591, p < .05 therefore multivariate tests are reported ε = .28. A repeated-measures ANOVA revealed that the perceived size of the 'divided' part of the stimulus was significantly affected by the number of vertical lines crossing it, V = 0.87, F (1.11, 7.80) = 14.7, $p < .05$. A z-test revealed a significant decrease compared to the actual physical size of the stimulus in the perceived size of a horizontal line when a single 'tick' was present ($p<.01$). Three more z-tests revealed a significant increase compared to the actual physical size of the stimulus in the perceived size of a horizontal line when 8, 10, 12 'ticks' were present ($p<.01$).

3.6.4 Discussion

The aim of this experiment is to observe how the prominence of the Oppel-Kundt illusion is affected around and beyond nine ‘ticks’. Results generated followed the same pattern to those in Experiment 4.

The control condition acts as a confirmation that participants are able to match accurately the two components of our stimulus, as the mean PSE for this condition is 6.13°. Moreover, the presence of a single ‘tick’ at the midpoint was found to reduce the apparent size of the standard component of the stimulus by 13.2%, giving a mean PSE of 5.32°. As indicated by a z-test this effect was found to be significant.

Interestingly, there were no significant differences between the three conditions when eight, ten or twelve vertical ‘ticks’ were present, revealing a relatively constant Oppel-Kundt illusion. In all three conditions the Oppel-Kundt illusion was found to be significant. Additionally, taking into account results from Experiment 4 as well, it appears that the size of the Oppel-Kundt illusion is relatively constant from eight to twelve vertical ‘ticks’, inducing a 5% increase in the perceived size of the horizontal line.

Finally, it is noteworthy that by increasing the range of values used for the variable stimulus we managed to capture both ends of the psychometric function for all five conditions, thus generating more accurate mean PSE values.

3.7 General Conclusion

This chapter focused on the effect of the number of lines on the Oppel-Kundt illusion and in investigating the bisection component of the vertical-horizontal illusion as described by Mamassian and de Montalembert (2010). In order to achieve this we carried out a series of five experiments using the method of constant stimuli in which we have found a significant main effect of the number of vertical lines on the perceived size of the horizontal.

In the Experiment 1 we failed to find significant differences in the apparent size of a horizontal line when one vertical of the same size abutted the former. We assigned this lack of illusory percept to two possible reasons; (a) the presence of the end 'ticks' which might had been acting as terminators, therefore allowing the viewer to make veridical size judgments by looking at the lower part of the stimulus where perception was not interrupted by any 'divisions' and (b) to the fact that the vertical line did *not* actually bisect the horizontal, but only abutted it. After carrying out Experiment 2, which was a repetition of Experiment 1, with the absence of the end 'ticks' we concluded that their presence was not responsible for the absence of an illusory percept and suggested that this arises from the fact that the vertical lines do not *cross* the horizontal but only abut it.

Consequently, in subsequent experiments we altered the size and position of the vertical lines in order to determine the effect of these factors on the bisection illusion. More specifically, the size of the vertical line was reduced to 1/10th of that of the horizontal line and instead of simply touching the horizontal, the vertical was crossing it. As a result, although no illusory percept was observed in Experiments 1 and 2 in an inverted 'T' configuration, we did find evidence of a bisection illusion in Experiments 3, 4 and 5. In Experiment 3, two independent stimuli were compared; a bisected to an unbisected one and the former appeared 6.8% smaller than the latter when the two were exactly the same size. In Experiment 4, when the two stimuli were merged into a single one, the reduction in the apparent size of the bisected horizontal line increased to 10.3% making the illusion more prominent. Finally, when the size range of the variable component of the stimulus was increased (Experiment 5), this 'bisection' illusion effect was found to be inducing a 13.2% reduction in the apparent size of a horizontal line.

Considering the model proposed by Mamassian and de Montalembert (2010) consisting of two components, anisotropy and bisection, in these two experiments we expected to find a 16% decrease in the size of a bisected line by virtue of the latter component. The reason for this is the lack of the anisotropy illusion since lines of the same orientation were compared. However, the absence of an illusory percept as a whole is rather surprising. Based on this evidence, we challenge the 'bisection' component of the vertical-horizontal illusion as described by Mamassian & de Montalembert as we failed to observe an underestimation of the bisected line (in the present case, the horizontal) in an inverted 'T' configuration, when this was compared to another horizontal line of the same size. We are going to investigate further the vertical-horizontal illusion and the two components proposed by Mamassian & de Montalembert will be further examined.

As far as the Oppel-Kundt illusion is concerned, consistently throughout all experiments investigating the effect of five lines, irrespective of size and position we fail to observe an Oppel-Kundt illusion. Consequently, we deduce that the presence of five lines allows for veridical size judgment of a horizontal stimulus. Presumably there are two factors at work one reducing the apparent size of a horizontal line when a single line is present and a second factor increasing the apparent size of a horizontal line when eight to ten lines are present. When there are five lines these two opposing factors cancel out.

In Experiment 1, results generated revealed a significant increase in the perceived size of a horizontal line when nine vertical lines abutted it, illustrating the classic Oppel-Kundt illusion. Although the illusion was evident in Experiment 2, the effect was reduced to 2.7% compared to 4.5% from Experiment 1, possibly due to the absence of end ‘ticks’ acting as terminators giving a clearer indication of the length of the horizontal line.

In Experiment 3 when the size and position of the nine vertical lines changed we generated a significant 4.9% increase in the perceived size of the horizontal line. Similarly, in Experiment 4 when the two stimuli were merged into a single one the perceived size of the horizontal line was found to be significantly longer by 6.6% when nine vertical ‘ticks’ were abutting the former.

In Experiment 5 we decided to investigate the Oppel-Kundt illusion around and beyond nine vertical ‘ticks’ and also increase the range of the variable component values in order to capture both ends of the psychometric function for all types of stimuli to generate a more accurate mean PSE for each participant. The challenge in Experiments 1, 2 and 4 was that the range of values used failed to capture the right end of the psychometric function. More specifically, it is evident that the range of stimuli used was not appropriate to capture the upper end of psychometric functions , even when the difference between the two was 0.9°. It is possible that this has affected the calculation of the PSE.

By using a wider range of values in Experiment 5, we managed to show that the presence of eight, ten or twelve vertical ‘ticks’ generate a relatively constant and significant Oppel-Kundt effect. Interestingly, there were no significant differences between the three conditions when eight, ten or twelve vertical ‘ticks’ were present, revealing that the size of the Oppel-Kundt illusion is not significantly different between these three conditions. These results are in accordance with Piaget and Osterrieth (1953) and Obonai (1933), who suggested a maximum Oppel-Kundt effect around nine vertical lines. A future study could be carried out, using a stimulus with more than twelve vertical 'ticks' to observe the effect on the Oppel-Kundt illusion. Taking into account the fact that the maximum illusory percept occurs around nine vertical lines (Piaget and Osterrieth, 1953; Obonai, 1933) we hypothesise that there will be a decrease in the size of the Oppel-Kundt illusion as the number of vertical 'ticks' increases beyond twelve.

To conclude, we have generated results suggesting that for a bisection illusion to exist the bisector has to be *crossing* the 'bisectee'. Moreover, the Oppel-Kundt illusion was found to be significant with ten vertical 'ticks' crossing the horizontal. Therefore we predict that the greatest illusory percept would be generated by the stimulus illustrated in Figure 3.23 below as the left side will be underestimated by more than 10% and the right side will be overestimated by approximately 5%. In a future study, participants could be asked to indicate which one of the two sides of such a figure appears longer. The size of the side with a single vertical 'tick' (on the left in **Error! Reference source not found.**) will be varied from shorter to longer and the position of the single 'tick' will be changed accordingly so that it will, in all instances, be in the middle.

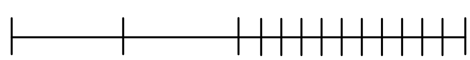


Figure 3.23 Stimulus predicted to generate a greater illusory percept.

3.8 Chapter Summary

A series of five experiments were carried out in the present chapter and evidence generated suggests that a change in the perceived size of a horizontal line is apparent mainly when vertical lines *cross* a horizontal. More specifically, when a single vertical tick crosses a horizontal line the 'bisection' effect ranges from approximately 7 to 13%, decreasing the perceived size of the horizontal. A relatively constant and significant Oppel-Kundt effect (5%) has been observed with eight to twelve vertical lines and the etiology behind this will be investigated in Chapter 4. Finally, we challenge the 'bisection' component of the vertical-horizontal illusion as described by Mamassian & de Montalembert as we failed to observe an underestimation of the bisected line (in the present case, the horizontal) in an inverted 'T' configuration, when this was compared to another horizontal line of the same size. This will be investigated further in Chapter 5.

Chapter 4 - Displacement of adjacent lines in the Oppel-Kundt illusion

The aim of this Chapter is to determine whether adjacent vertical lines in the graduated part of an Oppel-Kundt stimulus displace one another, inducing an increase in the perceived size of the stimulus as a whole.

4.1 Introduction

In the Oppel-Kundt illusion, a horizontal line filled with vertical lines appears longer, compared to an unfilled horizontal line of equal size. In Chapter 3 we showed a relatively constant and significant Oppel-Kundt effect (5%) when eight to twelve vertical lines crossed a horizontal line. Craven and Watt (1989) claimed that the average contour density, determined by the number of zero-crossings in a range of spatial scales (Watt, 1990), is responsible for the phenomenon implying that as the number of crossings increases the perceived size of the divided line will increase as well. When the Oppel-Kundt illusion was measured following adaptation of participants to parallel lines, no aftereffect was found demonstrating that this is not a product of an uninterrupted spatial calibration mechanism (Craven, 1995).

The aim of the present chapter is to determine whether adjacent vertical lines in an Oppel-Kundt stimulus displace one another in such a way to increase the perceived length of the stimulus as a whole. The idea behind this possible explanation arises from Ganz (1966) who reported that adjacent lines can induce shifts in their respective perceived positions in the visual system by interacting with one another. He proposed a lateral inhibition model able to accurately predict changes in the perceived location of the illusory stimulus, as a function of the retinal distance between adjacent lines. In psychophysics lateral inhibition is induced by contrast, and according to Ganz (1966) '…black solid figures appear blackest at their edges with white; white surfaces appear brightest at their edges with dark figures…' (p.133). Critically, this repulsion effect is minimal when two lines touch. Additionally, Carpenter and Blakemore (1973) reported that acute angles perceptually expand while obtuse angles contract, due to lateral inhibition in the orientation domain arising from the organisation of neurons in the visual cortex.

4.2 Experiment 6

4.2.1 Rationale

The aim of this experiment is to investigate whether the Oppel-Kundt illusion arises due to an apparent expansion of space induced by the existence of small adjacent ‘ticks’. This suggestion has been put forward by Ganz (1966), who proposed that shifts in the apparent position of contours arise when visual stimuli are located close to one another, as is the case in the Oppel-Kundt figure. We manipulated the number of vertical ‘ticks’ regularly-spaced on the standard stimulus with 0, 1 and 9 ‘ticks’ and participants were asked to indicate the position of a small ‘tick’ located under either of these relative to one of their end ‘ticks’ (i.e. left or right). As a result of vernier acuity, which is our ability to align two line segments with great accuracy, we expect participants to be extremely good at this task.

4.2.2 Method

Three conditions were interleaved; in the control condition (no vertical ‘ticks’) the position of either the left or the right final ‘tick’ of the stimulus was compared to one of seven comparator ‘ticks’, varying in position from slightly outwards to slightly inwards. The deviations from the standard position (3.17°) were -0.16, -0.11, -0.05, 0, 0.05, 0.11, 0.16 degrees. For the conditions B and C respectively, one or nine vertical ‘ticks’ were crossing the standard horizontal line in a regular manner and their length was identical to that of the end ‘ticks’ i.e. 0.61°. Figure 4.1 illustrates the stimuli used in this experiment.

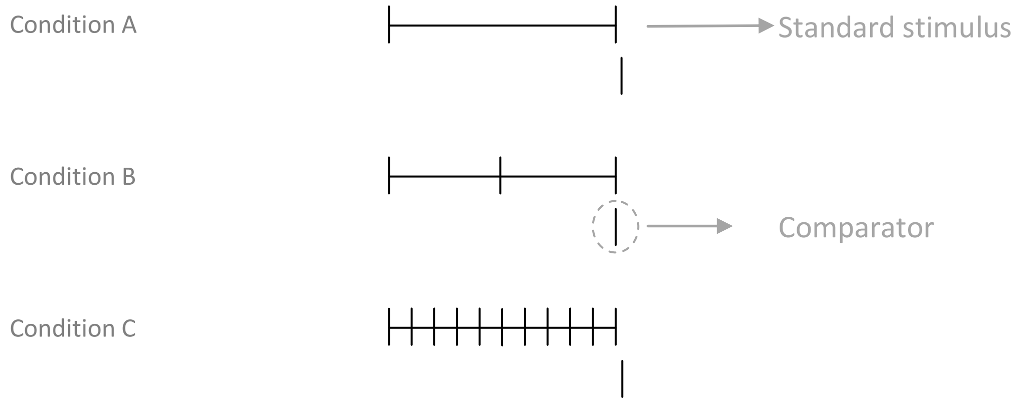


Figure 4.1 Stimuli used in Experiment 6. Participants were asked to indicate the position (i.e. left or right) of a small 'tick' relative to the position of the end 'tick' on the standard stimulus.

Each of seven naïve observers (five female) undertook 1050 trials; three types of stimuli each presented 25 times for seven comparator stimulus positions. Participants were asked to indicate the position (i.e. left or right) of a small 'tick' relative to the position of the end 'tick' on the figure right above it using a response box and the control condition was used to evaluate perceptual expansion of space occurs even in the absence of multiple adjacent 'ticks'. Stimuli were positioned one next to the other and presented simultaneously for 750ms. The luminance of the stimuli approached 0cd/m² whereas the background luminance was 20cd/m², so the contrast is approaching 1.00. The timeline for the experiment is shown in Figure 4.2.

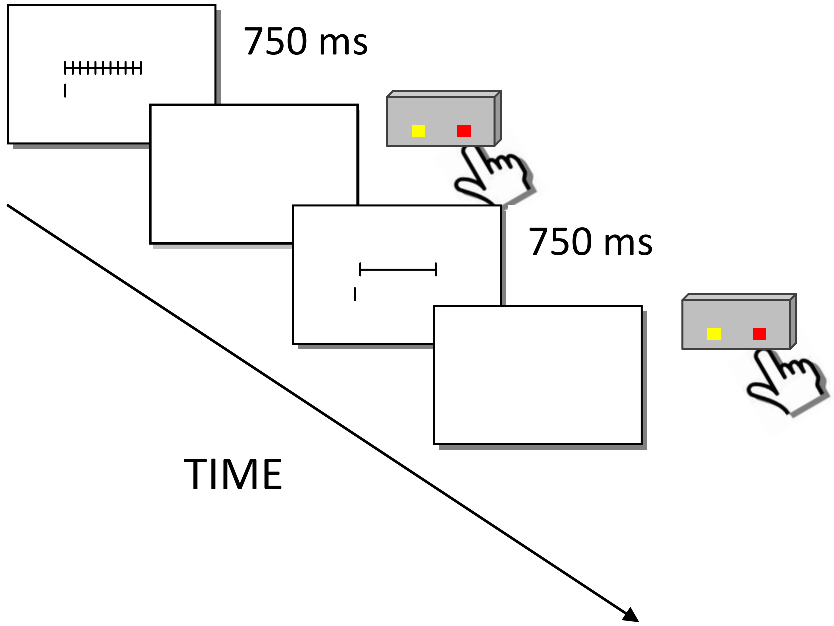


Figure 4.2 Timeline of Experiment 6 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

4.2.3 Results

Comparisons between the position of a small 'tick' and the end 'ticks' in three conditions were made so that psychometric functions could be determined and points of subjective equality (PSEs) calculated for seven participants. Figure 4.3 depicts the psychometric functions generated for a single participant for all three conditions. The orange curve represents the control condition (stimulus A-no 'ticks') and the mean PSE for this is 3.18° confirming that the participant is able to match the position of the two 'ticks' accurately. The green curve represents the condition when the position of the 'tick' is matched to the position of the final tick of stimulus B and the mean PSE is 3.18°, showing that the participant can carry accurately this comparison as well. The curves for the control condition and stimulus B are almost identical and superimposed on another in such a way so that only the curve for the latter is visible in Figure 4.3. The purple curve represents the condition when the position of the 'tick' is compared to the position of the end 'tick' of stimulus C and the mean PSE is 3.20°. This reveals a slight outward displacement of the perceived position of the end ‘tick’ in stimulus C.

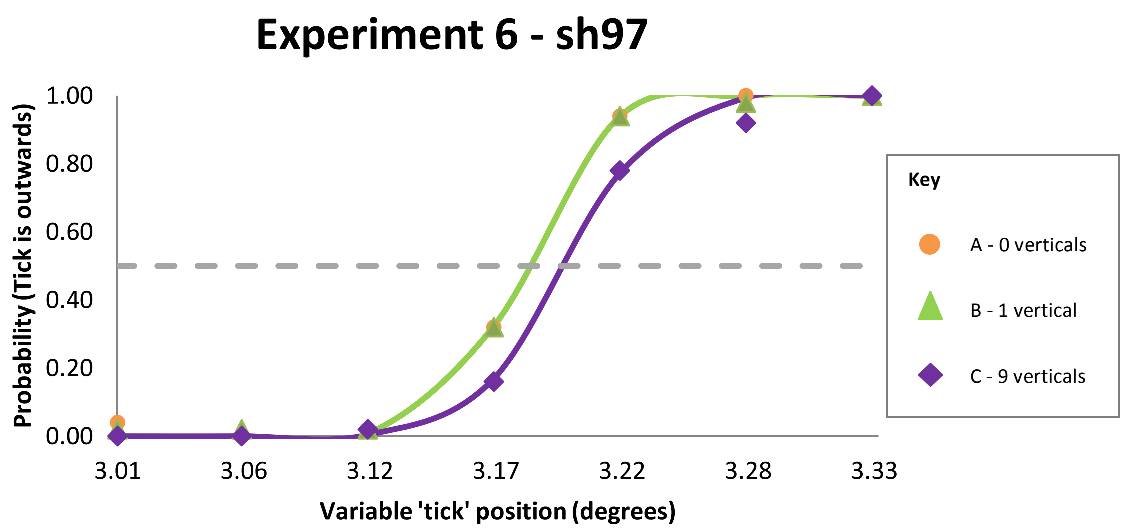


Figure 4.3 Psychometric functions for a single participant from Experiment 6. Psychometric functions of stimuli A and B are almost identical with the latter superimposed on the former.

Results for all participants are illustrated in Figure 4.4. The grey dotted line indicates the actual position of the end ‘tick’ in all three conditions (3.17°). Results show that participants could match the position of the independent vertical ‘tick’ to the position of the end ‘tick’ in the control condition. Similar results were generated with stimulus B, with a non-significant displacement of the end ‘tick’. However, there is a small but significant displacement of the end ‘tick’ in stimulus C by 0.015°. Taking into account the size of the horizontal line (6.1°) and the fact that displacement occurs both end ‘ticks’ at both sides of the stimulus, this would mean a total increase in the perceived size of the horizontal line of size by 0.5%.

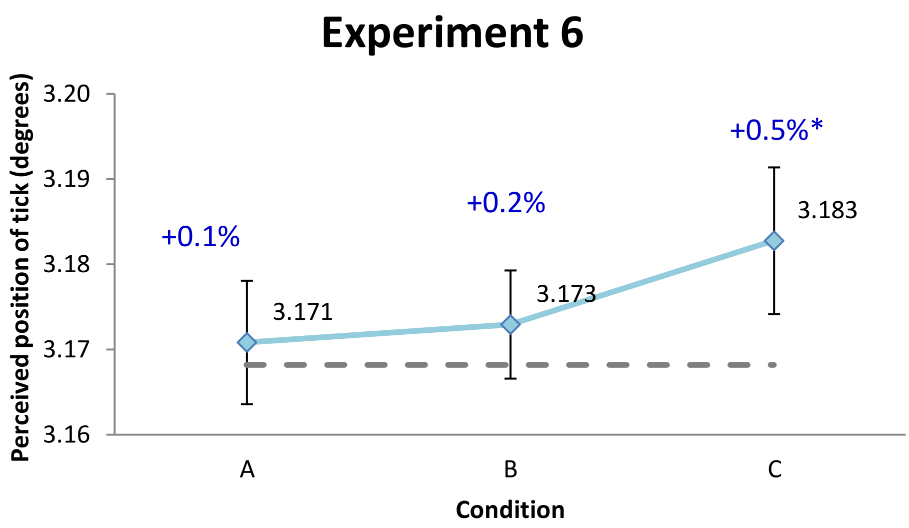


Figure 4.4 Results from Experiment 6, showing a significant displacement of the perceived position of a vertical tick for stimulus C of approximately 0.5% (N=7). Error bars show 95% confidence intervals.

A z-test revealed a significant displacement of the position of the end 'tick' in stimulus C, when nine 'ticks' crossed a horizontal line ($p<.01$).

4.2.4 Discussion

The aim of this experiment was to determine whether the increase in the perceived size of a graduated line arises due to an apparent expansion of space induced by the existence of small adjacent 'ticks'. Results generated suggest there is a significant displacement of the position of the end 'tick' in stimulus C, when nine vertical ticks cross a horizontal line in regular intervals. However, the size of this significant displacement is only 0.5% and is thus insufficient to account for the previously reported 4.9% increase in the perceived size of an identical figure in Experiment 3, Chapter 3.

4.3 Experiment 7

4.3.1 Rationale

Following from the previous experiment, the aim of Experiment 7 is to investigate whether the slight displacement in the apparent position of the end 'ticks' in an Oppel-Kundt figure with nine vertical 'ticks' is a local effect. We manipulated the number of vertical 'ticks' regularly-spaced on the standard stimulus as well as the position of the comparison 'tick' and participants were asked to compare the position of the latter to either the ultimate or penultimate 'tick' in three conditions.

4.3.2 Method

Three conditions were interleaved; in the control condition (identical to condition C in Experiment 6) the position of either the left or the right final 'tick' of the stimulus was compared to one of seven comparator 'ticks', varying in position from slightly outwards to slightly inwards. The deviations from the standard position (3.17°) were -0.16, -0.11, -0.05, 0, 0.05, 0.11, 0.16 degrees. In condition D, only the ultimate and penultimate 'ticks' on either side of the horizontal line were present without manipulating their size, position or the size of the horizontal line. In condition E, nine vertical 'ticks' were crossing the standard horizontal line in a regular manner and their length was identical to that of the end 'ticks' i.e. 0.61°. Figure 4.5 below illustrates the stimuli used in this experiment.

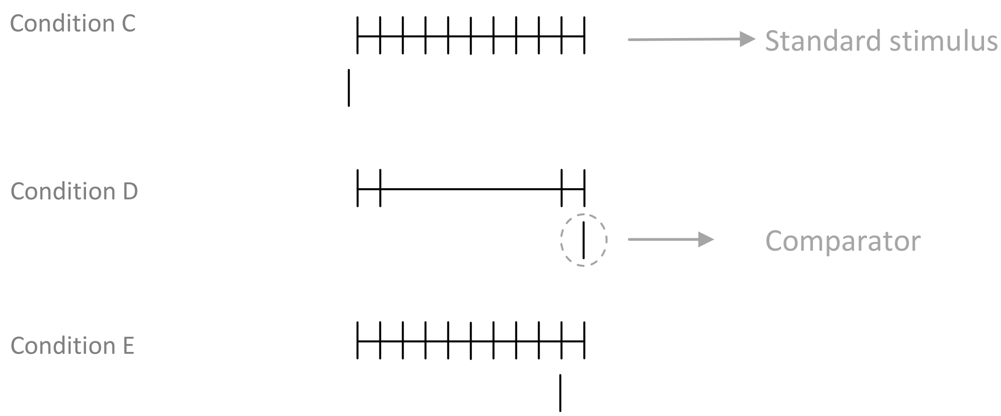


Figure 4.5 Stimuli used in Experiment 7. Participants were asked to indicate the position (i.e. left or right) of a small 'tick' relative to the position of either the end (C, D) or penultimate (E) 'tick' on the standard stimulus.

Each of nine naïve observers (eight female) undertook 1050 trials; three types of stimuli each presented 25 times for seven comparator stimulus positions. In conditions C and D participants were asked to indicate the position (i.e. left or right) of a small 'tick' relative to the position of the *ultimate* 'tick' on the figure right above it using a response box and the control condition was used to evaluate perceptual expansion of space occurs even in the absence of multiple adjacent 'ticks'. In condition E, participants were asked to compare the position of the small 'tick' to the position of the *penultimate* 'tick' on the standard stimulus. Stimuli were positioned one next to the other and presented simultaneously for 750ms. The luminance of the stimuli approached 0cd/m² whereas the background luminance was 20cd/m², so the contrast is approaching 1.00. The timeline for the experiment is shown in Figure 4.6 below.

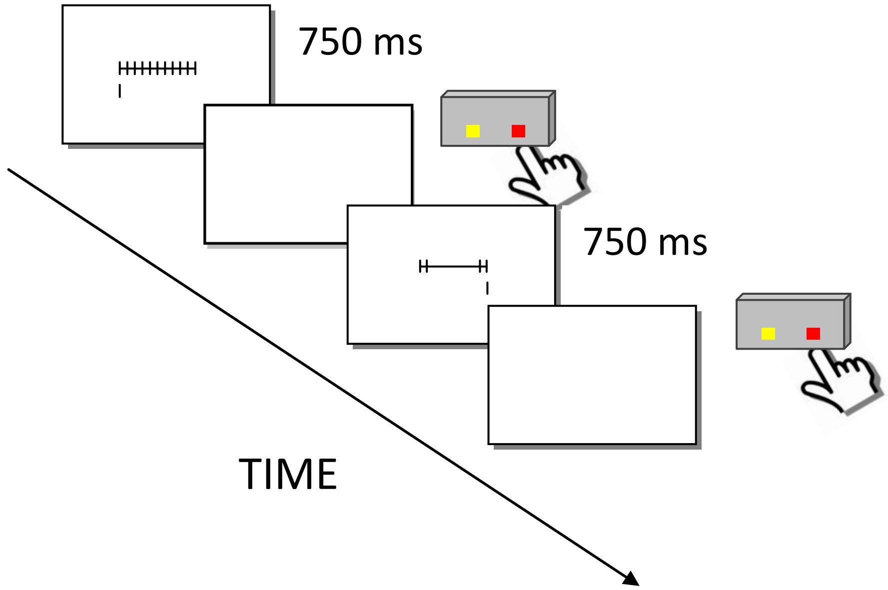


Figure 4.6 Timeline of Experiment 7 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

4.3.3 Results

Comparisons between the position of a small vertical 'tick' and the end 'ticks' in conditions C and D were made so that psychometric functions could be determined and points of subjective equality (PSEs) calculated for nine participants. In condition E, comparisons were carried out between the position of the small 'tick' and the penultimate tick of the standard stimulus. **Error! Reference source not found.** illustrates the psychometric functions generated for a single participant for conditions C and D. Condition C was repeated in this experiment in order to provide a baseline and allow comparison with the other two conditions. The purple curve represents condition C with a mean PSE of 3.20°, revealing a slight outward displacement of the perceived position of the end 'tick' when nine 'ticks' cross a horizontal, consistent with Experiment 6. The blue curve represents condition D, with a mean PSE of 3.18°, showing a similar but even smaller effect compared to condition C.

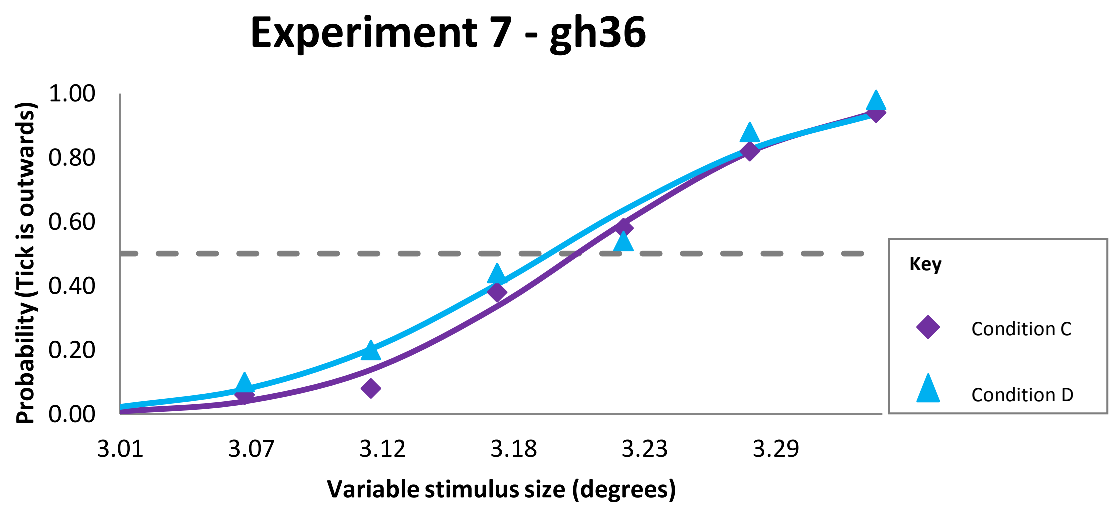


Figure 4.7 Psychometric functions for conditions C and D from a single participant Experiment 7.

Error! Reference source not found. below illustrates condition E, when the position of the comparator 'tick' was compared to the position of the penultimate 'tick' of the standard stimulus with nine vertical 'ticks' crossing the horizontal. The mean PSE was 2.60°, very similar to the actual position of the 'tick' (2.58°).

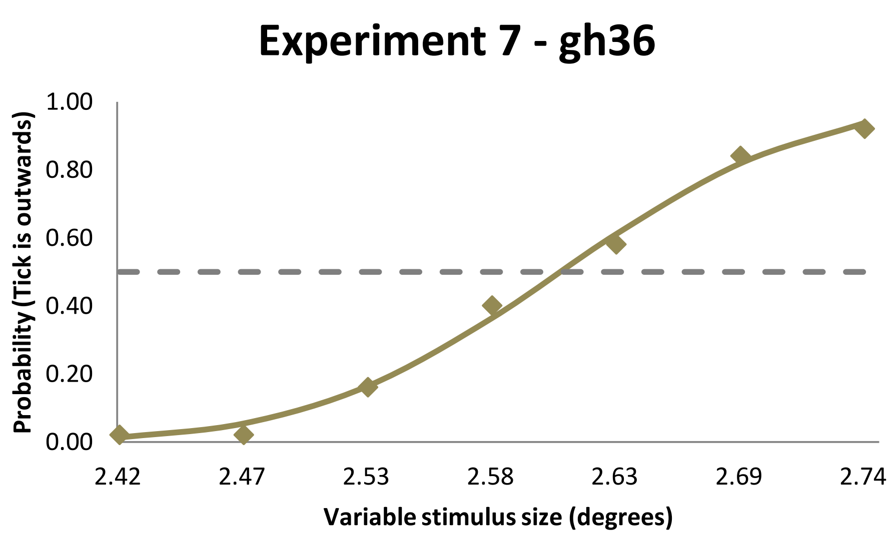


Figure 4.8 Psychometric functions for condition E from a single participant for Experiment 7.

Results for all participants are illustrated in Figure 4.9, replicating findings from Experiment 6 for condition C. Condition D showed a slight but significant outward displacement of the end 'tick' by 0.3%, whereas no significant displacement was observed for condition E.

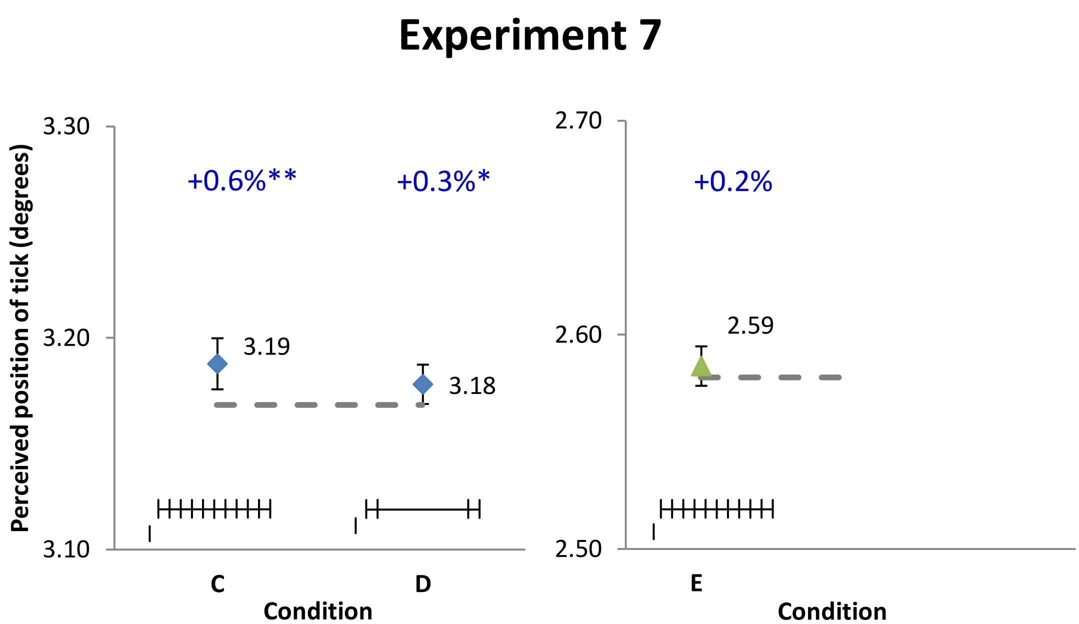


Figure 4.9 Results from Experiment 7, showing a slight but significant displacement of the perceived position of the final ticks for conditions C and D (N=9). Stimuli for each condition are illustrated. The dotted horizontal lines show the true position of the 'ticks'. Error bars show 95% confidence intervals.

Two z-tests revealed a significant displacement of the position of the end 'ticks' in condition C (*p<.01*) and condition D (*p<.05*).

4.3.4 Discussion

The aim of Experiment 7 was to determine whether the observed outward displacement of the end 'tick' in condition C, Experiment 6 is a local effect induced by the penultimate 'tick'. Consequently, in condition D we removed all 'ticks' from the horizontal line except the end and penultimate ‘ticks’ on either side in order to determine the significance of the latter on the perceived position of the former. Results generated in the present Experiment, condition D have shown a small significant displacement of the end ‘tick’ caused by the effect of the penultimate ‘tick’, confirming that this is a local effect. In condition E, we wanted to determine whether there is a significant displacement of the perceived position of the penultimate ‘tick’ and results generated showed no significant difference in its perceived location.

4.4 Chapter Summary

Two experiments were carried out in the present chapter and evidence generated suggests that the increase in the perceived size of a horizontal line in an Oppel-Kundt figure can only be partly explained in terms of repulsion between adjacent lines. Specifically, whereas the size of the Oppel-Kundt illusion in a figure consisting of a horizontal line and nine equally-spaced vertical ‘ticks’ is 5%, displacement of adjacent lines can only account for 0.5%. Taking into account the precision of our vernier acuity when aligning two lines segments (Li et al., 2012), this result is interesting as it demonstrates that vernier acuity can be compromised when comparing the end ‘tick’ of an Oppel-Kundt stimulus to an independent vertical ‘tick’.

Chapter 5 - Size judgment of simple lines

The aim of this chapter is to investigate a discrepancy between results generated in Chapter 3 and the 'bisection' component of the vertical-horizontal illusion as described by Mamassian and de Montalembert (2010). A new model describing size perception of lines in simple stimuli will be introduced and evaluated.

5.1 Introduction

In Chapter 3 we reported an absence of Mamassian and de Montalembert's (2010) 'bisection' component in the vertical-horizontal illusion when comparing the horizontal segment of an inverted 'T' configuration to a horizontal line of the same size. We ruled out any factors potentially affecting the appearance of the 'bisection' illusion such as the presence of end 'ticks' in the horizontal lines and in some cases the relatively low number of repetitions carried out per participant. Following this discrepancy between results presented in Chapter 3 and Mamassian and de Montalembert' s (2010) model we decided to extend our investigation in order to determine and evaluate factors affecting the vertical-horizontal illusion.

Mamassian and de Montalembert (2010) investigated the size of the vertical-horizontal illusion in inverted 'T', horizontal 'T', cross and 'L'-shaped configurations by using the method of constant stimuli to compare the two segments of the stimuli they used. One of the segments was in blue and the other in red touching at one point. The aim of the present chapter is to confirm the significance of the two independent components of the vertical-horizontal illusion, specifically anisotropy and bisection, as described by Mamassian and de Montalembert which are also in agreement with previous studies (Künnapas, 1955; Charras and Lupianez, 2009).

We will evaluate and test these components by using exactly the same configurations as Mamassian and de Montalembert (2010) did in their study, but instead of comparing two segments within the same configuration we will carry out comparisons between the vertical or horizontal segment of one of our stimuli to another independent vertical or horizontal line. First we will evaluate the 'anisotropy component' of their model in which the size of a vertical line is always overestimated when compared to a horizontal one of the same size due to its orientation.

Moreover, following evidence from Chapter 3 we will investigate their 'bisection' component as described by Mamassian and de Montalembert by which the horizontal segment of an inverted 'T' configuration is underestimated by approximately 16% when compared to the vertical segment of the same configuration. Based on these findings, Mamassian and de Montalembert claimed that their investigation confirmed that the 'bisection' component results in the *underestimation* of the bisected line instead of an *overestimation* of the bisecting line. However, as previously mentioned, evidence from Chapter 3 illustrated a veridical size judgment of the horizontal segment when this was compared to another horizontal line.

Finally, Mamassian and de Montalembert (2010) describe how the shape of psychometric functions reveals the nature of their 'bisection' component. As explained in Chapter 3, they claimed that according to the proposed model the bisection component generates a reduced sensitivity for the '+' compared to the 'L' configuration as indicated by a shallower psychometric function. This was taken as a confirmation that the bisection component results in the *underestimation* of the bisected line instead of an *overestimation* of the bisecting line. Figure 5.1 below illustrates results generated by Mamassian and de Montalembert (2010) and as can be seen the two curves are almost identical (L-curve in red, +-curve in pink). This assertion was only a speculation and not proven experimentally by comparing the horizontal segment of each of the two stimuli to another simple horizontal line.

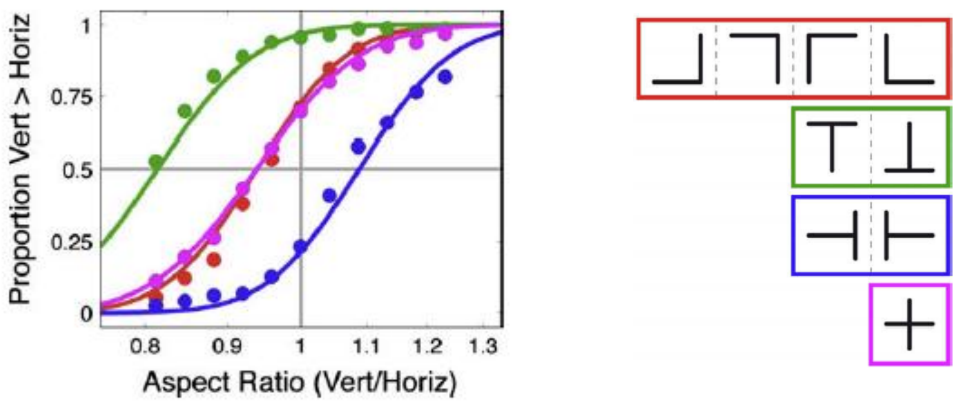


Figure 5.1 Results generated by Mamassian and de Montalembert (2010, Fig.2) showing the proportion of times the vertical line was perceived as longer than the horizontal within a single stimulus for the four classes of stimuli (N=24).

5.2 Experiment 8

5.2.1 Rationale

The aim of this experiment is to investigate the 'anisotropy' component of the vertical-horizontal illusion, as described by Mamassian and de Montalembert (2010), with observers comparing the apparent length of a horizontal and a vertical line. We manipulated the length of either the horizontal or the vertical line while the two were one next to another or one on top of the other.

5.2.2 Method

Two conditions were interleaved; in one condition a horizontal and a vertical line were positioned along the horizontal axis, one next to the other and in the other condition the two lines were positioned along the vertical axis, one above the other. Both conditions were fully counterbalanced so that in each one, half of the trials the horizontal line was acting as the standard stimulus and in the other half the vertical line was acting as the standard stimulus. The standard stimulus in each case was 6.1 degrees long and was compared with one of seven comparator stimuli which was either a simple horizontal or vertical line, varying in size from slightly smaller to slightly longer than the standard. The deviations from the standard width were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the comparator stimulus ranging between 5.2° to 7.0°. Figure 5.2 below illustrates the stimuli used in this experiment.

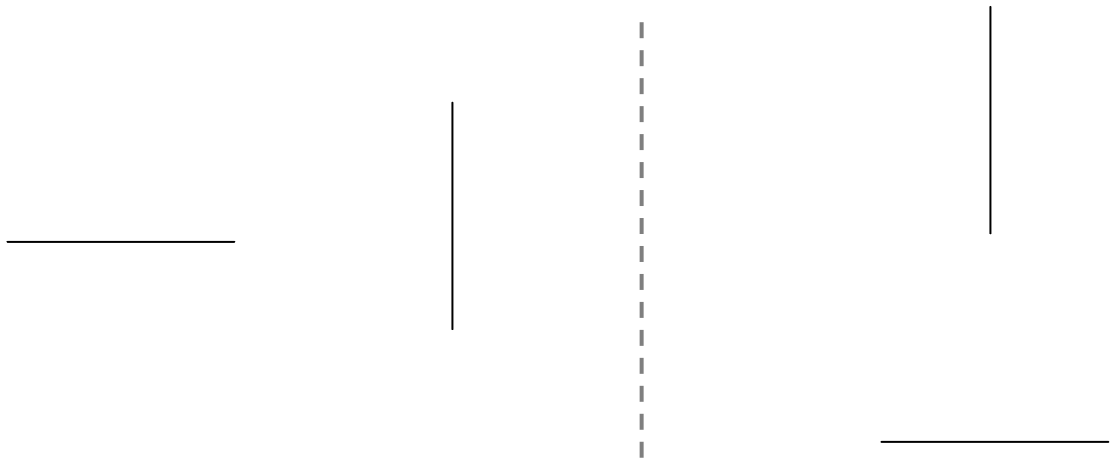


Figure 5.2 Stimuli used in Experiment 6 were positioned either next to each other or one on top of the other. In each one of these two settings, in half of the trials the comparator stimulus was a horizontal line, while in the rest of the trials the comparator stimulus was the vertical line.

Each of eleven naïve observers (six female) undertook 336 trials; eight pairs of stimuli each presented six times for seven comparator stimulus sizes. Participants were asked to indicate the longer line using a response box. Stimuli were positioned one next to the other and presented simultaneously for 500ms. The luminance of the stimuli was approximately 20cd/m² and the background approaching 0cd/m², so the contrast approached 1.00. The timeline for the experiment is shown in Figure 5.3 below.

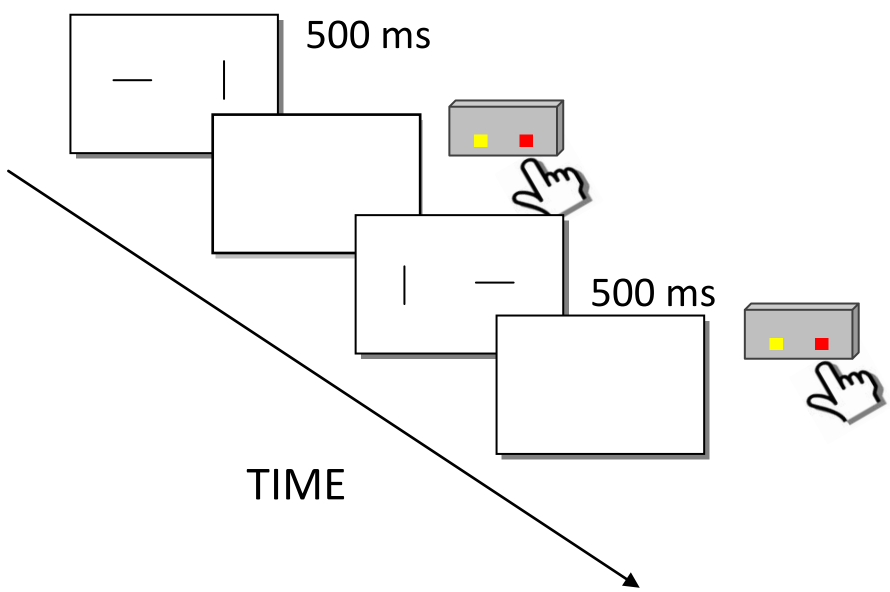


Figure 5.3 Timeline of Experiment 6 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

5.2.3 Results

Comparisons between a horizontal and a vertical line were made so that psychometric functions could be determined and points of subjective equality (PSEs) calculated for eleven participants. For each condition 95% confidence intervals were calculated.

Figure 5.4 depicts the psychometric functions generated for a single participant for both conditions when the horizontal line (green) acted as a standard and when the vertical line (orange) acted as a standard. The PSE for each curve lies at the crossing point between itself and the grey dotted line. Comparisons were carried out in the horizontal as well as the vertical axis in order confirming that there are no significant differences when participants carry out size judgments of simple lines. From Figure 5.4 below it is evident that the participant matched a vertical to a standard horizontal line of 6.1°, the former had to be 5.51° for the two to be perceived identical in size. Moreover, when they had to match a horizontal to a standard vertical line of length 6.1°, the former had to be 6.68° for the two to be perceived identical in size.

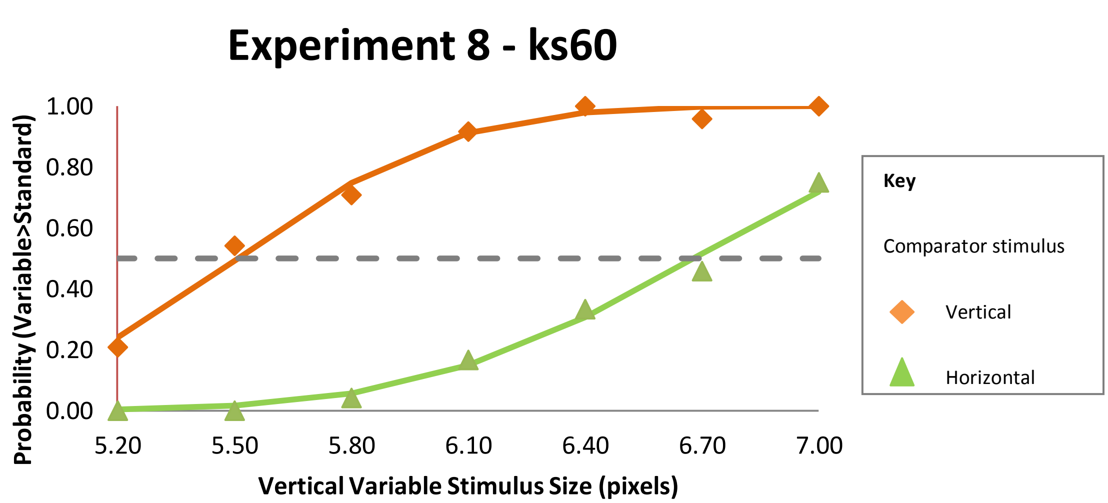


Figure 5.4 Psychometric functions for a single participant from Experiment 8.

Results for all participants are illustrated in Figure 5.5 *s*howing that the mean PSE when a vertical was matched to a standard horizontal line was 5.67° and when a horizontal was matched to a standard vertical line the mean PSE was 6.55°. A z-test revealed that when a vertical line was compared to a horizontal line of the same size the length of the former was significantly overestimated by approximately 7%, (*p<.01*). Similarly, another z-test revealed that the size of a horizontal line was found to be significantly underestimated by approximately 7% (*p<.01*).

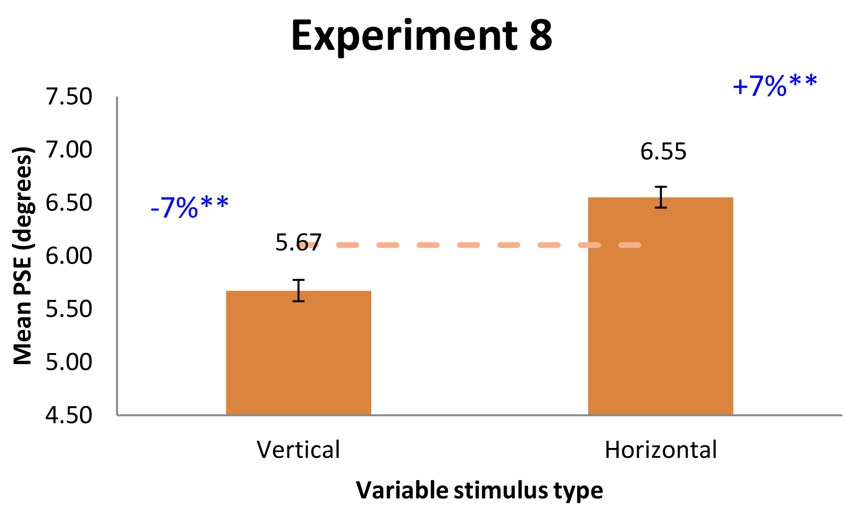


Figure 5.5 Results from Experiment 8, showing a significant underestimation of the horizontal line compared to the vertical by approximately 7% (N=11). Error bars show 95% confidence intervals.

5.2.4 Discussion

The present experiment was the beginning of an attempt to untangle the components affecting the size perception of horizontal and vertical lines in various shapes such as an inverted 'T', a horizontal 'T', a cross and an L-shape. More specifically, we investigated the 'anisotropy' component as described by Mamassian and de Montalembert (2010), by comparing simple horizontal and vertical lines. Results generated revealed that the size of a vertical line is significantly overestimated by approximately 7% when compared to a horizontal of the same size, whereas the size of a horizontal line is significantly underestimated by approximately 7% when compared to a vertical of the same size. This result is in accordance with findings by Mamassian and de Montalembert, who suggested that the anisotropy component makes a vertical line appear 6% longer than a horizontal one of the same size, because of its orientation.

5.3 Experiment 9

5.3.1 Rationale

The aim of this experiment is to scrutinize Mamassian and de Montalembert's (2010) 'bisection component'. We changed the position of a vertical line abutting a horizontal, along the horizontal axis, in order to observe how the perceived size of the latter varies. We manipulated the size of a comparator horizontal line and observers were asked to compare this to the horizontal segment of one of three configurations; an L-shape, an asymmetrical inverted 'T' and a regular inverted 'T' configuration.

5.3.2 Method

Three conditions were interleaved; in all cases the horizontal component of an 'L'-shape, a configuration in which the vertical segment abutted the horizontal three quarters of its length and an inverted 'T' was compared with one of seven comparator horizontal lines, varying in size from slightly smaller to slightly longer than the standard. Both the vertical and the horizontal segments of the standard stimuli were 6.1° long. The deviations from the standard width were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the comparator stimulus ranging between 5.2° to 7.0°. Figure 5.6 below illustrates the stimuli used in this experiment.

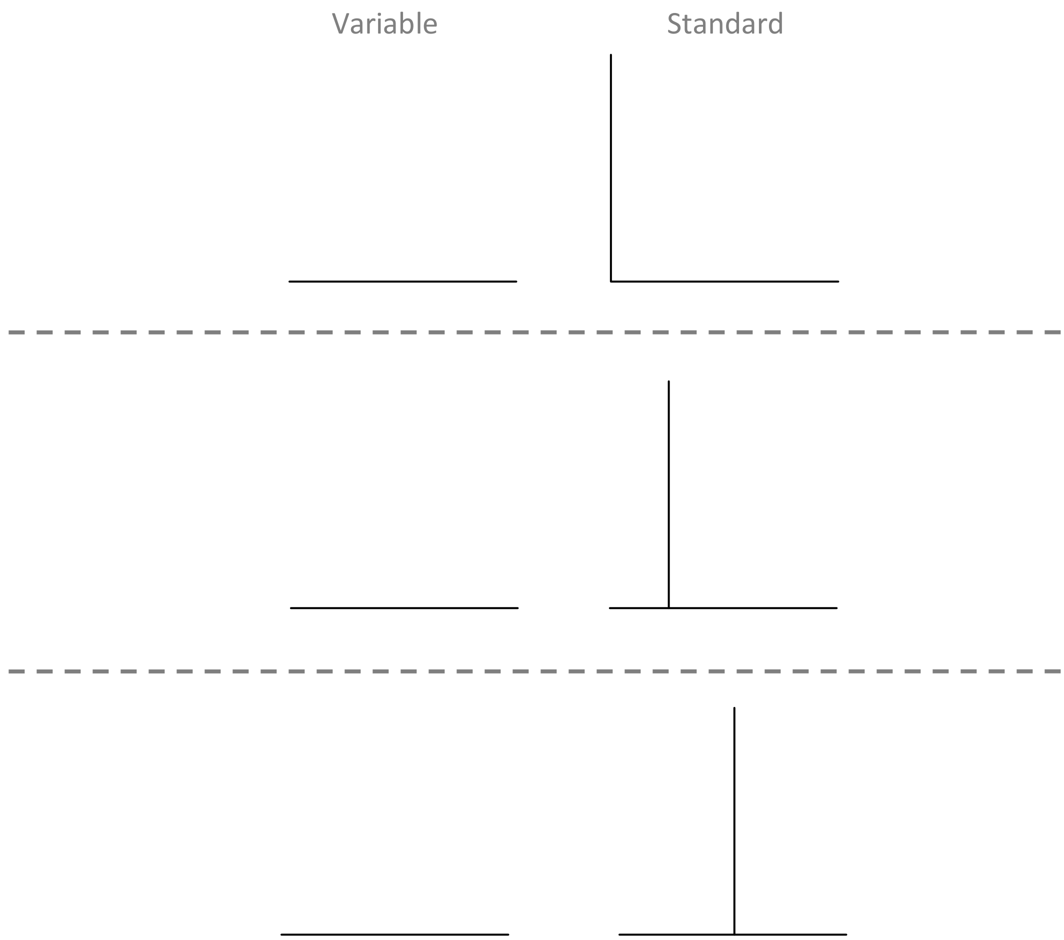


Figure 5.6 Stimuli used in Experiment 9. The comparator stimulus was always a simple horizontal line positioned either on the left or the right of each one of the three standard stimuli.

Each of three naïve observers (one female) undertook 1050 trials; six pairs of stimuli each presented 25 times for seven comparator stimulus sizes. Participants were asked to indicate the longer horizontal line using a response box. Stimuli were positioned one next to the other and presented simultaneously for 750ms. The luminance of the stimuli was approximately 20cd/m² and the background approaching 0cd/m², so the contrast is close to 1.00. The timeline for the experiment is shown in Figure 5.7 below.

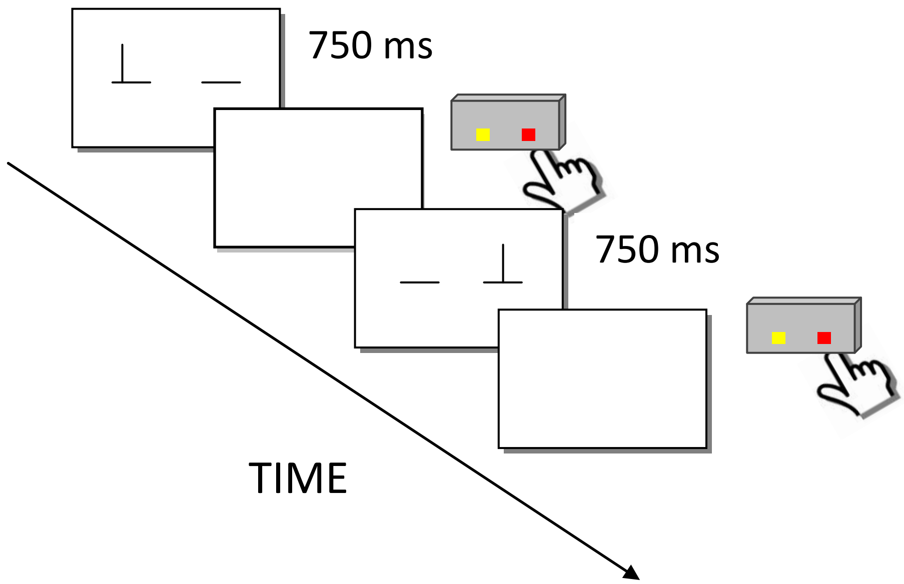


Figure 5.7 Timeline of Experiment 9 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

5.3.3 Results

Comparisons between a comparator horizontal line and the horizontal segment of each of the three simple shapes used as standard stimuli were made so that psychometric functions could be constructed and points of subjective equality (PSEs) calculated for three participants. Figure 5.8 depicts the psychometric functions generated for a single participant for all three conditions. The pink curve represents the L-shape condition and the mean PSE is 6.45°, showing that perceived size of the horizontal segment is increased. The yellow curve represents the configuration in which the vertical line abutted a horizontal three quarters along its length and the mean PSE is 6.29°, showing that the presence of the vertical segment does not significantly affect its perceived size in this specific configuration. Similarly, the perceived size of the horizontal segment in an inverted 'T' configuration, as shown by the purple curve is not affected by the presence of the vertical segment generating a mean PSE is 6.09°.

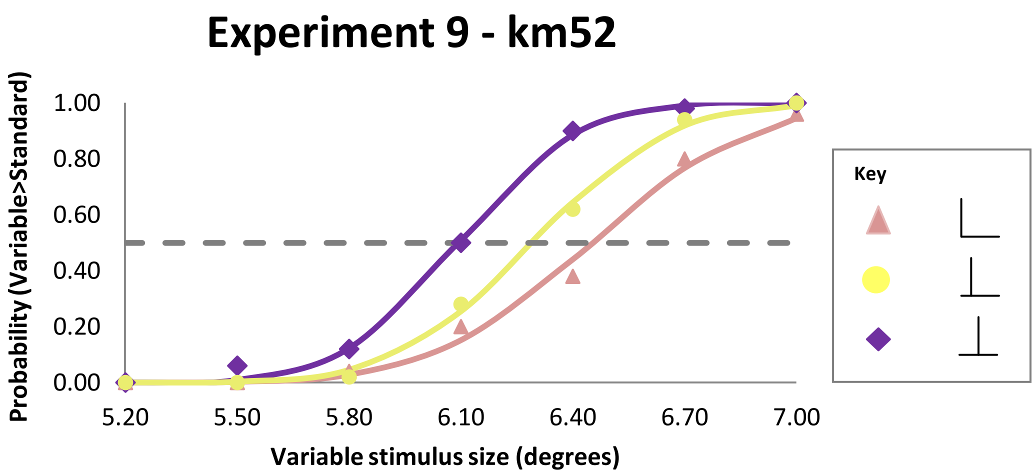


Figure 5.8 Psychometric functions for a single participant from Experiment 9.

Results for all participants are illustrated in Figure 5.9 below. The L-shape condition generated a mean PSE of 6.45°, and a z-test showed that the perceived size of the horizontal segment is significantly increased (*p<.05*). The mean PSE for the other two conditions is 6.21° and 5.90° respectively with z-tests showing that there are no significant variations of the perceived size of these horizontal segments (*p>.05*).

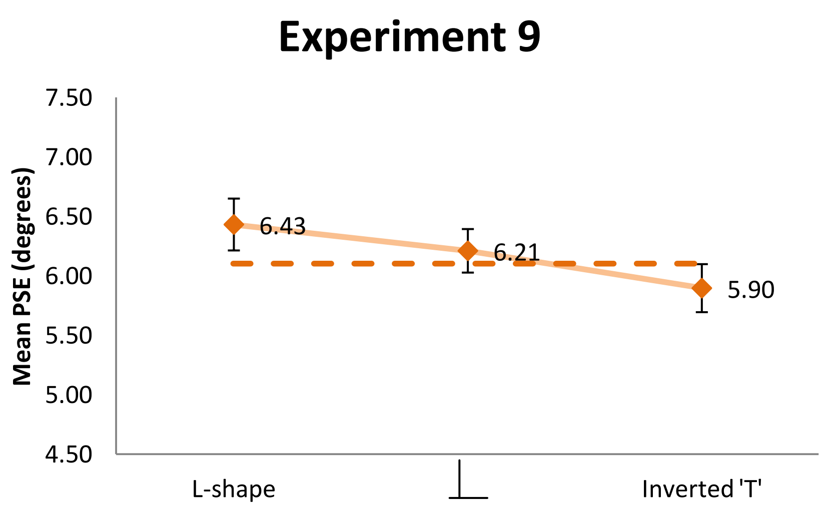


Figure 5.9 Results from Experiment 9, showing a significant overestimation of the perceived size of the horizontal segment of an L-shape (N=3). Error bars show 95% confidence intervals.

5.3.4 Discussion

The aim of the present experiment was to scrutinize the 'bisection' component as described by Mamassian and de Montalembert (2010). Confirming the results from Chapter 3 we observed no significant change in the perceived size of the horizontal segment in an inverted 'T' configuration. Additionally, there were no significant differences in the perceived size of the horizontal segment in a configuration in which the vertical segment abutted the horizontal three quarters of the way along its length. Interestingly, the perceived size of the horizontal segment in an L-shape was found to be significantly longer compared to its actual physical size. This result could not have been predicted by their model as it does not account for any changes in the perceived size of a line which one of its ends abutting on another line.

In light of the present results, we suggest that abutting plays a significant role in the size perception of lines within simple shapes. Consequently, we will incorporate this into a new model that will be described and evaluated in due course.

5.4 Experiment 10

5.4.1 Rationale

The aim of this experiment is to further investigate the ‘bisection’ component of the vertical-horizontal illusion, as described by Mamassian and de Montalembert (2010). We manipulated the size of an independent vertical line and asked observers to compare its length to the length of the vertical segment of one of three configurations; a horizontal ‘T’, a cross and an inverted ‘T’. Based on findings from the previous experiment we hypothesise that there is a difference between *abutting* and *crossing,* with the former increasing the perceived size of the abuttor and leaving unaffected that of the abuttee (see Figure 5.10) whereas the latter will decrease the perceived size of a line. Abutting occurs when one end of a line simply touches another line, without crossing it.

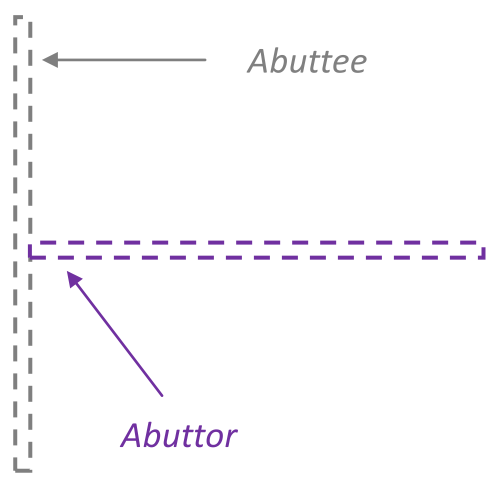


Figure 5.10 The abuttor has one of its ends simply touching another line; the abuttee.

5.4.2 Method

Four conditions were interleaved; in the control a standard vertical line was compared with one of seven comparator vertical lines, varying in size from slightly smaller to slightly longer than the standard. Stimuli were positioned along the vertical axis to prevent participants from carrying out size judgments by matching the position of their two ends. For the other three conditions, the vertical component of a horizontal 'T', a cross and an inverted 'T' was compared against the comparator stimulus. Both the vertical and the horizontal segments of the standard stimuli was 6.1° long. The deviations from the standard width were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the comparator stimulus ranging between 5.2° to 7.0°. Figure 5.11 below illustrates the stimuli used in this experiment.

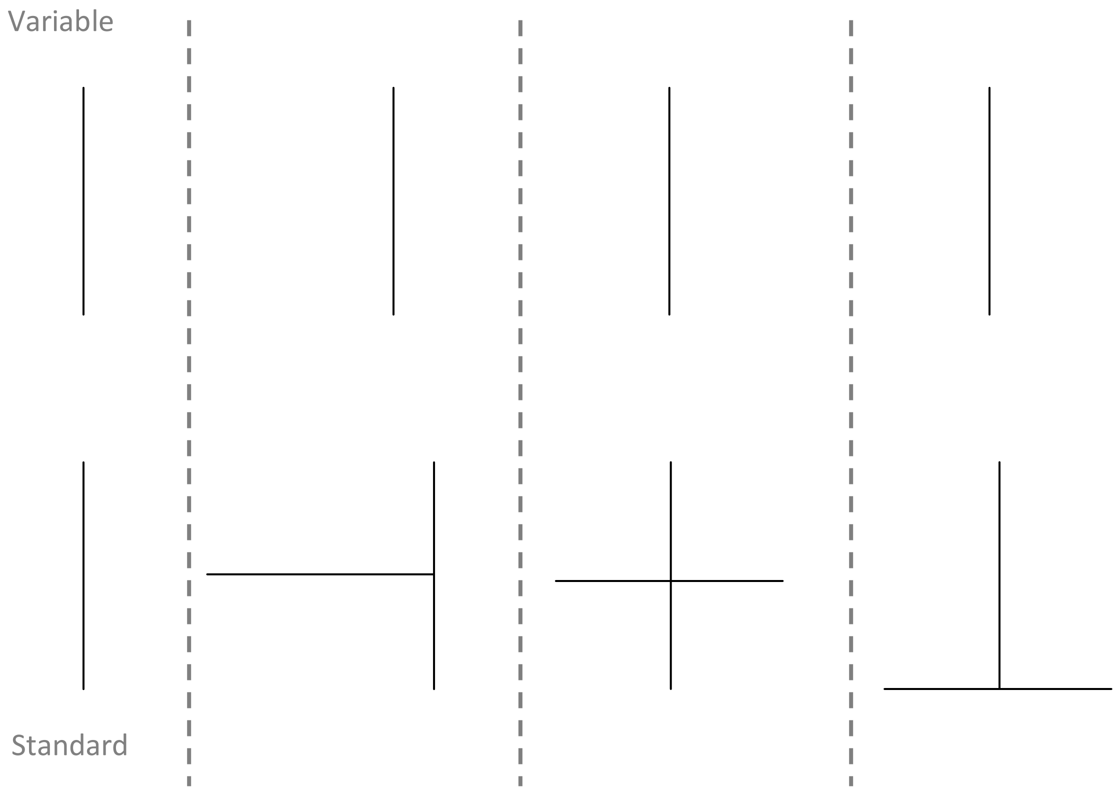


Figure 5.11 Stimuli used in Experiment 10. The comparator stimulus was always a vertical line located either above or below the standard stimulus. The control condition is illustrated in the first window on the left.

Each of seven naïve observers (four female) undertook 336 trials; eight pairs of stimuli each presented six times for seven comparator stimulus sizes. Participants were asked to indicate the longer vertical line using a response box and the control condition was used to evaluate whether or not participants were able to carry out the task. Stimuli were positioned one above the other and presented simultaneously for 500ms. The luminance of the stimuli was approximately 20cd/m² and the background approaching 0cd/m², so the contrast approached 1.00. The timeline for the experiment is shown in Figure 5.12 below.

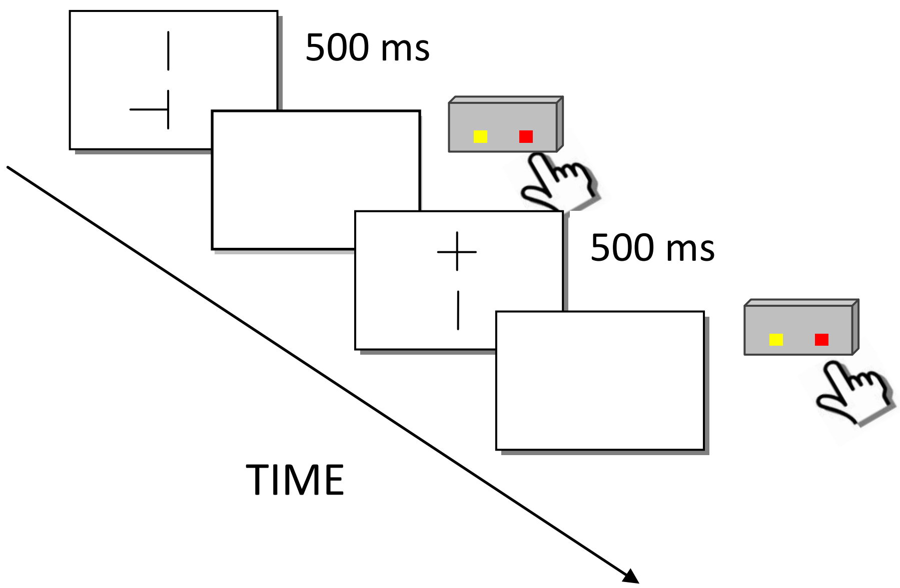


Figure 5.12 Timeline of Experiment 10 showing two trials. Presentation of stimulus pairs was random throughout the experiment.

5.4.3 Results

Comparisons between a vertical line and the vertical segment of each of the three shapes used as standard stimuli were made so that psychometric functions could be constructed and points of subjective equality (PSEs) calculated for seven participants. Figure 5.13 depicts the psychometric functions generated for a single participant for all four conditions. The orange curve represents the control condition and the mean PSE for this is 6.06° confirming that the participant is able to match two vertical lines presented on the vertical axis. The green curve represents the horizontal 'T' condition and the mean PSE is 6.02°, showing that size perception of the vertical segment remains unaffected by the presence of the horizontal line. The blue curve represents the cross condition and the mean PSE is 5.93°, showing that bisecting a vertical line reduces its apparent size. Finally, the purple curve represents the inverted 'T' condition and the mean PSE is 6.58°, illustrating that the perceived size of the vertical segment in such a configuration increases due to abutting.

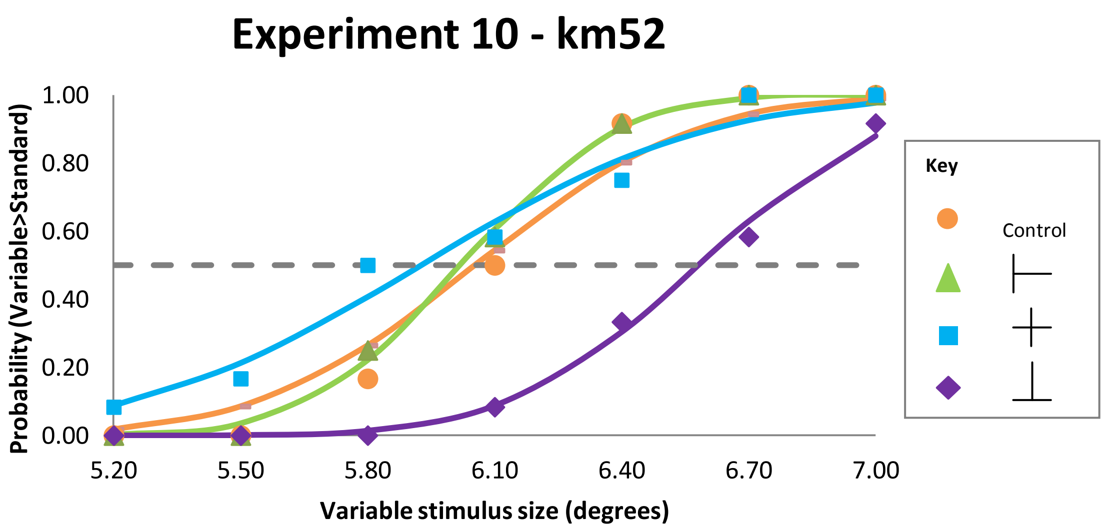


Figure 5.13 Psychometric functions for a single participant from Experiment 10.

Results for all participants are illustrated in Figure 5.14 below. The control condition shows that participants were able to match veridically the size of two simple vertical lines, generating a mean of 6.09°. Moreover, when comparing the size of a simple vertical line to the vertical segment of a horizontal 'T' the mean PSE was 5.91° and a z-test revealed no significant difference between the physical and perceived size of the latter (*p>.05*). However, for the vertical segment of the cross configuration to be perceived equal in size with the simple vertical line, the latter had to be approximately 7% shorter, generating a mean PSE of 5.65°. A z-test revealed that this value was significantly different from 6.1° (*p<.01*) i.e. the actual physical size of the vertical segment in the cross configuration. Finally, for the vertical segment of the inverted 'T' configuration to be perceived equal in size with the simple vertical line, the latter had to be approximately 9% longer, generating a mean PSE of 6.62°. A z-test revealed that this value was significantly different from 6.1° (*p<.01*) i.e. the actual physical size of the vertical segment.

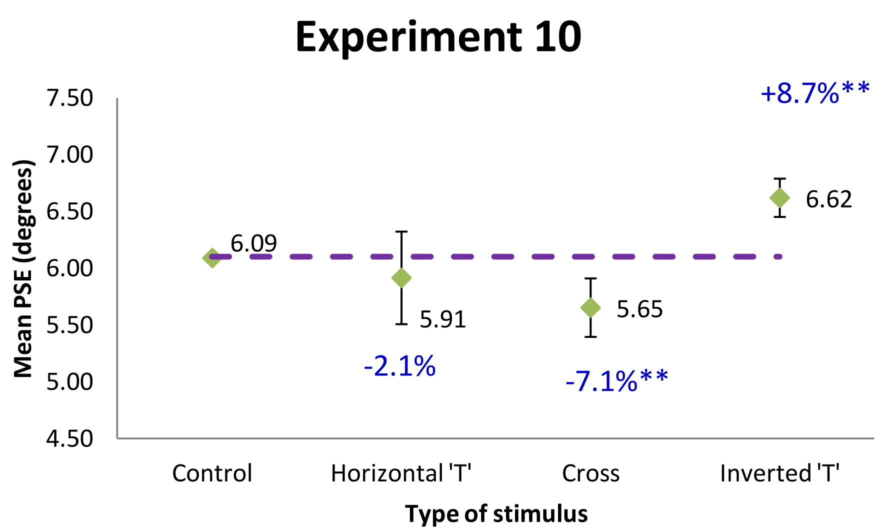


Figure 5.14 Results from Experiment 10 show a significant 7.1% underestimation of the perceived size of the vertical segment in a '+' and a significant 8.7% overestimation of the perceived size of the vertical segment in an inverted 'T' (N=7). Error bars show 95% confidence intervals; error bar on control condition is smaller than symbol.

5.4.4 Discussion

The aim of this experiment was to examine the 'bisection' component of the vertical-horizontal illusion, as described by Mamassian and de Montalembert (2010) by comparing the vertical segment of different configurations to an independent vertical line. According to Mamassian and de Montalembert the size of the 'bisection' component was calculated to be approximately a 16% decrease in length by comparing the vertical and horizontal segments within different configurations such as the inverted 'T', the cross and the L-shape. It is important to note here that Mamassian and de Montalembert state that '...The bisection bias is present in the 'T' configuration of the vertical-horizontal illusion where the horizontal segment is bisected by a dividing vertical line…' (p.956). Moreover, this same 'bisection' effect is present in a cross figure consequently implying that the *crossing* of two lines should be perceptually the same as when one line, either horizontal or vertical *abuts* another line orthogonal to it.

In contrast, in Chapter 3 results have illustrated a veridical size judgment of the horizontal segment of an inverted 'T' configuration when this was compared to another independent horizontal line. This contradicts Mamassian and de Montalembert's assertion that the horizontal segment of an inverted 'T' configuration undergoes a 16% reduction in its perceived size by virtue of the bisection component. In view of results from Chapter 3 and the present chapter, we propose an improved model to describe changes in the perceived size of lines within simple shapes. This **ABC** model consists of three components: anisotropy (**A**), abutting (**B**) and crossing (**C**). Anisotropy represents the overestimation of the perceived size of a vertical line compared to a horizontal one. Abutting refers to the overestimation of the perceived size of a line, either vertical or horizontal, that has one end simply touching or *abutting* a second line. Lastly, Crossing refers to the underestimation of the perceived size of a line, either vertical or horizontal, which crosses another one orthogonal to it. Table 5.1 in the following page illustrates predictions for the perceived size of the vertical segment in accordance with Mamassian and de Montalembert's simple model, as well as predictions derived from the new **ABC** model we propose.

According to Mamassian and de Montalembert the perceived size of the vertical segment in the horizontal 'T' condition would be reduced compared to its actual physical size by virtue of their bisection component. On the contrary we hypothesise that size perception of the vertical segment in such a shape would be veridical as it does not *cross* or has one of its ends *abutting* another line. Furthermore, according to their model the perceived size of the vertical segment in the cross condition would be reduced compared to its actual physical size by virtue of their bisection component. The **ABC** model agrees with this, as it predicts that any line which crosses another one should look smaller than it actually is. Lastly, in an inverted ‘T’ configuration Mamassian and de Montalembert would predict that the perceived size of the vertical segment should be veridical as it is not bisected. On the contrary the **ABC** model predicts that due to the fact that one end of it abuts on a horizontal line, its perceived size should increase.

PREDICTIONS			
Type of stimulus	⊣	+	⊥
Mamassian & de Montalembert	↓	↓	Veridical
ABC model	Veridical	↓	↑

Table 5.1 Predictions for perceived size of vertical segment within the cross, horizontal ‘T’ and inverted ‘T’ figures when compared to a comparator vertical line. Green denotes that a prediction was confirmed, whereas red indicates the opposite.

Results in the present experiment satisfied all three predictions generated by the **ABC** model. More specifically, the perceived size of the vertical segment of the horizontal ‘T’ condition was found not to be significantly different from the control thus challenging the definition of the ‘bisection’ component as described in Mamassian and de Montalembert’ s simple model. In addition, the perceived size of the vertical segment in a cross configuration was found to be approximately 7% smaller, satisfying our prediction that a ‘crossing’ component plays a vital role in size perception of simple line size. This result satisfied the qualitative nature of Mamassian and de Montalembert’ s ‘bisection’ component as there is an observed reduction in the size of the vertical line. However, this prediction is not satisfied quantitatively as the reduction was only 7% and not 16% as they suggested. Finally, the perceived size of the vertical segment in an inverted ‘T’ configuration was found to be significantly longer by 9% compared to its actual size. This was not and could not have been predicted by their model as they do not predict any changes in the perceived size of a line which has its one end abutting on another line. Importantly, the thickness of the ‘abuttee’ (i.e. the horizontal line) is such that adding this to the length of the ‘abuttor’ (i.e. vertical line) would lead to an insignificant increase in the latter’s length and cannot account for the 9% increase in its perceived size.

Interestingly, Mamassian and de Montalembert (2010) investigated whether there is a difference in sensitivity when discriminating vertical and horizontal lengths and found a reduced sensitivity demonstrated, as they claim, by a shallower psychometric function for the cross compared to the L-shape. Despite the fact that the two psychometric functions look very similar, this led them to the assertion that in an inverted ‘T’ configuration ‘…the bisection parameter was a shortening of the bisected line rather than a lengthening of the bisecting line…’ (p.961). However, it is important to highlight that this assertion was not proven experimentally by comparing the vertical segment of an inverted-T configuration to a simple vertical line as we did in the present experiment.

5.5 Experiment 11 - Part A

5.5.1 Rationale

The aim of the first part of this experiment is to investigate whether predictions derived from the new **ABC** model regarding the perceived length of lines affected by the three components individually identified and described in previous experiments are valid. Observers were asked to compare the apparent length of a vertical to a horizontal line. More specifically we manipulated the size of an independent vertical line which was compared against the horizontal segment of each of the three standard stimuli; a cross, an inverted 'T' and an L-shape.

5.5.2 Predictions

Based on findings from previous experiments in this chapter, we have generated a series of predictions for each one of three stimulus types, summarised in Table 5.2 in the following page. It is important to note, that all predictions made based on the **ABC** model assume a linear summation of the three components. Also, it must be clarified that the use of the word 'model' throughout this chapter is referring to a descriptive model aiming shed light on the factors affecting the vertical-horizontal illusion by to isolating them. It is by no means a mathematically sophisticated model and should not be treated like one.

In a cross figure, when comparing its horizontal segment with a vertical comparator line we expect **anisotropy** and **crossing** to be affecting size perception. More specifically, the horizontal segment of this figure will appear shorter by approximately 7% due to the anisotropy component. This reduction will be enhanced by the fact that the horizontal line is crossing a vertical by an additional 7%, leading to an approximate total reduction in the perceived size of the horizontal segment of the cross figure by 14%, relative to the comparator vertical line.

In an inverted ‘T’ configuration, when comparing the horizontal segment with a vertical comparator line we only expect anisotropy to be affecting size perception, by reducing the perceived size of the horizontal segment of the inverted ‘T’ configuration by 7%.

In an L-shape, when comparing the horizontal segment with a vertical comparator line we expect **anisotropy** and **abutting** to be affecting size perception. More specifically, the horizontal segment of this figure will appear approximately 7% shorter because of anisotropy, but this reduction will be compensated by the fact that the horizontal line is abutting a vertical making the former appear 9% longer. Consequently, the combined effect of these components will induce an increase in the perceived size of the horizontal segment of the L-shape by approximately 2% relative to the comparator vertical line.

Predictions from the ABC model			
Comparator stimulus			
Type of standard stimulus			
Components	**-A+C**	**-A**	**-A+B**
Predicted size of illusion	-14%	-7%	2%

Table 5.2 Summary of predictions derived from the ABC model, assuming a linear summation of the three components.

5.5.3 Method

Three conditions were interleaved; in all cases the horizontal component of a cross, an inverted 'T' and an 'L'-shape was compared with one of seven comparator vertical lines, varying in size from slightly smaller to slightly longer than the standard. Both the vertical and the horizontal segments of the standard stimuli were 6.1° long. The deviations from the standard width were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the comparator stimulus ranging between 5.2° to 7.0°. Figure 5.15 below illustrates the stimuli used in this experiment. Please note although all parts of the stimuli used in the experiment were the same colour, here the parts to be compared are shown in blue for the purpose of clarity.

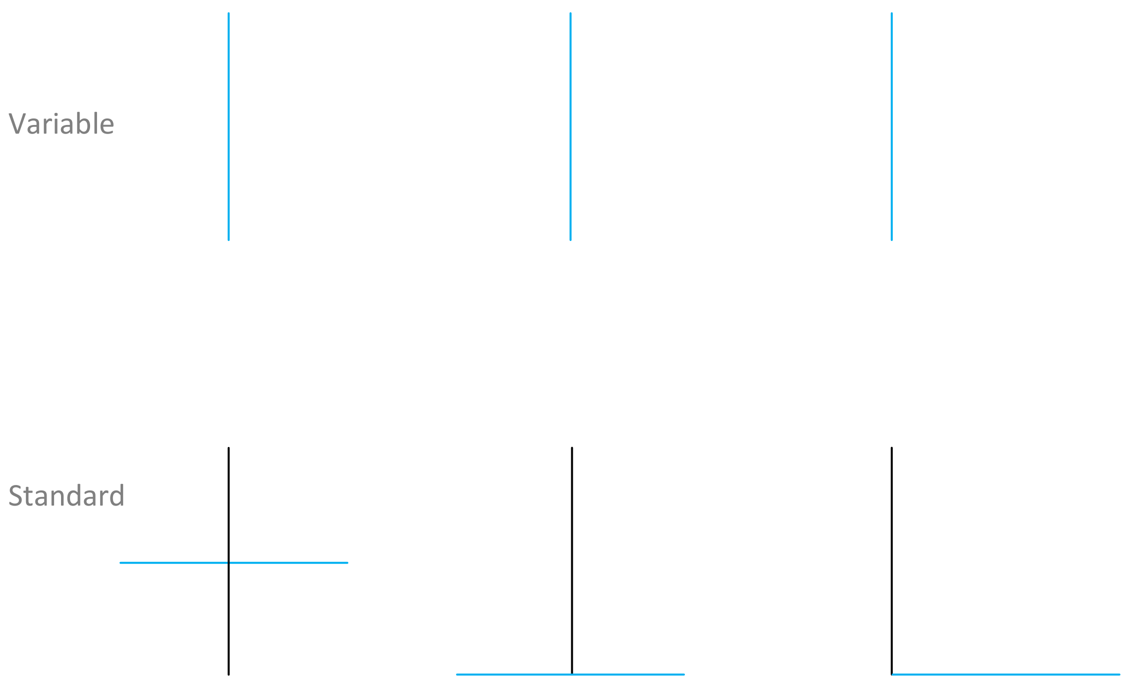


Figure 5.15 Stimuli used in Experiment 11a - the comparator stimulus was always a vertical line located either above or below the standard stimulus.

Each of eight naïve observers (seven female) undertook 840 trials; six pairs of stimuli each presented 20 times for seven comparator stimulus sizes. Participants were asked to indicate the longer line using a response box. Stimuli were positioned one above the other and presented simultaneously for 750ms. The luminance of the stimuli was approximately 0cd/m² and the background approaching 20cd/m², so the contrast is

1.00. The timeline for the experiment is shown in Figure 5.16 below.

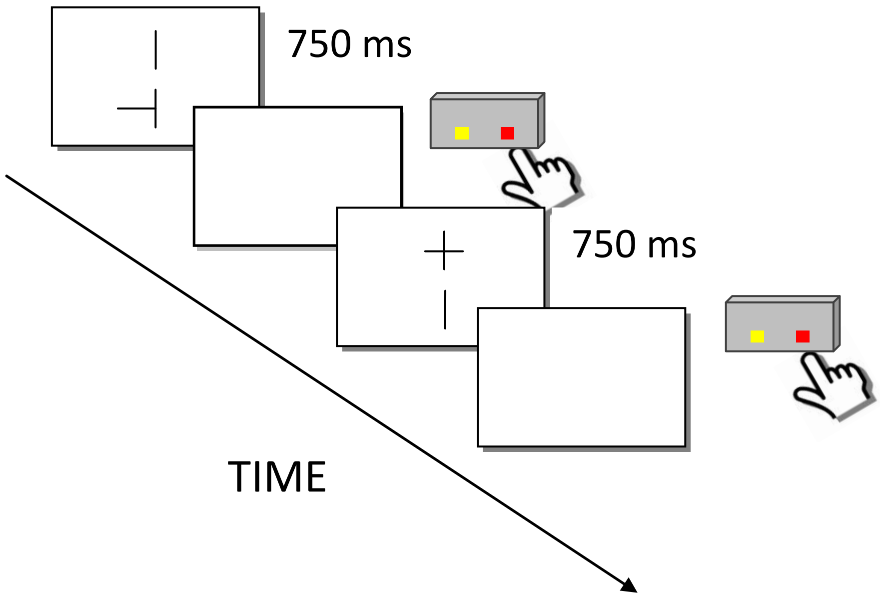


Figure 5.16 Timeline of Experiment 11a showing two trials. Presentation of stimulus pairs was random throughout the experiment.

5.5.4 Results

Comparisons between a comparator vertical line and the horizontal segment of each of the three shapes used as standard stimuli were made so that psychometric functions could be constructed and points of subjective equality (PSEs) calculated for seven participants. Figure 5.17 depicts the psychometric functions generated for a single participant for all three conditions. The blue curve represents the cross condition and the mean PSE is 5.56°, showing that size perception of the horizontal segment is greatly decreased when compared to an independent vertical line. The purple curve represents the inverted 'T' condition and the mean PSE is 5.70°, showing that the perceived size of the horizontal segment is also decreased. Finally, the pink curve represents the L-shape condition and the mean PSE is 6.01°, illustrating that the perceived size of the horizontal segment in such a configuration is almost veridical when compared to a vertical comparator line.

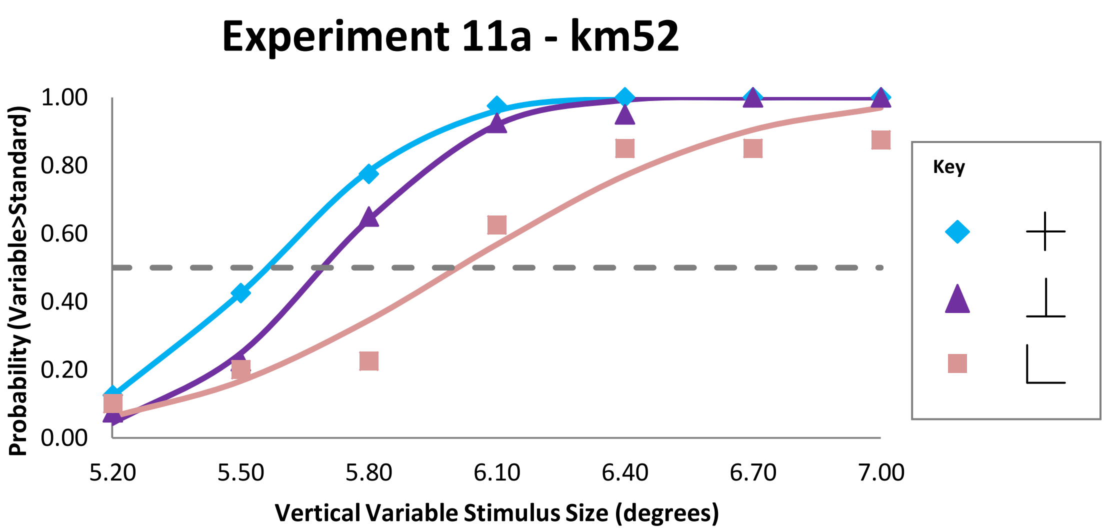


Figure 5.17 Psychometric functions for a single participant from Experiment 11a.

Results for all participants are illustrated in Figure 5.18 below. When comparing the size of a simple vertical line to the horizontal segment of a cross configuration the mean PSE was 5.23° and a z-test revealed that this was significantly different from the actual physical size of the stimulus ($p<.01$). The size of this reduction was found to be approximately 14%. For the horizontal segment of the inverted 'T' configuration the mean PSE was 5.76° and a z-test revealed that this was also significantly different from the actual physical size of the stimulus ($p<.01$). The size of this reduction was found to be approximately 6%. Finally, the mean PSE for the vertical segment of the L-shape was found to be 6.35° and a z-test confirmed that this was significantly different from the actual physical size of the stimulus ($p<.01$). The size of this increase was found to be approximately 4%.

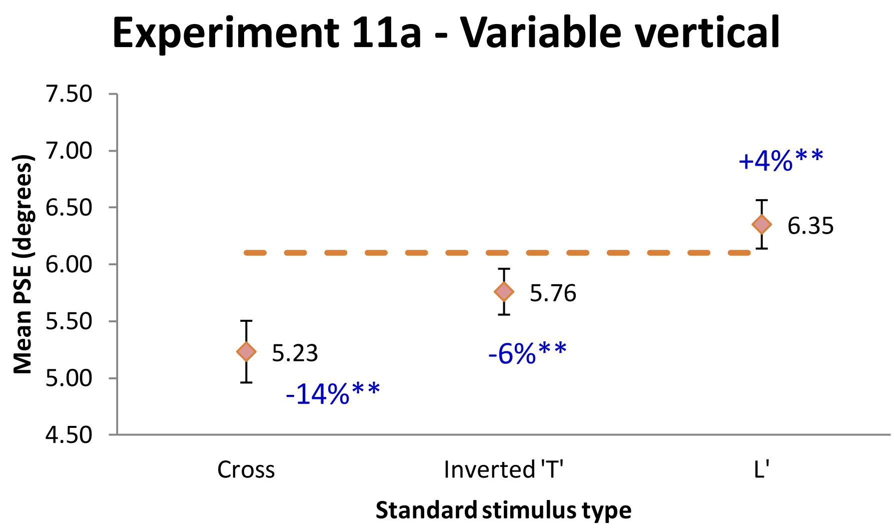


Figure 5.18 Results from Experiment 11a (N=8). Error bars show 95% confidence intervals.

5.5.5 Discussion

The aim of the present experiment was to validate predictions from the **ABC** model regarding the perceived size of lines and evaluate the significance of its three components. Based on findings from previous experiments, we generated a series of predictions for each one of the three stimuli used and these will be compared to results from this experiment.

When comparing the size of a simple vertical line to the horizontal segment of a cross configuration the predicted perceived size of the latter was expected to be 14% shorter by virtue of **A** and **C** each inducing an equal additive reduction of 7%. Results generated a mean PSE of 5.23° confirming a significant reduction in the perceived size of the horizontal segment of the cross configuration when compared to a comparator vertical line. As predicted the size of this reduction was found to be approximately 14%. Consequently the importance of the anisotropy and crossing components in such a figure has been confirmed not only qualitatively but quantitatively as well.

Furthermore, it was predicted that the perceived size of the horizontal segment of an inverted ‘T’ configuration would be 7% shorter when compared to the vertical comparator line, by virtue of **A**. Results showed that the mean PSE was 5.76° confirming a significant reduction in the perceived size of the horizontal segment when compared to the comparator vertical line by approximately 6%. Therefore, this second prediction was also validated.

In addition, when comparing the horizontal segment of an L-shape with a vertical comparator line we expect **A** and **B** to be increasing the perceived size of the former by approximately 2%. More specifically, the horizontal segment of this figure will appear 7% shorter because of the anisotropy component, an effect which will be compensated by the fact that the horizontal line is abutting the vertical increasing the perceived size of the former by 9%. Results showed that the mean PSE was 6.35° confirming a significant 4% increase in the perceived size of the horizontal segment of the L-shape.

To conclude, predictions drawn from previous experiments were tested and confirmed by these results. It is evident that the three components can provide a coherent explanation for the variations in perceived size of lines in different configurations.

5.6 Experiment 11 - Part B

5.6.1 Rationale

The aim of this part of the experiment is to investigate whether predictions based on the new **ABC** model regarding the perceived size of lines affected by the three components individually identified and described in Experiment 10 are valid. Observers were asked to compare the apparent length of a horizontal to a vertical line. More specifically we manipulated the size of an independent horizontal line which was compared against the vertical segment of each of the three standard stimuli; a cross, an inverted 'T' and an L-shape.

5.6.2 Predictions

Based on findings from previous experiments in this chapter, we have generated a series of predictions for each one of three stimulus types, summarised in Table 5.3 in the following page. As in the first part of Experiment 11, all predictions made based on the **ABC** model assume a linear summation of the three components.

In a cross configuration, when comparing the vertical segment with a horizontal comparator line we expect **anisotropy** and **crossing** to be affecting size perception. More specifically, the vertical segment of this figure will appear 7% longer because of **anisotropy** but this increase will be counterbalanced by **C** inducing a 7% reduction in the perceived size of the horizontal. Consequently, the combined effect of these components will add up to zero allowing for a veridical size perception of the vertical segment in a cross figure relative to the comparator horizontal line.

In an inverted ‘T’ configuration, when comparing the vertical to a horizontal comparator line we expect **anisotropy** and **abutting** to be affecting size perception. More specifically, the vertical segment of this figure will appear 7% longer because of **anisotropy** and this increase will be enhanced by **abutting** increasing the perceived size of the vertical line by 9%. Consequently, the combined effect of these two components will induce a 16% increase in the perceived size of the vertical segment of the inverted ‘T’ configuration, relative to the comparator horizontal line.

In an L-shape configuration, similarly to the inverted ‘T’, when comparing its vertical segment with a comparator line we expect **anisotropy** and **abutting** to be affecting size perception. The vertical segment of this figure will appear 7% longer because of **anisotropy** and this increase will be further enhanced by the fact that the vertical line is abutting a horizontal making the former appear 9% longer. Consequently, the combined effect of these two components will be identical to that in the inverted ‘T’ configuration, inducing a 16% increase in the perceived size of the vertical segment of the L-shape, relative to the comparator horizontal line.

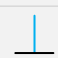
Predictions from the ABC model			
Comparator stimulus			
Type of standard stimulus			
Components	**A+C**	**A+B**	**A+B**
Predicted size of illusion	0%	16%	16%

Table 5.3 Summary of predictions derived from the ABC model, assuming a linear summation of the three components.

5.6.3 Method

Three conditions were interleaved; in all cases the vertical component of a cross, an inverted 'T' and an 'L'-shape was compared with one of seven comparator horizontal lines, varying in size from slightly smaller to slightly longer than the standard. Each of nine naïve observers (seven female) were asked to indicate the longer line using a response box. All other experimental details are identical to those in Experiment 11a. Figure 5.19 below illustrates the stimuli used in this experiment and Figure 5.20 in the following page shows the timeline.

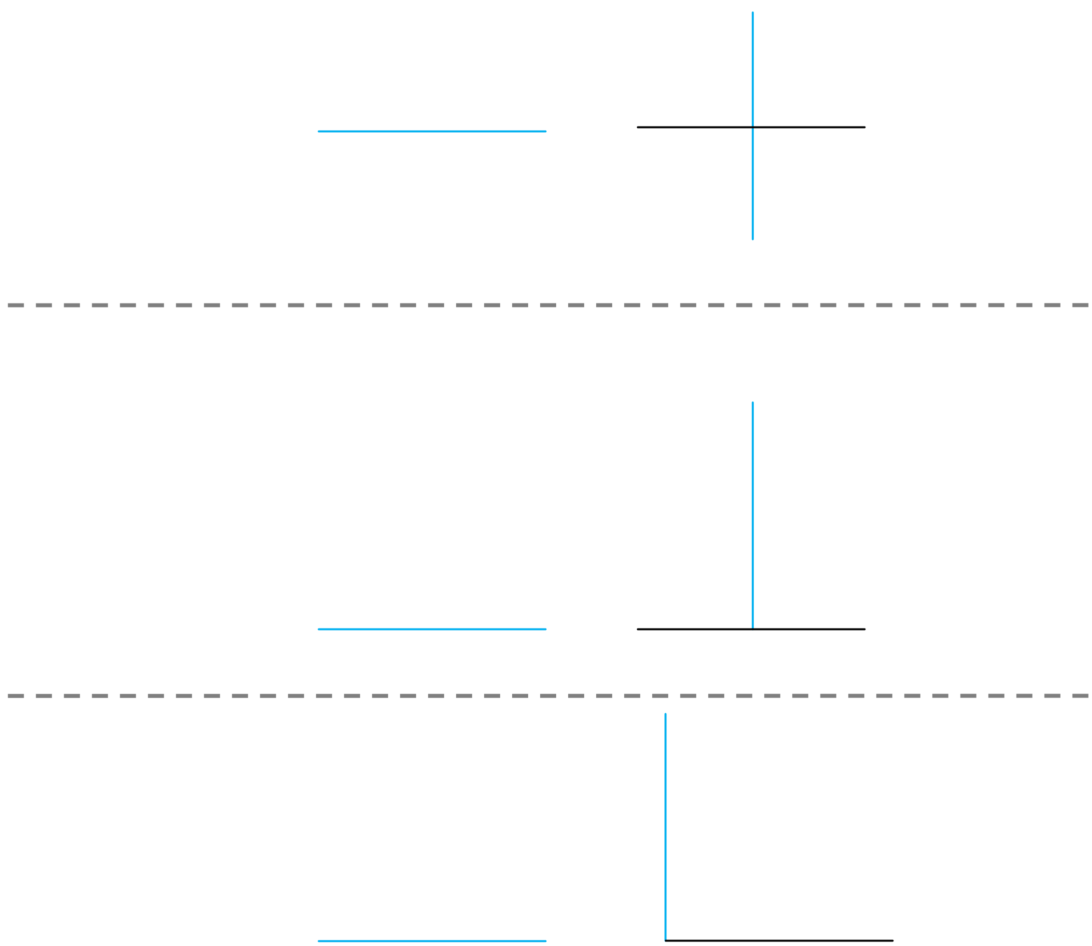


Figure 5.19 Stimuli used in Experiment 11b. The comparator stimulus was always a horizontal line located on either the left or the right of the standard stimulus.

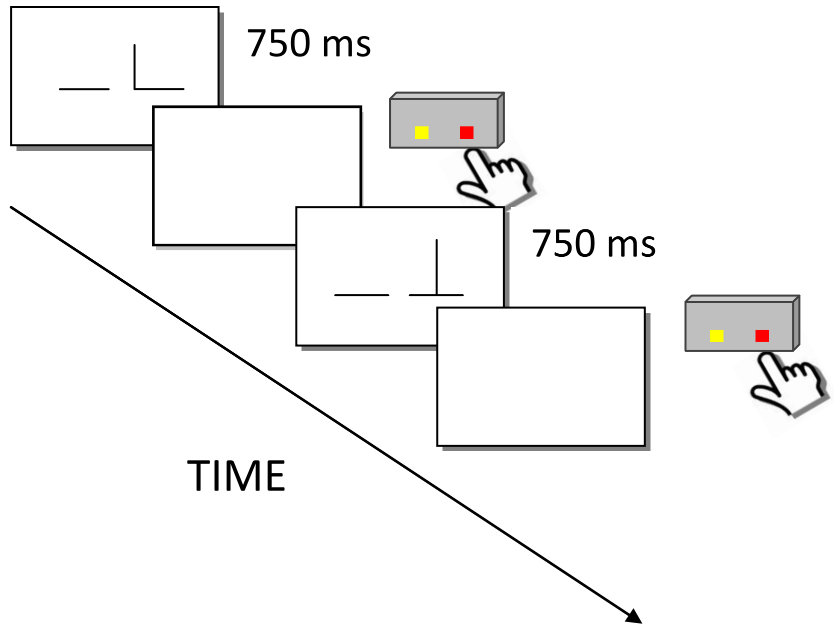


Figure 5.20 Timeline of Experiment 11b showing two trials. Presentation of stimulus pairs was random throughout the experiment.

5.6.4 Results

Comparisons between a comparator horizontal line and the vertical segment of each of the three shapes used as standard stimuli were made so that psychometric functions could be constructed and points of subjective equality (PSEs) calculated for seven participants. Figure 5.21 depicts the psychometric functions generated for a single participant for all four conditions. The blue curve represents the cross condition and the mean PSE is 6.19°, showing that size perception of the horizontal segment remains fairly unchanged. Moreover, the purple curve represents the inverted ‘T’ condition and the mean PSE is 6.47°, showing that the perceived size of the horizontal segment is increased. Finally, the pink curve represents the L-shape condition and the mean PSE is 6.79°, illustrating that the perceived size of the horizontal segment in such a configuration greatly increases when compared to a vertical comparator line.

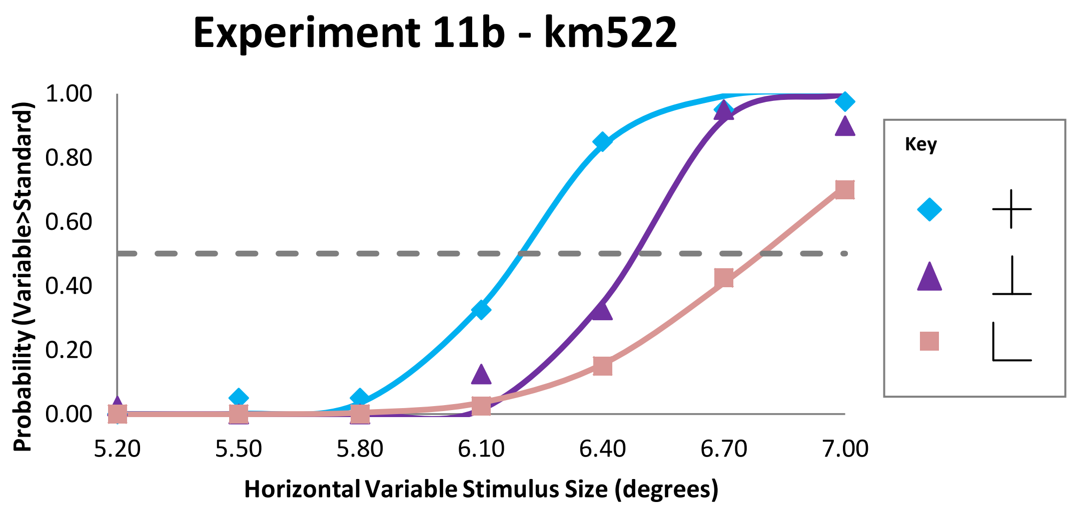


Figure 5.21 Psychometric functions for a single participant from Experiment 11b.

Results for all participants are illustrated in Figure 5.22 below. When comparing the size of a simple vertical line to the horizontal segment of a cross configuration the mean PSE was 5.98° and a z-test revealed that this was not significantly different from the actual physical size of the stimulus (*p>.05*). The size of this reduction was found to be approximately 2%. For the horizontal segment of the inverted 'T' configuration the mean PSE was 6.52° and a z-test revealed that this was significantly different from the actual physical size of the stimulus (*p<.01*). The size of this increase was found to be approximately 7%. Finally, the mean PSE for the vertical segment of the L-shape was found to be 6.99° and a z-test confirmed that this was significantly different from the actual physical size of the stimulus (*p<.01*). The size of this increase was found to be approximately 15%.

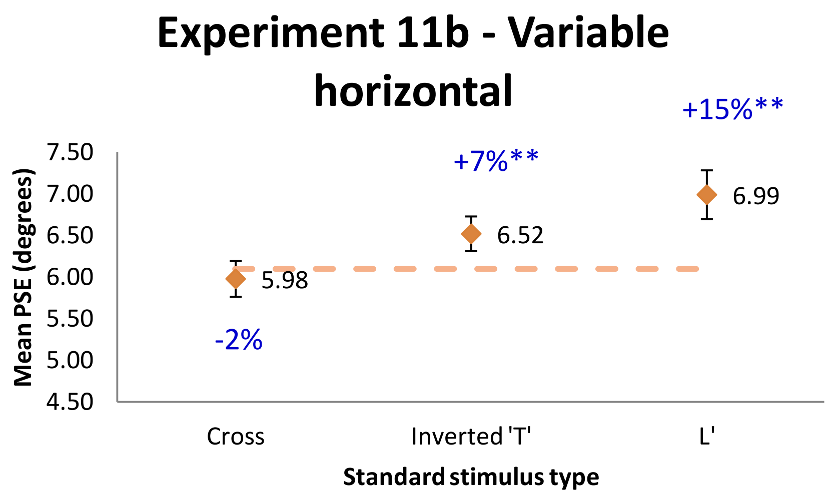


Figure 5.22 Results from Experiment 11b, showing a significant overestimation of the perceived size of the vertical segment in an inverted 'T' and an L-shape configuration compared to a simple vertical line by approximately 7% and 15% respectively (N=9). Error bars show 95% confidence intervals.

5.6.5 Discussion

The aim of the present experiment is to validate additional predictions derived from the **ABC** model regarding the perceived size of lines and evaluate the significance of its three components. Based on findings from previous experiments, we generated a series of predictions for each one of the three stimuli used and this will be compared to results from this experiment.

When comparing the size of a simple horizontal line to the vertical segment of a cross configuration the predicted perceived size of the latter would be veridical by virtue of **A** and **C**. Results generated a mean PSE of 5.98° confirming a veridical size judgment of the vertical segment in the cross configuration when compared to a comparator vertical line. The minor reduction was found to be non-significant as illustrated by the 95% confidence intervals and a z-test. Consequently the importance of the anisotropy and crossing components in such a configuration has been confirmed not only qualitatively but quantitatively as well.

Furthermore, it was predicted that the perceived size of the vertical segment of an inverted ‘T’ configuration would be 16% shorter when compared to a comparator horizontal line, by virtue **A** and **B**. Results showed that the mean PSE was 6.52° confirming a significant increase in the perceived size of the vertical segment when compared to the comparator horizontal line by approximately 7%. Although the prediction has been confirmed qualitatively by an increase in the perceived size of the vertical segment, the size of the effect was approximately half than the predicted.

In addition, similarly to the previous condition, when comparing the vertical segment of an L-shape with a vertical comparator line we predicted a 16% increase by virtue of **A** and **B**. Results showed that the mean PSE was 6.99° confirming a significant 15% increase in the perceived size of the horizontal segment of the L-shape. Therefore, this third prediction was confirmed.

To conclude, with the exception of the inverted ‘T’ configuration, predictions drawn from the **ABC** model have been confirmed both quantitatively and qualitatively, showing that the three components can provide a coherent explanation for the variations in perceived size of line in present different configurations.

5.7 General conclusion - Evaluation of the ABC model

The aim of the series of experiments in the present chapter was to investigate extensively the simple model proposed by Mamassian and de Montalembert (2010) describing quantitatively the overestimation of the vertical segment compared to the horizontal in the vertical-horizontal illusion. More specifically, the validity and significance of their two independent components, anisotropy and bisection, were evaluated.

Experiment 8 dealt with the anisotropy component of the simple model proposed by Mamassian and de Montalembert (2010). A simple and direct measure of this effect was carried out by comparing the perceived size of horizontal and vertical lines. In accordance with their results, this experiment showed that the perceived size of a vertical line is approximately 7% longer when compared to a horizontal of the same size. Similarly, the perceived size of a horizontal line was found to be approximately 7% shorter when compared to a vertical of the same size. This difference was found to be significant and was attributed to the difference in orientation between the two lines.

Subsequently, the aim of Experiment 9 was to scrutinize the 'bisection' component as described by Mamassian and de Montalembert (2010). Evidence derived from Chapter 3 suggested no significant decrease in the perceived size of the horizontal segment in an inverted 'T' configuration by virtue of Mamassian and de Montalembert's 'bisection' component. It is important to remember that researchers considered both the horizontal segment of an inverted 'T' as well as that of a cross configuration to be 'bisected' by a vertical line. This experiment investigated changes in the perceived size of the horizontal segment of an L-shape, a configuration in which the vertical segment abutted the horizontal three quarters of its length and an inverted 'T'. A significant increase was only observed on the length of the horizontal segment of an L-shape.

Given that Mamassian and de Montalembert's simple model does not account for any changes in the perceived size of a line which has one of its ends abutting on another line, we decided to incorporate this new component into an improved model-the **ABC** model.

The aim of Experiment 10 was to further inspect the 'bisection' component of the vertical-horizontal illusion, as described by Mamassian and de Montalembert (2010) by comparing the vertical segment of a horizontal 'T', a cross and an inverted 'T' to an independent vertical line. In accordance with Chapter 3, results from Experiment 10 challenged the definition of 'bisection' as the perceived size of the vertical segment of the horizontal 'T' condition was not found to be significantly different. In addition, the perceived size of the vertical segment in a cross configuration was found to be approximately 7% smaller, demonstrating that a 'crossing' component plays an important role in size perception of simple line size. However, although this result satisfied the qualitative nature of Mamassian and de Montalembert's 'bisection' component, it did not do so quantitatively as it was only found to be 7% and not 16% as suggested. Finally, a 9% significant increase was observed in the perceived size of the vertical segment in an inverted 'T' configuration. This could not have been accounted for by their model as they do not predict any changes in the perceived size of a line which has its one end abutting on another line.

Based on results from Chapter 3 and Experiments 8-10 in the present chapter we proposed an improved model to describe changes in the perceived size of lines within simple shapes. This **ABC** model consists of three components: anisotropy (**A**), abutting (**B**) and crossing (**C**). Anisotropy represents the overestimation of the perceived size of a vertical line compared to a horizontal one by approximately 7%. Abutting refers to the overestimation of the perceived size of a line, either vertical or horizontal, that has its one end simply touching or *abutting* a second line by approximately 9%. Lastly, Crossing describes the underestimation of the perceived size of a line, either vertical or horizontal, which crosses another one orthogonal to it by approximately 7%. As previously mentioned and similarly to Mamassian and de Montalembert's (2010) simple model, the ABC model is only a descriptive model aiming to isolate and characterize factors affecting the vertical-horizontal illusion. It is by no means a mathematically sophisticated model and should not be treated like one.

The next step was to confirm the validity of the **ABC** model by testing one or simultaneously two components in different configurations. Based on findings from previous experiments, we generated a series of predictions for each one of the three stimuli used and compared these to results from Experiment 11. In Experiment 11a, the horizontal segment of a cross, an inverted 'T' and an L-shape was compared to an independent vertical line and all three predictions made were confirmed by results. In Experiment 11b, the vertical segment of a cross, an inverted 'T' and an L-shape was compared to an independent horizontal line two out of three predictions made were confirmed qualitatively as well as quantitatively by results. These are displayed in Table 5.4 Summary of predictions generated based on the ABC model and results from Experiment 11a and 9b.Table 5.4 below.

Predictions from the ABC model						
Comparator stimulus	|	|	|	—	—	—
Standard stimulus	+	⊥	└	+	⊥	└
Components	**-A+C**	**-A**	**-A+B**	**A+C**	**A+B**	**A+B**
Predicted size of illusion	-14%	-7%	2%	0%	16%	16%
Results from Experiment 11	-14%**	-6%**	4%**	0%	7%**	15%**

Table 5.4 Summary of predictions generated based on the ABC model and results from Experiment 11a and 9b.

Taking into account the fact that predictions involving the abutting component in an L-shape were confirmed it is not clear why the size of the illusion in an inverted 'T' configuration was only confirmed qualitatively and not quantitatively, failing to show an increase of approximately 16% in the perceived size of the vertical segment. It could be suggested that the size of the **B** could vary depending on the position of the vertical line relative to the horizontal. However, the size of the abutting component in Experiment 10 was estimated using an inverted 'T' configuration.

Compared to the simple model proposed by Mamassian and de Montalembert (2010), the **ABC** model has provided a better explanation for the variations in perceived size of lines. Following results from the present chapter as well as Chapter 3, it is evident that their definition of 'bisection' was imprecise as they considered both the horizontal segment of an inverted 'T' and that of a cross configuration to be 'bisected'. By making this assumption, they concluded that the bisection component was a shortening of the bisected line; a statement which appears to be valid only when one line *crosses* another. Results in Chapter 3, have shown that the size of a horizontal line in an inverted 'T' remains veridical and Experiment 10 has shown that *truly* bisected lines exist in a cross configuration.

Furthermore, Mamassian and de Montalembert claimed that the perceived size of a bisecting line is not increased. Following these arguments, a necessity arose to redefine 'bisection'. A line is truly bisected when a second line crosses it. Consequently, there is no difference between a bisected and a bisecting line as they both cross another line. This crossing induces a decrease in the perceived size of both lines by virtue of **C**, as described in the **ABC** model. Finally, the 'bisecting' line in an inverted 'T' configuration is in fact the ‘abuttor’, which undergoes an increase in its perceived line because one of its ends is touching the horizontal line.

An independent reader could possibly question the existence of any illusory effect at all in any of the configurations used in the present chapter and argue that any difference in the perceived size of horizontal or vertical lines is driven by observer bias. This issue was recently investigated by Morgan et al. (2012) using the method of single stimuli (MSS) who looked for shifts in the central tendency of psychometric functions without any loss of precision. When in doubt, experienced observers were directed into favouring one response over the other and results generated by Morgan et al. showed a shift in observers’ psychometric functions away from the natural mean without any evident implications on the shape of the psychometric function. However, significant results generated in the present chapter are illustrated not only by a difference in the mean but also a change in the shape of the psychometric function for each condition. Noteworthy is the fact that all participants were *naive* towards the purpose of each experiment or any past literature that could favour their responses towards a specific response.

To conclude, in light of these findings it is evident that the **ABC** model, compared to Mamassian and de Montalembert’s simple model, provides a more comprehensive explanation for the perceived size of line in various configurations. However, the abutting component needs to be explored further. This could be done by comparing the horizontal segment of a horizontal ‘T’ configuration to an independent vertical line (see Figure 5.23). The predicted effect would be a 2% increase in the perceived size of the latter by virtue of **A** and **B**. More specifically, **A** would decrease the perceived size of the horizontal segment by 7%, whereas **B** would increase it by 9%.

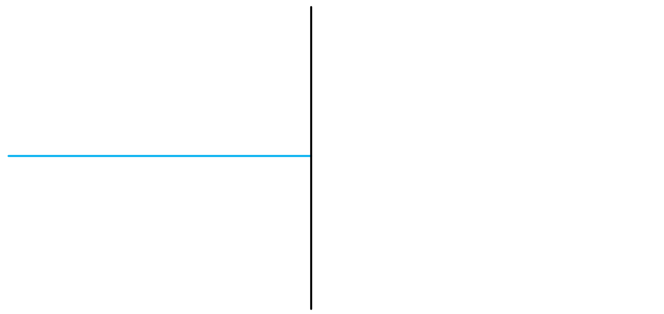


Figure 5.23 An illustration of a potential future experiment to clarify the abutting component of the ABC model.

5.8 Chapter Summary

A series of four experiments was carried out in the present chapter and an improved model for the vertical-horizontal illusion was proposed, consisting of three components. The effects of **anisotropy**, **abutting** and **bisection** were found to affect the perceived size of lines by +7%, +9% and -7% respectively. Although abutting needs to be explored further, the **ABC** model is able to provide a coherent qualitative explanation for the variations in perceived size of lines in various configurations.

Chapter 6 - The Neural correlates of the Helmholtz's squares illusion

The aim of this chapter is to determine whether the resulting non-veridical visual experience arising from the Helmholtz's squares illusion can be matched to analogous patterns of brain activity in primary visual cortex, V1, using functional Magnetic Resonance Imaging.

Introduction In the present chapter we are proceeding on to a consideration of the neural basis of an illusion of filled extent, namely the Helmholtz's squares illusion. As previously mentioned in Chapter 1, in the Helmholtz's squares illusion (1867) a square filled with horizontal lines would look taller than a square filled with vertical lines and a square filled with vertical lines would look wider than the one filled with horizontal ones (see Figure 6.1). Similarly to the Oppel-Kundt illusion, perceptual expansion only occurs orthogonally to the orientation of the lines, in a single dimension, causing the Helmholtz's *squares* to be perceived as *rectangles* instead.

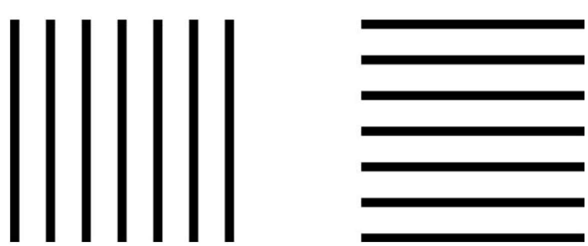


Figure 6.1 The original Helmholtz's squares; the vertically-striped square (left) looks wider whereas the horizontally-striped square look taller (right).

Given the lack of empirical evidence from Helmholtz, a few teams of researchers focused on investigating this illusion of filled extent. Yoshioka et al. (2004) measured the apparent size of a square filled with horizontal or vertical lines and in accordance with Helmholtz's original theory, subjects perceived the horizontal square as being taller than the vertical square and the vertical square being wider than the horizontal. Additionally, Imai (1982) reported that a horizontally striped square was perceived 14.0% taller than its actual size and a vertically striped square 4.06% wider than its actual size. Noteworthy, is the asymmetry of the Helmholtz's square effect which favours the vertical dimension and serves as an indication that another illusion may be present. It is believed that the vertical-horizontal illusion which induces an apparent increase in the size of a vertical line compared to a horizontal line of identical size is the cause of this asymmetry.

Thompson and Mikellidou (2011) investigated the effect of the stimulus duty cycle on the size of the Helmholtz's squares illusion. The duty cycle is described as the fraction of each cycle which is white; thus a duty cycle of 0.9 will have a narrow dark bar that occupies 10% of each cycle of the pattern. Results showed that when two patterns have the same height, the horizontally-striped pattern was perceived as 4.1 – 10.1% taller and a vertically-striped square was perceived as 1.3 – 6.5% wider, depending on the duty cycle. These results confirmed and quantified the Helmholtz's square illusion and showed that the illusory percept is greater with smaller duty cycles (i.e. narrow black lines on a white background).

Interestingly, results generated by Thompson and Mikellidou (2011) using 3D cylinders showed that the Helmholtz's squares illusion decreased as the size of the cylinders increased. This result is in accordance with Long and Murtagh (1984) and Obonai (1954) who found that the effect of another illusion of filled extent, namely the Oppel-Kundt illusion, diminished with larger stimuli.

With regards to brain activity induced by visual experience, it has been conventionally hypothesised that activity in early visual processing brain areas such as V1 corresponds to physical input from the retina, whereas activity in higher visual areas such as V4 and V5 corresponds to perceptual experience. Despite the fact that Fischer et al. (2011) emphasized that object representation in V1 is more accurately predicted by retinal rather than percept-based coordinates, some unique information on perceived position was also evident. In addition, both Murray et al. (2006) and Sperandio, Chouinard and Goodale (2012) challenged this previously well-accepted notion by demonstrating that V1 is not strictly retinotopic.

Murray et al. (2006) have shown that the cortical area activated in V1 by an object in the visual field varies according to perceived angular size. In their study, a distant object appearing to occupy a larger portion of the visual field activated a larger part of V1 compared to an object of identical angular size which appeared to be nearer and thus smaller. Additionally, Sperandio, Chouinard and Goodale (2012) have shown that as the size of an afterimage increased, activation in V1 became more eccentric, potentially playing a very important role in size constancy. This study was carried out by creating an afterimage projected on a screen placed at various distances, while keeping the retinal size of the stimulus constant.

Following evidence that the topographic map in V1 can be dynamically changed in accordance with the perceived size of an object (Sterzer &Rees, 2006) Chapter 6 consists of a single experiment separated into two parts. The aim of the psychophysics part of Experiment 12 is to recruit a sample of participants who experience a large Helmholtz's squares illusion such that they perceive a minimum of 7% difference between the width of a vertically and a horizontally striped square of identical dimensions. Subsequently, these participants will take part in the second part of Experiment 12 which will be carried out in an fMRI scanner to determine whether activity in V1 can be linked to perceptual experience. Similarly to Schwarzkopf, Song and Rees (2011), taking into consideration morphological variations between individuals a retinotopic map will be constructed for each individual using the conventional rotating wedge and expanding ring sections of a high contrast, moving, dashboard pattern (DeYoe et al., 1996; Dumoulin et al., 2003; Engel et al., 1997; Engel et al., 1994; Sereno et al., 1995) and this will be used to predict the location of brain activity induced by specific contrasts.

6.1 Experiment 12 - Psychophysics experiment

6.1.1 Rationale

The aim of this experiment is to use the ideal Helmholtz's squares pair as defined by Thompson and Mikellidou (2011) which will induce the greatest illusory percept and recruit participants for the neuroimaging part of Experiment 12. Observers are asked to compare the apparent width of two squares; a horizontally-striped and a vertically-striped one. We manipulated the width of the horizontally-striped square and this was compared against the width of a standard vertically-striped square. Participants chosen to take part in the neuroimaging part of the study experienced a Helmholtz's squares effect greater than 7% in this behavioural experiment.

6.1.2 Method

Two conditions were interleaved; in the control a standard horizontally-striped square 6.6° long was compared with one of seven comparator stimuli composing of another horizontally-striped square, varying in size from slightly smaller to slightly longer than the standard. The deviations from the standard length were -0.9, -0.6, -0.3, 0, 0.3, 0.6, 0.9 degrees, with the length of the variable stimulus ranging between 5.7° to 7.5°. For the other condition, the width of a variable horizontally-striped square was compared against a standard vertically-striped square of width 6.6°. Figure 6.2 below illustrates the stimuli used in this experiment.

Stimuli were positioned one next to the other approximately 3° away from the centre and presented simultaneously for 600ms. The luminance of the stimuli was 20cd/m² for 300ms, followed by 0cd/m² for 300ms, whereas the luminance of the background constant at 10cd/m². Consequently, the stimuli and background were equiluminant across time to avoid adaptation. Each square consisted of seven lines, the duty cycle was 0.1 and the spatial frequency was 1.30 cycles/degree. An example of the stimuli used in shown in Figure 6.2 below.

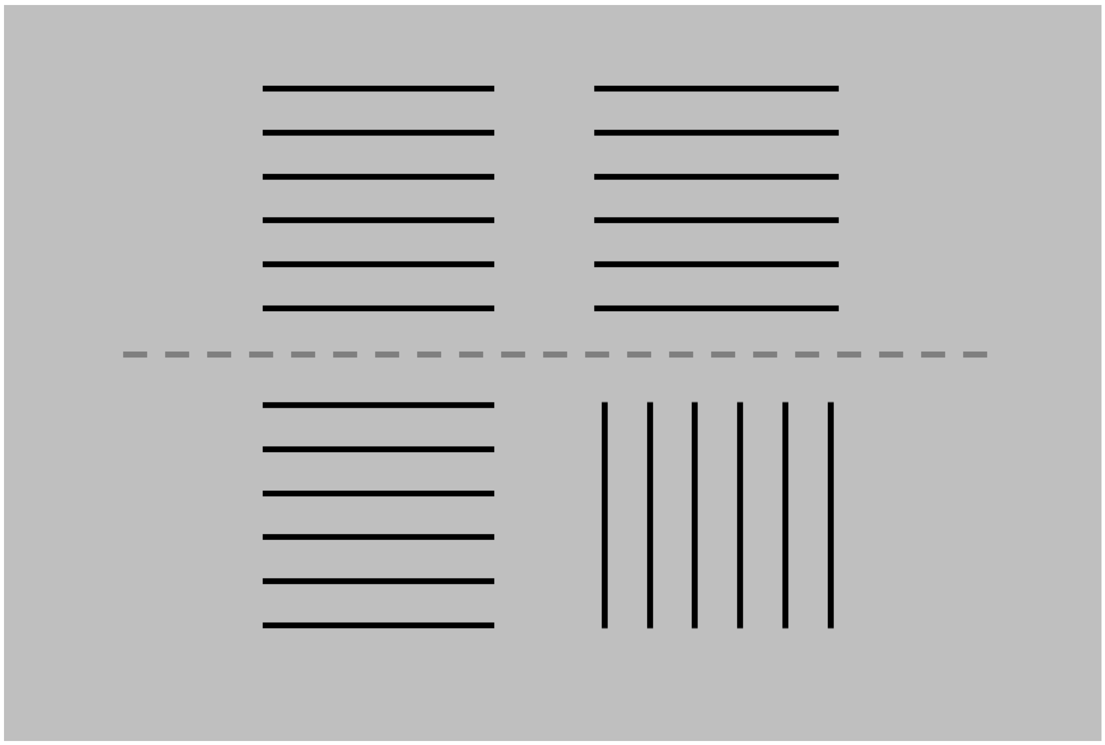


Figure 6.2 Stimuli used in the Helmholtz’s squares illusion psychophysics experiment. The variable stimulus was always a horizontally-striped square compared to either another horizontally-striped square or a vertically-striped one. Despite the colour of the stimuli in this image being black, in the experiment it was alternating between white (20cd/m²) for 300ms and black (0cd/m²) for 300ms on a grey background.

Each of twenty-two naïve observers (eighteen female) undertook 1400 trials; two pairs of stimuli each presented a hundred times for seven variable stimulus sizes. Participants were asked to indicate the wider square using a response box and the control condition was used to evaluate whether or not participants were able to carry out the task. The timeline for the experiment is shown in Figure 6.3.

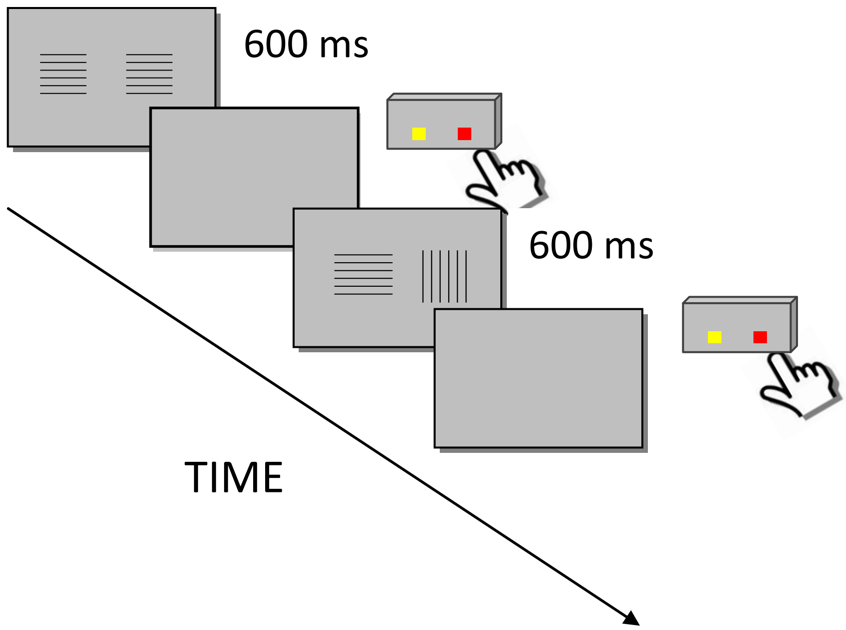


Figure 6.3 Timeline of Experiment 12 – Psychophysics showing two trials. Presentation of stimulus pairs was random throughout the experiment.

6.1.3 Results

Comparisons between a horizontally-striped square and the two conditions were made so that psychometric functions could be determined and points of subjective equality (PSEs) calculated for all participants. Moreover, 95% confidence intervals were calculated. Figure 6.4 depicts the psychometric functions generated for a single participant for both conditions. The PSE for each curve lies at the crossing point between itself and the grey dotted line. The functions for the control condition and the comparison between a vertically-striped to a horizontally-striped square are shown in grey and light purple colour respectively. The PSE for the former condition is 6.62° confirming that participants could accurately carry out a comparison between two horizontally-striped squares. On the other hand, the PSE 7.16° for the latter condition is shallower and shows a right shift.

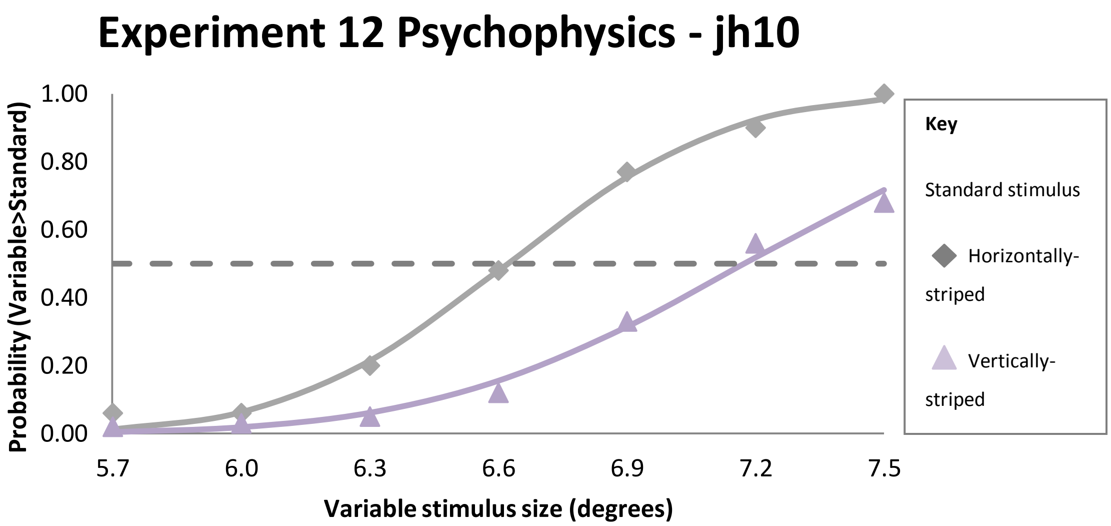


Figure 6.4 Psychometric functions for a single participant from Experiment 12-Psychophysics. Error bars show 95% confidence intervals.

Participant	Control	HV	% Difference
jx56	6.56	7.38	12.5
ce51	6.57	7.17	9.16
enb50	6.59	7.09	7.67
fl59	6.62	7.79	17.8
ejt51	6.61	7.16	8.32
va55	6.59	7.13	8.13
ytc50	6.63	7.34	10.7
ag86	6.62	7.29	10.1
ejp52	6.61	7.12	7.64
ms10	6.57	7.29	10.8
hsme50	6.62	7.23	9.21
jh10	6.62	7.17	8.33
wyc50	6.63	7.59	14.5

Table 6.1 Summary of results from Experiment 12-Psychophysics (N=13).

Thirteen participants (ten female) who perceived the width of a vertically-striped square at least 7% wider than that of a horizontally-striped square of identical dimensions were chosen to take part in the subsequent neuroimaging experiment. Results are illustrated in Figure 6.5 below, showing an average overestimation of the perceived with of a vertically-striped square by 10.4%.

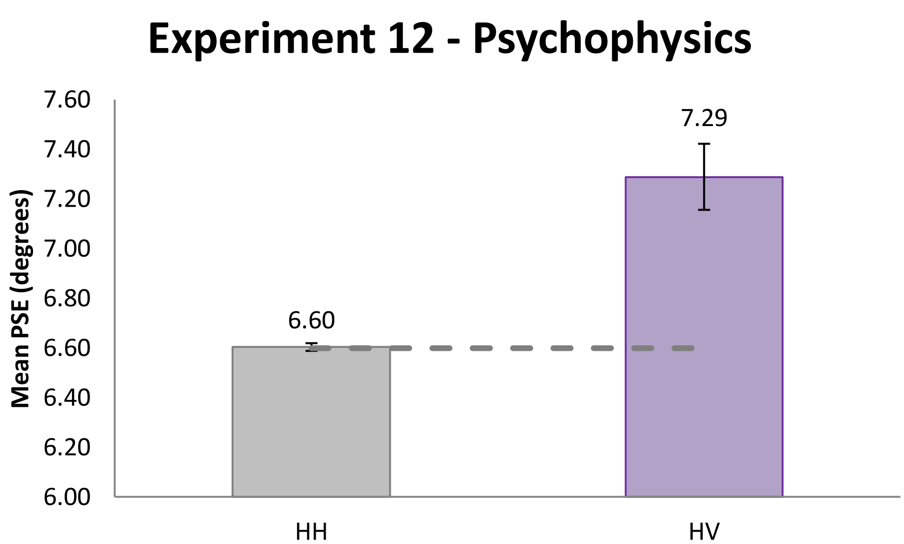


Figure 6.5 Results from the first part of Experiment 12, showing a significant overestimation of the perceived width of a vertically-striped square by approximately 10% (N=13). Error bars show 95% confidence intervals.

A z-test showed a significant increase in the perceived width of a vertically-striped square, when this was compared to a horizontally-striped square of identical dimensions (*p<.01*).

6.1.4 Discussion

The aim of this experiment was to use the ideal Helmholtz's squares pair as defined by Thompson and Mikellidou (2011) to recruit participants for the neuroimaging part of Experiment 12. We only investigated the Helmholtz's squares illusion in the horizontal dimension by manipulating the width of a horizontally-striped square to match that of vertically-striped square and determine the point of subjective equality for each specific participant.

Initially twenty-two observers took part in the experiment but only thirteen were chosen to participate in the subsequent neuroimaging part of the experiment. The selection was carried out based on the size of the Helmholtz's squares illusion experienced by each observer, which had to be more than 7%, as we wanted to increase the chances of brain activity induced by the illusory percept. Individual PSEs were calculated for each participant and the mean PSE for the thirteen participants was found to be 7.29° demonstrating an average effect of 10.4%.

6.2 Experiment 12 - Neuroimaging experiment

6.2.1 Rationale

The aim of this experiment is to use the ideal Helmholtz's squares pair as defined by Thompson and Mikellidou (2011) which will induce the greatest illusory percept and determine whether activity in primary visual cortex reflected the illusory percept or physical dimensions of the stimuli. Observers recruited from the psychophysics part of Experiment 12 will be viewing pairs of squares consisting of vertical and horizontal stripes either *physically* identical or *perceptually* identical *in size*, in a functional Magnetic Resonance Imaging scanner. When squares were *perceptually* identical we manipulated the width of the horizontally-striped square to match perceptually that of the vertically-striped square. Concurrently, observers were asked to carry out a central fixation task in order to avoid any eye movements, which could potentially abolish any effects we are aiming to measure.

6.2.2 Method

The main principle behind the fMRI technique is the association of cerebral blood flow with neuronal activation; an increase in blood flow is indicative of an active brain region. The basic measure of fMRI is the blood-oxygen-level-dependent (BOLD) contrast which is calculated by comparing the change in magnetization between oxygenated and deoxygenated blood. Specifically, following activation in a specific brain area, there is a decrease in oxygenated blood which is compensated by an increase in cerebral blood flow to that area (Logothetis & Wandell, 2004). In the presence of a large magnetic field such as the one induced by the MRI scanner, deoxyhaemoglobin present in deoxygenated blood induces field inhomogeneities, in terms of cerebral blood flow, which are the source of BOLD contrast and can be detected in the MRI signal (Chen & Ogawa, 2000).

Participants

Eight observers (ages 18-25) were recruited based on their performance on the psychophysics experiment described previously in the present Chapter. Experimental protocols were approved by the York Neuroimaging Centre (YNiC) Science and Ethics Committee.

Scanning

Functional and structural MRI data were acquired using an 8-channel, phase-array head coil on a GE 3-Tesla Signa HD Excite scanner at the York Neuroimaging Centre, University of York.

Structural data: Multi-average, whole-head T1-weighted anatomical volumes were acquired for each participant (TR=7.8ms, TE= 3ms, TI= 450ms, FOV=290x290x176, 256x256x176 matrix, flip angle= 20°, 1.13 x 1.13 x 1.0 mm^3). The sequences used was 3DFSPGR (on the GE Signa Console); imaging parameters provided good gray-white contrast allowing the segmentation of anatomical data into gray and white matter, and subsequent visualization in volume and inflated cortical views.

Functional data: Gradient recalled echo pulse sequences were used to measure T2* BOLD data (TR=2000ms, TE=30ms, FOV=256mm, 128x128 matrix, 26 contiguous slices with 2.5mm slice thickness). Images were read out using an EPI sequence. Magnetization was allowed to reach a steady state by discarding the first five volumes, an automated feature on the scanner used.

Data analysis

Data were analyzed using publicly available tools (http://white.stanford.edu/software/). Most analysis was performed in MATLAB (The Mathworks, Natick, MA, USA) using the mrVista toolbox.

Anatomical data: Individual hemispheres of acquired anatomical volumes were segmented into white and gray matter volumes using the Freesurfer4 "autorecon" script (http://surfer.nmr.mgh.harvard.edu) followed by manual topology checking using mrGray, part of the Stanford "VISTA" toolbox. Cortical surfaces (gray matter) of each subject were constructed and rendered in three dimensions from this segmentation for data visualization using mrMesh, a visualization tool available in the "VISTA" toolbox (Wandell, Chial, & Backus 2000). Functional volumes were motion corrected within each run and across runs using FSL's MCFLIRT Images were also corrected for spatial inhomogeneity. The EPI volumes were initially aligned to individual high-resolution anatomical volumes manually and subsequent alignments were refined with an automated procedure. This procedure allowed the parameters derived from the analysis of the functional data to be visualized on the inflated cortical surface.

Functional data (Retinotopies): Functional images were corrected for spatial inhomogeneity (mrInitRet). Motion correction was achieved using FSL's MCFLIRT (Jenkinson et al. 2002). Functional time series were high-pass filtered to remove baseline drifts. Percent signal change was computed for each voxel by dividing by and subtracting its mean amplitude value over time. The strength of stimulus-synchronized activity at each voxel was assessed using coherence. Coherence (C) is defined as the Fourier amplitude of the BOLD signal at the stimulus fundamental frequency ($f0 = 8$) divided by the sum of amplitudes of frequency bins around the fundamental ($C = A(f0) / \Sigma (A(f)^2)$). The visual field representation of each voxel in cortex was derived by using the Fourier phase at the stimulus frequency, corresponding to the relative delay of the cyclical response (Engel et al., 1997; Wandell et al., 2005). Functional data were averaged across scans for four repeated scans within a session for each individual. Functional data were manually aligned to the high resolution anatomical volume and visualized in 3D.

Functional data (Experimental): For the Helmholtz's squares data standard general linear model (GLM) analyses were applied to spatially unsmoothed data using mrVista software.

6.2.3 Stimuli

Computer-generated visual stimuli were presented using a LCD projector (Dukane ImagePro 8942) and were rear projected onto an acrylic screen situated in the bore of the MRI scanner, behind the participant's head. Participants viewed the stimuli via a mirror mounted on the head coil.

Standard retinotopic mapping stimuli were used: a rotating wedge to map polar angle, and an expanding annulus to map eccentricity (DeYoe et al., 1996; Dumoulin et al., 2003; Engel et al., 1997; Engel et al., 1994; Sereno et al., 1995). Stimuli were generated with MATLAB and controlled by the ViSaGe Visual Stimulus Generator (Cambridge Research Systems, UK). Rings and wedges stimuli were unmasked portions of a 100% contrast radial checkerboard with 8 rings and 24 radial segments on a mean gray background. Contrast reversal rate was 6 Hz. Each scan contained either the expanding annulus or rotating wedge. A red fixation cross was placed in the centre of the stimulus. The wedge stimulus was a 90 deg wedge of the flickering checkerboard, rotating about the centre of the screen. The ring stimulus comprised three rings of the checkerboard which increased in angular extent (to a maximum of 15 deg) as it moved out from the centre of the visual field; each ring was replaced by a new ring at the centre as the existing ring approached the edge of the visual field. Both the wedge and ring stimuli had a period of 36 seconds and were repeated for 7 full cycles.

To determine whether regions of the early visual cortex have a representation for perceptual differences two experimental runs were carried out during a single session for each participant. In each run, two conditions were used; in one the Helmholtz's squares pair consisting of a horizontally-striped and a vertically-striped square of identical dimensions (6.6x6.6°) were presented simultaneously. In the other condition, the Helmholtz's squares pair consisted of a horizontally-striped and a vertically-striped square, with the width of the former adjusted to be *perceptually* identical in width to that of the latter. Each square consisted of seven lines, the duty cycle was 0.1 and the spatial frequency was 1.30 cycles/degree. The luminance of the stimuli alternated between 20cd/m² for 0.3s, followed by 0cd/m² for 0.3s for the 9s block duration, whereas the luminance of the background was kept constant at 10 cd/m². Consequently, the stimuli and background were equiluminant across time.

Two runs were carried out for each participant and within a single run, each one of the two conditions was repeated sixteen times. Both runs were fully counterbalanced, so that for each condition the horizontally-striped square was presented equal times on the left and the right visual field. For each one of the eight participants, the width of the horizontally-striped square was determined by the individual PSEs generated in the previously described psychophysics experiment and it matched *perceptually* that of the vertically-striped square. These two conditions were incorporated into a pseudo-randomised block design and duration of condition presentation was 9s followed by an empty screen for 9s.

Participants were asked to fixate on a small central square and count the number of times the position of a randomly moving smaller red square was at twelve o'clock (see Figure 6.6). Following the end of each one of the two sessions, participants were asked to indicate this number and accuracy was calculated for each individual. Considering the duration and the high-demand of the task it was decided that a 70% accuracy or above was satisfactory to serve the purposes of our study. This central fixation task was used for two reasons; primarily we wanted to ensure that observers would stay awake and secondly we wanted the two squares to fall on exactly the same position on either side of the fovea, for the whole experimental session.

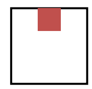


Figure 6.6 The fixation task used in the Helmholtz's squares illusion neuroimaging experiment.

6.2.4 Contrasts and Predictions

One control and four other contrasts were carried out and these are displayed and described thoroughly in due course. The aim of the control condition was to determine the stimulus representation in V1. The stimuli with a ***** (star) next to them, are physically wider than the rest and for each participant the size of these was determined by the individual mean PSE generated in the psychophysics experiment. For the 'Illusion' and 'Perceptually Matched' contrasts described subsequently, it is important to note that differential activity due to perceived height might be evident when contrasting a vertically-striped to a horizontally-striped square within the same hemisphere. However, since we did not measure or control any of the stimuli used in the vertical dimension, predictions are only going to be made for the horizontal dimension. Subsequent images will show brain activity in two colours; orange to code for the 'active' condition greater than the 'control' and blue for the 'control' greater than the 'active'.

Stimulus Representation

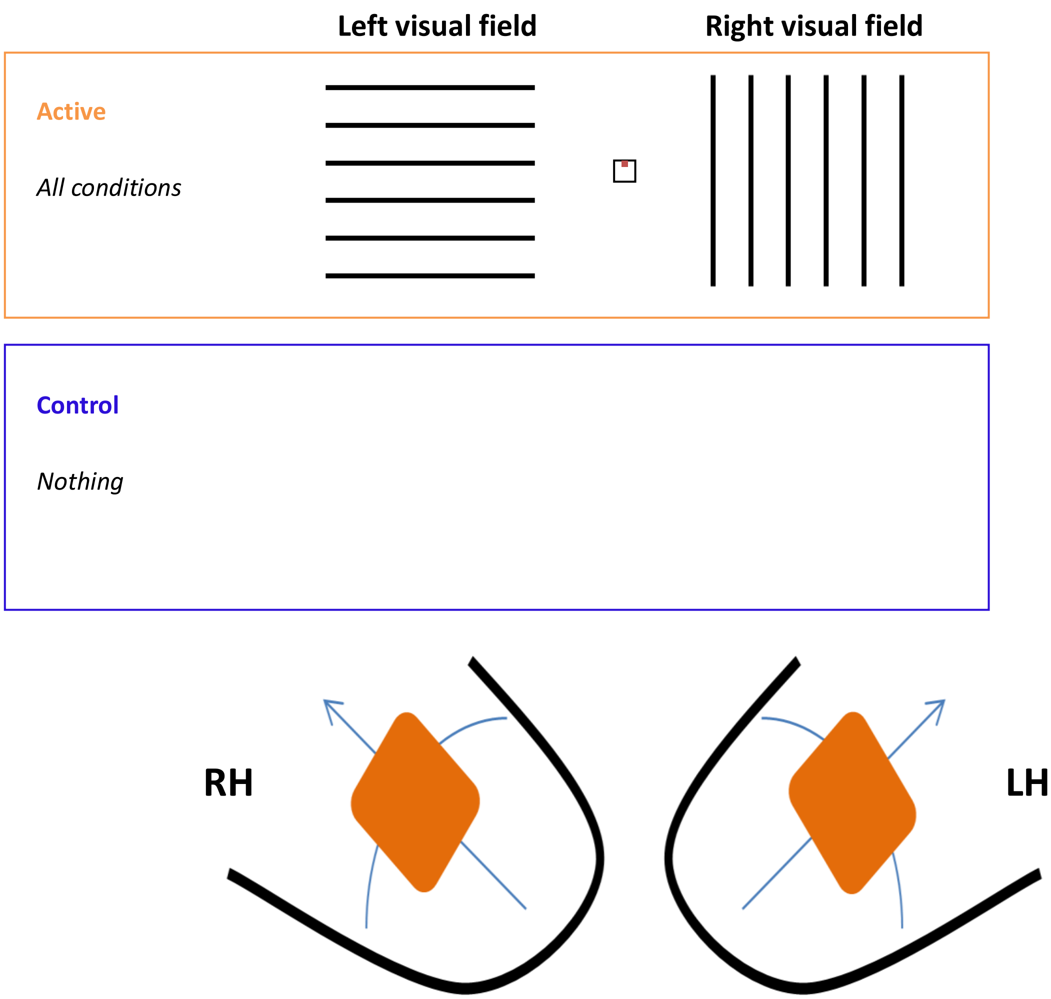


Figure 6.7 A schematic of the predicted activations for the Stimulus representation contrast. With participants carrying out the central fixation task, the vertically-striped square is projected onto the left hemisphere and the horizontally-striped square is projected onto the right hemisphere of the brain.

The stimuli presented to the right visual field will be projected onto the left hemisphere. In this contrast we expect to determine the stimulus representation in the left V1, consequently we predict the appearance of an orange square in the left hemisphere.

The stimuli presented to the left visual field will be projected onto the right hemisphere. In this contrast we expect to determine the stimulus representation in the right V1, consequently we predict the appearance of an orange square in the right hemisphere

Illusion

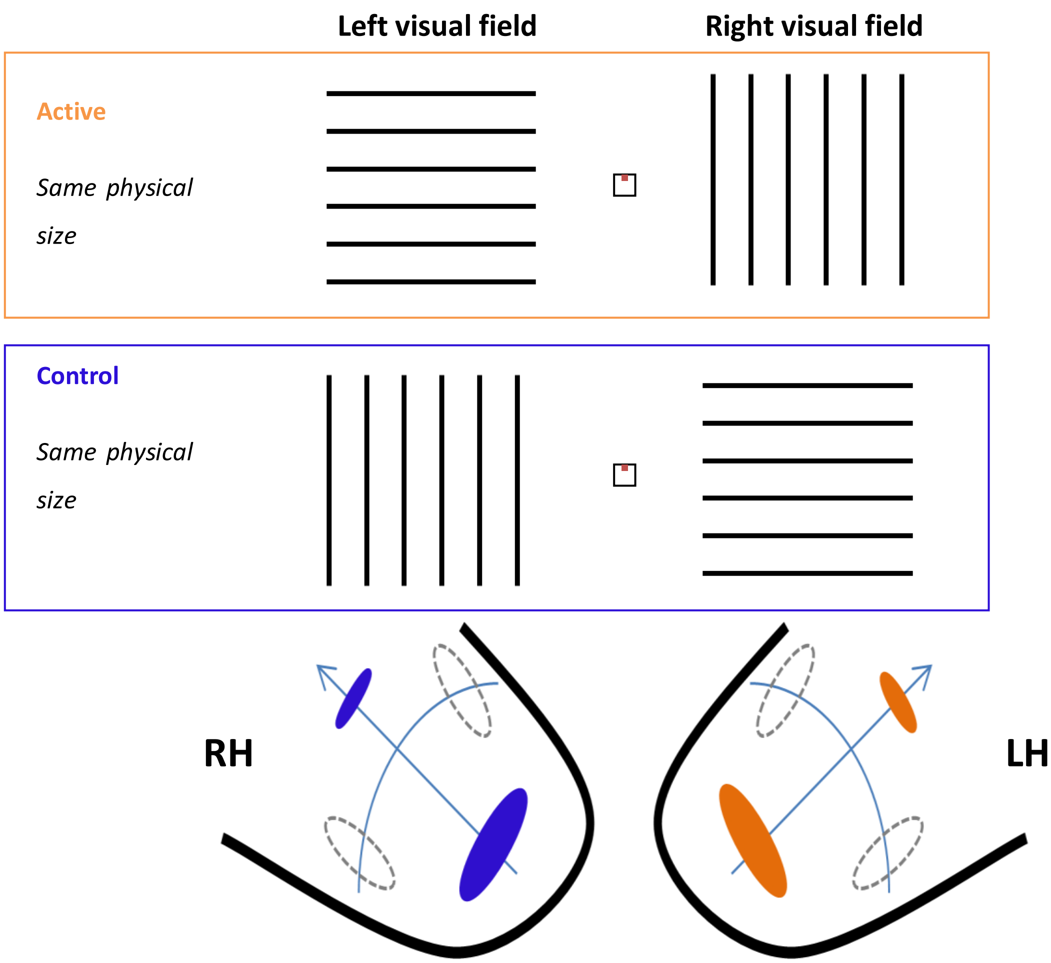


Figure 6.8 A schematic of the predicted activations for the Illusion contrast. With participants carrying out the central fixation task, stimuli in the right visual field are projected onto the left hemisphere and stimuli in the left visual field projected onto the right hemisphere of the brain.

Since the stimuli to be contrasted in this case have identical physical dimensions, we expect that any activity observed in V1 would be solely due to *perceptual* differences and it would provide evidence that V1 registers *perceptual* differences between visual stimuli.

The stimuli presented to the right visual field, a vertically-striped square for the active condition and a horizontally-striped square for the control condition of identical dimensions will be projected onto the left hemisphere. Since the vertically-striped square (active) is *perceptually* wider than the horizontally-striped square (control), we predict the appearance of orange clusters along the representation of horizontal meridian in the left hemisphere.

The stimuli presented to the left visual field, a horizontally-striped square for the active condition and a vertically-striped square for the control condition of identical dimensions will be projected onto the right hemisphere. Since the vertically-striped square (control) is *perceptually* wider than the horizontally-striped square (control), we predict the appearance of blue clusters along the representation of the horizontal meridian in the right hemisphere.

The grey dotted clusters nearer the representations of the vertical meridian in either hemisphere represent brain activity which might arise due to perceived differences in height between a vertically-striped and a horizontally-striped square with the former appearing taller than the latter.

Physical differences in width (presented in left hemifield)

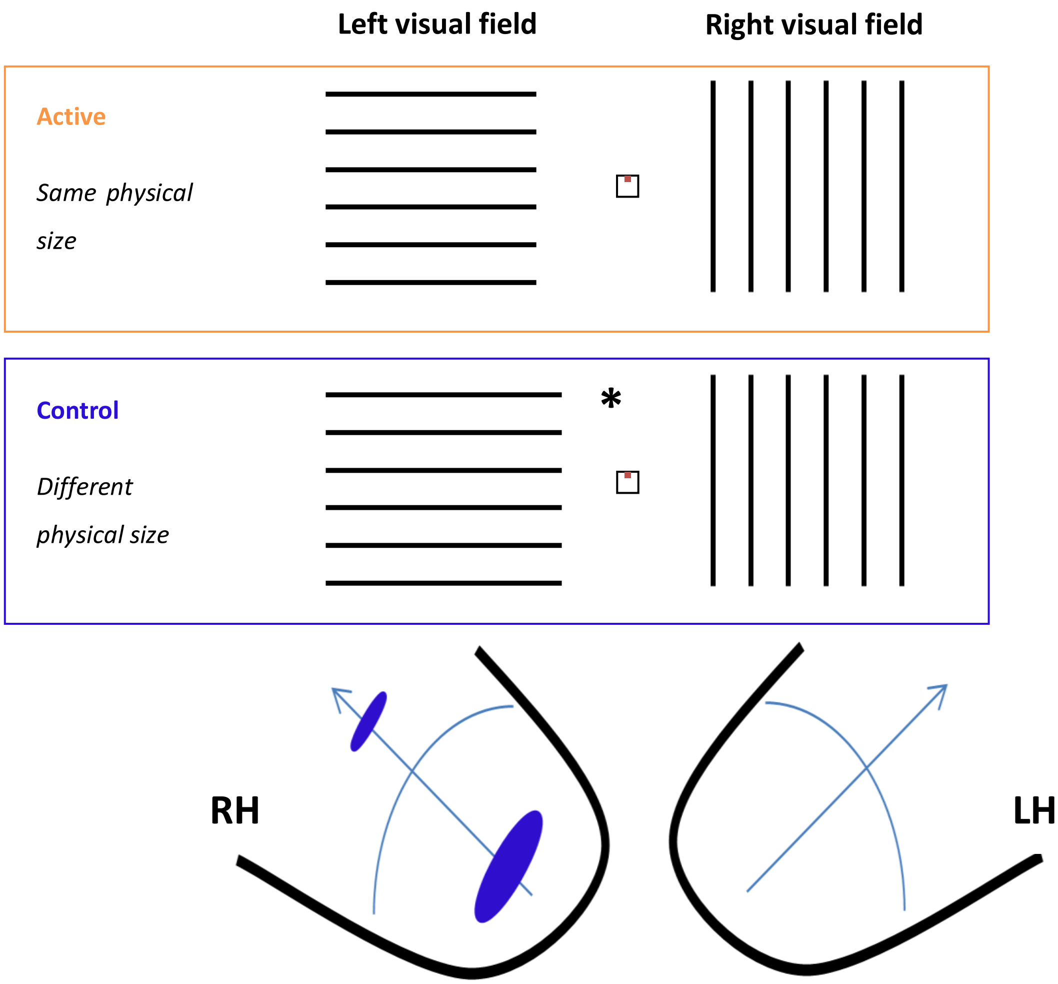


Figure 6.9 A schematic of the predicted activations for the Physical differences in width (presented in the left hemifield) contrast. With participants carrying out the central fixation task, stimuli in the right visual field are projected onto the left hemisphere and stimuli in the left visual field projected onto the right hemisphere of the brain.

The stimuli presented to the right visual field, two identically vertically-striped squares for both the active condition and the control condition will be projected onto the left hemisphere (LH). Since the stimuli are identical in both size and orientation we expect no difference in activity between the two conditions in the left hemisphere for this specific contrast.

The stimuli presented to the left visual field, two horizontally-striped squares for both the active and the control conditions will be projected onto the right hemisphere. Since the horizontally-striped square in the 'control' condition is physically wider than the horizontally-striped square in the 'active' condition we predict the appearance of blue clusters along the representation of the horizontal meridian in the right hemisphere. Such activity will be supporting the notion of V1 registering *physical* differences between visual stimuli.

Physical differences in width (presented in right hemifield)

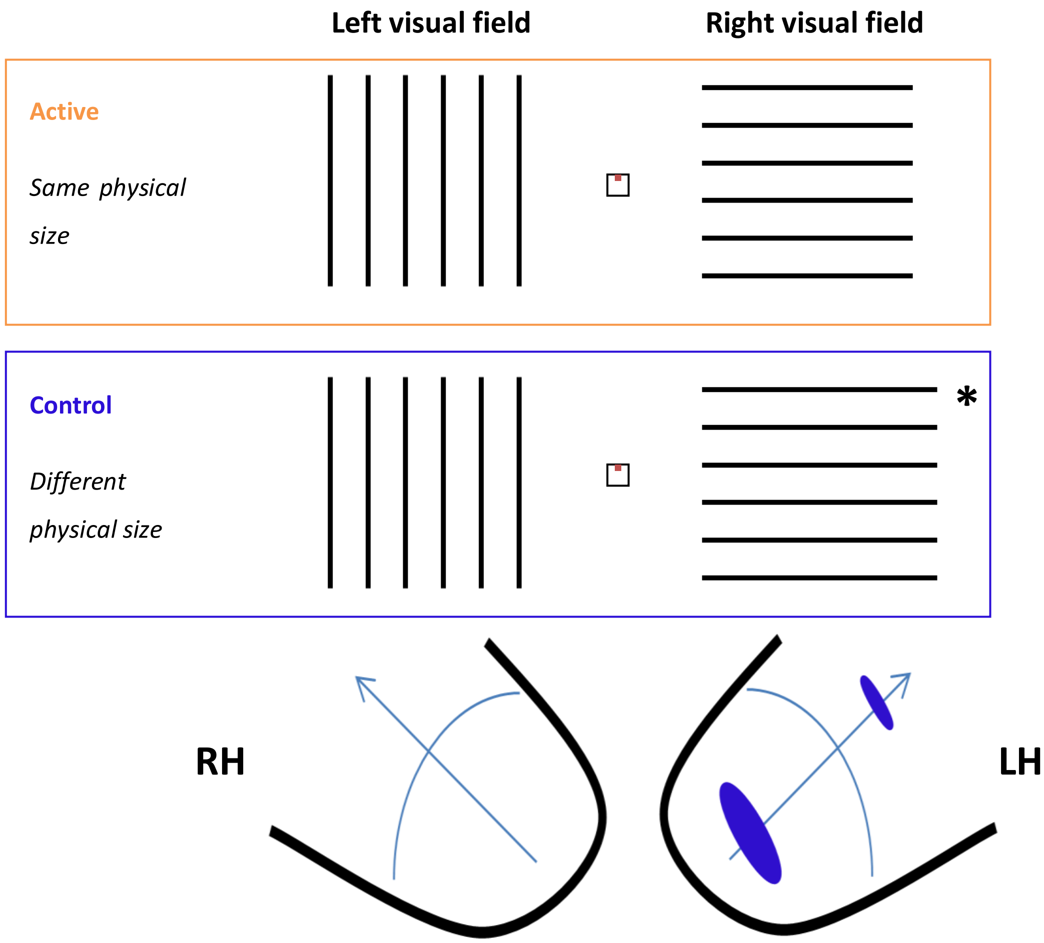


Figure 6.10 A schematic of the predicted activations for the Physical differences in width (presented in the right hemifield) contrast. With participants carrying out the central fixation task, stimuli in the right visual field are projected onto the left hemisphere and stimuli in the left visual field projected onto the right hemisphere of the brain.

The stimuli presented to the right visual field, two horizontally-striped squares for both the active and the control conditions will be projected onto the left hemisphere. Since the horizontally-striped square in the 'control' condition is physically wider than the horizontally-striped square in the 'active' condition we predict the appearance of blue clusters along the representation of the horizontal meridian in the left hemisphere. Such activity will be supporting the notion of V1 registering *physical* differences between visual stimuli.

The stimuli presented to the left visual field, two identically vertically-striped squares for both the active condition and the control condition will be projected onto the right hemisphere (RH). Since the stimuli are identical in both size and orientation we expect no difference in activity between the two conditions in the right hemisphere for this specific contrast.

Perceptually matched

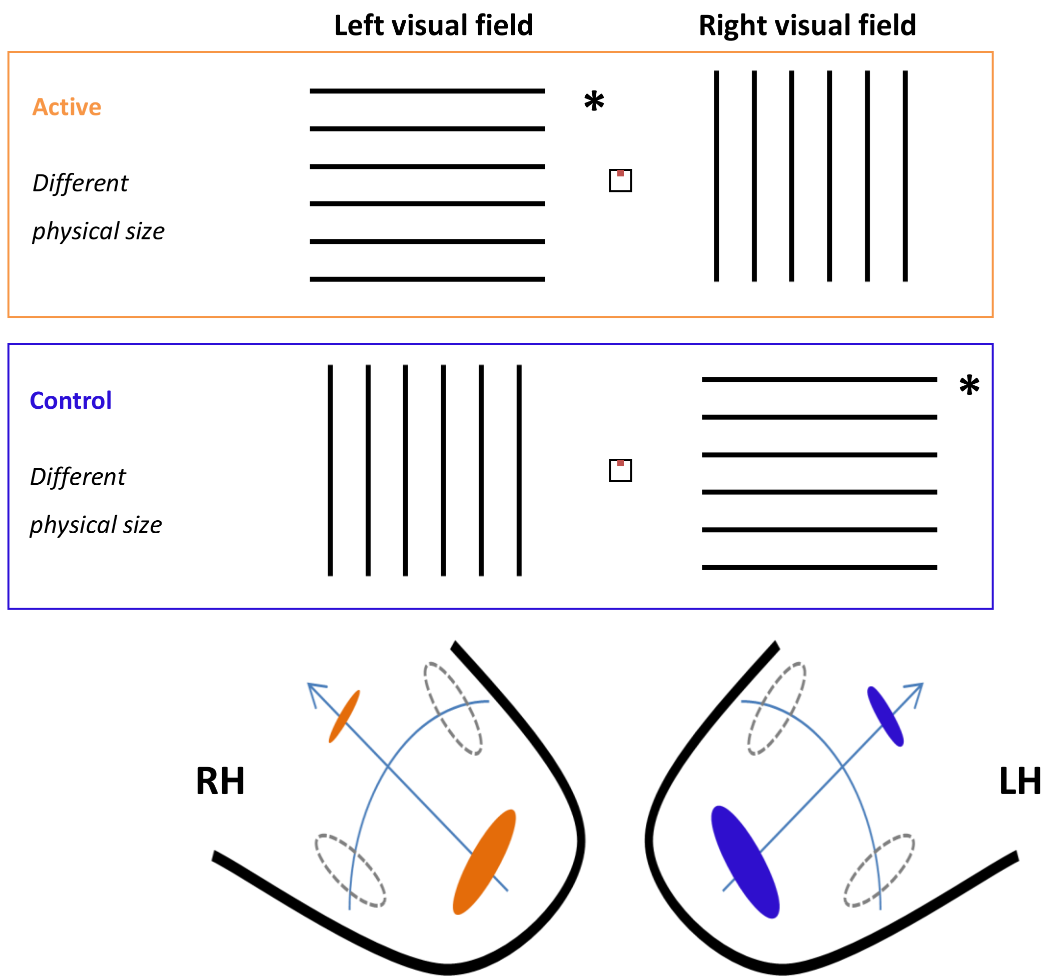


Figure 6.11 A schematic of the predicted activations for the Perceptually matched contrast. With participants carrying out the central fixation task, stimuli in the right visual field are projected onto the left hemisphere and stimuli in the left visual field projected onto the right hemisphere of the brain.

The stimuli presented to the right visual field, a vertically-striped square for the active condition and a horizontally-striped square for the control condition will be projected onto the left hemisphere. Since the horizontally-striped square (control) is physically wider than the vertically-striped square (active), we predict the appearance of blue blobs at the representation of the horizontal meridian in the left hemisphere. But, this pattern should only emerge if V1 registers *physical* and not perceptual differences in width. The alternative is that no clusters will be observed, consistent with V1 reflecting the illusion, registering perceptual differences.

The stimuli presented to the left visual field, a horizontally-striped square for the active condition and a vertically-striped square for the control condition will be projected onto the right hemisphere. Since the horizontally-striped square (active) is physically wider than the vertically-striped square (control), we predict the appearance of orange clusters at the representation of the horizontal meridian in the right hemisphere. Again, this pattern should only emerge if V1 registers *physical* and not perceptual differences in width. The alternative is that no clusters will be observed, consistent with V1 reflecting the illusion, registering perceptual differences.

The grey dotted shapes along the vertical meridian in either hemisphere represent brain activity which might arise due to perceived differences in height between a vertically-striped and a horizontally-striped square with the former appearing taller than the latter.

6.2.5 Results

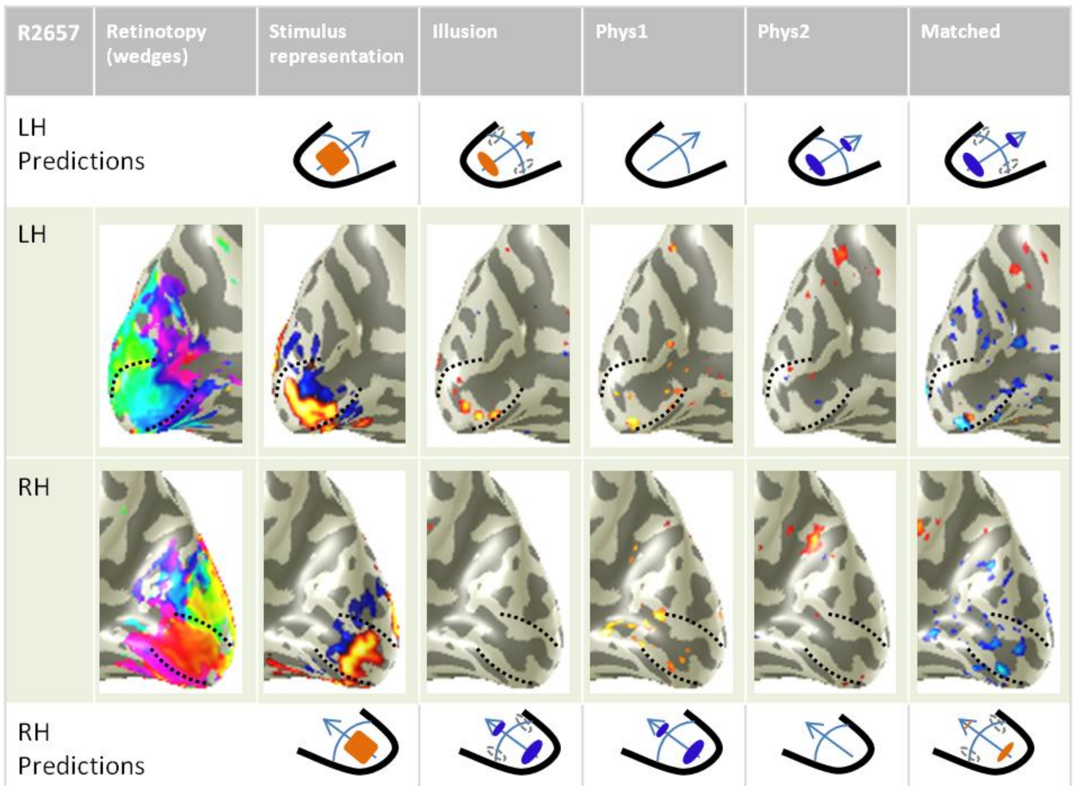
Neuroimaging data for eight observers are illustrated in subsequent figures. Four participants failed to attend the neuroimaging session and data from a single participant were discarded because different imaging parameters were used.

Table 6.2 below illustrates data for eight participants; the mean PSE was calculated to 7.29° and the effect of the Helmholtz's squares illusion was found to be 10.6%. Participants' accuracy for the fixation task ranged between 70-97% with an average of 87%.

Participant	Control PSE	HV PSE	% Difference
R3106	6.56	7.38	12.5
R3109	6.57	7.17	9.16
R2657	6.59	7.09	7.67
R3111	6.62	7.79	17.8
R3113	6.61	7.16	8.32
R3110	6.59	7.13	8.13
R3107	6.63	7.34	10.7
R3112	6.62	7.29	10.1

Table 6.2 Summary of results from the Experiment 12- Psychophysics (N=8).

Table 6.3 below illustrates prediction sketches as well as cortical surface meshes for both hemispheres from participant R2657. Predictions for the left hemisphere (LH) are shown in the first row, followed by left hemisphere data in the second row, right hemisphere (RH) data in the third row and right hemisphere predictions in the fourth row. Starting from the left, the retinotopic mapping data from the wedges stimuli are shown in the second column, followed by the stimulus representation, 'Illusion', 'Physical differences in width-presented in left hemifield' (Phys1), 'Physical differences in width-presented in right hemifield' (Phys2) and 'Perceptually Matched' contrasts. Subsequent tables illustrating data for the remaining seven participants will follow the same structure.



Thresholds ±10 ±2 ±3 ±2 ±2

Table 6.3 Retinotopic maps and cortical mesh surfaces for each contrast for participant R2657.

The black dotted lines in each cortical surface mesh represent the lower and upper vertical meridians of area V1 as defined by the polar angle maps (see the first column in each table) generated using the rotating wedges stimuli. The average percentage accuracy in the fixation task for this participant for the two runs was 91%.

The stimulus representation contrast (second column in Table 6.3) shows the position of the Helmholtz's squares in V1 for both hemispheres. The 'Illusion' contrast (third column) in LH partly satisfies our prediction showing activation along the horizontal meridian, whereas in RH the absence of activation is in disagreement with the predictions. The prediction for the 'Physical differences in width-presented in left hemifield' contrast (fourth column) in both hemispheres is not satisfied as the activation does not agree with the prediction sketches. The cortical surface mesh for the 'Physical differences in width-presented in right hemifield' contrast (fifth column) in LH shows weak activation (blue) along the edges of the stimulus representation and no activation in RH. Finally, results for the 'Perceptually Matched' contrast (sixth column) in LH agree with the prediction that V1 registers physical differences between stimuli whereas in RH no evidence of activation due to physical differences in the horizontal dimension is evident. However, interestingly we observe activation in the lower and upper vertical meridians in both hemispheres possibly arising due to *perceived* differences in height between the two squares as previously described.

Table 6.4 below illustrates prediction sketches as well as cortical surface meshes of both hemispheres for participant R3106. The average percentage accuracy in the fixation task for this participant for the two runs was 90%.

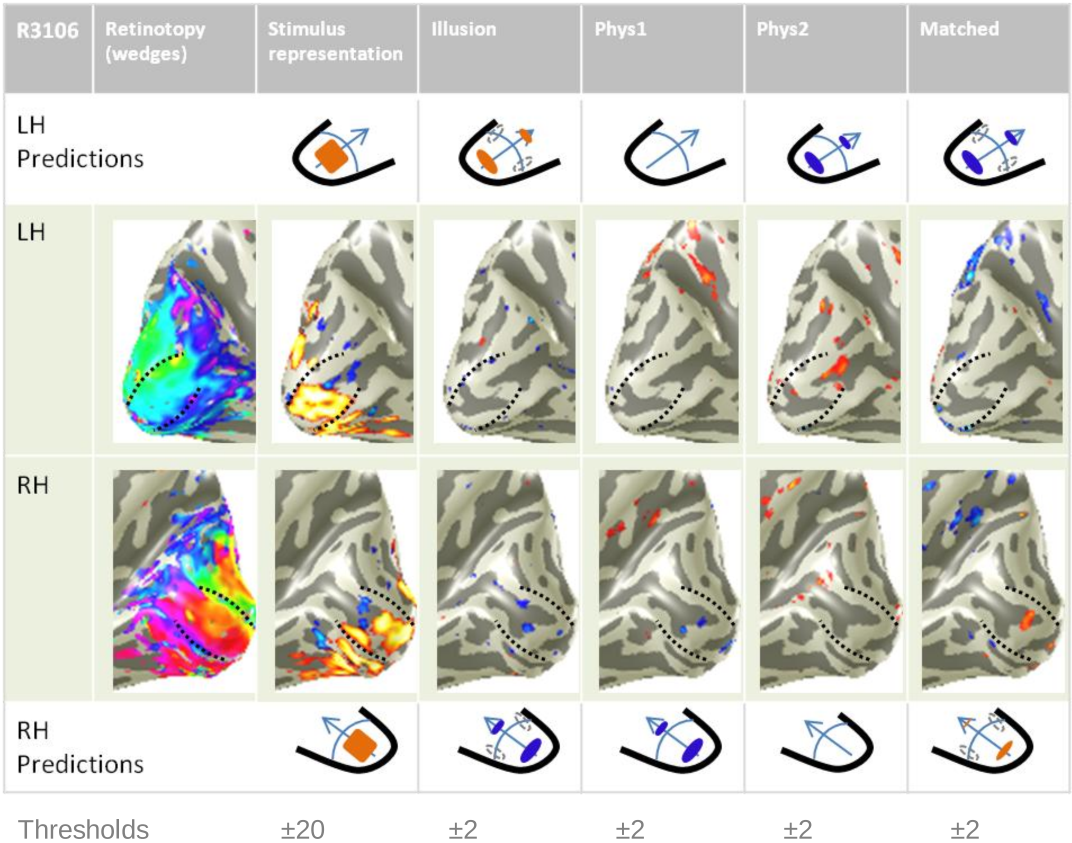


Table 6.4 Retinotopic maps and cortical mesh surfaces for each contrast for participant R3106.

The stimulus representation contrast shows the position of the Helmholtz's squares in V1 for both hemispheres. The 'Illusion' contrast in LH does not satisfy our prediction as no activation is evident, whereas in RH activation is shown on the representation of the horizontal meridian satisfying the prediction. The 'Physical differences in width-presented in left hemifield' contrast (fourth column) in both hemispheres satisfy the prediction as no activation in evident in LH and in RH activation is evident along the horizontal meridian. The cortical surface mesh for the 'Physical differences in width-presented in right hemifield' contrast (fifth column) in LH does not satisfy the prediction, whereas the absence of activation in RH satisfies the prediction. Finally, activation along the horizontal meridian for the 'Perceptually Matched' contrast (sixth column) in both hemispheres is consistent with the prediction that V1 registers physical differences of visual stimuli.

Table 6.5 below illustrates prediction sketches as well as cortical surface meshes of both hemispheres for participant R3107. The average percentage accuracy in the fixation task for this participant for the two runs was 82%.

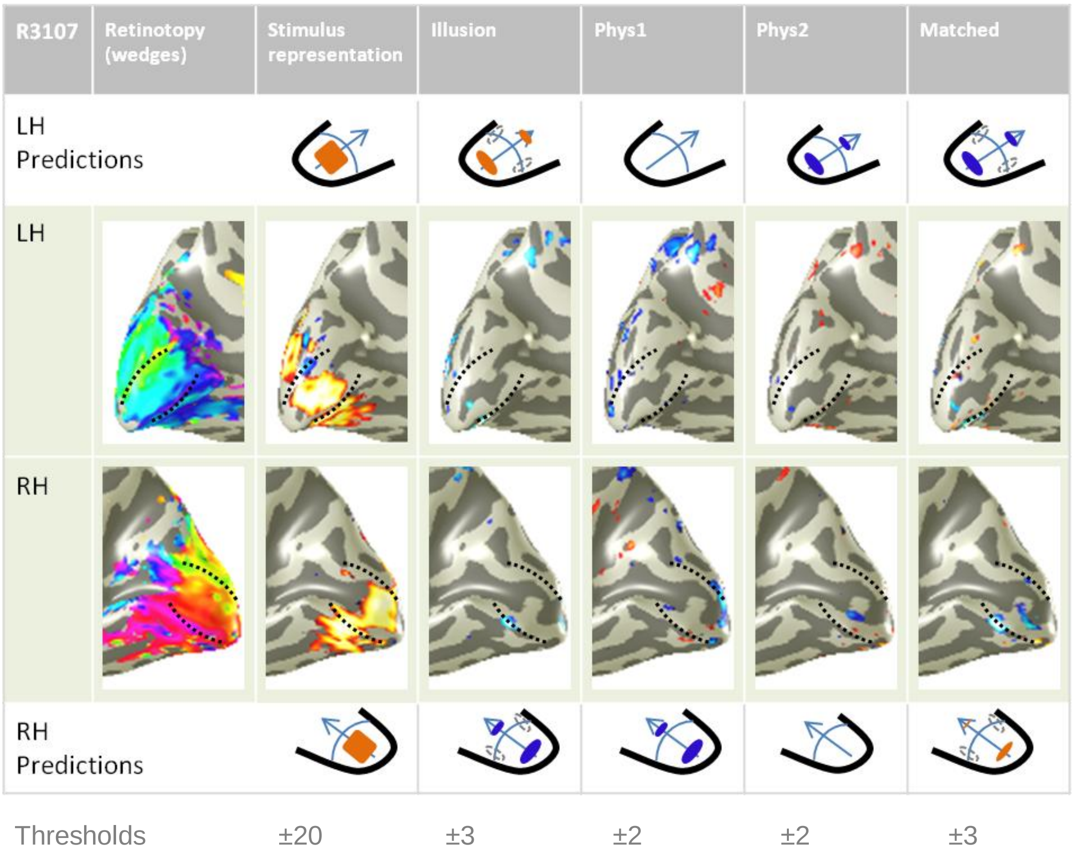
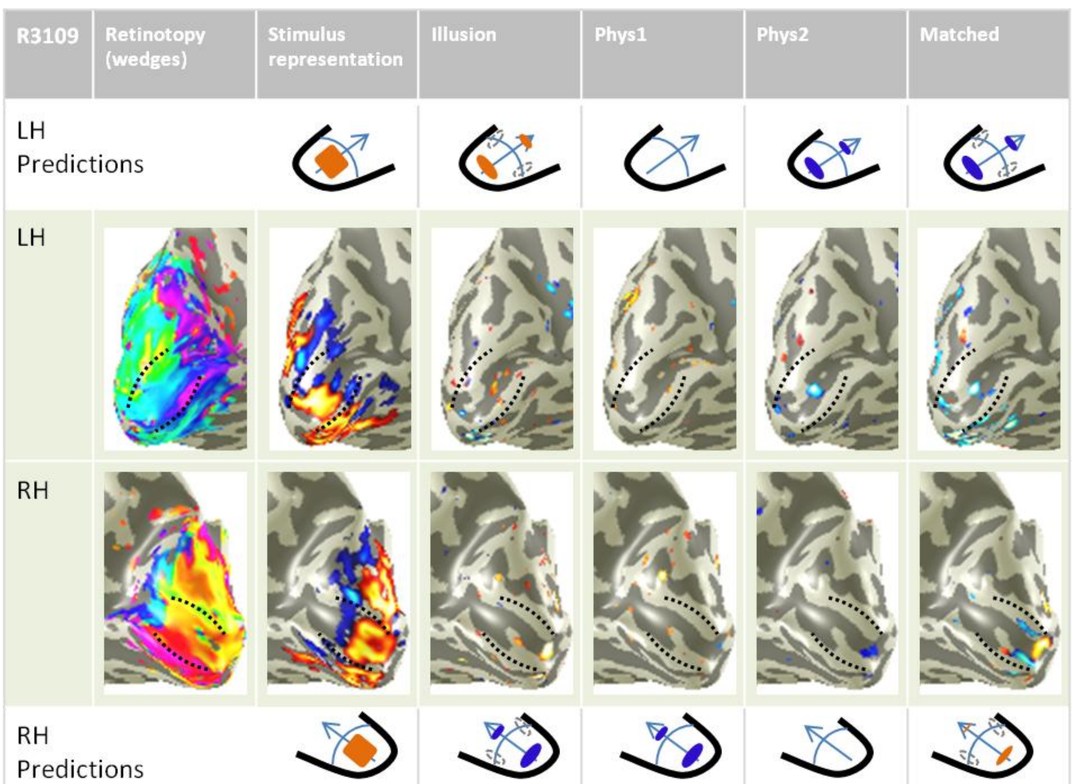


Table 6.5 Retinotopic maps and cortical mesh surfaces for each contrast for participant R3107.

The stimulus representation contrast shows the position of the Helmholtz's squares in V1 for both hemispheres. The 'Illusion' contrast in LH does not satisfy our prediction as no activation is evident, whereas in RH weak activation is shown along the horizontal meridian satisfying the prediction that V1 retains some information about perceptual experience. The 'Physical differences in width-presented in left hemifield' contrast (fourth column) in both hemispheres satisfy the prediction as no activation in evident in V1 in the LH and in RH activation is evident along the horizontal meridian. The cortical surface mesh for the 'Physical differences in width-presented in right hemifield' contrast (fifth column) shows some activation along the horizontal meridian in LH and some activation is also evident in RH in disagreement with our prediction. Finally, activation along the horizontal meridian for the 'Perceptually Matched' contrast (sixth column) in both hemispheres is consistent with the prediction that V1 registers physical differences of visual stimuli. In this contrast some activation along the vertical meridian in both hemispheres in also present.

Table 6.6 below illustrates prediction sketches as well as cortical surface meshes of both hemispheres for participant R3109. The average percentage accuracy in the fixation task for the two runs was 87%.



Thresholds ±10 ±3 ±3 ±2 ±3

Table 6.6 Retinotopic maps and cortical mesh surfaces for each contrast for participant R3109.

The stimulus representation contrast shows the position of the Helmholtz's squares in V1 for both hemispheres. The 'Illusion' contrast in LH satisfies our prediction, whereas in RH activation shown does not agree with our prediction. The 'Physical differences in width-presented in left hemifield' contrast (fourth column) in both hemispheres satisfy the prediction as no activation in evident in V1 in the LH and in RH weak activation is evident along the horizontal meridian. The cortical surface mesh for the 'Physical differences in width-presented in right hemifield' contrast (fifth column) shows strong activation along the horizontal meridian in LH and some activation is also evident in RH in disagreement with our prediction. Finally, activation along the horizontal meridian for the 'Perceptually Matched' contrast (sixth column) in both hemispheres is consistent with the prediction that V1 registers physical differences of visual stimuli. Interestingly, in RH some activation is evident along the vertical meridian as well, creating a square.

Table 6.7 below illustrates prediction sketches as well as cortical surface meshes of both hemispheres for participant R3110. The average percentage accuracy in the fixation task for the two runs was 84%.

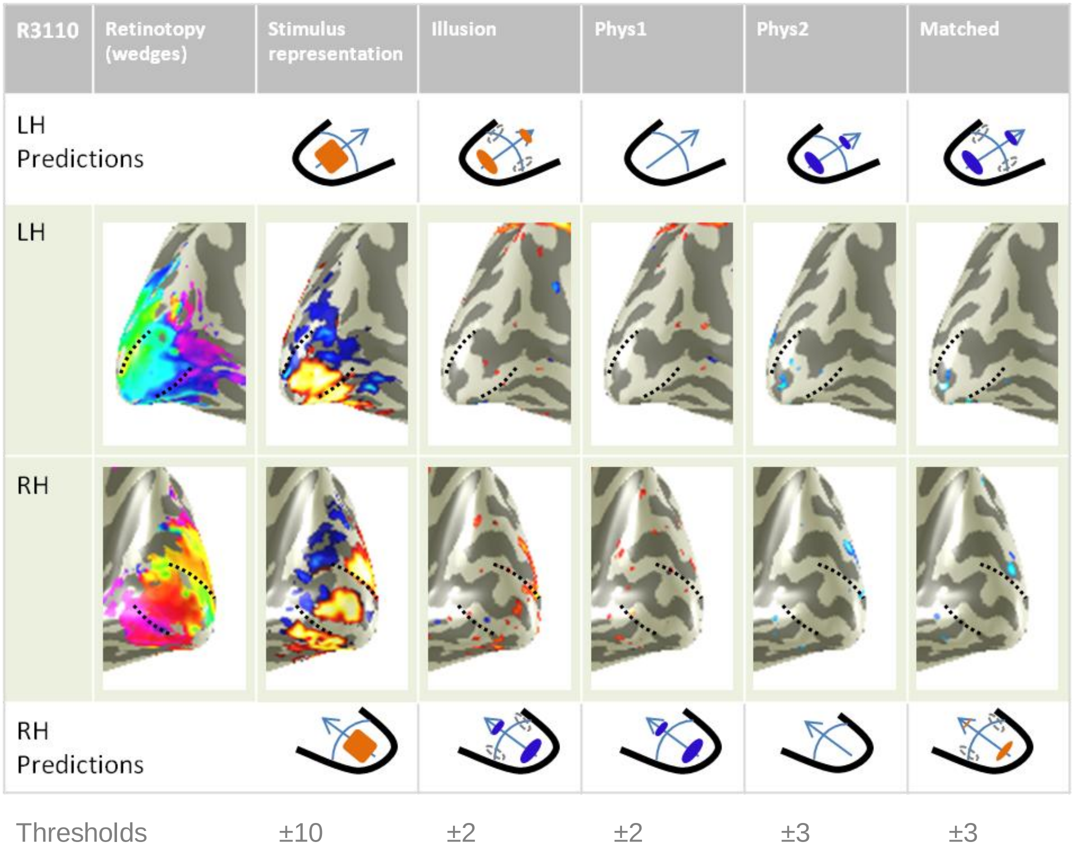


Table 6.7 Retinotopic maps and cortical mesh surfaces for each contrast for participant R3110.

The stimulus representation contrast shows the position of the Helmholtz's squares in V1 for both hemispheres. The cortical surface mesh for 'Illusion' contrast shows weak activation in LH in agreement with our prediction, whereas in RH activation shown does not agree with our prediction. The 'Physical differences in width-presented in left hemifield' (fourth column) contrasts in LH satisfies the prediction as no activation in evident in V1, whereas in RH the absence of any activation is in disagreement with the prediction. The cortical surface mesh for the 'Physical differences in width-presented in right hemifield' contrast (fifth column) shows strong activation along the horizontal meridian in LH and no activation in RH; both results satisfy our predictions. Finally, results for the 'Perceptually Matched' contrast (sixth column) in LH agree with the prediction that V1 registers physical differences between stimuli whereas in RH no evidence of activation due to physical differences in the horizontal dimension is evident.

Table 6.8 below illustrates prediction sketches as well as cortical surface meshes of both hemispheres for participant R3111. The average percentage accuracy in the fixation task for the two runs was 75%.

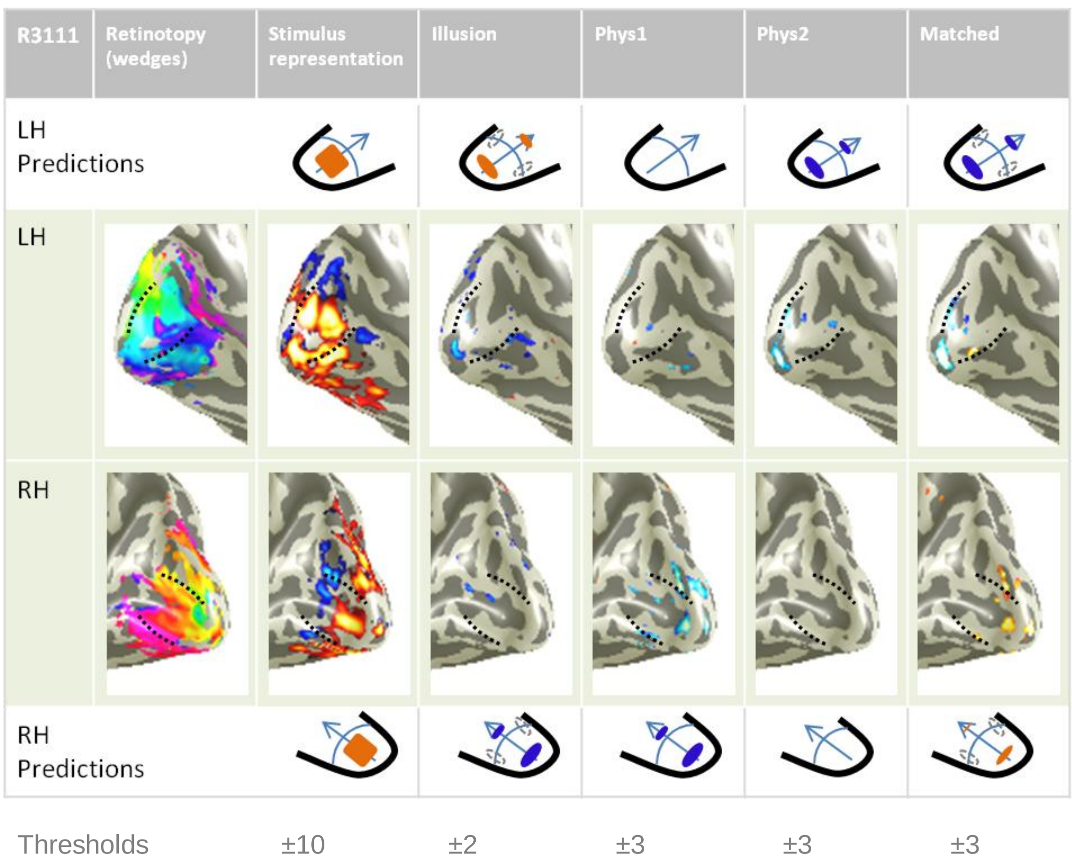


Table 6.8 Retinotopic maps and cortical mesh surfaces for each contrast for participant R3111.

The stimulus representation contrast shows the position of the Helmholtz's squares in V1 for both hemispheres. The activation in LH for the 'Illusion' contrast is not consistent with the prediction, whereas activation in RH does agree with our prediction. The 'Physical differences in width-presented in left hemifield' contrast (fourth column) in both hemispheres satisfies the prediction as no activation in evident in LH and in RH activation is evident along the horizontal meridian. Predictions are also satisfied for the 'Physical differences in width-presented in right hemifield' (fifth column) contrast, with strong activation in LH and absence of activation along the horizontal meridian in RH. Finally, activation along the horizontal meridian for the 'Perceptually Matched' contrast (sixth column) in both hemispheres is consistent with the prediction that V1 registers physical differences of visual stimuli. Interestingly, in LH some activation along the vertical meridian is also evident.

Table 6.9 below illustrates prediction sketches as well as cortical surface meshes of both hemispheres for participant R3112. The average percentage accuracy in the fixation task for the two runs was 93%.

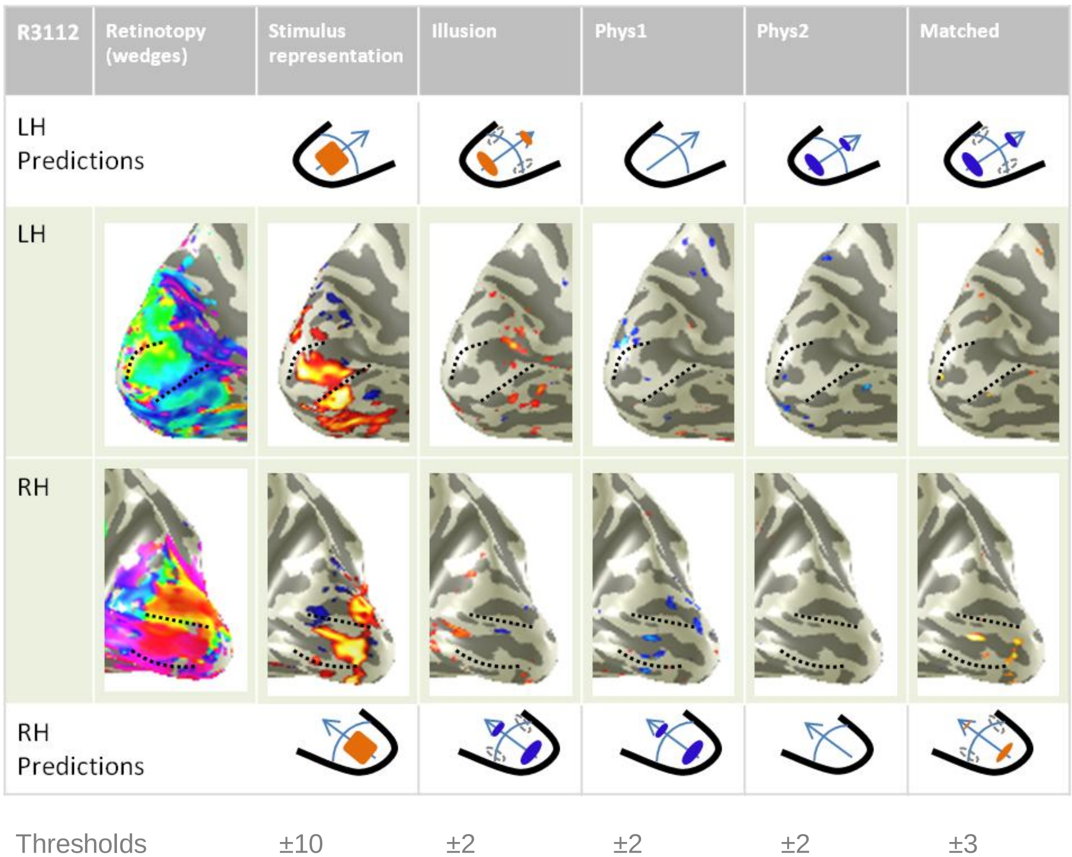


Table 6.9 Retinotopic maps and cortical mesh surfaces for each contrast for participant R3112.

The stimulus representation contrast shows the position of the Helmholtz's squares in V1 for both hemispheres. The activation in LH for the 'Illusion' contrast confirms our prediction, whereas the opposite is true for activation in RH. The 'Physical differences in width-presented in left hemifield' contrast (fourth column) in both hemispheres satisfies the prediction as no activation in evident in LH and in RH activation is evident along the horizontal meridian. Predictions are also satisfied for the 'Physical differences in width-presented in right hemifield' contrast (fifth column), with weak activation in LH and absence of activation along the horizontal meridian in RH. Finally, results for the 'Perceptually Matched' contrast (sixth column) in RH agree with the prediction that V1 registers physical differences between stimuli whereas in LH no evidence of activation due to physical differences in the horizontal dimension is evident.

Table 6.10 below illustrates prediction sketches as well as cortical surface meshes of both hemispheres for participant R3113. The average percentage accuracy in the fixation task for the two runs was 97%.

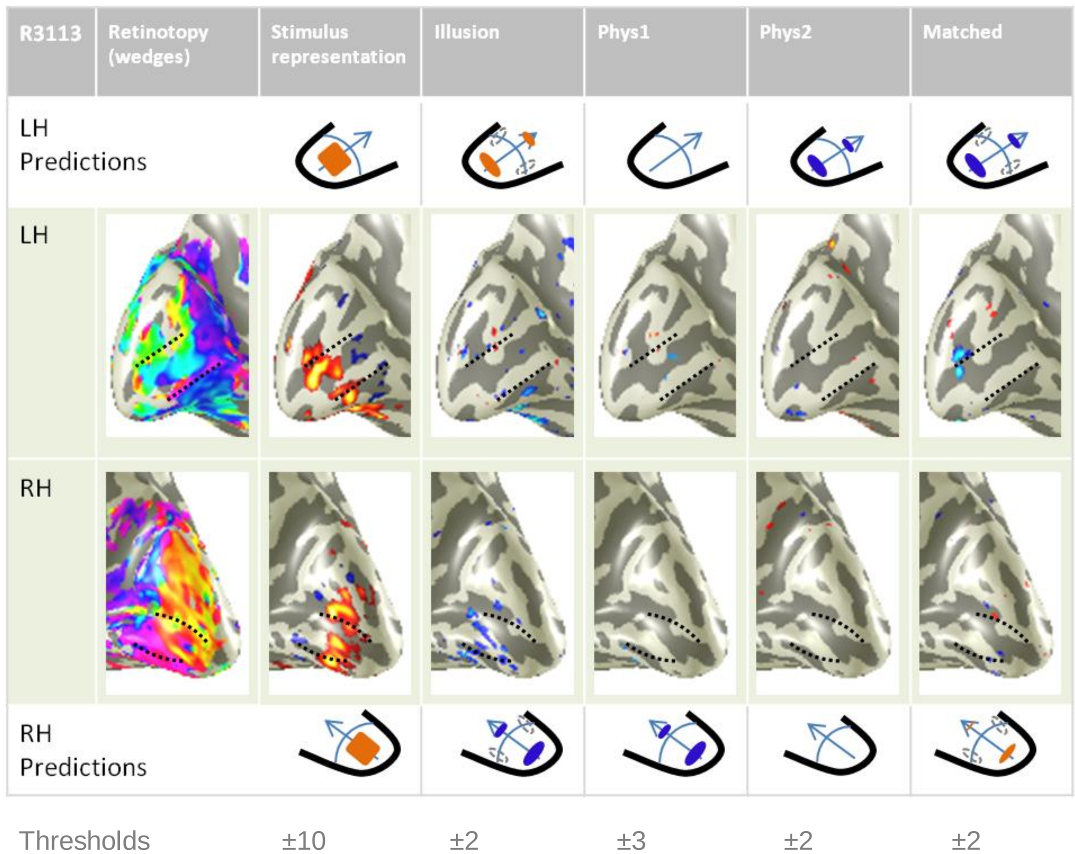


Table 6.10 Retinotopic maps and cortical mesh surfaces for each contrast for participant R3113.

The stimulus representation contrast shows the position of the Helmholtz's squares in V1 for both hemispheres. The activation in LH for the 'Illusion' contrast does not satisfy our prediction, whereas the prediction is satisfied for the RH. The 'Physical differences in width-presented in left hemifield' contrast (fourth column) in both hemispheres is not in agreement with our prediction. Predictions are also satisfied for the 'Physical differences in width-presented in right hemifield' contrast (fifth column), with weak activation in LH and absence of activation along the horizontal meridian in RH. Finally, results for the 'Perceptually Matched' contrast (sixth column) in LH agree with the prediction that V1 registers physical differences between stimuli whereas in RH no evidence of activation due to physical differences in the horizontal dimension is evident.

Results for eight participants are summarized in Table 6.11 below. Consequently, sign tests were been performed for each condition to determine significance of results in relation to our hypotheses. For the 'Perceptually matched' condition, results which are consistent of V1 registering physical differences are interpreted as a confirmation of the hypothesis and vice versa.

	'Illusion'		Phys1		Phys2		'Perceptually Matched'	
Participant	LH	RH	LH	RH	LH	RH	LH	RH
R2657	+	-	-	-	+	+	+	-
R3106	-	+	+	+	-	+	+	+
R3107	-	+	+	+	+	-	+	+
R3109	+	-	+	+	+	-	+	+
R3110	+	-	+	-	+	+	+	-
R3111	-	+	+	+	+	+	+	+
R3112	+	-	+	+	+	+	-	+
R3113	-	+	-	-	+	+	+	-
Confirming Hypothesis	**4**	**4**	**6**	**5**	**7**	**6**	**7**	**5**

Table 6.11 Summary of results; '+' represents a satisfied prediction, whereas '-' represents a prediction not satisfied.

Results from eight participants across hemispheres which confirmed our predictions were counted and a sign test was carried out to determine significance. For our hypotheses to be confirmed at *p<.05*, at least 12 out of 16 hemispheres must satisfy our predictions for the 'Illusion' and 'Perceptually matched' contrasts. Results from Phys1 and Phys2 contrasts were collated as there is no evidence in the literature to suggest that physical differences would be represented differently in V1 in the two hemispheres. Consequently, for the 'Physical differences in width' contrast at least 22 out of 32 hemispheres must satisfy our predictions for our hypothesis to be confirmed (*p>.05*).

For the 'Illusion' contrast only 8 out of 16 hemispheres satisfied our predictions and results generated were found to be non-significant. For the 'Physical differences in width' contrast results were significant (*p<.05*), with 24 out of 32 hemispheres satisfying our prediction. For the 'Perceptually Matched' contrast 12 out of 16 hemispheres followed our predictions and a sign test showed that results were significant (*p<.05*) supporting the notion that V1 registers *physical* differences between stimuli.

Despite the fact that we did not record eye movements during the fMRI session, participants were asked to carry out a demanding fixation task and their accuracy allowed evaluation of whether they were paying sufficient attention to the central fixation task. We inspected cortical surface meshes for two participants R3113 and R3111 with the 'best' and 'worst' performance in the central fixation task respectively and found no systematic differences between the two. We concluded that cortical activity did not vary when the percentage accuracy was in the region of 70-100%.

6.2.6 Discussion

Results generated by the neuroimaging experiment of the Helmholtz's squares illusion revealed that activity in V1 is better associated with *physical* differences of visual stimuli rather than *perceived* differences.

More specifically, in the 'Illusion' contrast it was predicted that clusters of activity along the representation of horizontal meridian would be evident in both hemispheres due to *perceptual* width differences between a horizontally and a vertically-striped square. Only eight out of sixteen hemispheres satisfied our predictions showing that V1 might retain some information about the perceived width of the Helmholtz's squares, but a sign test showed that this effect was non-significant.

In the 'Physical differences in width' contrast we predicted that due to differences in *physical size* between the two horizontally-striped squares activity would be evident along the horizontal meridian. Twenty-four out of thirty-two hemispheres satisfied the prediction and a significant sign test confirmed that V1 registers *physical* differences in the horizontal dimension between two horizontally-striped squares.

In the 'Perceptually Matched' contrast we predicted that if V1 registered *physical* differences, rather perceptual difference, both hemispheres would exhibit activity along the representation of the horizontal meridian. On the contrary, if the opposite was true no observed activity was expected along the horizontal meridian. Thirteen out of sixteen hemispheres satisfied the prediction that V1 registers *physical* differences and generated a significant result, showing that activity in V1 is strongly associated with physical differences in the dimension of the stimuli.

Finally, despite the fact that all interpretations of activation patterns have been carried out carefully and cautiously we acknowledge that these may be subject to errors, as they have been performed by experimenters instead of a sophisticated statistical analysis tool for neuroimaging data. Consequently, we consider this study a foundation which is subject to further analysis in order to reach definite conclusions.

6.3 General Conclusion

The aim of the present chapter was to employ neuroimaging methods in order to complement the study of illusions of filled extent using psychophysics methods. Firstly, a psychophysics experiment was carried out to determine the point at which a horizontally-striped square was *perceptually* identical in terms of width to a vertically-striped square, as indicated by the PSE for each individual participant. Subsequently, an fMRI experiment was carried out to determine whether activity in V1 can be linked to *perceptual* experience rather than purely *physical* differences between visual stimuli.

Results generated by the neuroimaging experiment of the Helmholtz's squares illusion revealed a significant effect in V1 associated with *physical* differences between visual stimuli rather than *perceived* differences. This result contradicts findings from Murray et al. (2006) who showed that as the perceptual size of the stimulus increased, the pattern of activation in V1 also increased. Murray et al. (2006) investigated the influence of perceived object size on representations in V1 by presenting a stimulus of constant physical size while varying its *perceived* size by changing the apparent depth.

In agreement with Murray et al. (2006) a dynamic change in the topographic map of V1 due to the *perceived* size of an object was shown by Fang et al. (2008) who carried out comparisons between the size of two 3D rings at close and far apparent depths in a 3D scene. The former was found to occupy a more eccentric portion of the visual field, relative to the close ring but this effect was significantly reduced when the focus of attention was narrowed with a demanding central fixation task. This reduction in activity was taken as evidence of feedback projections from higher visual areas, processing 3D depth cues, to lower visual areas.

In line with present findings, Fischer et al. (2011) showed that activity in V1 was strongly associated to the retinal position of the stimuli while retaining some unique information about *perceived* position. Fischer et al. (2011) carried out an fMRI study with participants performing a five-alternative forced-choice position discrimination task using Gabor stimuli and they focused their analysis on trials in which misperception of stimulus position was evident. Similarly, results from the present Helmholtz's squares neuroimaging study have shown that, although non-significant, some illusion-related activity is evident in V1.

Despite evidence generated by Murray et al. (2006), Fang et al. (2008) and Fischer et al. (2011) it is not clear whether information about *perceptual* experience in V1 represents the existence of initial percept-based processing in V1 itself or feedback projections from higher visual areas such as the Lateral Occipital cortex and the posterior fusiform gyrus which exhibit strong percept-centered activity (Fischer et al., 2011).

In the present Helmholtz's squares neuroimaging experiment, in addition to ensuring the fixed position of the stimuli on either side of the fovea, the central fixation task essentially drew the attention away from the Helmholtz's squares pair, eliminating the amount of top-down processing. By reducing the amount of processing allocated to the Helmholtz's squares in higher-order areas, the amount of feedback projections from these to V1 were eliminated to reveal intrinsic processing in V1. Therefore, evidence generated strongly suggests that when the illusion is 'cancelled' (in the 'Perceptually Matched' contrast) activity in V1 closely follows the *physical* dimensions of the stimulus. Consequently it can be inferred that intrinsic processing in V1 is not inducing illusion-related activity and it is likely that feedback from other areas dominates the results of other studies. It is also possible that experiments using size constancy (Murray et al., 2006; Fang et al., 2008) to generate various perceptual sizes from identical retinal images can induce illusory-related activity in V1, whereas the Helmholtz's squares illusion in the absence of any 3D cues is unable to do so.

Due to the subtle nature of the signals arising from illusory percept, future research could involve acquiring more data from additional participants to increase the power of the results. Also, a further Region of Interest (ROI) analysis could be carried out and the task could be manipulated in order to shift the focus of attention from the centre to the Helmholtz's squares to determine whether activity that has been previously associated with *perceptual* experience in V1 is in reality induced by feedback projections from higher order areas.

6.4 Chapter Summary

Two experiments were carried out in the present chapter to investigate whether activity in V1 can be linked to *perceptual* experience. A psychophysics experiment determined the individual PSE for each participant and this was followed by a neuroimaging experiment observing activity in V1. Results generated revealed a significant effect in V1 associated with *physical* differences between visual stimuli rather than *perceived* differences. By eliminating the amount of top-down processing allocated to the Helmholtz's squares in higher-order areas, and consequently feedback projections from these to V1 we concluded that intrinsic processing in V1 is not responsible for inducing illusion-related activity and it is likely that feedback from other areas dominates the results of other studies.

Chapter 7 – Summary and general conclusion

This chapter summarises and discusses the main findings from experiments presented throughout this thesis. It also proposes possible future research directions.

7.1 Summary of Thesis Findings

The aim of the thesis was to investigate the conditions under which the Oppel-Kundt illusion becomes most apparent, provide a more coherent explanation for the vertical-horizontal illusion in simple figures and also determine the role of visual brain area V1 in the processing of the Helmholtz's squares illusion.

Chapter 3

The aim of this chapter was to investigate how the position and number of vertical lines in an Oppel-Kundt figure affect the size of the illusory percept. A series of five experiments were performed by manipulating the size, position and number of vertical lines on a horizontal line. The results showed that when a vertical 'tick' *crosses* a horizontal line in the middle, the size of this 'bisection' effect ranges from approximately 7 to 13%, reducing the perceived size of the horizontal line. However, we did not observe any underestimation of the bisected line in an inverted 'T' configuration (in the present case, the horizontal), when this was compared to another horizontal line of the same size. This evidence challenged the validity of the 'bisection' component of the vertical-horizontal illusion as described by Mamassian & de

Montalembert (2010) and it was decided that a thorough investigation and evaluation of their model would be carried out in Chapter 5. Secondly, a relatively constant and significant Oppel-Kundt effect was observed when eight to ten vertical 'ticks' crossed a horizontal, inducing approximately a 5% increase in the perceived size of the latter. Thirdly, evidence showed that an increase in the perceived size of a horizontal line is apparent only when vertical lines *cross* a horizontal.

Chapter 4

This chapter is a continuation of Chapter 3 and the aim was to determine whether the illusory percept arising in a classic Oppel-Kundt figure can be assigned to repulsion between adjacent 'ticks' which displace one another in such a way to increase the perceived length of the stimulus as a whole, as suggested by Ganz (1966). Evidence generated by two experiments suggests that the increase in the perceived size of a horizontal line in an Oppel-Kundt figure which is typically ~5% as shown in Chapter 3 cannot be exclusively explained by repulsion between adjacent lines as this was found to account only for 0.5% of the perceived size increase. Consequently the explanation provided by Ganz (1966) involving repulsion of adjacent contours can be ruled out as a complete explanation for the Oppel-Kundt illusion.

Chapter 5

Following evidence from Chapter 3, the aim of this chapter was to evaluate the simple model of the vertical-horizontal illusion proposed by Mamassian and de Montalembert (2010) and provide an alternative, more coherent explanation with an additional parameter. Specifically, Mamassian and de Montalembert carried out direct comparisons between the two segments in inverted 'T', horizontal 'T', cross and 'L'-shaped configurations and claimed that two components drive differences between their perceived size; namely 'anisotropy' and 'bisection'. According to their claims the former induces a 6% increase in the perceived size of a vertical line compared to a horizontal whereas the latter induces a 16% decrease in the perceived size of a *bisected* line. However, in Chapter 3 we failed to observe a decrease in the perceived size of the horizontal segment in an inverted ‘T’ configuration when this was compared to an independent horizontal line. Consequently, we proposed a new model, namely the **ABC** model consisting of three components; **anisotropy, abutting and crossing.** A series of four experiments was carried out in the present chapter providing evidence for support for the **ABC** model. The effects of **anisotropy**, **abutting** and **crossing** were found to affect the perceived size of lines by +7%, +9% and -7% respectively. It was concluded that the **ABC** model can provide a comprehensive explanation for the variations in the perceived size of vertical and horizontal lines in simple shapes.

Chapter 6

In Chapter 6 an fMRI study was carried out investigating the role of visual brain area V1 in the processing of another illusion of filled extent, the Helmholtz’s squares illusion. Firstly, a psychophysics experiment was carried out in order to determine the individual PSE for each participant and this was followed by a neuroimaging experiment measuring activity in V1. Participants were asked to carry out a demanding central fixation task while viewing the Helmholtz’s squares presented simultaneously one next to the other. Results revealed a significant effect in V1 associated with *physical* differences between visual stimuli rather than *perceived* differences. By eliminating the amount of top-down processing allocated to the Helmholtz’s squares in higher-order areas, and consequently feedback projections from these to V1 we concluded that intrinsic processing in V1 is not completely responsible for inducing illusion-related activity as previously suggested and it is likely that feedback from other areas dominates the results of other studies (Murray et al., 2006; Fang et al., 2009).

7.2 Future Research

Future research could focus on exploring the **abutting** component of the **ABC** model. Despite the fact that predictions involving the abutting component in an L-shape were confirmed, in an inverted 'T' configuration the size of the illusion was only confirmed qualitatively and not quantitatively, failing to show an increase of approximately 16% in the perceived size of the vertical segment. As suggested in Chapter 5 this could be done by comparing the horizontal segment of a horizontal 'T' configuration to an independent vertical line and the predicted effect would be a 2% increase in the perceived size of the latter by virtue of **anisotropy** and **abutting**.

In relation to the Helmholtz's squares illusion, future research could involve acquiring more data from additional participants to increase the power of the results. Also, it would be interesting to perform a Region of Interest (ROI) analysis in V1 and possibly higher visual areas to determine the origin of such illusory percept in the brain. Finally, the task could be manipulated in order to focus attention on the Helmholtz's squares and determine whether activity that has been previously associated with *perceptual* experience in V1 is in reality induced by feedback projections from higher order areas. Interestingly, additional research could focus on determining whether evidence of *perceptual* experience in V1 arises only when size constancy is involved, as it was the case in Murray et al. (2006).

7.3 Conclusion

The findings of this thesis have important implications for the Oppel-Kundt, vertical-horizontal and Helmholtz's squares illusions. Results determined that an increase in the apparent size of a horizontal line only occurs when vertical lines are crossing it and also confirmed that the maximum Oppel-Kundt effect occurs with eight to ten small vertical 'ticks'. Additionally, this thesis has proposed a more comprehensive model explaining the variations in size of vertical and horizontal lines in simple figures, compared to the existing model described by Mamassian and de Montalembert (2010). Finally, an fMRI study of the Helmholtz's squares illusion has provided evidence to support the notion that any activity in V1 previously related to *perceptual* experience is likely to be arising due to feedback projections from higher visual areas. Instead, results revealed a significant effect in V1 associated with *physical* differences between visual stimuli rather than *perceived* differences.

References

Avery, G.C., & Day, R.H. (1969). Basis of the horizontal vertical illusion. *Journal of Experimental Psychology, 81,* 376-380.

Blakemore, C., Carpenter, R.H.S., & Georgeson, M.A. (1970). Lateral inhibition between orientation detectors in the human visual cortex. *Nature, 228, 37-39.*

Blakemore, C., & Tobin, E.A. (1972). Lateral inhibition between orientation detectors in the cat's visual cortex. *Experimental Brain Research, 15,* 439-330.

Bulatov, A., Bertulis, A., & Mickiene, L. (1997). Geometrical illusions: study and modeling. *Bio. Cybern., 77,* 395-406.

Charras, P., & Lupianez, J. (2009). The relevance of symmetry in line length perception. *Perception, 38,* 1428-1438.

Charras, P., & Lupianez, J. (2010). Length perception of horizontal and vertical bisected lines. *Psychological Research, 74,* 196-206.

Chen, W., & Ogawa, S. (2000). Principles of BOLD functional MRI. In C.T.W. Moonen, P.A. Bandettini, A.L. Baert (Eds.), *Functional MRI* (103-113). Germany: Springer-Verlag GmbH.

Coren, S., & Girgus, J.S. (1978). *Seeing is deceiving: The Psychology of visual illusions.* Hillsdale: New Jersey.

Cormack, E.O. & Cormack, R.H. (1974). Stimulus configuration and line orientation in the horizontal-vertical illusion. *Perception & Psychophysics, 16,* 208–212.

Craven B.J., & Watt, R.J. (1989). The use of fractal image statistics in the estimation of lateral spatial extent. *Spatial Vision, 4*(4), 223-239.

Craven, B.J. (1993). Orientation dependence of human line-length judgments matches statistical structure in real-world scenes. *Proceedings of the Royal Society of London, B, 253,* 101–106.

Craven, B. J. (1995). Temporal properties of the filled-space illusion. *Perception, 24,* 80.

DeValois, R.L., & DeValois, K.K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research, 31,* 1619-1626.

DeYoe, E.A., Carman, G.J., Bandettini, P., Glickman, S., Wieser, J., Cox, R., Miller, D., Neitz, J., (1996). Mapping striate and extrastriate visual areas in human cerebral cortex. *Proceedings of the National Academy of Science U.S.A., 93,* 2382–2386.

Dumoulin, S.O., Hoge, R.D., Baker Jr., C.L., Hess, R.F., Achtman, R.L., Evans, A.C., 2003. Automatic volumetric segmentation of human visual retinotopic cortex. *NeuroImage, 18*, 576–587.

Engel, S.A., Rumelhart, D.E., Wandell, B.A., Lee, A.T., Glover, G.H., Chichilnisky, E.J., Shadlen, M.N., 1994. fMRI of human visual cortex. *Nature, 369*, 525.

Engel, S.A., Glover, G.H., Wandell, B.A., (1997). Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cerebral Cortex, 7*, 181–192.

Fang, F., Boyaci, H., Kersten, D., & Murray S.O. (2008). Attention-dependent representation of a size illusion in human V1. *Current Biology, 18,* 1707-1712.

Finger, F. W., & Spelt, D. K. (1947). The illustration of the horizontal–vertical illusion. *Journal of Experimental Psychology, 37*, 243–250.

Fischer, J., Spotswood, N., & Whitney, D. (2011). The Emergence of perceived position in the visual system. *Journal of Cognitive Neuroscience, 23* (1), 119-136.

Ganz, L. (1966). Mechanism of the figural-aftereffects. *Psychological Review, 73(*2), 128-150.

Giora, E., & Gori (2010). The perceptual expansion of a filled area depends on textural characteristics. *Vision Research, 50*(23), 2466-2475.

Girgus, J. S., & Coren, S. (1975). Depth cues and constancy scaling in the horizontal vertical illusion: The bisection error. *Canadian Journal of Psychology, 29*, 59–65.

Gregory, R. L. (1963). Distortion of visual space as inappropriate constancy scaling. *Nature, 199*, 678–680.

Gregory, R. L. (1970). *The intelligent eye*. New York: McGraw-Hill.

Helmholtz, H. von (1925). The monocular field of vision. In J.P.C. Southhall (Ed.). *Helmholtz's Treatise on Physiological Optics: The Perceptions of Vision* (Vol.3), (Translated from the Third German Edition of Handbuch der physiologischen Optik (first published in 1867, Leipzig: Voss), pp.154-242. Menasha, Wisconsin: The Optical Society of America.

Hess, R., Negishi, K., & Creutzfeldt, O. (1975). The horizontal spread of intracortical inhibition in the visual cortex. *Experimental Brain Research, 22,* 415-419.

Hirsch, J., DeLaPaz, R.L., Relkin N.R., Victor, J., Kim, K., Li, T., Borden, P., Rubin, N., & Sharley, R. (1995). Illusory contours activate specific regions in human visual cortex: Evidence from functional magnetic resonance imaging. *Proceedings of the National Academy of Science USA, 92,* 6469-6473.

Howe, C.Q, & Purves, D. (2002). Range image statistics can explain the anomalous perception of length. *Proceedings of the National Academy of science, 99* (20), 13184-13188.

Imai, S. (1982). The mystery of the appearance of horizontally and vertically striped clothes (in Japanese). *Psychology, 29,* 12.

Jenkinson, M., Bannister, P., Brady, M. & Smith, S. (2002). Improved optimization for the robust and accurate linear registration and motion correction of brain images. *Neuroimage 17*, 825-41.

Künnapas, T. M. (1955). An analysis of the 'vertical-horizontal illusion'. *Vision Research, 49* (2), 134-160*.*

Künnapas, T. M. (1955b). Influence of frame size on apparent length of a line. *Journal of Experimental Psychology, 50*, 168–170.

Künnapas, T. M. (1957a). Vertical horizontal illusion and surrounding field. *Acta Psychologica, 13*, 35–42.

Künnapas, T.M. (1957). The vertical-horizontal illusion and the visual field. *Journal of Experimental Psychology, 53,* 405-407.

Künnapas, T. M. (1958). Influence of head inclination on the vertical horizontal illusion. *The Journal of Psychology, 46*, 179–185.

Kundt, A. (1863). Annalen der Physik und Chemie. Untersuchungen uber AugenmaÞ und optische Tauschungen. *Poggendorff Annalen*, *120,* 118-158.

Li, R.W., Brown, B., Edwards, M.H., Ngo, C.V. Chatt, S.W., & Levi, D.M. (2012). Reduced sampling efficiency causes degraded Vernier hyperacuity with normal aging: Vernier acuity in position noise. *Nature: Scientific reports, 300.*

Liu, J.V., Ashida, H., Smith, A.T., & Wandell, B.A. (2006). Assessment of stimulus-induced changes in human V1 visual field maps. *Journal of Neurophysiology, 96,* 3398-3408.

Logothetis, N.K., & Wandel, B.A. (2004). Interpreting the BOLD signal. *Annual Reviews of Physiology, 66,* 735-*769.*

Long, G. M., & Murtagh, M.P. (1984). Task and size effects in the Oppel-Kundt and irradiation illusions. *Journal of General Psychology, 111,* 229-240.

Mamassian, P., & de Montalembert, M. (2010). A simple model of the vertical-horizontal illusion. *Vision Research, 50* (10), 956-962.

Morgan, M.J., Dillenburger, S.R., Raphael, S., & Solomon, J.A. (2012). Observers voluntarily shift their psychometric functions without losing sensitivity. *Attention, Perception & Psychophysics, 74,* 185-193.

Murray, S.O., Boyaci, H., & Kersten, D. (2006). The representation of perceived angular size in human primary visual cortex. *Nature Neuroscience, 9,* 429-434.

Obonai, T. (1954). Induction effects in the estimates of extent. *Journal of Experimental Psychology, 47,* 57-60.

Oppel, J. J. (1855). Uber geometrisch-optische Tauschungen. *Jahresbericht des Frankfurter Vereins, 1854-1855, p.37-47.*

Oyama, T. (1960). Japanese studies on the so-called geometrical-optical illusions. Psychologia*, 3,* 7–20.

Piaget, J., & Osterrieth, P. A. (1953) Recherches sur le développement des perceptions: x v i i. L'évolution de l'illusion d'Oppel–Kundt en fonction de l'âge. *Arch de Psychol, 34,* 1–38.

Pollock, W. T. & Chapanis, A. (1952). The apparent length of a line as a function of its inclination. *Quarterly Journal of Experimental Psychology, 4,* 170–178.

Prinzmetal, W., & Gettleman, L. (1993). Horizontal vertical illusion: One eye is better than two. *Perception and Psychophysics, 53*, 81–88.

Rentschler, I., Hilz, R., Sutterlin, C., & Noguchi, K. (1981). Illusions of filled lateral and angular extent. *Experimental Brain Research, 44,* 154-158.

Ramsden, B. M., Hung, C. P. Roe, & A. W. (2001). Real and illusory contour processing in area V1 of the primate:a cortical balancing act. *Cerebral Cortex, 11*, 648-665.

Robinson, J. O. (1972). *The psychology of visual illusion.* 1st ed. Hutchinsons, (MI Mich.).

Sanders, A. F., & Kappers, A. M. (2009). Factors affecting the haptic filled-space illusion of dynamic touch. *Experimental Brain Research, 192,* 717-722.

Schwarzkopf, D. S., Song, C. & Rees, G (2011). The surface area of human V1 predicts the subjective experience of object size. *Nature Neuroscience, 14,* 28-30.

Sekuler, R., & Blake, R. (2002). *Perception* (4th Edition). New York:McGraw-Hill Higher Education.

Sereno, M.I., Dale, A.M., Reppas, J.B., Kwong, K.K., Belliveau, J.W., Brady, T.J., Rosen, B.R., Tootell, R.B., (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science, 268*, 889–893.

Sheth, B.R., Sharma, J., Rao, S.C., & Sur, M., (1996). Orientation maps of subjective contours in visual cortex. *Science*, *274*, 2110-2115.

Shipley, W. C., Nann, B. M. & Penfield, M. J. (1949). The apparent length of tilted lines. *Journal of Experimental Psychology, 39, 548-551.*

Sperandio I., Chouinard, P. A. and Goodale, M. A. (2012). Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. *Nature Neuroscience, 15*(4), 540-542.

Sterzer, P., & Rees, G. (2006). Perceived size matters. *Nature Neuroscience, 9*(3), 302-304.

Sugawara, M., & Morotomi (1991). Visual evoked potentials elicited by subjective contour figures. *Scandinavian Journal of Psychology, 32*(4), 352-357.

Suzuki, S., & Cavanagh, P. (1997). Focused attention distorts visual space: An attentional repulsion effect. *Journal of Experimental Psychology: Human Perception and Performance, 23,* 443-463.

Taya, S., & Miura, K. (2007). Shrinkage in the apparent size of cylindrical objects. *Perception, 36*, 3-16.

Thompson, P., & Mikellidou, K. (2011). Applying the Helmholtz illusion to fashion: horizontal stripes won't make you look fatter. i-*Perception, 2*(1), 69-76.

Tong, F. (2003). Primary visual cortex and visual awareness. *Nature Reviews Neuroscience, 4,* 219-229.

von Collani, G. (1985). The horizontal-vertical illusion in photographs of concrete scenes with and without depth information. *Perceptual and motor skills, 61*(2), 523-531.

von der Heydt, R., & Peterhans, (1989). Mechanisms of contour perception in monkey visual cortex. I. Lines of pattern discontinuity. *Journal of Neuroscience, 9,* 1731-1748.

Wandell, B.A., Chial, S. & Backus, B.T (2000). Visualization and measurement of the cortical surface. *Journal of Cognitive Neuroscience, 12,* 739-52.

Wandell, B.A., Brewer, A.A. & Dougherty, R.F (2005). Visual field map clusters in human cortex. Philosophical Transactions of the Royal Society B: Biological Sciences, 360, 693-707.

Watt, R. J. (1990). The primal sketch in human vision. In A. Blake & T. Troscianko (Eds.), *AI and the Eye*, J. Wiley & Sons, New York, p.147-180.

Whitaker, D., McGraw P.V., & Levi, D. M. (1997). The influence of adaptation on perceived visual location. *Vision research, 37,* 2207-2216.

Whitney, D., Goltz, H.C., Thomas, C.G., Gati, J.S., Menon, R.S. & Goodale, M.A. (2003). Flexible retinotopy: Motion-dependent position coding in the visual cortex. *Science, 302,* 878-881.

Williams, P.A., & Enns, J.T. (1996). Pictorial depth and framing have independent effects on the horizontal-vertical illusion. *Perception, 5,* 308-330.

Wolfe, U., Maloney, L.T., &Tam, M. (2005). Distortions of perceived length in the frontoparallel plane: Tests of perspective theories. *Perception and Psychophysics, 67,* 967-979.

Woodworth, R.S. (1938). *Experimental Psychology.* New York: Holt, Rinehart and Winston.

Yang, T. L., Dixon, M. W., Proffitt, D. R., (1999). Seeing big things: Overestimation of heights is greater for real objects than for objects in pictures. *Perception, 28,* 445-467.

Yoshioka, T., Ichihara, S. & Akutsu, H. (2004). Effects of illusory stripes on the Helmholtz illusion. *Perceptual Motor Skills*, *99*(2), 495-500.

Zanforlin, M. (1967). Some observations on Gregory's theory of perceptual illusions. *Quarterly Journal of Experimental Psychology, 19*, 193-197.