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The assumed light source direction : evidence from different populations

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The Assumed Light Source Direction: Evidence from Different Populations

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Abstract

The experiments in this thesis measured light source biases in different populations to investigate why observers assume that light originates from above and to the left. All the experiments use the same greyscale stimulus, the "honeycomb", which consists of a hexagon surrounded by six hexagons. Light and dark edges give the impression of the stimulus being lit from one side, although there is no explicit light source in the picture. Participants viewed the honeycomb presented at different orientations and stated whether they perceived the central hexagon as pushed in or out compared to the surrounding hexagons. Participants' light biases were calculated from these judgements, the angle at which they assumed the light was originating.

The effect of long term experience is explored in Chapters Two and Three, showing that the cultural experience of language modulates the left lighting bias as biases were significantly reduced in a group of first language Hebrew speakers, who read and write from right to left, compared to English speakers. However, the experience of hemispatial neglect, an attentional disorder commonly seen after stroke, does not cause a shift in the light bias. The role of hemispheric asymmetry is examined in Chapters Three, Four, and Five by measuring the effects of lesions after stroke, simulated lesions in healthy participants, and the natural decline of hemispheric asymmetry with ageing. These experiments show that the lighting bias is modulated by hemispheric asymmetry; however the specific role of the right hemisphere is not clear. Chapter Five shows the lighting bias shifts to the right with age, as the right hemisphere degenerates, yet conversely Chapters Three and Four found that a disruption of the right hemisphere causes a leftward shift in participants' light biases, regardless of lesion location.

These findings make a significant contribution to the light assumptions literature, showing that the left lighting bias is caused by an interaction between fixed factors, hemispheric asymmetry, and also environmental experience.

Chapter One. Literature Review

The retinal image is two dimensional; observers must use various depth cues in order to recover the three dimensional shape of surfaces. There are a multitude of cues including binocular disparity, occlusion, motion, surface reflectance, texture, and shading. However, these cues can often be interpreted in multiple ways. For instance Figure 1.1 shows two sets of stimuli which are equally consistent with two lighting directions separated by 180˚ degrees; directly above, and directly below. Therefore each sphere can either be perceived as either a bump or a crater. In these cases interpretation is guided by extra-retinal prior knowledge about the environment. This involves making assumptions based on prior experience in order to quickly interpret the shape of objects (Cavanagh & Lecerc, 1989; Mamassian, Landy, & Maloney, 2001).

Shading is a cue that indicates depth by showing which areas of a surface are oriented toward a light source (O'Shea, Banks, & Agrawala, 2008); a convex surface will be lighter on the side which is oriented toward a light source. As such, in order to use shading to interpret the shapes in Figure 1.1, observers must use knowledge and prior experience to assume the light source is originating from above or below the scene. As such, prior assumptions aid observers to quickly recover the three dimensional scenes around them.

Assumptions include the judgement that there is a single light source and that the light source is located above, rather than below the scene (Cavanagh & Lecerc, 1989; Kleffner & Ramachandran, 1992; Mamassian, Knill, & Kersten, 1998). The assumption of a single light source is evident by the fact that two groups of spheres with opposite shading (Figure 1.1) cannot be perceived as simultaneously convex or concave. If an observer were to mentally reverse the perception of one group, from convex to concave, the group with opposite shading would reverse to convex automatically. Additionally, the assumption of the light source placed above the scene means a shaded grey sphere will usually be reported as convex when lighter at the top and concave when lighter at the bottom. These assumptions are thought to reflect environmental regularities as sun light, a single light source, as well as most artificial lights are placed above the observer (Ramachandran, 1988). Therefore it makes ecological sense for observers to assume there is a single light source above the scene, as statistically, that source of light is the most likely. However, some evidence suggests these assumptions may not be, at least exclusively, ecological but also innate. Hershberger (1970) reared chickens in cages lit from below and trained them to discriminate between convex and concave dents. When shown photographs of dents the chickens interpreted the depth in the photographs as though the dents were lit from above, despite never experiencing overhead lighting.

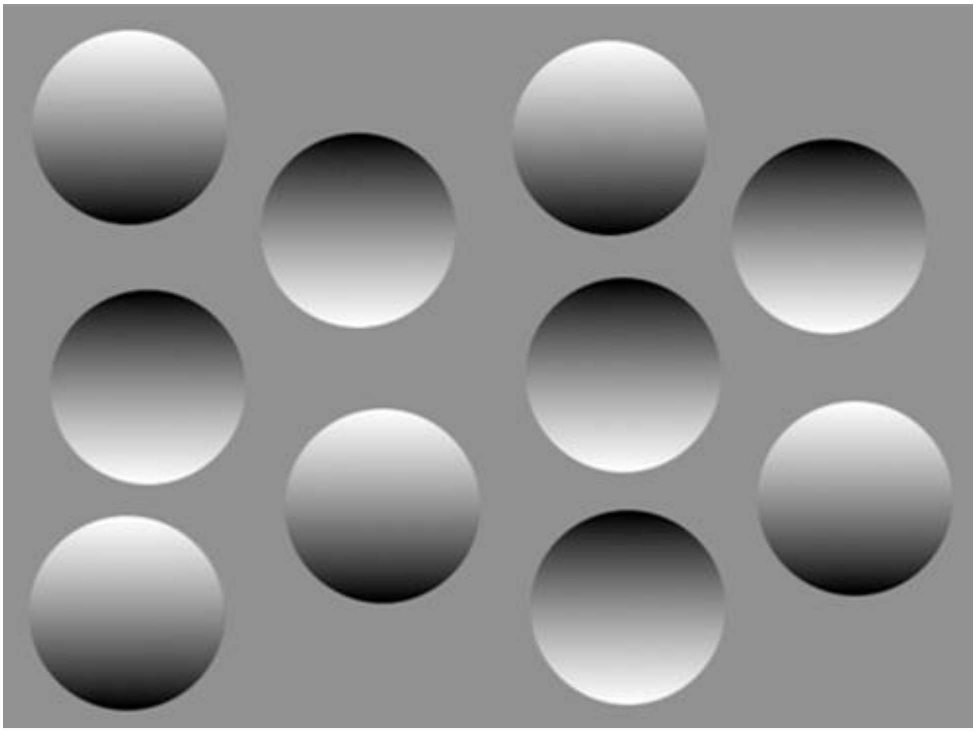

Figure 1.1: A group of spheres with two opposite shading directions, one as though lit from above and the other as though lit from below (adapted from Vision Research Lab, UCL, n.d.).

Intriguingly, Sun and Perona (1998) found that during a visual search task observers were faster at detecting a single target with the opposite shading among convex and concave hemispheres when the shading was consistent with the light source being placed above and left of vertical by as much as 60˚. This suggests that the above and left lighting was most compatible with the observers' prior assumptions about light sources; therefore those scenes were processed faster. An above and left assumption makes less ecological sense than an assumption of directly overhead lighting because humans have not evolved with the sun shining from the left more often than from the right. For this reason the left lighting assumption is of great interest.

Left lighting assumptions

Observers not only assume left lighting when performing a shape from shading task, but also when choosing where to place a light source in a scene without a shading cue. This can be seen in paintings, where an artist has had free choice in where the light source is placed. In a sample of 225 paintings from a range of periods, Sun and Perona (1998) found that artists most often choose a lighting direction left of vertical by 30-60˚. Similarly, Mamassian (2008) reported that of 659 paintings displayed in the Louvre museum spanning many centuries and styles, 84% of portraits and 67.3% of non-portraits depicted a light source from the above left. The reason for this could simply be that artists place illumination on the left to prevent them from painting in a shadow cast by their hand (Ruskin, 1857), which has resulted in more paintings with above left illumination. However, this is unlikely to be the lone factor causing the left lighting in paintings because the same asymmetry is seen more recently in modern magazine advertising (Thomas, Berkitt, Patrick, & Elias, 2008) in which painting in shadow would not be an issue. This suggests artists and advertisers simulate left lighting because that is where they assume or prefer the light to be. Furthermore there is evidence to suggest these left lit advertisements may be more effective. Hutchinson, Thomas, and Elias (2011) found observers rate brands more positively and express a higher intention to purchase when the advertisements contain above left, compared to above right, illumination. This shows that not only do observers assume above left lighting when making shape from shading judgments, but also that observers have a preference or a processing advantage for scenes which are compatible with this assumption.

Sun and Perona (1998) highlighted the left lighting assumption using a visual search task among shaded spheres. Subsequent reports have confirmed that the assumed light source direction is biased to the left of the observer using different tasks, such as shape classification of shaded spheres (Adams, 2007; Elias & Robinson, 2005; McManus, Buckman, & Woolley, 2004). Novel stimuli have also been generated specifically for the purpose of assessing observers' light source assumptions. The "polo mint" stimulus comprises of a ring divided into eight sectors, one of which has opposite shading to the remaining seven (Gerardin, de Montalembert, & Mamassian, 2007; see Figure 1.2). Therefore the stimulus can either be perceived as a convex ring with a section missing or a concave ring with a section protruding, depending on the direction of shading. Mamassian and Goutcher (2001) used bright and dark parallel lines on a grey background. These gave the illusion of either wide or narrow strips protruding from the background, the strips appearing to be narrowest when the light source was simulated above. Participants judged whether the strips were narrow or wide and the illumination position in which the strips were most frequently judged to be "narrow" was deemed the preferred illumination position.

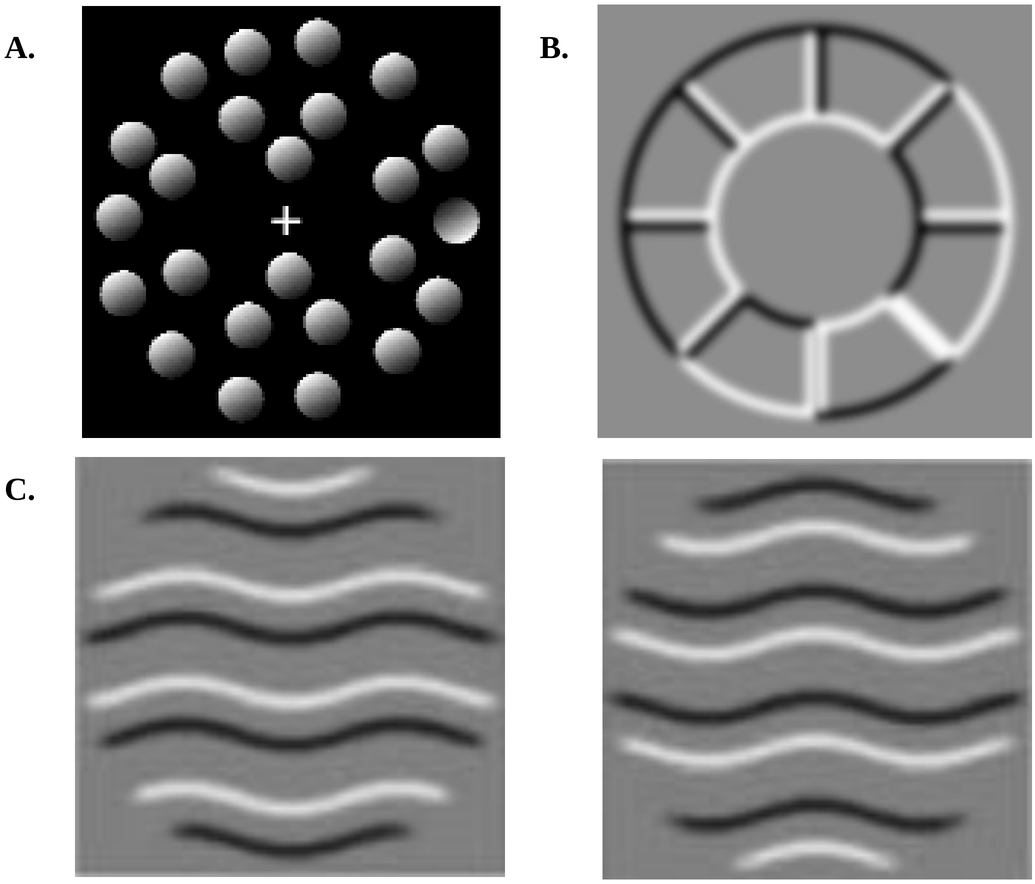

Figure 1.2: Stimuli used to measure light source biases. **A.** Visual search task used by Sun and Perona (1998); participants detected the sphere with the opposite shading. **B.** “Polomint” stimulus pictured as either a convex ring with a section missing, or a concave ring with a section protruding (Gerardin et al., 2007). **C.** Parallel lines giving the illusion of narrow (left) and wide (right) strips protruding from the background (Mamassian & Goutcher, 2001).

In shape from shading tasks designed to investigate observers’ lighting assumptions, lighting can be described by two angles, slant and tilt. Slant is the angle between the direction of light and the viewing direction thus it describes the angle of the illumination relative to the observer. Tilt is the angle between the projection of the light direction and the vertical axis in the frontal plane, meaning the tilt of the lighting direction describes the location of the illumination relative to the objects on screen. Shape from shading experiments use different illumination tilts and measure the resulting shape discrimination or target detection. This gives a measure of the distribution of participants' light from above assumptions, showing how probable they assume it is that the light is illuminating from each of the tilt angles. The mean of the distributions are then calculated to give an angle which represents the assumed illumination position for each observer.

Although the left lighting bias is consistently present across experiments and tasks, the strength of the bias is not. Group averages range from -5.1˚ (Adams, 2007) to -26.1˚ (Mamassian & Goutcher, 2001), which shows lighting assumptions may be affected by factors such as the type of stimuli being viewed, viewing time, restriction of binocular depth cues, or even individual differences among participants.

Kleffner and Ramachandran (1992) found that reaction times for detecting a target sphere with the opposite shading to the distracters did not increase linearly with the number of distracters, only when the shading gradients were vertical. When the shading gradients were horizontal there was an increase in reaction time, suggesting parallel search when convex and concave shapes are easily distinguished and serial search when they are not. Adams (2007) showed that the light prior is correlated in individuals across a visual search task with multiple items, a shape processing task requiring judgment of a selected target, and reflectance judgements. These findings indicate there is a single process responsible for perceived shape across the different tasks, suggesting perceived shape from shading may be a pre-attentive feature. However, further evidence suggests it may not be so simple. Champion and Adams (2007) used haptic training in the same procedure as Adams et al. (2004) and found that unlike the shape judgements, visual search performance did not indicate a change in participants' lighting assumptions after training. Champion and Adams attribute these results to differences in processing during visual search and shape judgement tasks; preattentive processing takes place in a visual search task where only speedy shape detection is required. In contrast, shape judgement tasks implement subsequent stages of processing which can take additional information into account such as recent experience from haptic training. This conclusion is supported by a later experiment which showed that head tilt has a greater effect in visual search tasks than shape judgement tasks, suggesting that in the shape judgment task additional processing allowed for some compensation of the head tilt (Adams, 2008).

Other left biases in visual processing

The left light source bias is not the only left bias demonstrated by human observers. When shown a chimeric face, a face composed of a left and right half showing a different expression, there is a preference to recognise facial emotions or identity using the side which appears in the left visual field (Campbell, 1978; David, 1989; Luh, Rueckert, & Levy, 1991). Also, when asked to mark the centre point of a horizontal line, healthy subjects show a tendency to overestimate the length of the left side (Bowers & Heliman, 1980, see Jewel & McCourt, 2000 for review). This is true even for lines which are meaningful, such as visual analogue scales for reporting pain (McKechnie & Brodie, 2008). Finally, observers show preferences in aesthetic judgements for pictures which depict the majority of weight in the left visual space and for pictures depicting left to right motion, such as with implied movement of transport (Christman & Pinger, 1997; Mead & Mclaughlin, 1992).

These biases are thought to reflect a right hemispheric advantage in the processing of visual information. The hyper-attention toward the leftward features of a chimeric face has been attributed to a right hemisphere dominance for face processing (Levy, Heller, Banich, & Burton, 1983). The right hemisphere, in particular the intraparietal sulcus is implicated in line bisection performance, as seen in imaging studies using healthy participants (Fink et al., 2000; Fink, Marshall, Weiss, & Zilles, 2001) and the disruption of line bisection performance after lesions in this area (Rorden, Fruhmann Berger, Karnath, 2006). Furthermore research has consistently shown that leftward bisections are more extreme when participants use their left hand, regardless of their hand writing preference (Failla, Sheppard, & Bradshaw, 2003; Jewell & McCourt, 2000; Scarisbrick, Tweedy, & Kulansky, 1987). This has been attributed to further increased activation of the right hemisphere with the use of the left hand, exacerbating hemispheric asymmetry (Kinsbourne, 1970; Kinsbourne, 1977).

Beaumont (1985) found that when viewing pictures containing one or two objects, participants looked to the right of the point of interest. Beaumont states this is to ensure the majority of the picture falls within the left visual field and thus will be processed by the right hemisphere. Levy (1976) argues that viewing pictures activates the right hemisphere which leads to an attentional bias in the contralateral direction, toward the left visual field. An attentional bias then causes greater perceptual weight to be placed upon stimuli in the left visual field. Similarly, Kinsbourne’s activation orientation theory states that there is a greater leftward bias in spatial attention due to the enhanced activity of the right hemisphere, which increases the salience of stimuli within the left hemispace (Kinsbourne, 1970; Kinsbourne, 1977). This could explain the preference for images lit from the left such as paintings (Mamassian, 2008) and advertisements (Hutchinson et al., 2011) in which the left illumination may be preferred because it highlights the side on which greater perceptual weight is placed, and thus the side which contains more salient stimuli.

Factors implicated in light source biases

Specific cerebral location

Evidence of other visual attentional biases suggests the right hemisphere may cause the left lighting bias (Kinsbourne, 1970; Kinsbourne, 1977; Levy, 1976). This raises the question of whether there is a more specific cerebral location which modulates light assumptions. Neurological evidence for the neural basis of the left lighting assumption comes from de Montalembert, Auclair, and Mamassian (2010) who measured the lighting assumptions of six patients with left hemispatial neglect (HN), one patient with right HN and healthy aged-matched controls participants. HN is a neurological syndrome, common after stroke and it most frequently presents after right hemisphere parietal damage (Vallar & Perani, 1986). HN patients fail to orient or respond to stimuli in the contralesional space (Heilman, Watson, & Valenstein, 1979) which impacts drastically on their lives. They may fail to dress the left side of their body or walk into objects on their left. The bias towards the right occurs not only for external stimuli but also for mental representations of the environment, for instance when recalling features of familiar landscapes (Bisiach & Luzzatti, 1978; Vuilleumier, Ortigue & Brugger, 2004). de Montalembert et al. investigated the effect HN has upon the mental representation of light sources.

Although some of the patients showed an ipsilesional shift in their assumption of the light position, there was no correlation between HN severity and light source assumptions. Of the patients with left HN, three of the patients showed a lighting bias which was right of vertical, one patient showed a bias of overhead lighting, and the remaining two patients showed left light biases slightly farther to the left than the control participants. The three patients who assumed the light sources were right of vertical had cortical lesions within the frontal, tempororal, and parietal areas of the brain, whereas the remaining patients had subcortical lesions. It was concluded that the fronto-temporo-parietal network modulates the lighting bias and damage to this area results in an inability to imagine light sources in the neglected space, thus the light sources are assumed to be right of vertical. In order to confirm that this network modulates the lighting bias, patients with damage to this network but without HN should also have been tested, to measure the effects of lesion that occur independently of attentional deficits.

Research into the cerebral basis of shape from shading using healthy observers has suggested that the estimation of the light source direction depends on a low level mechanism, within early visual areas (Humphrey et al., 1997; Mamassian, Jentzsch, Bacon & Schweinberger, 2003; Gerardin, Kourtzi, & Mamassian, 2010). Gerardin et al. (2010) asked participants to perform a shape from shading task with the "polo mint" stimulus whilst in a magnetic resonance imaging (MRI) scanner. Participants' behavioural responses showed that on average they estimated the light source to be 22.5˚ left of vertical. Using multivoxel pattern analysis (MVPA), activations after viewing trials which simulated left lighting were compared to activations for trials which simulated right lighting. Activation in early visual areas, including retinotopic areas, was modulated by lighting direction whereas activation in higher visual areas (such as the parietal lobes) was not. Gerardin et al. conclude the prior for assuming above left lighting is processed in early visual areas, with the argument that if the prior was fed in a top down manner from higher areas, they too would show activity for discriminating left and right lighting. Mamassian et al. (2003) report similar conclusions in an event related potential (ERP) experiment which showed early activation in low level visual areas correlated with the perception of shape from shading; and furthermore that shape is disambiguated within 100ms of stimulus onset. These findings conflict with the neurological evidence of de Montalembert et al. (2010) which suggested higher cortical areas modulate the lighting bias. If, instead, prior assumptions about lighting are stored in early visual areas this suggests the left lighting bias is modulated by different networks than other left visual processing biases which have been attributed to cortical right hemispheric hyperactivity.

Reference frames for "above"

If prior knowledge of lighting is stored in early visual areas, this raises the question of where knowledge of "above" is stored. To address this question one can change the orientation of an observer's head relative to the shaded stimuli. Behavioural evidence has demonstrated that as participants' heads are tilted, their shape from shading judgements change shift in the same direction. For instance if an observer views an image from an upside-down position they respond as though the shape is lit from below (Howard, Bergstrom, & Ohmi, 1990; Ramachandran, 1988; Wenderoth & Hickey, 1993). This suggests that "above" is also judged in early visual areas with reference to retinal coordinates, rather than participants' objective knowledge of above and below.

Interestingly, Adams (2008) found that although retinotopic coordinates dominate participants' shape from shading decisions, gravitational coordinates can also be utilised in specific tasks. Participants performed shape judgements and visual search tasks with their heads either upright or tilted by 45˚ or 60˚ to the left or right. When a fast and efficient visual search amongst an array of 16 objects was required, participants' light biases were shifted farther in the direction of their head tilt than when shape discrimination of one highlighted object was required. This suggests reference frames are employed differently depending on task demands. Although the head and retinal coordinates are apparently consistently used as a reference frame for above, during the shape judgement tasks additional cues to gravitational above may be incorporated, allowing observers to attempted to compensate for their misalignment.

This shows that head tilt causes a shift of the observers' lighting bias in the same direction. This raises the question of whether the left bias regularly measured in other experiments was due to the participants naturally tilting their heads to the left. McManus et al. (2004) measured the spontaneous head tilt of participants by photographing them standing naturally in front of a wall of horizontal lines. In the photographs a straight horizontal line was drawn across the face exactly intersecting the centre of the eyes. The angle that the line deviated from the horizontal lines in the background was taken as the measurement of head tilt. Across two experiments, McManus et al. found a significant correlation between participants' light bias, an average of 9˚ to the left, and head tilt. This suggests that left light source assumptions may not be due to an assumption that light sources are left of vertical. Instead, the assumption may be of overhead lighting but perception of above is altered by head orientation. However, the finding has not been replicated. Furthermore, the majority of experiments control for head tilt by using a chin rest or bite bar; therefore even if head tilt can explain the left bias measured by McManus et al., it cannot explain the left biases measured in other experiments. Adams (2007) measured whether head tilt could still affect judgements in other experiments by producing an after effect when the head was fixed. Using the same procedure as McManus et al., participants' natural head tilt was measured, as well as their lighting bias while their head position was fixed. There was little variation in head tilt between participants and it could not account for the variation in participants' light biases.

Putnam, Nooman, and Bellia (1996) found no correlation between head tilt and handedness, footedness, or eye dominance, suggesting that spontaneous head tilt is independent of cerebral dominance. Moreover, Putnam et al. found a rightward head tilt more common, present in 59% of participants, and also that tilt direction was stable over a period of 2-9 days. If spontaneous head tilt was a cause of the left light source bias it would seem logical that the majority of observers spontaneously tilt their heads to the left. Putnam et al.'s findings question the conclusion that spontaneous head tilt causes left light source assumptions in most observers. This suggests that although head tilt may modulate light source biases due to the reliance of retinal rather than gravitational coordinates as a reference frame (Adams, 2008; Howard et al. 1990; Ramachandran, 1988; Wenderoth & Hickey, 1993), it is not the cause of the left lighting bias in experiments where fixation is fixed.

Handedness

Sun and Perona (1998) reported a correlation between handedness and light source bias, with left handed participants demonstrating a weaker leftward bias than right handed participants (7.9˚ and 23.3˚ to the left respectively). This was consistent with differences between left and right handed groups in other visual processing tasks such as line bisection tasks (Bowers & Heliman, 1980; Scarisbrick, et al.,1987) and chimeric faces tasks (Hoptman & Levy, 1988; Levy et al., 1983). These differences have been attributed to cerebral dominance (Beaumont, 1985; Bowers & Heliman, 1980; Scarisbrick, et al., 1987) and would appear to support the conclusions of de Montalembert et al. (2010) that lighting assumptions shift to the right when the right hemisphere is no longer dominant.

Instead, Sun and Perona (1998) suggested that the habit of positioning light sources relative to objects of interest may underlie this correlation, for instance on the side opposite to the writing hand to avoid casting a shadow over their work. Thus, right handed individuals would preferentially place a desk lamp on their left, and therefore would have more experience with light originating from the left than from the right. This alters observers' opinions of "normal" lighting until the assumption is that light usually originates from the above left. However, to avoid writing in shadow, left handed individuals would have to do the opposite and place the desk lamp on the right. The authors suggested that left handed individuals have a reduced left bias rather than a mirrored symmetric bias to the above right because not all light sources can be manipulated by the observer. They suggest that most light sources in the environment are suited to the predominantly right handed population, which results in lighting in the environment being placed to benefit right handed people. Thus, right handed observers consistently experience optimal lighting, left of objects of interest, whereas left handed observers are exposed to a wider range of light source directions, thus modifying their lighting bias.

Subsequent studies have failed to confirm an effect of handedness in the assumed light source direction (Mamassian & Goutcher, 2001; McManus et al., 2004), including performance in similar visual search tasks (Adams, 2007). The reason why Sun and Perona (1998) measured a strong correlation when it has failed to be replicated is unclear, although Mamassian and Goutcher (2001) suggest cerebral dominance does affect light source assumptions and that there may have been several participants with left cerebral dominance among Sun and Perona’s left handed population.

Visual field preferences

Mamassian and Goutcher (2001) suggested that biases in the assumed direction of the light source reflect a visual field preference, similar to the left bias found in other visual processes. As mentioned above, observers predominantly rely upon the right side of a face for recognition and emotion judgements (Campbell, 1978; David, 1989; Luh, et al., 1991). Mamassian and Goutcher state that in order for the left side of a stimulus to be optimally perceived it must be properly illuminated. This could change light source assumptions both directly and indirectly. When performing a shape from shading task the light source is not explicitly present in the scene. Instead mental representations of the light source must be used to identify the shape. It could be that as the left side of visual stimuli are preferred, when an observer is shown an ambiguous shaded object they internally represent the illumination above and left of the scene, as they would prefer. Alternatively, as higher perceptual value is placed predominantly on the left side of stimuli, observers manipulate light sources in their environment so the left side has the greater illumination.

Within the natural environment scenes are often complex, containing multiple objects. In these cases the left side of convex objects will be brighter across the visual field. As above and left lighting becomes the most common lighting direction for the observer, this affects their assumptions about normal lighting. So when performing a shape from shading task their assumption represents the lighting direction that is normal for their environment. This latter proposal is compatible with Sun and Perona's (1998) suggestion of light and object orientation, except rather than manipulating light sources and objects due to handedness, manipulations occur because higher perceptual value is placed on the left side of visual stimuli.

Right hemisphere specialisation has been implicated in other left visual field biases in visual processing (Beaumont, 1985; Bowers & Heliman, 1980; Scarisbrick, et al., 1987). Therefore, if a visual field bias does alter observers' perception of normal lighting, this suggests hemispheric asymmetry may be ultimately, although indirectly, responsible for the left light source assumption.

Experience

The above evidence suggests that left light source biases may be learned, based on our experience with light sources, rather than an innate and fixed preference. Thomas, Nardini, and Maraschal (2010) investigated the development of shape perception by showing children of different ages and also a group of adults the "polo mint" stimulus (see Figure 1.2). In some stimuli presentations the "light from above" assumption and the "convexity" assumption (the tendency to perceive an ambiguous shape as convex rather than concave often regardless of the light position; Symons, Cuddy, & Humphrey, 2000) were compatible, and in other presentations they were not. When resolving the conflicting assumptions the young children, aged 4-5, assumed the stimulus was convex regardless of lighting direction. However the 6-8 year olds and 9-12 year olds showed the same resolution as the adults, which was to assume overhead lighting instead of convexity. Furthermore, the preference for left compared to right lighting increased with age group. Therefore the left lighting bias is not innate or fixed. Instead, young children assume stimuli in their environment are convex, which the authors state is likely due to their regular interactions with convex rather than concave objects.

Gori, Del Viva, Sandini, and Burr (2008) found that the ability to properly integrate visual and haptic cues does not develop until 8-10 years of age. Prior to this, one or other cue is dominant, regardless of its reliability. Although the task was measuring height estimations rather than light source assumptions, the fact that cross-modal integration development is delayed suggests young children make estimates about their environment differently to adults, despite the environmental information being the same. As children grow older and they learn to integrate information from multiple cues, their assumptions about lighting in their environment develops, beginning with an assumption of above lighting and developing into an assumption of above left lighting throughout childhood. Therefore long term experience can modify light source assumptions. Further testing with age groups older than 9-12 but pre-adulthood would help to identify the age at which adult assumptions are established, which would provide more information on why the assumption is for above left.

It is not only long term experience which can alter light source assumptions. Adams, Graf, and Ernst (2004) measured participants' baseline lighting bias using a shape judgment task with shaded spheres. Then, in a training phase haptic representations of the spheres were presented alongside the visual presentation. However the haptic information represented a shift of the participants' lighting bias by 30˚ to the left or right. Therefore some haptic sphere presentations were incompatible with their baseline assumptions, meaning some spheres which looked convex felt concave or vice versa. This training phase affected subsequent judgements of visually presented sphere stimuli. Participants with a shift of 30˚ to the right in the training phase showed a shift from their baseline bias of 13.8˚ to the right; those with a shift of 30˚ to the left showed a shift of 17.6˚ to the left. This modification of perceived shape generalised to a different task, suggesting that the assumed light source direction was updated rather than the shape assigned to specific spherical stimuli. Adams et al. concluded that assumptions about the environment are constantly being updated based on evidence. They therefore predicted the participants' light assumptions would return to baseline quickly once normal interactions with the environment resumed. If light source assumptions are indeed constantly being updated this suggests that the factor(s) causing this left assumption must be continually present in the environment.

Later evidence, however, suggests this is not the case. In a similar haptic training design, Adams, Kerrigan, and Graf (2010) found that the effects of the training were still evident days after the original session, despite the participants presumably experiencing their environment as usual between sessions. Similarly, in a previous study of experience-dependent visual learning, participants decided whether target bars among distracters were horizontal or vertical, with increasingly shorter presentation times. Participants' sensitivity to quicker presentation times increased over training sessions 1-3 days apart. The effects of this training were still present over a period of two to three years (karni & Sagi, 1993). Although this task was slightly different and training improved visual detection rather than modifying environmental assumptions, it still demonstrates the long term effects of training in a visual learning task.

Context dependant assumptions

If light source assumptions can be so quickly modified by an environment, it would be most advantageous to retain assumptions about light sources specific to different environments, so shape perception can be accurate for different lighting contexts. Adams et al. (2004) found that a shift in light source assumptions can generalise to previously unseen stimuli which would suggest that there is a single light source assumption which is constantly updated for each new environment. However, using a similar training session with incompatible visual and haptic spheres to induce a shift in light assumptions, Adams et al. (2010) recorded training induced shifts days and even weeks after the training session. This contrasts the earlier findings for it suggests that the participants learned the shifted light source assumption applied exclusively to the experimental context, which explains why it was not updated by their natural environmental interactions between testing sessions.

To address this disparity, Kerrigan and Adams (2013) created different contexts within a haptic training session by illuminating the stimuli with a green or a red light. In the red lit trials the visual and the haptic stimuli were compatible with the participants' baseline assumptions. During the green lit trials the haptic stimuli were consistent with a light source shifted 30˚ to the left or right, the same as the procedure in Adams et al. (2004). In a post-training shape judgement task, light biases changed significantly more for the green stimuli than the red stimuli, with the shift for green stimuli comparable to the original experiment using haptic training (Adams et al., 2004). Interestingly, however, shifts from baseline also occurred for the red stimuli although to a lesser extent. This suggests that although the different colour contexts were learned, assumptions were still updated by training across contexts. Importantly, it also shows that observers are able to associate specific lighting with different contexts, presumably in order to aid their shape recognition in these contexts.

Summary

Many reasons for the left lighting bias have been posited. Some have failed to be replicated such as handedness and spontaneous head tilt. Other findings have demonstrated modulation of light biases, such as haptic training and specific lesion locations, and yet these have failed to explain why the assumption remains above and left for healthy observers. The remainder of this thesis aims to answer this question.

Chapter 2. Cultural Experience*

Chapter Overview

The current chapter assesses the contribution of cultural factors affecting habitual scanning direction, in determining the assumed light source direction. Left and right handed first language English and Hebrew participants, who read and write from left to right and from right to left, respectively, judged the shape of shaded stimuli. Both groups showed biases above and to the left; however the first language Hebrew participants showed a significantly smaller bias. In neither group was the light bias affected by participants' handedness. Findings show that the bias in the assumed light source direction is affected by cultural factors, likely related to the habitual scanning direction employed by participants when reading and writing their first language script.

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Observers use various depth cues in order to recover the three dimensional shape of surfaces from their retinal image. Shading is one such cue. When judging the shape of shaded objects while no information is present about the position of the light source, people tend to assume that the light source is located above, rather than below the object itself (Cavanagh & Lecerc, 1989). Therefore a shaded grey sphere will usually be reported as convex when lighter at the top and concave when lighter at the bottom. This assumption reflects an environmental regularity as sun light and most artificial lights are placed above the observer (Ramachandran, 1988). Research into the cerebral basis of shape from shading has suggested that the estimation of the light source direction depends on a low level mechanism, within early visual areas (Gerardin et al., 2010; Humphrey et al., 1997; Mamassian et al., 2003). Behavioural data have offered some confirming evidence to this idea, for example, demonstrating that the light source is predominantly represented in retinal or head-centric coordinates (Howard et al., 1989; Kleffner & Ramachandran, 1992; Wenderoth & Hickey, 1993) but gravitational influences on shape judgements have also been found (Yonas, Kuskowski, & Sternfels, 1979; Adams, 2008).

Intriguingly, using a visual search task, Sun and Perona (1998) found that observers were faster at discriminating the shape of convex and concave hemispheres when the shading was consistent with the light source being placed above and left of vertical by as much as 60˚. Subsequent reports have confirmed that the assumed light source direction is biased to the left of the observer (Mamassian & Goutcher, 2001; McManus et al., 2004; Gerardin et al., 2007; Thomas et al., 2010). Yet the reason for this bias remains unclear.

Sun and Perona (1998) reported a correlation between handedness and left bias, with left handed observers demonstrating a weaker leftward bias than right handed participants. The authors suggested that the habit of positioning light sources on the side opposite to the hand used to write, to avoid casting a shadow with their writing hand, may underlie this correlation. Thus, right handed individuals would preferentially place a desk lamp on their left, and therefore would have more experience with light originating from the left than from the right. It was posited that left handed individuals have a reduced left bias rather than a mirrored symmetric bias to the above right with the fact that the environment is suited to the predominantly right handed population, which results in lighting in the environment being placed to benefit right handed people. Thus, Sun and Perona attribute the handedness difference to experience interacting with the environment.

Even though subsequent studies have failed to confirm a handedness difference in the assumed light source direction (e.g., Mamassian & Goutcher, 2001; McManus et al., 2004), the suggestion that biases are influenced by learning and experience has received experimental support. Thomas et al. (2010) investigated the development of shape perception and found that young children, before age 6, assumed the stimulus was convex regardless of lighting direction, but the left bias arises around the time when children achieve literacy. Furthermore, Adams et al. (2004) modified the shape judgements of shaded spheres by implementing a training phase whereby haptic information about visually presented spheres was incompatible, meaning some spheres which looked convex felt concave or vice versa. This modification of perceived shape generalised to a different task, suggesting that the assumed direction of the light source was updated rather than the shape assigned to specific spherical stimuli. These studies support the assumption that the left bias depends on learned regularities in the environment.

Mamassian and Goutcher (2001) suggested instead that biases in the assumed direction of the light source reflect a visual field preference, similar to the left bias found in other visual processes. For example there is a preference to recognise faces using the right side, which appears in the left visual field (Campbell, 1978). Similarly, line bisection tasks show a tendency for healthy subjects to overestimate the length of the left side (Bowers & Heliman, 1980). These results are thought to reflect a right hemispheric advantage in the processing of visual information (Scarisbrick, et al., 1987).

If the left lighting bias does reflect a visual field preference then it may be that it is also mediated by hemispheric dominance. This could also explain the handedness effect reported by Sun and Perona (1998) because the probability of atypical cerebral lateralisation increases with left handedness. There is consistent evidence that right hemisphere language dominance is more likely to occur in left handed individuals (Isaacs, Barr, Nelson, & Devinski, 2006; Knecht et al., 2000). However evidence for cerebral dominance in attention and visuospatial tasks is more mixed. Masure and Benton (1983) administered a line orientation judgement task to fifteen non-right handed patients with right or left hemisphere frontal and temporal lobe lesions. Six of the eight patients with right hemisphere lesions performed significantly worse than the control participants whereas all of the left hemisphere patients performed within the normal range. Furthermore three of the right hemisphere patients who showed a deficit in this task were also aphasic. These results suggest that visuospatial functions are mediated primarily in the right hemisphere in both handedness groups, even when the right hemisphere is also dominant for language. However a different study with a larger number of patients with left hemisphere lesions (21 left handed and 57 right handed) and more comprehensive visuospatial tasks found that the left handed patients were significantly more impaired, particularly on tests requiring visuo-perceptual and spatial organisational skills (Borod, Carper, Naeser, & Goodglass, 1985). This suggests cerebral dominance for visuospatial processing can differ in left and right handed individuals because the left handed patients had more left hemisphere representation of non-verbal functions. However it is not evidence of a completely switched cerebral dominance in these left handed patients; simply that it is more bilateral in some left handed people.

Several studies have demonstrated that visual field biases are influenced by cultural factors: for example Hebrew and Arabic participants, who read from right to left, show a right side preference in tasks using nonverbal stimuli (Chokron & De Agostini, 2000) and a reversal of the line bisection bias (Chokron & Imbert, 1993). Vaid and Singh (1982) administered a chimeric faces task to 131 right handed and 31 left handed participants in four different language groups, Hindi (left to right reading) Urdu/Hindi (bi-directional), Arabic (right to left) and illiterates. The Hindi readers and Arabic readers showed opposing preferences for the left and right halves of the faces respectively, although the bias was not as strong in the Arabic readers and was not statistically different from the bi-directional readers and illiterates who did not show a preference. There was no effect of handedness, however there were relatively few left handed participants and there were an unequal number in each language group.

There is no experimental or neuropsychological evidence for reversed cerebral lateralisation in people with right to left reading habits. This suggests that lifelong learned habits, including scanning direction, affect visual processes commonly attributed to hemispheric dominance. Vaid and Singh (1982) conclude that reading direction and cerebral lateralisation interact, because if reading direction were the sole determinant then the Hindi and the Arabic readers would have showed mirror symmetric biases. The authors attribute the lack of handedness effect to cultural effects. Vaid and Singh state a lesser acceptance of left handedness in Muslim cultures could have led to the inclusion of some latent left handed participants in the right handed sample.

The current study tested right and left handed English and Hebrew participants on a shape from shading task, designed to measure participants' assumed light source direction. If the assumed light source bias is related to the observer's experience of handedness, as proposed by Sun and Perona (1998), then a difference between the left and right handed participants would be expected in both groups. An effect of handedness may also be expected if cerebral dominance mediates the lighting bias. However as mentioned above this effect is unlikely to be seen without a large number of strongly left handed participants. On the other hand, if cultural factors influence the assumed light source direction, then the Hebrew participants may demonstrate opposite or smaller biases than the English participants.

Gerardin et al. (2007) suggested that previously used stimuli, including spheres (Sun & Perona, 1998) and undulated stripes, (Mamassian & Goutcher, 2001) may not have contained much salient depth. To address this, a new stimulus, the "honeycomb" was created as a stimulus in which it is easy to perceive depth and which a multitude of different lighting tilts can be simulated. Gerardin et al. found differences in shape judgements of the polomint stimulus over seven levels of blur. However in the higher three levels of blur participants reported the ring shape as convex the majority of the time. As such, different levels of blur should be used to investigate whether the honeycomb stimulus has an optimal level of blur, which would be seen in participants' reaction times.

Experiment one: First Language English Group

In the first experiment we estimated the assumed light source direction in right and left handed first language English speakers using a novel stimulus. The stimulus consisted of a central hexagon surrounded by six shaded hexagons. Participants reported whether the central hexagon appeared pushed in or out compared to the surrounding hexagons (see Figure 2.1). The stimulus was presented in different orientations, allowing the assumed light source directions to be estimated.

Participants

Sixteen (ten right handed) undergraduate students at Bangor University were recruited and received course credit for their participation (aged 18-26). Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). All participants had normal or corrected to normal vision. Participants' first language was English. The experiment was approved by Bangor University's ethical committee and complied with the declaration of Helsinki.

Apparatus and stimuli

Participants were tested in a dimly lit room. A LaCie Electron 22blue CRT monitor was used to present the stimuli. The screen resolution was set at 1024x768 pixels. A chin rest was used to ensure that participants maintained a constant distance of 60cm from the screen.

The stimuli were drawn using proprietary software (Inkscape, Software Freedom Conservancy, Inc. Brooklyn, NY) and presented on E-Prime (Psychology Software Tools, Pittsburgh, PA). The stimuli consisted of seven hexagons on a grey background; each edge was either brighter or darker than the background (see Figure 2.1). The pattern of these light and dark edges gives the impression that the inner hexagon and the outer hexagons have a different shape. In both the left and the right presentations of the stimulus in Figure 2.1, observers can perceive the central hexagon as pushed in and the surrounding hexagons as protruding out or vice versa. Extra-retinal knowledge must therefore be utilized in order to recover either of these shape options. Observers' prior distributions state the light is likely to originate from above and unlikely to originate from below; as such observers usually perceive the central hexagon as protruding out in the left presentations and pushed in in the right presentations. The stimulus size was 14.3˚ diameter. This stimulus orientation was varied over 24 levels, 15˚ apart.

The new stimulus was presented in three different levels of blur by applying three low pass Gaussian filters and measured the bias and variability of responses in each level of blur. Level of blur is expressed as a percentage, where 100% corresponds to a blurring radius of 1/8 of the stimulus perimeter. The blur levels used were 1.0% 1.4% and 1.8%.

A.

B.

C.

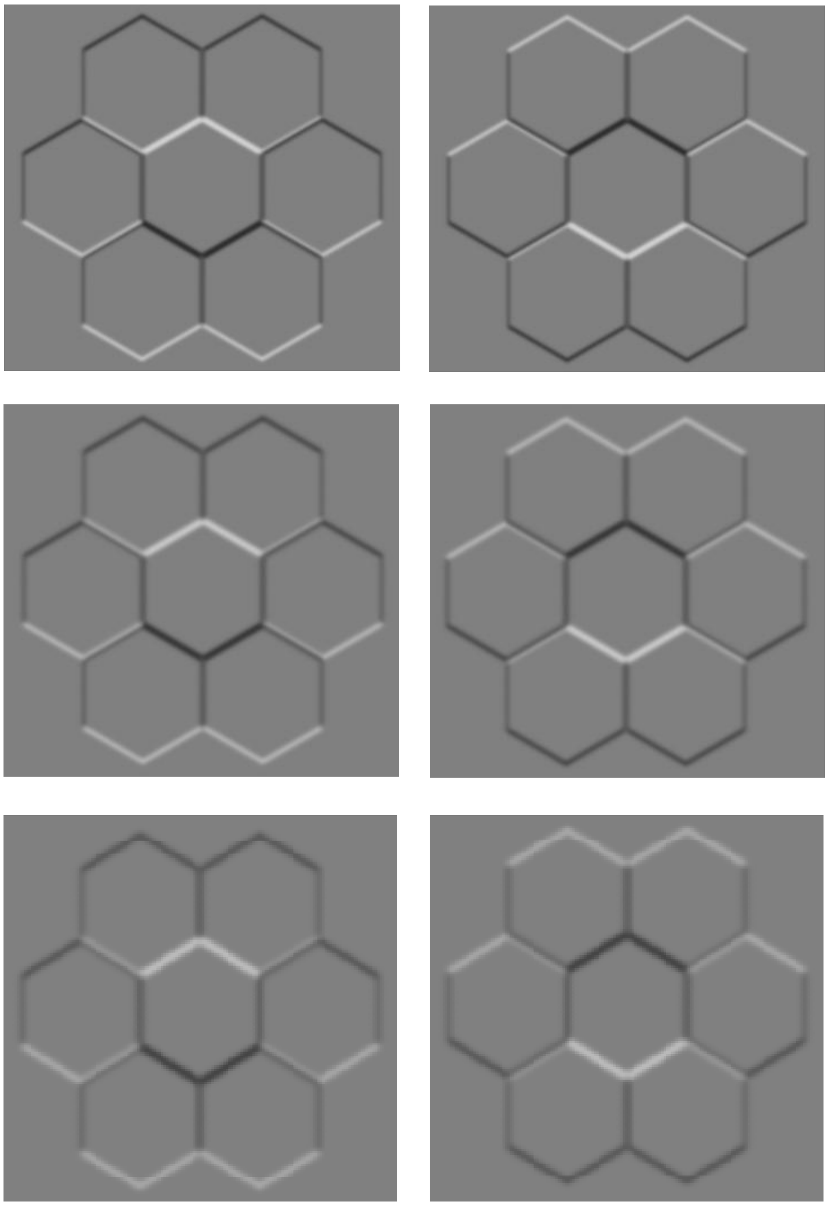


Figure 2.1: Experimental stimulus with three levels of blur with light and shadow as though lit from 0˚ (left) and 180˚ (right). The standard deviation of the Gaussian filter applied was **A**. 1.0%. **B**. 1.4 %. **C**. 1.8%.

Procedure

Each participant's handedness was tested using the Edinburgh Handedness Inventory. Prior to the data collection blocks, participants completed a practice block of 24 trials. Five testing blocks consisted of 144 trials presented in a random sequence. Each trial began with a central fixation cross presented for 1000ms followed by the stimulus, presented for 500ms (1,000ms in the practice trials). Immediately after the stimulus presentation a prompt appeared on screen containing the following written question "is it in (left) or out (right)?". Participants pressed one of two keys indicating whether they perceived the centre hexagon to be pushed in or out.

Results and discussion

The relation between the proportion of convex judgements ("out" response) and the stimulus orientation was estimated for each participant using a multivariate logistic regression:

$$\mathrm{p}(\mathrm{C}|\theta) = \frac{1}{1 + e^{-\mathrm{f}(\theta)}}$$

This is the most appropriate model because the dependent variable is binomial (participants could only respond "in" or "out").

The independent variables included a constant term and a series of sine and cosine functions of the stimulus orientation, θ, in the image plane:

$$f(\theta) = \alpha_0 + \alpha_1 \cdot \cos(\theta) + b_1 \cdot \sin(\theta)$$

The assumed light source direction was then computed using the following formula:

$$O_{light\_source} = \tan^{-1}\left(\frac{b_1}{\alpha_1}\right)$$

Negative values for the assumed light source direction indicate biases to the left of vertical. Figure 2.2 shows the proportion of trials in which a typical participant reported the central hexagon to be pushed out as a function of the orientation of the stimulus.

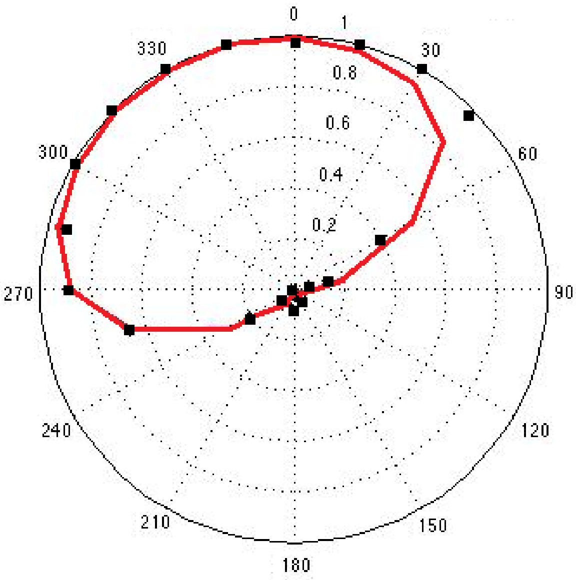


Figure 2.2: Data for one representative participant whose assumed light source was estimated to be 22.5˚ to the left of the vertical. The filled squares show the proportion of "out" responses for each stimulus orientation. The line shows the model fit. The 0˚ orientation corresponds to stimuli where the central hexagon was brightest at the top.

In order to establish whether a participant's reports were significantly modulated by the orientation of the stimulus, we computed the ratio of the log-likelihoods of two models.

The log-likelihood of each model $f(\theta)$ was computed using the following expression:

$$\Lambda = \sum_{i=1}^{n} \log\left(\frac{1}{1+e^{-f(\theta_i)}}\right) + \sum_{j=1}^{m} \log\left(1 - \frac{1}{1+e^{-f(\theta_j)}}\right)$$

Where Λ is the log-likelihood of the model, *i* is an index over trials where the participant reported a convex central hexagon and *j* is an index over trials where the participant reported a concave central hexagon, *m* is the total number of trials where the participant reported a convex central hexagon and *n* is the total number of trials where the participant reported a concave central hexagon.

The first model included only the constant term as an independent variable, the second model included also the first terms of the harmonic series. These models were compared because the model which contained only a constant term accounted for any convexity/concavity response bias independent of the stimulus orientation. The model containing the first terms of the harmonic series assumed instead that there is a periodic relation between the probability of reporting central hexagon as either sticking in or out from the background and the orientation of the stimulus, whose frequency is one cycle per full rotation of the stimulus.

The ratio of the log-likelihoods has an approximately chi squared distribution with two degrees of freedom. Data from participants whose log-likelihood ratio was associated with a p-value greater than 0.01 were not included in the group level analysis. None of the participants in the English group met this criterion.

The data fitting procedure we used is not based on some theoretical prediction, but rather on analytical convenience. Therefore computing the goodness of fit would not provide by itself theoretically relevant information. Additionally, we found that estimates of the light source direction obtained from fitting extended harmonic series did not differ substantially from those obtained by fitting the model mentioned above containing only the sinusoids and cosinusoids of the fundamental frequency, suggesting that using more complex models did not change the ultimate result.

Effect of blur

A repeated measures ANOVA with blur (three levels) as an independent factor, shows blur to have no significant effect on reaction time, $F(2, 28) = .45$, $p = .65$, $\eta^2_p = .031$.

The mean bias was similar across blur levels 1.0, 1.4, and 1.8 percent (means= -25.72, -27.31, & -22.4 respectively). A one factor (blur) repeated measures ANOVA shows no significant difference in bias between blur levels, $F(2,28)= .92$, $p=.41$, $\eta^2_p=.062$. z3Data obtained with different blur levels were collapsed in subsequent analyses.

Effect of handedness

The light source bias in the right and left handed groups is shown in figure 2.3. Most of the right handed participants were strongly right handed (laterality score range = 80 - 100, mean = 94) whereas scores were more varied among the left handed group, with only one participant scoring -100 (laterality score range = 0 - -100, mean = -58).The light bias was slightly larger for the left handed (mean=-29.18˚, SE=5.51) than the right handed (mean=-25.46˚, SE=4.58) participants. However, an independent t-test showed no significant difference between left and right handed participants $t(14)= -.51$, $p= .62$. Similarly, the Spearman's correlation between strength of handedness and assumed light source direction was not significant, r= -.03, $p= .46$.

The honeycomb stimulus demonstrated a consistent left lighting bias in English readers. The magnitude of the bias is similar to Mamassian and Goutcher (2001) and Gerardin et al. (2010) who reported biases of -26.1˚ and -22.5˚ respectively. These two experiments also asked participants to judge the shape of single centrally presented stimuli.

Our findings confirm there is no effect of handedness on assumed light source direction, in agreement with previous reports (Mamassian & Goutcher, 2001; McManus et al., 2004). Neither was there an effect of blur, contrary to Gerardin et al. (2007). The current experiment used only three different levels of blur, whereas Gerardin et al. presented seven blur conditions and with the greatest level of blur the individual segments were indistinguishable. This suggests the nonsignificant effect of blur was due to the similarity between each level.

Experiment Two: First Language Hebrew Group

We then estimated the assumed light source in first language Hebrew participants. If cultural factors influencing habitual scanning direction also affect the processing of shaded stimuli then the Hebrew participants may show a smaller left bias, or a right bias. To test further the effect of handedness, we tested right and left handed participants.

Participants

Seventeen participants (nine right handed) from Ben-Gurion University of the Negev in Israel, aged 20-25, took part in the experiment for course credit. All were first language Hebrew and had normal or corrected to normal vision. Participant's handedness was established by self-report. The experimental protocol was approved by Ben-Gurion University.

Apparatus and Stimuli

Stimuli were displayed on a Dell LDC screen placed at a distance of 60cm from the observers, held constant by a chin rest. As in Experiment 1 stimuli were presented at 24 different orientations 15˚ apart, with a stimulus size of 17.6˚ diameter. As there was no effect of blur in Experiment 1 the middle level of blur was chosen for this experiment.

Procedure

A training block consisting of 24 trials with a stimulus presentation of one second preceded four blocks of 240 trials each. Each of the stimulus orientations was presented 40 times in a random order. The rest of the procedure was identical to the procedure used in Experiment 1.

Results

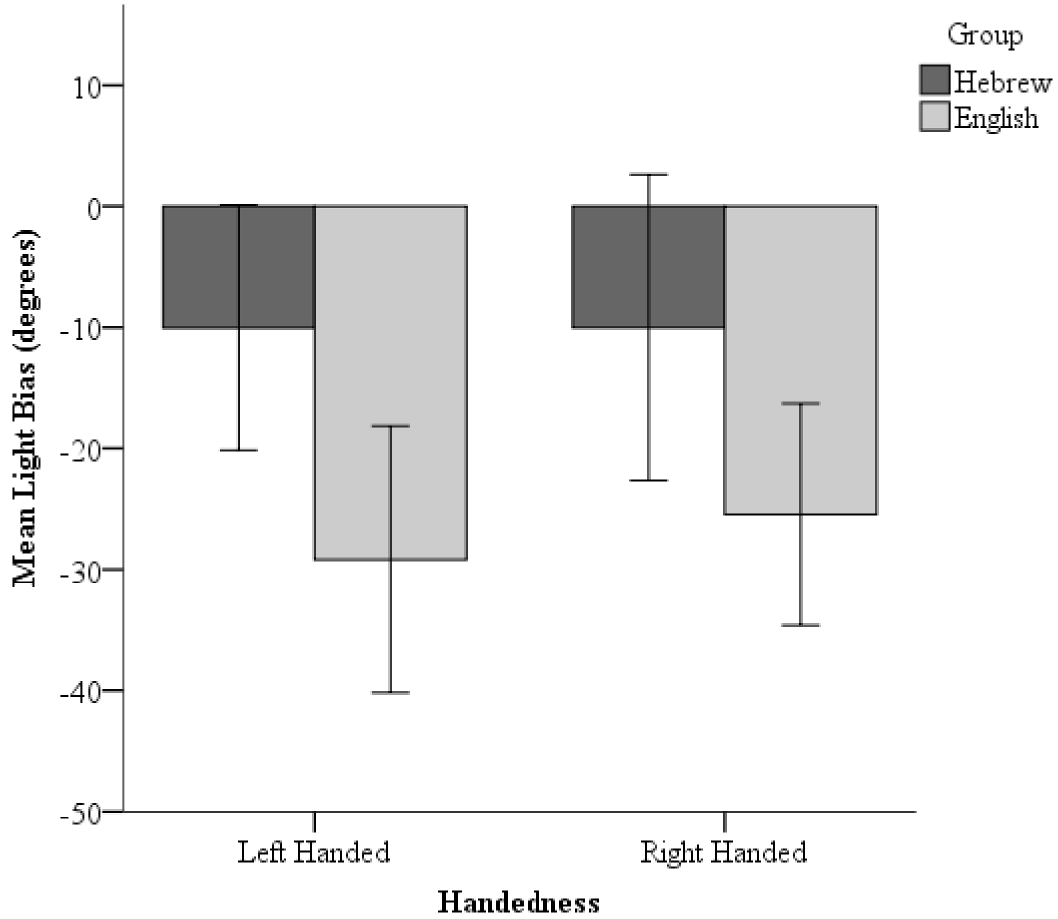
Two (right handed) participants showed log-likelihood ratios of *p*=.56 and *p*=.49, suggesting that their responses were not modulated by the stimulus' orientation, so their results were excluded from the study. A left handed participant was also excluded as their results were consistent with the assumption that the light was coming from below rather than above. This is because an assumption from below is highly unusual, both within the experiments in this thesis and also in the literature. As such this particular result could be indicative of something other than the participant's lighting bias; for example it is possible that the participant made a mistake when pressing the keys, which would reverse their responses. As there is no way to verify this, the safest thing is to remove the participant.

The assumed light source direction did not differ significantly between right handed (Mean= -10.01˚, SE= 6.31) and left handed (Mean= -10.03˚, SE=5.06) Hebrew participants, $t(13)=-.003, p=.99$.

The average bias for the Hebrew readers was -10.02˚ (range = -34.79 - 22), while the average bias for the English readers was -26.86˚ (range = -51.16 - 0.73; see Figure 2.3). Only one English reader showed a bias which was not left of 0˚, whereas three of the Hebrew readers showed a bias right of 0˚.

A factorial ANOVA with handedness (right and left) and group (English and Hebrew) as factors showed a significant effect of group $F(1,26)=10.14$, $p=.004$, $\eta^2_p=.28$. The main effect of handedness was not significant $F(1,26)=.12$, $p=.73$, $\eta^2_p=.01$, nor was the interaction of handedness and group $F(1,26)=.12$, $p=.74$, $\eta^2_p<.001$.

A.



B.

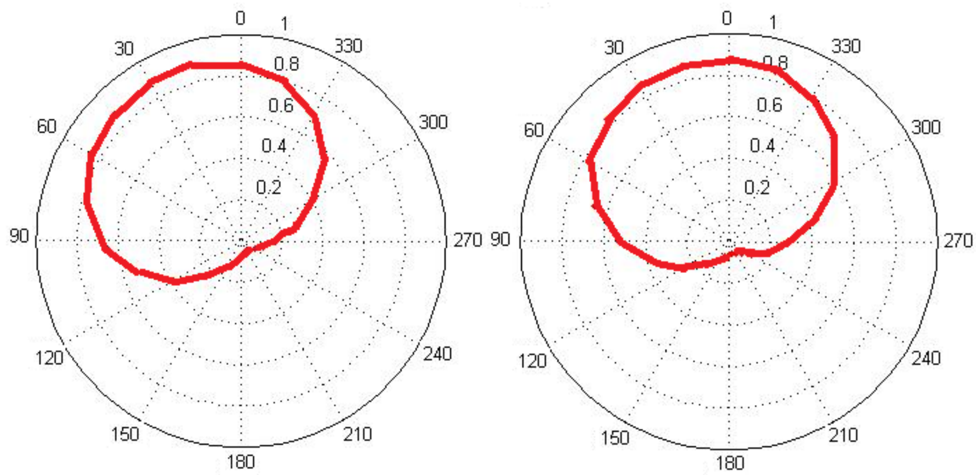


Figure 2.3: **A.** Graph displaying the mean light bias in degrees for the left and right handed participants in the English and Hebrew speaking groups. Negative bias scores indicate scores left of vertical. Error bars indicate ±1SE. **B.** Polar plots displaying the prior distributions of the English (left) and Hebrew (right) groups.

General Discussion

Several conclusions can be drawn from this study: first, the light source bias is not influenced by the observer's handedness. Second, cultural factors may affect the assumed direction of the light source. Finally, regardless of handedness and experience, there appears to be a default bias to place the light source left of vertical.

Sun and Perona (1998) found that the bias in the assumed light source direction was related to handedness. In agreement with subsequent studies (Mamassian & Goutcher, 2001; McManus et al., 2004) we did not find any difference between left and right handed participants. This suggests that left and right handed observers do not use different strategies when orienting objects relative to light sources. This questions why Sun and Perona (1998) reported a strong correlation when it has failed to be replicated multiple times. Sun and Perona attribute the effect of handedness to different interactions with objects relative to light sources. However this conclusion is not based on any evidence. It may be more informative in the future if alongside a handedness assessment participants also reported some of their light manipulations. For instance, if they have a desk, where do they place the lamp? This would give at least a rough estimate of whether there is a difference in object and light source manipulations between left and right handed individuals. Mamassian and Goutcher (2001) suggest that several of the six left handed participants among Sun and Perona's left handed population may have had opposite cerebral dominance and that this caused the difference between the left and right handed groups. This conclusion suggests that hemispheric dominance does mediate the lighting bias. While the data in this chapter do not support this because there was no effect of handedness, an absence of evidence for cannot be taken as evidence against, particularly with the small sample size of left handed participants.

There was, however, a difference in the direction of the assumed light source between first language English and Hebrew participants. Although the participants in both language groups displayed a left bias, the bias was significantly smaller in the Hebrew than the English participant group. Similar results have been found in visual processing of objects and faces. Right-to-left readers do not show the same left visual processing bias as left-to-right readers, demonstrating instead a preference for the right side of objects (Chokron & De Agostini, 2000; Chokron & Imbert, 1993) and a reduced left visual field bias in face processing (Gilbert & Bakan, 1973). Chokron and De Agostini (2000) state that reading direction can affect the way attention is directed, resulting in observers directing attention toward the side on which they begin reading. Therefore Hebrew readers may direct their attention toward the right of stimuli and place higher perceptual value on the right side of objects. This would result in different object and light manipulations within their environment and subsequently affect their lighting preferences.

There is a difference between processing faces and objects and performing a shape from a shading task because the former requires forming judgements on visible properties of the stimulus, whereas the latter requires the participant to form a mental representation of the light source which is not visible on the screen. Our results imply that habitual scanning direction affects the internal layout of the mental representations. Chokron and De Agostini (2000) state that reading habits interact with hemispheric asymmetry to not only determine our pattern of habitual scanning but also our allocation of attention and our mental representations of our surroundings. Independent support for this interpretation comes from a study with hemispatial neglect patients, who have a deficit in mentally representing stimuli in the left visual field (Bisiach & Luzzatti, 1978; Vuilleumier et al., 2004). A recent study found in some patients with neglect a diminished left bias for the assumed light source direction (de Montalembert et al., 2010).

Hebrew participants did not show the opposite rightward bias, but rather a smaller left bias than the English participants. There are two possible explanations for this finding. First, it is possible that the default assumed direction of light is left but is being modified by habits related to the customary reading direction. Adams et al. (2004) found that individual's light source assumptions are quickly modified by new information, and predicted that the bias will return to the above left when this new information is no longer relevant. Therefore, Hebrew observers could have a reduced left bias because of reading direction and experience in their environment, but the bias remains left for this is the default bias caused by some unrelated default factor such as hemispheric dominance. This is in line with Vaid and Singh (1982) who found differences between left to right and right to left readers in a chimeric faces task and yet the rightward bias in the Arabic reading group was not as strongly rightward as the leftward bias in the Hindi reading group. Vaid and Singh attribute this pattern to the mediating effect of both hemispheric interaction and reading direction on non-linguistic spatial tasks.

An alternative explanation may be based on the fact that Hebrew readers are not pure right to left readers. For example, although letters are written from right to left in Hebrew, numbers are written from left to right. In addition, children in Israel generally learn English starting from 4th grade. All our Hebrew participants were University students, with some exposure to English in varying levels. Maas and Russo (2003) tested the directional preference in the mental representation of spatial events in three groups of students at an Italian University: Italian students, Arab students tested in Italian, Arab students tested in Arabic, and a fourth group of Arab students attending University in their home country. Opposite directional biases were found in Italian and Arab students studying in their home countries; however the Arab students studying in Italy, whether responding in Italian or Arabic did not show a significant bias in either direction. This shows that not only can the reading direction you are exposed to from an early age affect the visual processing bias, but also that exposure to more than one reading direction can modify processing biases. The findings of Vaid and Singh (1982) suggest this is the less likely explanation because they report similar findings with a different group of right to left readers. Arabic differs from Hebrew in that numbers are not written from left to write. Furthermore, the Arabic readers recruited by Vaid and Singh, unlike the Hebrew readers in Experiment two, had only a rudimentary knowledge of English. Therefore, the Hebrew readers' exposure to left to right scanning is less likely to be the cause of the reduced left, rather than symmetric right bias.

In order to eliminate the possibility that the group differences in this chapter were due to differences in experimental parameters, a second group of first language English participants were tested using the same equipment and procedure as Experiment Two. These were the results reported in the published version of this chapter (Appendix A). When the experimental procedure and equipment is consistent between groups there is still a significant difference between language groups. In this sample the average bias was -29.79˚ and every participant showed a bias to the left of 0˚. As such the group difference cannot be attributed to experimenter induced effects.

In summary, handedness does not contribute to the lighting bias. Instead it appears to be cultural habits that affect the bias, particularly the exposure to the direction in which a language is read.

Chapter 3. Effects of Lesion and Attentional Deficits.

Chapter Overview

The current chapter measured lighting biases in another population of observers who preferentially attend to the right side of stimuli. Hemispatial neglect (HN) is common after right hemisphere stroke, patients fail to orient or respond to stimuli in the contralesional space and scan scenes from the right side. Three patients with chronic left HN were recruited, as well as five right hemisphere patients without HN, and five left hemisphere patients. Despite preferentially attending to the right side of stimuli for over a year, the HN patients displayed lighting biases which were no different to the right hemisphere stroke patients. There was, however, an effect of hemisphere, with the right hemisphere patients both with and without HN showing biases which were significantly leftward compared to the left hemisphere patients, whose biases were similar to the control group. This suggests firstly that the right hemisphere does modulate the lighting bias, although a specific cortical or subcortical area is not apparent. Second, the fact that HN patients did not show a rightward lighting bias suggests HN in chronic patients does not cause an inability to imagine light in the neglected space.

Chapter Two showed that reading direction affects light source assumptions as first language Hebrew speakers showed a significantly less extreme left bias compared to first language English participants. Scanning direction can result in observers directing attention toward the side on which they begin reading (Chokron & De Agostini, 2000). This leads observers to place higher perceptual value on that side and thus light sources in their environment are manipulated so that the preferred side is illuminated.

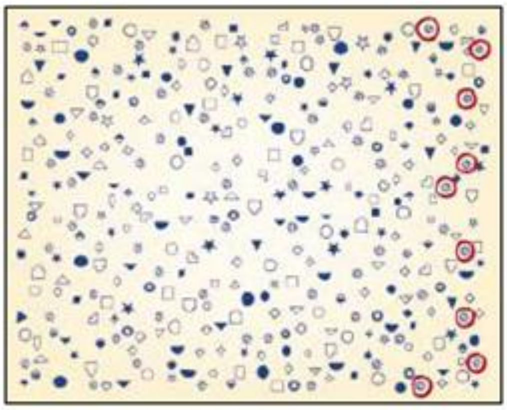
If scanning direction was the only factor affecting light source assumptions then the Hebrew participants would be expected to show a rightward bias rather than a reduced left bias. The reduced left bias could be explained by the language experience of the participants who were all University students with an exposure to English and thus to multiple opposing reading directions. Alternatively it is possible that although the light bias can be modified by scanning direction, other factors may cause the bias to remain left of vertical. Another population who scan objects and scenes from right to left can further test the effect of scanning direction on light source assumptions.

Hemispatial Neglect

Hemispatial neglect (HN) is common after stroke with prevalence estimates ranging from 25% (Pedersen et al., 1997) to 62-72% (Stone et al., 1991) although it most frequently presents after right hemisphere parietal damage (Posner, Walker, Friedrich, & Rafal, 1984; Vallar & Perani, 1986). Due to the heightened frequency after right hemisphere stroke it most commonly manifests as a deficit in attending toward the left hemispace. HN patients fail to orient or respond to stimuli in the contralesional space (Heilman et al., 1979). Naturally this impacts drastically on patients' daily lives, they may fail to fully dress or shave themselves, ignore someone talking to them from their contralesional side, or begin reading and writing in the centre of the page. Despite the major effect on their lives, patients are often unaware of, or indifferent to, their condition (Vallar, Bottini, & Sterzi, 2003).

The deficits can also be measured in various paper and pencil tests where ipsilesional and contralesional responses are compared. These include cancellation tasks which require patients to detect target shapes, often among distracters, copying or spontaneous drawing tasks, and line bisection tasks (see Figure 3.1). Assessment of daily life activities can also be administered such as asking patients to demonstrate how they would shave. Although these tests can be a more sensitive indicator of the patient's deficit in everyday life (Azouvi et al., 1996), Azouvi et al. (2002) state that if time is limited, administering a cancellation task with many distracter items, a copying task, and a spontaneous drawing task will highlight neglect in up to 70% of patients.

A.



B.

Figure 3.1: Typical performance of a neglect patient in a cancellation task where only the extreme ipsilesional targets have been marked (**A.**) and a clock drawing from memory where the contralesional numbers have been omitted (**B.**; adapted from Husain & Rorden, 2003).

The ipsilesional bias occurs not only for external stimuli but also for mental representations. For instance, when recalling features of familiar landscapes such as street scenes or maps, patients recall more ipsilesional than contralesional landmarks (Bisiach & Luzzatti, 1978; Vuilleumier et al. 2004) or make errors when drawing simple objects from memory such as clocks (Husain & Rorden, 2003; see Figure 3.1B). Like all aspects of HN, prevalence estimates of representational HN vary. Some studies detected representational HN in roughly one third of patients diagnosed with HN (Bartolomeo, Bachoud-L´evi, Azouvi, & Chokron, 2005; Bartolomeo, D'Erme, & Gainotti, 1994) whereas Guariglia, Palermo, Piccardi, Iaria, and Incoccia (2013) found representational HN was as common as perceptual HN among a group of 96 patients with right hemisphere lesions.

This ipsilesional preference leads to a different scanning behaviour. Azouvi et al. (2002) administered a test battery to 206 right hemisphere stroke patients, an average of 11 weeks after stroke. Tests included standard paper and pencil assessments as well as tests of motor function and hemianopia. The most sensitive individual measure was the starting position in a shape cancellation task, with a right sided starting point detecting HN in 50.5% of patients (85% presented HN in at least one measure), showing that HN patients, unlike healthy controls, begin scanning stimuli from the right side.

Dijkerman et al. (2003) recorded eye movements of three HN patients in a size judgement task for rectangles on the left and right side of the screen. Contrary to the control participants, all three patients directed the majority of their initial saccades rightward from the central fixation cross in order to scan the stimuli from right to left. This demonstrates that HN patients scan stimuli from right to left. However this scanning is not always systematic. When searching for targets among distracters, patients will often revisit rightward targets they have already detected and neglect targets on the left (See Figure 3.2; Chedru, Leblanc, & Lhermitte, 1973; Mannan et al., 2005; Sprenger, Kompf, & Heide, 2002). Therefore there are similarities between the habitual scanning developed by reading direction, seen by the Hebrew readers in Chapter Two, and HN patients, but as well as scanning from the right, HN patients spend a great proportion of time fixating on the right side of stimuli.

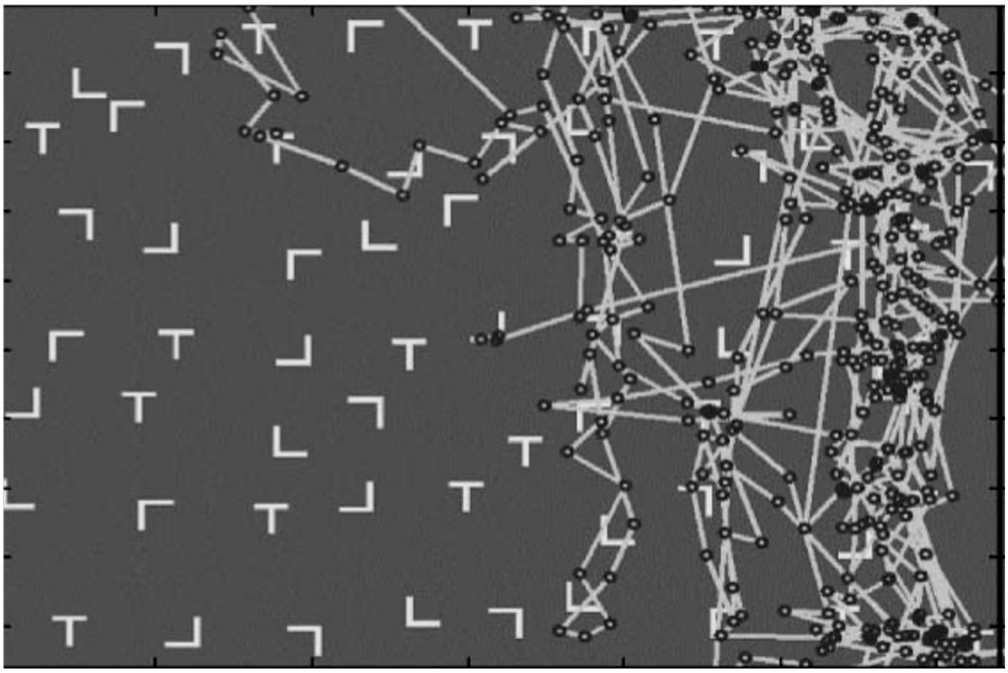


Figure 3.2: Performance of an HN patient searching for Ts among L shapes, showing fixation points (dots) and scan paths (Adapted from Mannan et al., 2005).

This rightward shift of attention, habitual scanning from the right side of stimuli, and deficit in imagining information on the left raises the question of whether HN patients continue to show a leftward lighting bias or instead a bias shifted to the right.

de Montalembert et al. (2010) measured the lighting assumptions of six patients with left HN and one patient with right HN using the “polo mint” stimulus (Gerardin et al., 2007; see Figure 1.2). Participants reported the side (left or right) or the shape (convex or concave) of the odd sector while a light source was simulated in four different directions. The mean bias for the control group was -5.23˚ with a standard deviation of 4.05. The authors state this average left bias is in line with previous research, however the average bias is reduced compared to another group of participants tested using the same stimulus and method, who showed an average group bias of -22.3˚ (Gerardin et al., 2010). The cause of this difference is not clear; it may be due to differences in stimulus parameters such as stimulus size, or possibly age, although age of participants is not reported in Gerardin et al. (2010); it only states that participants were university students.

Among the patients there was no correlation between light source assumption and severity of HN. The patient with right HN showed a stronger left light source bias than the control participants. Of the patients with left HN, three showed a rightward lighting bias, one showed a reduced left bias, and the remaining two showed an extreme left bias. The three patients who showed a rightward lighting bias had cortical lesions within the frontal, temporal, and parietal areas of the brain whereas the remaining patients had subcortical lesions. de Montalembert et al. concluded that the fronto-temporo-parietal network modulates light source assumptions and damage to this area results in an inability to mentally represent light sources in the neglected space. Thus the light source assumptions are shifted to the right in these patients. These findings contradict previous findings using healthy participants. Mamassian et al., (2003) and Gerardin et al., (2010) both concluded that activation in early visual areas, including retinotopic areas, modulates shape discrimination from light sources rather than higher cortical areas.

While there was a clear dissociation between rightward biases in the patients with cortical lesions and biases matching the control participants in the patients with subcortical lesions, the conclusion of the fronto-temporo-parietal network is vague. The three patients with cortical lesions appear to have a range of lesions and little information is given about the size and precise location of the lesions. Once the researchers noticed a potential pattern of results by lesion location a lesion overlap analysis could have been performed to determine the exact areas of damage that these patients had in common. Furthermore, the role of this cortical area is not as clear as de Montalembert et al.

conclude because patient performance cannot be dissociated from HN. Therefore patients with similar lesions without HN should be tested in order to assess whether lighting biases can shift to the above right independently of HN. de Montalembert et al. (2010) recognise that the inclusion of patients without HN would have improved the study, but state this is difficult due to the high prevalence of HN after right hemisphere stroke.

The conclusion that damage to the fonto-temporo-parietal network results in an inability to mentally represent light sources in the neglected space assumes that the position of illuminants is explicitly represented while participants perceive shape from shading. The role of mentally representing the light source in space has been alluded to by Boring (1942) who recalled that dents in surfaces could be perceived as convex bumps if the observer imagined the light shining from below. However this does not indicate that imagining the light within the image is necessary to complete the task. If de Montalembert et al.'s (2010) conclusion is correct then these results are evidence against the arguments that recovering shape from shading is predominantly low level and preattentive (Adams, 2007; Gerardin et al., 2010; Mamassian et al., 2003). However, as mentioned above, further research is required before these findings can be considered valid.

The findings by de Montalembert et al. (2010) suggest that the light source bias may not be affected by attentional experience. Firstly, patients' biases did not correlate with HN severity. Secondly, de Montalembert et al. concluded that lesions to a specific right hemisphere cortical area caused the rightward light biases seen in three of the patients. All the patients tested by de Montalembert et al. (2010) were acute patients, with a range of 30-90 days from lesion onset. It may be that effects of attentional experience would be more pronounced in chronic HN patients who have preferentially attended to, and scanned scenes from, the right side for many months or years.

If a specific lesion in the right hemisphere shifts the lighting assumption to the right then this raises the question of whether patients with lesions to the contralateral homologue area (left hemisphere cortical patients) show a shift in the opposite direction. The one such patient tested by de Montalembert et al. (2010) with a left frontal-parietal lesion had a lighting bias which was farther to the left than the control group, suggesting this may be the case. de Montalembert et al. do not explain why they recruited only one patient with left hemisphere damage although it was presumably because only HN patients met their inclusion criteria and HN is less common after a left hemisphere stroke (Posner et al., 1984; Vallar & Perani, 1986). Regardless of the reason, concrete conclusions cannot be based on results from one participant. The confirmation of a specific cortical area which modulates the lighting bias would contribute significantly to the question of why light source assumptions are biased to the left.

The current experiment assesses firstly whether the experience of chronic HN affects light source biases. The reduced bias in the Hebrew group in Chapter Two suggests that the long term attentional deficit will lead to a reduced left bias, or possibly right bias, in the HN patients. The experiment also assesses whether the lesion specific deficits found by de Montalembert et al. (2010) can be replicated. If so, not only will the HN patients with cortical lesions show a rightward bias compared to the control group, but so will the patients who have similar lesions, but do not have HN.

Method

Participants

Thirteen patients with cortical and subcortical lesions in either the right or left hemisphere (see Table 1; mean age 62.3, SD 14.86) and 14 age matched controls (mean age = 62.64, SD = 11.18) without any neurological or medical condition were recruited. Patients were recruited from Bangor University’s Patient Panel. When joining the panel patients are invited to Bangor University for an MRI scan to determine precise lesion location and ensure there is no previous cerebral damage.

Patient inclusion criteria: i) Aged 18 or over. ii) Unilateral lesion of ischemic or haemorrhagic etiology. iii) No upper limit of time from stroke onset was applied (mean time = 45.23 months, SD = 34.68). iv) Awake, alert, and capable of understanding and participating in research.

Patient exclusion criteria: i) Presence of other neurological, psychiatric or medical conditions that would preclude active participation in research and/or alter the interpretation of the behavioral/imaging studies. ii) Evidence by CT or MRI of previous cerebral damage. iii) An inability to maintain wakefulness or follow task instructions.

Control inclusion criteria: i) Matched in age to a patient by no greater than two years. ii) Matched in gender to same patient. iii) Normal or corrected to normal vision.

Control exclusion criteria: i) Presence of any neurological condition. ii) Presence of any psychiatric or medical conditions that would preclude active participation in research and/or alter the interpretation of the results. iii) An inability to maintain wakefulness or follow task instructions.

Apparatus and stimuli

The honeycomb stimulus from Chapter Two, with the middle level of blur was used. Apparatus was the same as in Chapter Two.

Procedure

Neuropsychological tests

Prior to the experiment, all patients performed the following neuropsychological tests in order to assess the severity of spatial attention deficits. Multiple tests were used because a battery of tests has been reported as more sensitive than one test alone (Azouvi et al., 2002; Halligan, Cockburn, & Wilson, 1991). Furthermore, HN is a heterogenous condition, leading participants to display a range of deficits (Bisiach, Perani, Vallar, & Berti, 1986; Coslett, Bowers, Fitzpatrick, Haws, & Heilman, 1990) which are more likely to be detected and dissociated by multiple tests (Barrett et al., 2006; Ota, Fujii, Suzuki, Fukatsu, & Yamadori, 2001). The Mini Mental State Examination (MMSE; Folstein, Folstein, & McHugh, 1975) is a brief test of cognitive impairment. Aspects of orientation, language, registration, calculation, and recall are assessed. For example the questions "Where are we?: (state) (county) (town) (hospital) (floor)" to assess orientation. This test was used to exclude patients with possible dementia (score <24 of a possible 30).

The Starry Night test (Deouell, Sacher, & Soroker, 2005) is a computerised test which, importantly for this Chapter, is more sensitive in detecting deficits in recovering patients compared to the behavioural inattention test (BIT), a standardised battery of paper and pencil tests (Deouell et al., 2005). Participants detected visual targets (a blue square) among distracters (red dots). As recommended by Deouell et al. (2005) reaction times were compared for detection of the 63 targets on each side of the screen using a paired samples t-test, comparing homologous locations around the vertical meridian. Deficits in spatial attention were indicated by a significant difference in reaction times to left and right sided targets.

The Bells test (Gauthier, Dehaut, & Joanette, 1989) requires patients to circle 35 pictured bells randomly distributed over a landscape A3 sheet which also contains 280 pictures of random objects as distracters. The addition of distracter items increases the task demands, increasing the spatial bias in responding and as such increasing the sensitivity of the test (Barrett et al., 2006; Mennemeier, Morris, & Heilman, 2004). The number of targets omitted out of a possible 17 for the left and right side (the 35th target was central) of the sheet are compared. Gauthier et al. (1989) conclude that more than three omissions, to one side only, indicate the presence of HN. During the Bells test and the gap detection test the experimenter recorded the positions where the pen first marked the paper.

The gap detection test (Ota et al., 2001) requires patients to circle ten complete circles and draw a cross inside incomplete circles, ten with a gap on the left and ten with a gap on the right. The number of target omissions on each side of the page are measured as well as the number of incomplete circles mistakenly marked as complete circles. These two potential types of error give extra information about the type of HN the patient may have, for it is possible to dissociate between body centred neglect (failure to mark all targets which are in the contralesional space) and stimulus centred neglect (all targets on the page may be marked but incomplete circles with a gap on the contralesional side will be incorrectly marked as complete circles).

Finally, participants also completed two copying tests, one of a single flower and one of a house with two trees either side. An error was recorded when an element was incomplete (for example only the right side of a tree was drawn) and two errors were recorded when an element was omitted completely (the tree was completely omitted). There were a potential eight errors for the flower test and 12 for the house with trees either side.

If there was a discrepancy between test outcomes, for instance if a patient showed HN on some but not all of the tests, then they were grouped according to the most sensitive tests. As such a patient would be placed in the HN group if they showed a deficit on the starry night test and normal performance in the others. For the patients who did not complete the starry night test the Bells test was the most sensitive test. The other tests were used to gain additional information about type and severity of HN.

During the paper tests the measures were taped in place on the table in front of the participants, the centre of each measure being in line with the participants' trunk;

participants were free to move their eyes and head. Completion of the task was indicated by the patients whereby the examiner asked “are you finished?” and gave no feedback on performance.

Light Source Task

In the light source task participants viewed one practice block containing 15 trials, to familiarise the participants with the stimuli and responses, followed by two blocks of 120 trials. To ensure participants fully attended to the stimulus; participants stated their responses and the experimenter, who could not view the screen, pressed the appropriate button. Each stimulus was presented for up to 3000ms with the next trial beginning once the experimenter responded. If there was no response within 300ms a prompt appeared on screen saying “is it in or out?”.

Results

Patients 2, 5, and 8 consistently demonstrated HN based on the neuropsychological assessments (see Table 1). Patient 5’s copying task can be seen in Figure 3.3 as typical performance for a patient with HN. More petals are omitted on the left side of the flower and there is less detail in the leaf and stem on the left compared to the right side. Patient 1’s copying task shows equal detail on both sides of the flower. The gap detection test detected body centred HN in all patients and so the targets omitted on each side of the page are reported. This would have a potentially serious impact on the study if multiple objects were presented simultaneously; however as each trial involves the central presentation of a single stimulus the type of HN is not pertinent. None of the participants had an MMSE score <24. Recording the start point and direction of scanning during the cancellation tasks revealed that all the control patients began in the upper left corner and systematically marked targets from left to right across the page. As expected the HN patients first marked targets in the upper right corner of the page and scanned from right to left, although often in a less systematic way, revisiting already marked targets on the right which is common for HN patients (Mannan et al., 2005).

Figure 3.3: Performance on the flower copy task. The flower participants were asked to copy (left); performance by patient 1 (centre); performance by patient 5 (right).

Table 3.1. Summary of patients' demographics and neglect measures.

Patient	Age	Sex	Lesion Location (R: Right, L: Left)	Lesion onset (months)	Starry Night *p* value	Bells test (omissions L/R)	Gap detection test (errors L/R)	Copy tasks (errors L/R)
1	46	M	R Basal ganglia	28	.75	+	+	+
2	26	F	R Occipito-parietal	16	.0001*	4/1	1/1	+
3	64	M	R Frontal-parietal-temporal	51	Incomplete	2/+	+	+
4	56	F	R Insula	32	.98	+/2	2/+	+
5	74	M	R Temporo-parietal	33	.0001*	17/9	15/5	6/1
6	64	M	R Intraparietal	14	.24	+/1	+	+
7	64	F	R Thalamus	131	.22	4/5	+	+
8	63	M	R Parietal	17	Incomplete	17/5	Incomplete	7/+
9	51	F	L Frontal-parietal	90	.086	4/2	1/1	+
10	78	M	L Basal ganglia	75	.14	+	+	+
11	78	F	L Frontal-parietal	30	.14	6/6	1/+	+
12	77	M	L Parietal	51	.63	7/7	+	+
13	69	M	L Frontal-parietal	20	.600	+/3	+	+

Note. + = no errors; *=Significant *p* values

The formulae for analysing the light source bias results are described in Chapter Two. Patient 13 was excluded from the analysis as their responses were not significantly modulated by the stimulus, *p*=.95. The results for each participant's light bias can be seen in Figure 3.4. The means for each participant group were: age matched controls (mean= -5.96, SE= 7.22), HN patients (mean= -43.32, SE= 8.12), right hemisphere patients (mean= -49.34, SE= 6.95), and left hemisphere patients (11.52, SE= 25.95).

A one way ANOVA for the levels: controls, HN patients, right hemisphere patients without HN, and left hemisphere patients showed a significant effect of group $F(22, 3)=6.97$, $p=.002$, $\eta_p^2=.49$. Follow up tests with Bonferroni corrections show that only one patient group, the right hemisphere patients, differed from controls (*p*=.014). Among the patient groups the left hemisphere patients differed significantly from the right hemisphere patients (*p*=.007) and the HN patients (*p*=.043).

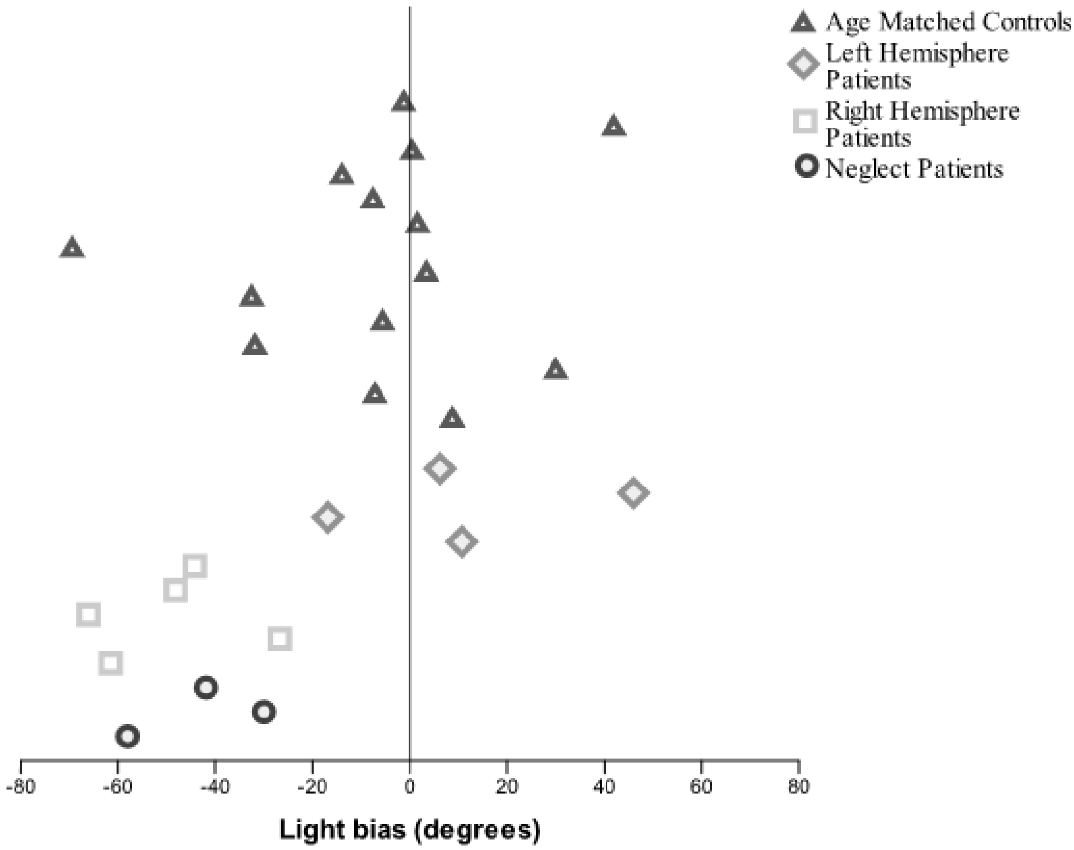


Figure 3.4: Participants' light bias, grouped by participant type. Negative values indicate those left of vertical.

The light assumptions of the control participants were normalised to a z-distribution to assess the deviation from normal performance in individual patients. Each patient's bias was transformed to a z-score based on the distribution of the control scores. A patient was considered to have a result significantly different to the control group if the z-score was greater than 1.64 (significance level of .05). The results of this analysis can be seen in Figure 3.5.

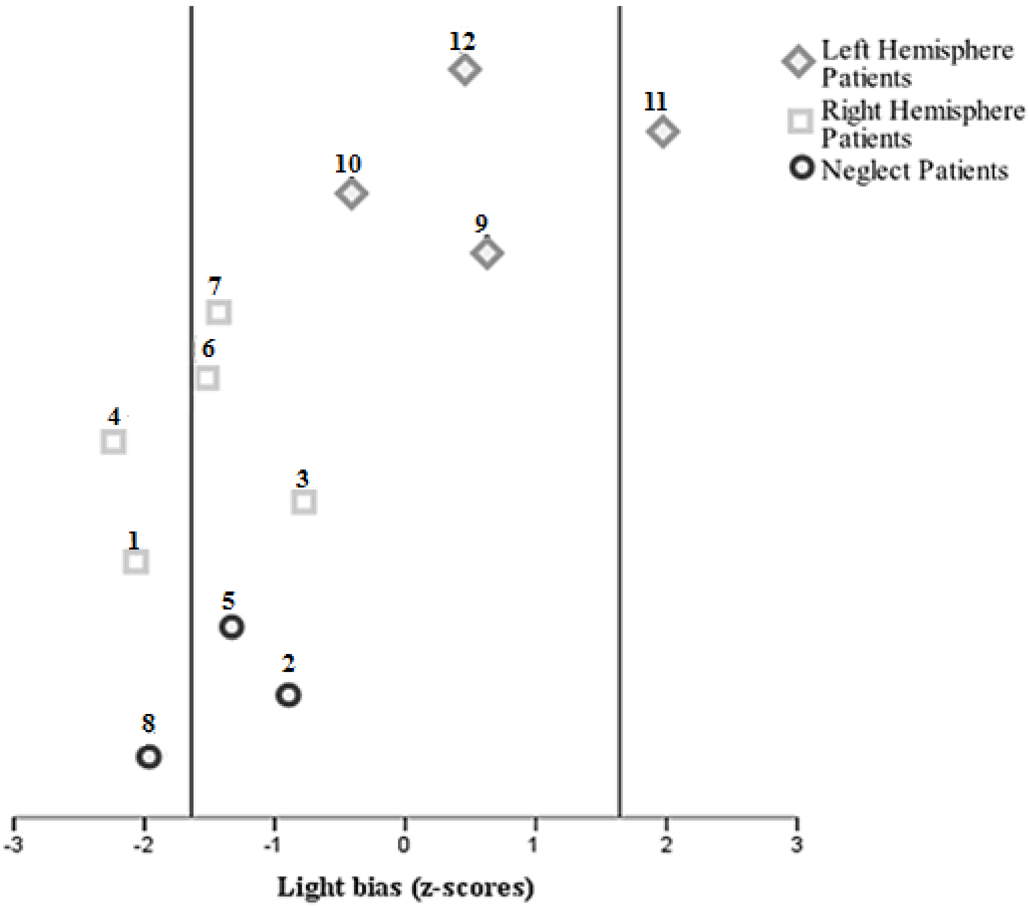


Figure 3.5: Participants' light assumptions converted to a z-score, grouped by participant type. Reference lines indicate significance thresholds at 1.64 and -1.64. Negative values indicate biases left of the control distribution. Patient numbers label their z-score.

As Figure 3.5 shows, the majority of the patients demonstrated light biases which were not significantly different to the control group. Among the four patients who did show a significantly different assumption there was a range of lesion sites. Importantly there is no lesion area exclusively related to light biases which are significantly different to the control group. Furthermore of the three patients with HN only one had a bias significantly different to the controls, and that was a more extreme left assumption, rather than the rightward assumption that was predicted. Therefore, in contrast to de Montalembert et al. (2010) and the experimental predictions, the results show that neither the experience of HN nor the fonto-temporo-parietal network can be implicated in affecting lighting biases.

Discussion

The current study found that chronic HN does not result in rightward lighting biases; all three HN patients showed assumptions which were farther left than the control group, although the difference was not significant. Furthermore the results of the HN patients were similar to the results of the right hemisphere patients without HN showing that the attentional deficit does not modulate light source assumptions in chronic patients. There was, however, an effect of hemisphere with right hemisphere patients both with and without HN showing a bias significantly more to the left of the left hemisphere patients, regardless of lesion site.

Contrary to the conclusions of de Montalembert et al. (2010), the HN patients with cortical lesions did not appear to have a deficit in imagining the light source on the left. One possibility for this difference in performance is that it could be indicative of different recovery rates for representational neglect compared to perceptual neglect. Different deficits within HN recover at different rates (Farne et al., 2004) and HN for imagined space has been observed independently of other manifestations of HN (Beschin, Cocchini, Della Sala, & Logie, 1997; Coslett, 1997; Guariglia, Padovani, Pantano, & Pizzamiglio, 1993). Therefore it is possible that although the HN patients demonstrated deficits in detecting external stimuli, their HN for imagined space had begun to recover.

A way to address this would be to include recall tests for imagined space in the neuropsychological assessments battery.

Predictions based on Chapter Two were that the experience of preferentially attending to the right and scanning scenes from right to left for many months would cause a reduced left bias, or a rightward lighting bias. The fact that lighting assumptions are still to the left after up to 33 months of HN suggests that despite preferentially attending to, and scanning scenes from the right side, there is some independent factor which makes the lighting biases in these patients different to the first language Hebrew group in Chapter Two.

Another interesting finding is that of hemispheric differences. Despite the non HN patient groups showing no attentional deficits in any of the neuropsychological assessments, they still showed group differences in the light source task. The left hemisphere group showed a pattern similar to the control group whereas the right hemisphere patients, both with and without HN, had light assumptions which were significantly leftward. There were a variety of lesions in each patient group and so the differences are not due to one specific lesion location.

Furthermore, the direction of these hemispheric differences is surprising. After damage to a hemisphere there is reduced activity in that area and also increased activity in the contralateral homologue area (Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005). However this imbalance is not permanent, Corbetta et al. (2005) found that networks had rebalanced to normal activity when patients were tested in the chronic stage after six months. This may explain the difference in the current findings compared to those by de Montalembert et al. (2010). de Montalembert et al.'s acute patients would have had both a reduction in activity in the right hemisphere due to the lesion and also increased activity in the contralateral hemisphere, whereas the chronic patients in the current study only had reduced activity in the damaged hemisphere. Therefore the ipsilesional shift in lighting biases measured by de Montalembert et al. could be due to the contralateral shift of attention caused by the hyperactive hemisphere, which was no longer hyperactive in the chronic patients recruited in the current study. However this explanation would predict that once the hyperactivity reduces and the normal balance is restored the ipsilesional shift would reduce and a normal left bias would be restored. While this may be the case with the left hemisphere patients, who displayed biases no different to the control group, the right hemisphere patients showed a bias farther to the left than the control group. As these hemispheric differences arise regardless of specific lesion location and without any evidence of attentional differences between the groups it is difficult to implicate the factor(s) causing these hemispheric differences.

Although the age matched controls showed a left lighting bias at the group level, the mean assumption was small compared to the English speaking group in Chapter Two (5.9˚ and 26.86˚ left of vertical respectively) and some of the control participants even showed rightward biases. The only other study to measure lighting assumptions in an “older” group of healthy participants (not the traditional undergraduate student age) was de Montalembert et al. (2010). In that study the age matched controls showed a mean bias remarkably similar to the controls in the current experiment (5.2˚ left of vertical). This suggests that the light source bias may change with age. This will be discussed further in Chapter Five.

In summary, HN may lead to a preference for the right side of objects and habitual scanning from right to left but in chronic patients this does not cause a deficit in the ability to imagine light sources on the neglected side. Lighting biases are, however, modified by right hemisphere damage with lesions causing a contralesional shift in light assumptions, although the reason for this shift is unclear.

Chapter 4. Disruption of Left Space in Healthy Participants.

Chapter Overview

Chapter Three found that patients with chronic HN showed lighting biases no different to the right hemisphere patients without HN. The biases for the right hemisphere patients were farther to the left than those of the left hemisphere patients and the age matched control participants. Chapter Four attempted to investigate the effect of disrupted mental representations of the left side of space, independent of the confounding factor of lesion location. Two different techniques, prism adaptation (PA) and transcranial direct current stimulation (tDCS) were used in an attempt to shift the representation of the left side of space in healthy participants. However, the extent to which these interventions were successful is unclear. There was no shift in participants' lighting biases after PA. After tDCS there was a significant interaction between session (real or sham stimulation) and time (pre and post stimulation), with a small leftward shift in the mean light bias after real stimulation and an equal and opposite shift after sham. However there was no evidence that the interventions successfully induced a rightward shift of attention.

Chapter Three showed that the left lighting bias does not shift to the right in chronic HN patients who have preferentially attended to the right side of stimuli for up to 33 months. Furthermore, Chapter Three showed there was an effect of hemisphere, with the right hemisphere patients showing more leftward light biases than the left hemisphere patients, regardless of attentional deficits or lesion location. This makes the role of attention in light biases unclear.

One way to further investigate the effects of attention is to induce HN like deficits in healthy individuals. This would temporarily induce a bias toward the right side of space without the confounding factor of lesion location. There are a number of non-invasive methods which have been used to disrupt function in healthy participants. Such methods include prism adaptation (PA), transcranial direct current stimulation (tDCS), and transcranial magnetic stimulation (TMS). Each technique will be discussed with reference to simulating HN in healthy participants.

Rossetti et al. (1998) demonstrated that when HN patients repeatedly point to targets whilst wearing prismatic goggles which shift the visual field 10˚ to the right, patients initially make errors and point to the right of the true target location. Gradually patients compensate for the visual field shift by reaching farther to the left in order to point to the targets accurately. Once the prismatic goggles are removed participants continue to display adaptation behaviours by exploring the left side of space more, thus alleviating HN symptoms, an intervention known as prism adaptation (PA). Left shifting prisms can also be used to simulate HN in healthy individuals; wearing the prism goggles results in an initial leftward error when reaching for targets which gradually reduces until targets are accurately reached. Once the goggles are removed participants still display compensatory behaviours and so an after effect causes a rightward shift in attention.

These after effects can be measured by asking participants to point directly ahead or at targets, without providing them with feedback on their arm position.

In healthy participants, the two hemispheres are engaged differently during PA (Clower et al., 1996; Inoue et al., 2000; Michel et al., 2003). Using PET Inoue et al. (2000) found an increase in activation of the left dorsal premotor cortex and left supplementary motor area during adaptation. Clower et al (1996) found selective activation of the posterior parietal cortex contralateral to the reaching limb during PA, which was not present in a separate task with similar sensory, motor, and cognitive demands. Loftus Nicholls, Mattingley, and Bradshaw (2008) suggest this increased activity in the left hemisphere mediates the rightward shift in attention.

PA with left shifting prisms has been shown to cause a rightward shift in line bisection and land mark errors, judgements of pre-bisected lines, in healthy individuals (Berberovic & Mattingley, 2003; Michel et al., 2003). It can also cause performance similar to HN patients in non-lateralised spatial tasks such as inducing a local features bias during the the processing of small letters arranged to form a large letter (Bultitude & Woods, 2010).

Girardi, McIntoshc, Michela, Vallar, and Rossetti (2004) asked participants to indicate the centre of a circle which had been either haptically or visually explored, before and after PA. In both conditions left shifting prisms resulted in a rightward shift in the estimation of centre. The shift occurred after both visual and haptic explorations and furthermore the magnitude of the shift did not correlate with any measurements of sensorimotor after effects, leading Girardi et al. to propose the changes in task performance reflected changes to the representation of space induced by the PA.

Further evidence that PA affects participants’ representation of space comes from Rode, Rossetti, and Boisson (2001) who reported the effects of the intervention on imagined space in HN patients. Patients imagined a map of France and recalled towns from that mental representation; more towns from the left side of the country were recalled after PA. Similar effects on mental representations can be seen in healthy participants. Loftus et al. (2008) presented participants with number triplets (such as 15, 36, 55) and asked them to judge whether the numerical distance to the left or right of the central number was greater. At baseline participants over estimated numerical distance to the left of the mental number line, whereas this overestimation was not present after PA with left shifting prisms. Loftus et al. state this is evidence that PA affects higher order mental representation of stimuli. The above evidence shows that PA can induce a rightward shift in attention for both stimuli in the environment and imagined stimuli. One conclusion from Chapter Three was that it is possible the HN patients demonstrated deficits in detecting external stimuli but HN for imagined space had begun to recover. Using PA with healthy participants may be able to address this issue without the confound of lesion.

Both TMS and tDCS are classed as brain stimulation techniques; both methods can be of great experimental and therapeutic benefit, not only in the area of HN. For instance both TMS (Slotema, Blom, Hoek, & Sommer, 2010; Speer et al., 2000) and tDCS (see Nitsche, Boggio, Fregni, & Pascual-Leone, 2009 for a review) have shown some level of success in treating depression. However the mechanisms of TMS and tDCS are quite different. TMS uses a coil placed over the head to create brief magnetic pulses; this triggers action potentials in the targeted area of the brain beneath the coil (Di Lazarro et al., 2004). Following this action potential is a brief period of reduced activity in those cells while the ion balance is restored. As such TMS can be used to induce transient disruption of cortical function in a targeted surface area of the brain (Edgley, Eyre, Lemon, & Miller, 1997; Pascual-Leone, Walsh, & Rothwell, 2000).

tDCS affects the resting state potential of neurons in the brain; a weak electrical current increases (anodal stimulation) or decreases (cathodal stimulation) excitability in the area underneath the electrodes (Nitsche & Paulus, 2000), not only during the stimulation period but also for several hours afterward if the current is applied for a 10-30 minute period (Bindman, Lippold, & Redfearn, 1962).

Both brain stimulation techniques have been used as therapeutic tools with HN patients, and as a method for inducing HN like deficits in healthy participants. Evidence shows TMS over the left parietal cortex improves HN symptoms in patients (Song et al., 2009, see Cazzoli, Muri, Hess, & Nyffleer, 2010 for review). Conversely, right parietal cortex stimulation induces HN like symptoms in healthy people, measured by judgements of pre-bisected lines (Fierro, Brighina, Piazza, Oliveri, Bisiach, 2001) and detection of targets presented simultaneously in the left and right visual field (Hilgetag, Theoret, & Pascual-Leone, 2001; Muggleton et al., 2006).

Sparing et al. (2009) used tDCS to show that anodal stimulation to the posterior parietal cortex (PPC) in either hemisphere biased attention toward the contralateral space whereas cathodal stimulation impaired contralateral performance in a visual detection task. Furthermore, HN patients performing the same task showed an improved performance after both cathodal stimulation to the left hemisphere and anodal stimulation to the lesioned right hemisphere, showing that tDCS is a valid rehabilitation tool for stoke patients.

Giglia et al. (2007) compared the use of cathodal stimulation to the right PPC alone to bilateral stimulation consisting of both cathodal stimulation to the right PPC and anodal stimulation to the left PPC simultaneously in healthy subjects. Participants completed a landmark task, judging the accuracy of pre-bisected 150mm long horizontal lines, as a baseline before stimulation and then at five minute intervals during the stimulation period and after stimulation ended. This landmark task was an effective choice of task because it employs the perceptual mechanisms of line bisection tasks while excluding any confound of motor behaviours. Furthermore the task was cognitively demanding; stimulus presentation time was 50ms and the vertical line bisection would only deviate from the true centre by 5mm. This ensured there would be no ceiling effects, and thus there were sufficient errors to judge the effectiveness of the stimulation. The bilateral stimulation affected participants' performance after only five minutes stimulation, whereas than cathodal stimulation only affected performance after ten minutes; however the effect did not last longer.

The bilateral stimulation approach is a more effective method for simulating HN because the right hemisphere readily directs spatial attention towards both the ipsilateral and contralateral side of space. In contrast, the left hemisphere displays a predominantly contralateral bias with only a minor representation of the left side of space (Bisiach & Vallar, 2000). As such, after a right hemisphere stroke it is not only the reduced activity in the lesioned hemisphere which contributes to HN severity but also the contralateral attentional bias from the intact and hyperactive left hemisphere (Mesulam, 2002). Therefore applying cathodal stimulation to the right hemisphere to simulate a lesion in that area is not sufficient; anodal stimulation applied over the left hemisphere simultaneously will simulate the hyperactivity of the left hemisphere after a right hemisphere stroke. This can also explain why both anodal stimulation over the lesioned hemisphere and cathodal stimulation over the left parietal cortex alleviated HN deficits in Sparing et al.'s (2009) study. For this reason tDCS may be more effective in simulating HN in healthy participants because the bilateral stimulation like that used by Giglia et al. (2011) can better represent the reduced activity in the lesioned hemisphere and the hyperactivity in the opposite hemisphere which is seen after stroke (Mesulam, 2002). TMS does not have this capability.

The current chapter uses two different methodologies across three experiments to disrupt the mental representation of leftward space and induce a rightward attentional shift in healthy participants. Experiment One used PA and Experiments Two and Three used tDCS to disrupt the representation of the left side of space in healthy participants in order to assess whether this affects their light source assumptions.

Experiment One: Prism Adaptation

Participants

Forty four participants (three left handed) mean age 19.65 participated for course credit; all had normal or corrected to normal vision.

Apparatus and Stimuli

The stimuli were the same as in Chapter Two, presented on a Hyundai ImageQuest P910+ monitor with a chin rest maintaining a distance of 60cm from the screen. Stimuli were presented at a visual angle of 12.36˚.

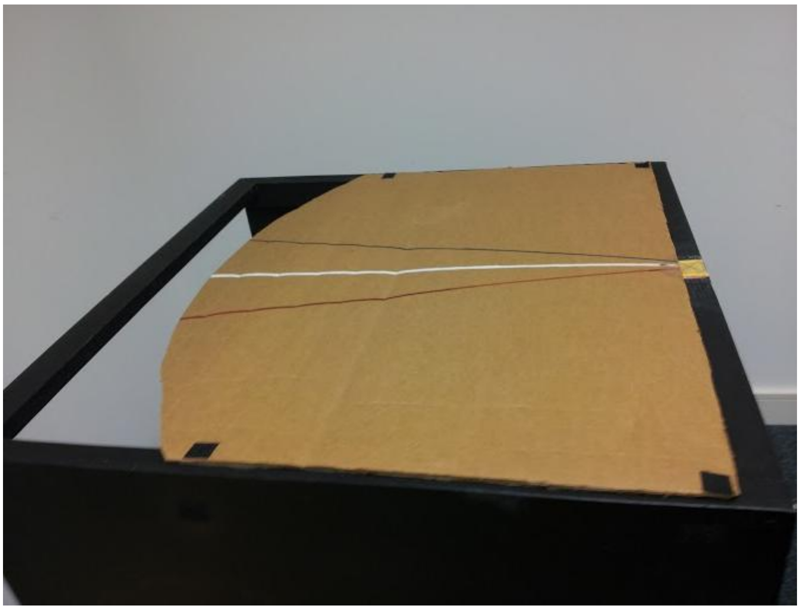
Participants were seated in a wheeled chair which could be manoeuvred between the computer screen and adaptation box by the experimenter.

Procedure

Pre-adaptation light bias task.

Similar to previous chapters, a training block containing 13 trials preceded two blocks of 120 trials presented in a random sequence, totalling 10 presentations of each stimulus orientation. Each trial began with a 1000ms fixation cross followed by the experimental stimulus, presented for 500ms (1,000ms in the practice trials). Participants pressed one of two keys (counterbalanced) indicating whether they perceived the centre hexagon to be pushed in or protruding out.

A.



B.

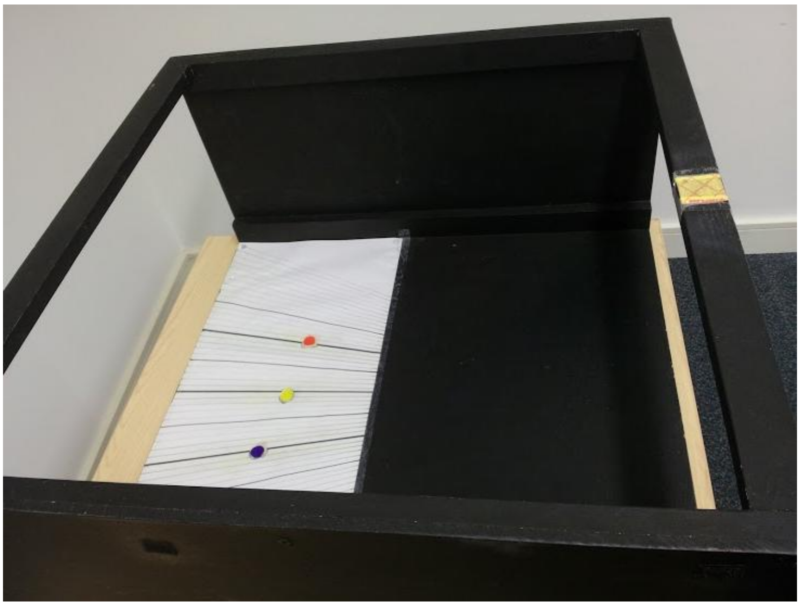


Figure 4.1: Prism adaptation box. **A**. Open loop pointing: participants rest their chin on the yellow square and point in line with each of the coloured lines. **B**. Prism adaptation: Wearing the goggles participants rest their chin on the yellow square and point to each of the coloured dots in sequence.

Pre-adaptation open-loop pointing.

Participants were turned to face a prism adaptation box 90cm wide x 35cm high x 70cm deep based on the description by Berberovic and Mattingley (2003; see Figure 4.1).

On the lid of the box were three lines disseminating from participants' midline at angles of -10˚, 0˚ and +10˚. During the open loop pointing task participants rested their chin on the top of the box and pointed under each line four times in a pseudorandom order as directed by the experimenter. These pointing movements were made with extended elbow and index finger and participants returned their hand to rest in front of their torso between each movement. The experimenter, positioned at the opposite end of the adaptation box, recorded pointing accuracy to the nearest .5˚ using markings on the underside of the lid.

Prism adaptation.

The lid of the adaptation box was removed to reveal the base of the box which had been fitted with three 1.5cm targets placed at angles of -10˚, 0˚ and +10˚ from participants' midline. Participants were fitted with welding goggles adapted to contain Risley biprisms which shifted the visual field 15˚ to the left. In a closed loop task, participants rested their chin on the edge of the box and made 150 pointing movements toward the targets in a specific sequence (left-middle-right-middle), returning their hand to their torso between each movement. To ensure a consistent, ballistic pointing speed these movements were performed in time with a metronome set to 1 Hz.

De-adaptation occurs quickly in healthy participants once they begin interacting with their surroundings as normal; as such participants closed their eyes at the end of the adaptation session and between each subsequent task, similar to Berberovic and Mattingley (2003).

Post-adaptation open-loop pointing.

The prism goggles were removed and adaptation was measured using the same procedure as the pre-adaptation open loop pointing.

Post-adaptation light bias task.

Participants completed the same experiment as described in the pre-adaptation test. Time spent completing this test varied between participants, to prevent de-adaptation before the end of the test all participants repeated the PA procedure between testing blocks one and two.

Late open-loop pointing.

The open-loop pointing task was performed a third time using the same procedure as described above to confirm the adaptation was sustained during the post adaptation task.

Results and Discussion

Two participants were excluded from the analysis as their responses were not significantly modulated by the stimulus, p=.8 and p=.95. A further four participants were discarded because their open loop pointing errors were not significantly modified by the PA, as confirmed by a paired samples t-test for each of their errors. As such it could not be concluded that the PA had effected their representation of space. Thus, there were 38 participants in the group level analysis.

The light biases measured before and after the PA intervention are displayed in figure 4.2. The pre-intervention bias (Mean= -24.11˚, SE=3.08) was not significantly different to the post-intervention bias (Mean= -25.67˚, SE=2.82), $t(37)= .87$, $p= .39$. Furthermore there was no significant correlation between the prism adaptation effects on the open loop pointing measurements and effects on the light bias measurements r= -.16, $p= .17$.

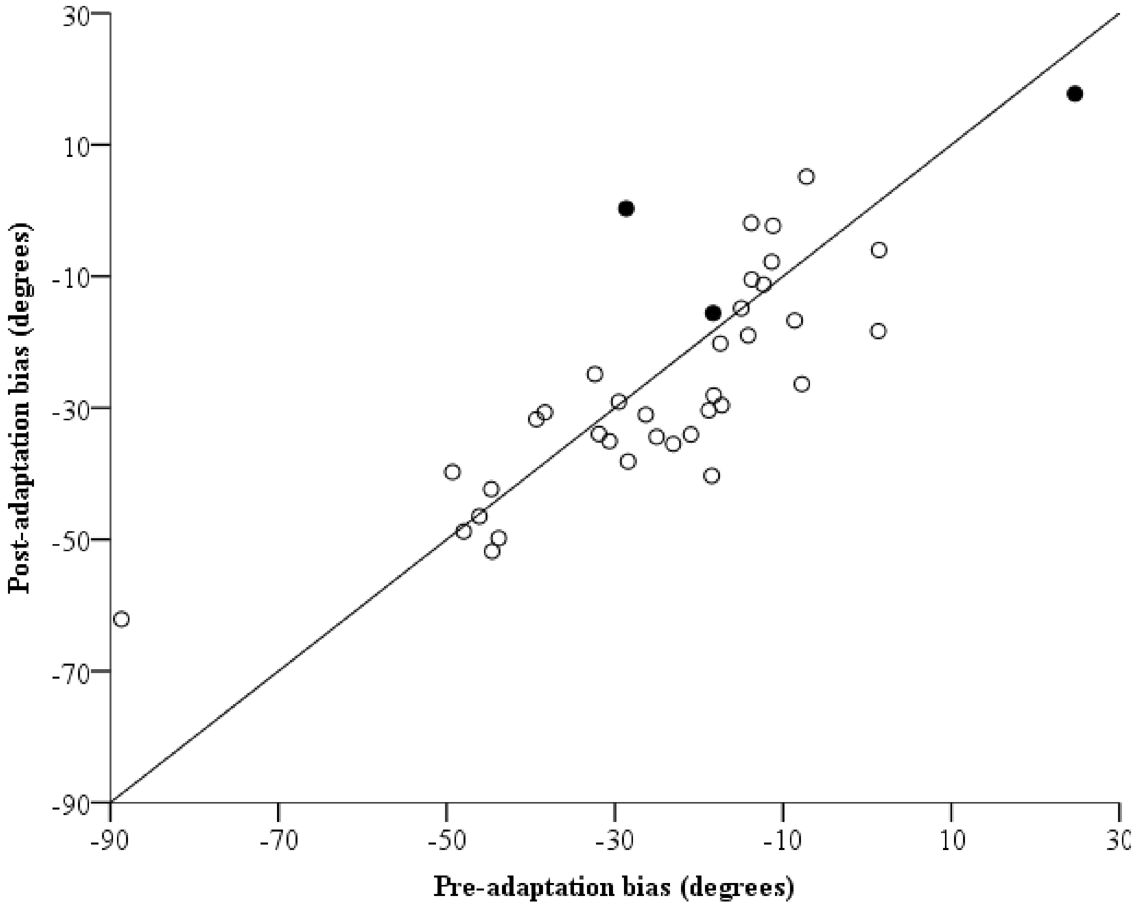


Figure 4.2: Participants' light biases pre and post prism adaptation. Negative values indicate biases left of vertical. Filled circles indicate left handed participants.

This experiment shows PA does not change the left lighting bias in healthy participants. The aim was to test whether disrupting the representation of the left side of space would affect participants' lighting biases. The fact that it did not suggests that either PA did not sufficiently disrupt the representation of the left side of space or that it was effective in this disruption but that the left lighting bias is driven by another independent factor.

Goedert, Chen, Foundas, and Barrett (2013) divided 24 acute HN patients according to deficit type using a computerised line bisection task. In some conditions participants' hand movements were reversed on the viewing screen, a technique adapted from Tegner and Levander (1991) who used mirrors. In the reversed condition patients with perceptual deficits moved their hand to the left so their bisections continued to be on their perceived right, whereas patients with motor deficits continued to make ipsilesional hand movements and thus bisected lines on their perceived left. Seven patients were categorised as displaying perceptual deficits only, five as having motor deficits only and the remaining 12 were categorised as showing both. Ten PA sessions were administered in total over two weeks. In addition HN severity was measured weekly over 5 weeks using the BIT and the Catherine Bergego Scale (Azouvi et al., 2003) together forming a large battery of functional impairment and paper and pencil assessments. Throughout the weekly sessions HN improved most in the motor deficits group and intermediate improvement was measured in the patients who showed both types of deficits. There was no improvement in the patients categorised as showing perceptual errors only.

A similar pattern was also reported in healthy participants. Using the same computerised line bisection task, Fortis, Goedert, and Barrett (2011) found PA selectively affected motor and not perceptual components of the task in a group of 84 healthy participants. Striemer and Danckert (2010) assert that this is because prism adaptation influences dorsal areas implicated in vision for action and therefore as a rehabilitation technique it improves motor behaviours but not perception. Therefore, the non-significant result in this experiment could be due to the PA method affecting only motor behaviours for the light source task is a perceptual task rather than a motor task.

Another intervention method should be used to dissociate between the possibilities that the non-significant result is due to either the PA technique, or the robust nature of the left lighting bias, remaining unaltered when HN like symptoms are induced. If the lighting bias changes with a different methodology then the previous non-significant result is due to the PA technique. However if the lighting bias remains unaltered then it suggests that the left lighting bias can remain when a representation of the left side of space is disrupted. In order to make this dissociation clearer participants should also complete a test commonly administered to HN patients as an independent measure of the intervention's effect on attention.

Experiment Two: Transcranial Direct Current Stimulation Over 10 Minutes

Participants

Twenty naive right handed participants (mean age = 24.9) with no history of neurological or psychiatric impairment participated. All had normal or corrected to normal vision.

Apparatus and Stimuli

Participants faced a faced an iiyama ProLite B1906S screen with a resolution of 1280 x 1024 at a distance of 50cm. As in previous experiments the honeycomb stimulus was presented at 24 different orientations 15˚ apart; stimulus size on this display was 10.84˚ diameter.

Participants also completed a line bisection task. The purpose of this test was to independently measure any lateralised shifts of attention as a result of the stimulation. Participants were shown 20 black horizontal lines on white A2 paper which were 1mm thick and ranged from 100mm to 404mm in length.

tDCS

One saline dampened 5x5cm sponge electrode was held in place by a rubber strap over the right parietal cortex, centred on P6 of the International EEG system (Koessler et al., 2009) and set as cathodal. The other electrode was placed over the left parietal cortex centred on P5 of the International EEG system and set as anodal. These locations were chosen because Giglia et al. (2011) showed stimulation in these locations induces HN like symptoms in healthy participants. Current was delivered from anode to cathode using a

Magstim DC Stimulator Plus (Magstim Ltd, Whitland, UK). During the real stimulation condition the current was ramped up to 1.5 mA over 15 seconds and then remained constant for 10 minutes. During the sham condition the current was ramped up as in the stimulation condition but then reduced to zero after 15 seconds. Participants were unable to tell the difference between this initial sensation and the stimulation condition, reporting feeling an itchy or tingling sensation for the first few seconds in both conditions.

Procedure

Participants completed both the light source task and the line bisection task twice during each session, pre and post stimulation. The procedure for the light source task was the same as in Experiment One. During the line bisection task the A2 sheet was placed in front of participants at their midline and participants were asked to intersect the centre of each line using their right hand. No time limit was applied. Deviation from true centre was measured to the closest .5mm.

All participants completed a real stimulation session and a sham session one week apart. Both task order (light source and line bisection) and session order (stimulation and sham) were counter balanced. During the 10 minute stimulation period participants sat in the dimly lit room and the experimenter did not communicate with them during this time.

Results and Discussion

Line Bisection

Participants' percentage deviations from true centre were calculated for each line using the following formula: (deviation/line length) x100. The mean percentage deviation was calculated for each administration of the line bisection test, so each participant had four mean percentage deviation scores, pre and post stimulation in the real and sham conditions. Figure 4.3 shows the mean percentage deviations for the baselines in the stimulation (mean= -0.08, SE= .36) and sham (mean= 0.17, SE= .32) conditions, as well as the post stimulation results for the stimulation (mean= 0.1, SE= .27) and sham (mean= 0.38, SE= .34) conditions. Negative scores indicate deviations to the left of the true centre.

A factorial ANOVA with condition (real stimulation and sham) and stimulation (pre and post stimulation) showed non-significant main effects of both condition $F(1,19)=.57$, $p=.47$, $\eta^2_p=.03$ and stimulation $F(1,19)=1.23$, $p=.27$, $\eta^2_p=.063$ as well as a non-significant interaction $F(1,19)=.005$, $p=.95$, $\eta^2_p<.001$. This suggests the stimulation did not successfully disrupt participants' representation of the left side of space.

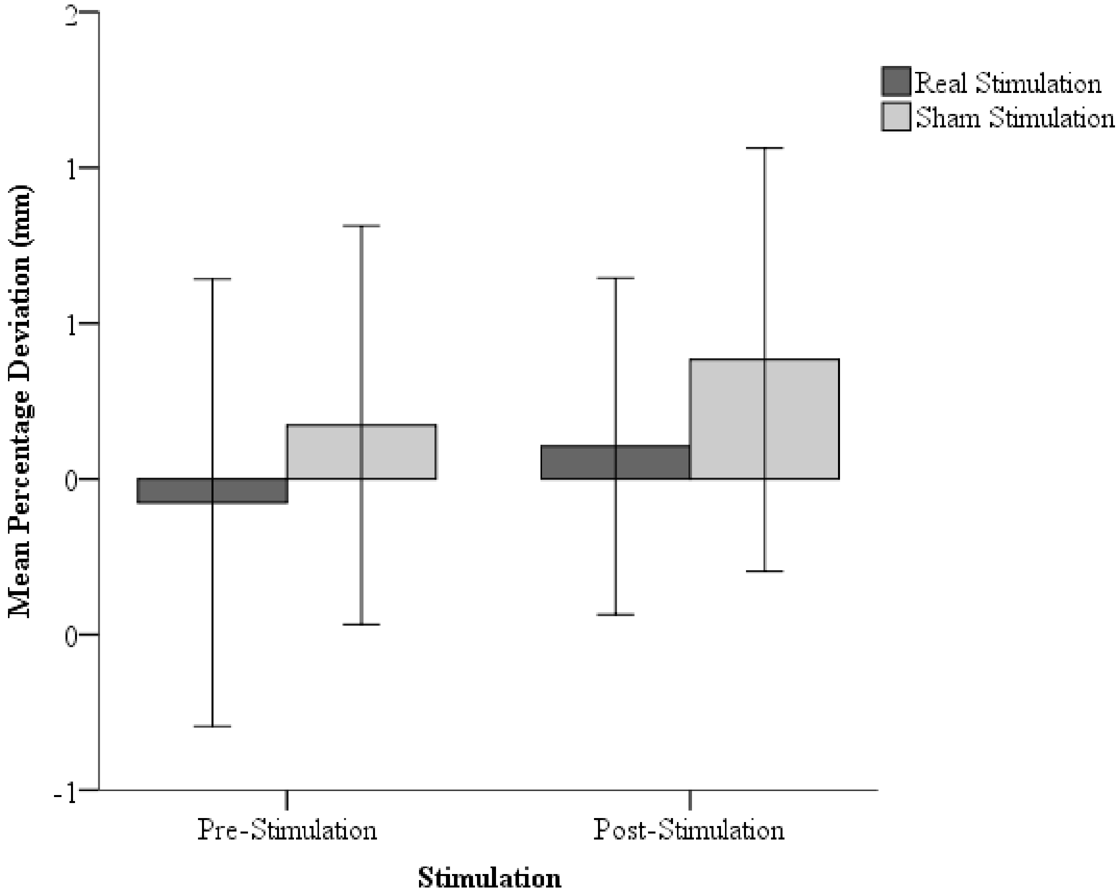


Figure 4.3: Graph representing the percentage deviations from true centre in millimetres, for the real stimulation and sham conditions, before and after the stimulation period. Negative scores indicate deviations to the left of the true centre. Error bars indicate ±1SE.

Light Source

Participants' light biases were calculated using the same formulae as in the preceding chapters. Figure 4.4 shows the mean light bias for the baselines in the stimulation (mean= -16.59˚, SE= 5.16) and sham (mean= -16.17˚, SE= 5.48) conditions, as well as the post stimulation results for the stimulation (mean= -19.59˚, SE= 6.21) and sham (mean= -19.09˚, SE= 6.04) conditions. The intervention of tDCS had a remarkably similar effect on the results in both the real and the sham stimulation conditions, with the mean bias shifting slightly to the left.

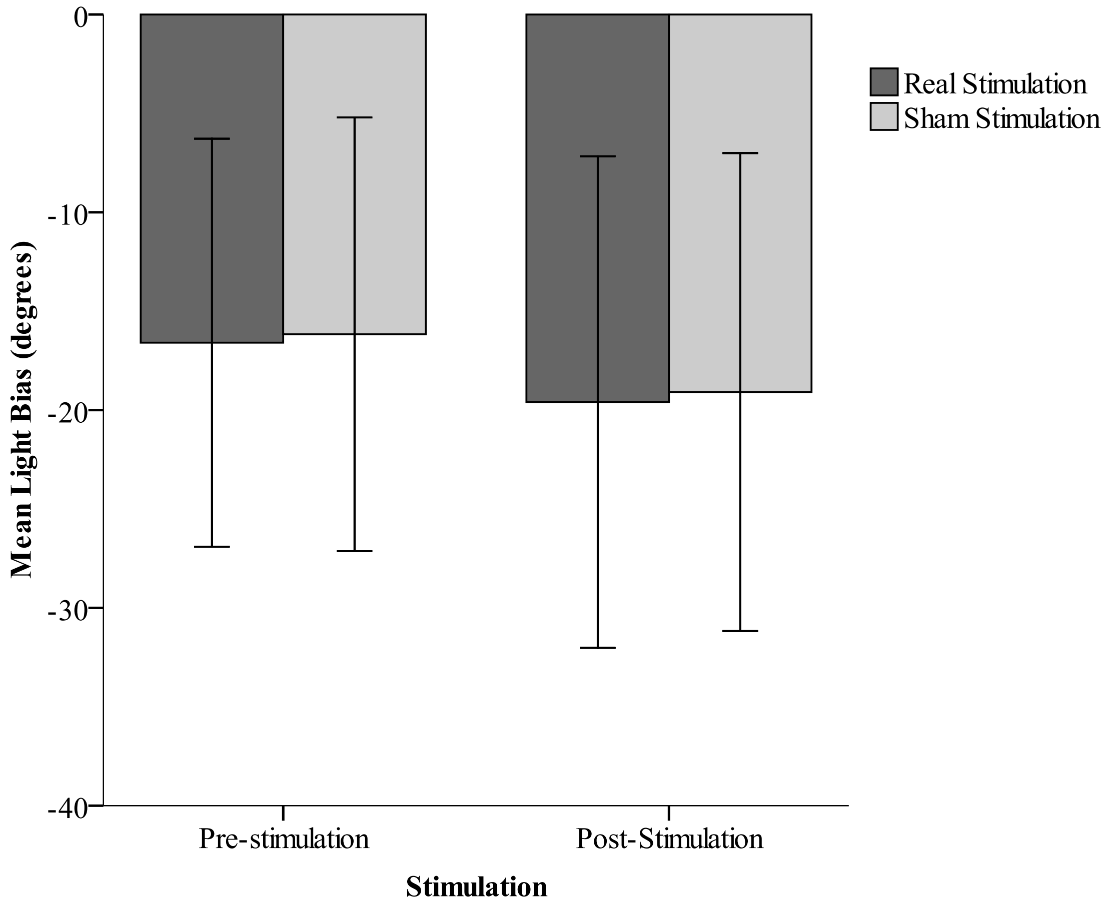


Figure 4.4: Graph displaying the mean light bias in degrees for the real stimulation and sham conditions, before and after the stimulation period. Negative bias scores indicate scores left of vertical. Error bars indicate ±1SE.

A factorial ANOVA with condition (real stimulation and sham) and stimulation (pre and post stimulation) showed non-significant main effects of both condition $F(1,19)=.023$, $p=.88$, $\eta^2_p=.001$ and stimulation $F(1,19)=1.27$, $p=.27$, $\eta^2_p=.063$ as well as a non-significant interaction $F(1,19)<.001$, $p=.99$, $\eta^2_p<.001$.

These results indicate that stimulation failed to induce HN like deficits in the healthy participants and also failed to modify participants' light biases. It is difficult to make conclusions about the effect of induced HN because it is not clear whether these two null results are linked or not. It is possible that the stimulation was ineffective in inducing HN deficits and as such there was also no effect on participants' light biases. Alternatively it is possible that the two are independent and if stimulation had successfully induced HN deficits participants' light biases would still have remained the same.

The reason that the stimulation did not show any effects could be due to the parameters chosen. It is unlikely that the electrodes were placed over inappropriate areas of the cortex because lesions to the right parietal cortex commonly cause HN (Perenin, 1997; Posner, et al., 1984; Vallar & Perani, 1986). Furthermore brain stimulation over these areas have produced HN like deficits of perception in previous tDCS (Giglia et al., 2011) and TMS (Fierro et al., 2001; Ghacibeh, Shenker, Winter, Triggs, & Heilman, 2007) experiments.

Another possibility is that the strength of the stimulation was not high enough, or the duration not long enough, to induce the desired deficits. Teo, Hoy, Daskalakis, and Fitzgerald (2011) found an effect of current intensity on modulation of working memory performance in healthy participants. Comparing performance after sham, 1mA, and 2mA intensities for 20 minute stimulation periods there was a significant difference between 2mA and sham but not between 1mA and sham. This is one of the few experiments to date that measures the effect of different current intensities on the same task. Although the task was related to working memory rather than attentional deficits it still shows that higher currents over a 20 minute period can have a larger impact on performance.

Finally, the line bisection test may also have not been sensitive enough to detect any minor shifts in lateralised attention. A line bisection task is not very cognitively demanding compared to the landmark task used by Giglia et al. (2011). Therefore a more sensitive measure of lateralised attention should be used in the future.

Experiment Three: Transcranial Direct Current Stimulation Over 20 Minutes

Experiment Three was implemented to address the issues raised in Experiment Two. It is predicted that a higher level of stimulation over a longer period of time will induce a rightward shift of attention. Also, that this shift will be more prominent in a more cognitively demanding spatial task than a line bisection task.

Participants

Fifteen right handed participants (mean age 24.8) with no history of neurological or psychiatric impairment participated. All had normal or corrected to normal vision. Participants from Experiment Two were excluded from this experiment.

Apparatus and Stimuli

Apparatus and stimuli in the light source task were the same as in Experiment Two.

Participants also completed the starry night test (Deouell et al., 2005) as described in Chapter Three as a more sensitive measure of lateralised shifts of attention compared to the line bisection task used in Experiment Two. The starry night test assessed participants' speed at detecting targets (blue squares) among distracters (red circles) in different locations on the screen. Targets and distracters could appear in any location on screen and were viewed at a visual angle of .46˚

tDCS

The same equipment was used as in Experiment Two. As in Experiment Two, one electrode was centred on P6 of the International EEG system (Koessler et al., 2009) and set as cathodal and the other electrode was centred on P5 and set as anodal. During the real stimulation condition the current was ramped up to 2.0 mA over 20 seconds and then remained constant for 20 minutes. During the sham condition the current was ramped up as in the stimulation condition but then reduced to zero after 15 seconds. During both the real and sham conditions participants reported feeling an itchy or tingling sensation for the first few seconds.

Procedure

All participants completed a real stimulation session and a sham session one week apart. Participants completed both the light source task and the starry night task twice during each session, pre and post stimulation. Both task order (light source and starry night) and session order (stimulation and sham) were counter balanced. During the stimulation and sham period participants sat with their eyes shut in the dimly lit room and the experimenter did not communicate with them during this time.

Light source

The procedure for the light source test was the same as in Experiment Two.

Starry night

The starry night test consisted of 147 trials. During each trial participants viewed an array of 49 randomly but evenly distributed red circles (distracters), one of which would disappear and reappear elsewhere every 50-250ms at random intervals. Thus, the distracter display was not fixed but constantly moving throughout each trial. The blue square (target) appeared after a random interval of 700-2100ms. Participants were instructed to respond by key press as soon as they detected the target. The target remained in place until the key press, or until 3000ms had passed. If the target was not detected after 3000ms that trial was recorded as a miss and the next trial began.

Results and Discussion

Starry Night

To analyse the results of the starry night test the screen coordinates were divided into seven equal columns. Trials were then categorised according to which column the target appeared in. All reaction times faster than 50ms were excluded to control for target anticipation. The "reaction time difference" is the difference in reaction time between targets presented in the three left and the three right columns. It was calculated by subtracting the median reaction time in milliseconds for the right targets from the median reaction time for the left targets; therefore a negative reaction time difference represented faster reaction times to targets on the left.

Figure 4.5 shows the mean reaction time difference for the baselines in the stimulation (mean= -3.37, SE= 4.68) and sham (mean= 5.93, SE= 4.04) conditions, as well as the post stimulation results for the stimulation (mean= 1.17, SE= 3.93) and sham (mean= -.97, SE= 4.88) conditions. Although the group means do shift in the direction that is expected after real stimulation because reaction times become faster for the targets on the right, this shift is minor and there is a large amount of between subject variance.

A factorial ANOVA with condition (real stimulation and sham) and stimulation (pre and post stimulation) showed non-significant main effects of both condition $F(1,13)=.78$, $p=.39$, $\eta^2_p=.05$ and stimulation $F(1,13)=.08$, $p=.77$, $\eta^2_p=.006$ as well as a non-significant interaction $F(1,13)=1.15$, $p=.3$, $\eta^2_p=.076$. This suggests the stimulation did not successfully induce a rightward shift in attention.

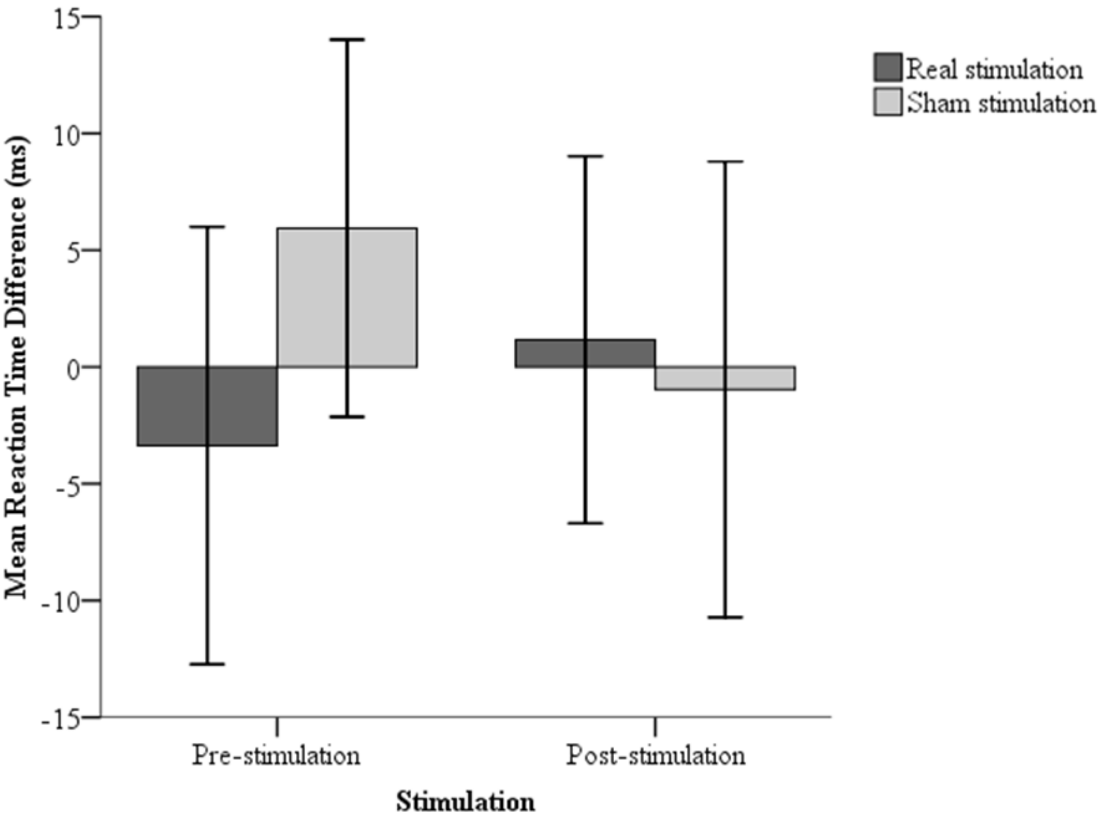


Figure 4.5: Graph representing the difference scores in milliseconds, for the real stimulation and sham conditions, before and after the stimulation period. Negative scores indicate faster reaction times for targets on the left. Error bars indicate ±1SE.

Light source

Participants' light biases were calculated using the same formulae as in the preceding chapters. Figure 4.6 shows the mean reaction time difference for the baselines in the stimulation (mean= -16.59˚, SE= 3.12) and sham (mean= -17.73˚, SE= 3.95) conditions, as well as the post stimulation results for the stimulation (mean= -19.36˚, SE= 3.45) and sham (mean= -13.51˚, SE= 3.18) conditions. The results in the real stimulation condition are very similar to the results in Experiment Two, with a small shift farther to the left after stimulation. However in this experiment after sham stimulation there was an equal shift to the right.

A factorial ANOVA with condition (real stimulation and sham) and stimulation (pre and post stimulation) showed non-significant main effects of both condition $F(1,13)=1.72$, $p=.21$, $\eta^2_p=.11$ and stimulation $F(1,13)=.14$, $p=.72$, $\eta^2_p=.01$. However the interaction did reach significance $F(1,13)=4.76$, $p=.047$, $\eta^2_p=.25$

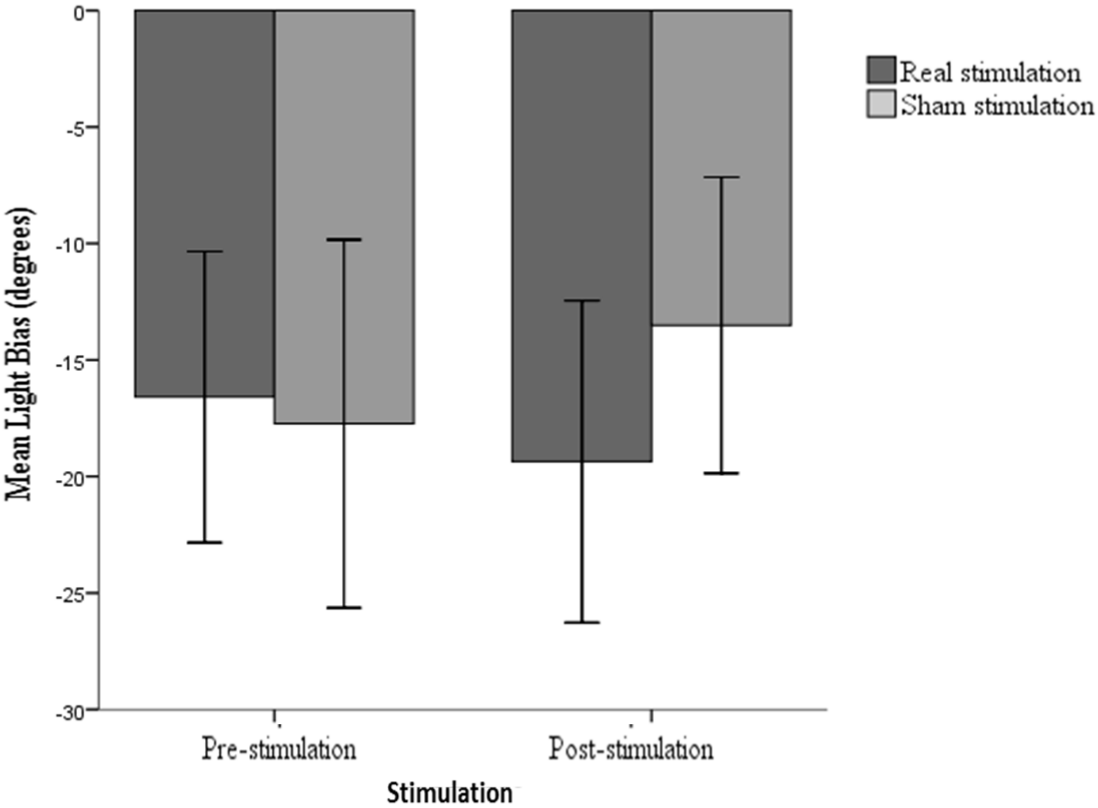


Figure 4.6: Graph displaying the mean light bias in degrees for the real stimulation and sham conditions, before and after the stimulation period. Negative bias scores indicate scores left of vertical. Error bars indicate ±1SE.

The results of the starry night test indicate that stimulation failed to induce HN like deficits in the healthy participants. Although the group average shift was in the predicted direction, this shift was small and there was high between subjects variability, therefore the shift did not reach statistical significance.

The reason why stimulation did not affect performance in the starry night test is unclear; the test was chosen for its sensitivity in detecting attentional deficits compared to more commonly used tests such as line bisection and cancellation tests (Deouell et al., 2005). Furthermore, previous research has reported inducing HN like deficits after stimulation over the posterior parietal cortices with lower stimulation than we used, and over a shorter amount of time (Giglia et al., 2007).

A second curious result is the shift that occurred in both the light source task and the starry night task after sham stimulation, which was in the opposite direction to the shift after real stimulation in both cases. The sham condition involved only 15 seconds of stimulation in order for participants to believe they were experiencing real stimulation, as such pre and post measures were expected to be the same. This highlights a potential methodological issue with sham sessions in tDCS experiments. Unlike TMS, the instantaneous effects of tDCS are under explored (Davis & Koningsbruggen, 2013) and so while 15 seconds of stimulation is very little compared to 20 minutes it cannot be assumed that those 15 seconds have no effect upon the brain.

Finally, the average light source biases measured in Experiments Two and Three were to the left but reduced compared to the group averages measured in Experiment One and the first language English group tested in Chapter Two, both of which showed similar group averages of -24.11˚ and -27.29˚ respectively. The procedure was the same across all experiments; the only difference which may have caused the reduced bias in this experiment was the smaller visual angle of the honeycomb stimulus. A correlation was performed between mean light bias and visual angle across the first language English groups in Chapter Two and the published version of Chapter Two, as well as the baseline biases measured in Experiments One, Two, and Three (see Figure 4.7). For Experiments Two and Three which contained two baseline measures (pre stimulation and pre sham) the mean was calculated using the results from the first session the participants completed. There was a strong negative correlation between visual angle and light bias, r= -.93, *p*=.012. This could explain some of the variance across studies within the literature. There is evidence of other visual processing biases becoming more lateralised with large stimulus presentations. For instance in line bisection tasks, larger lines result in larger deviations from true centre (Chokron & Imbert, 1993; see Jewell & McCourt, 2000 for review).

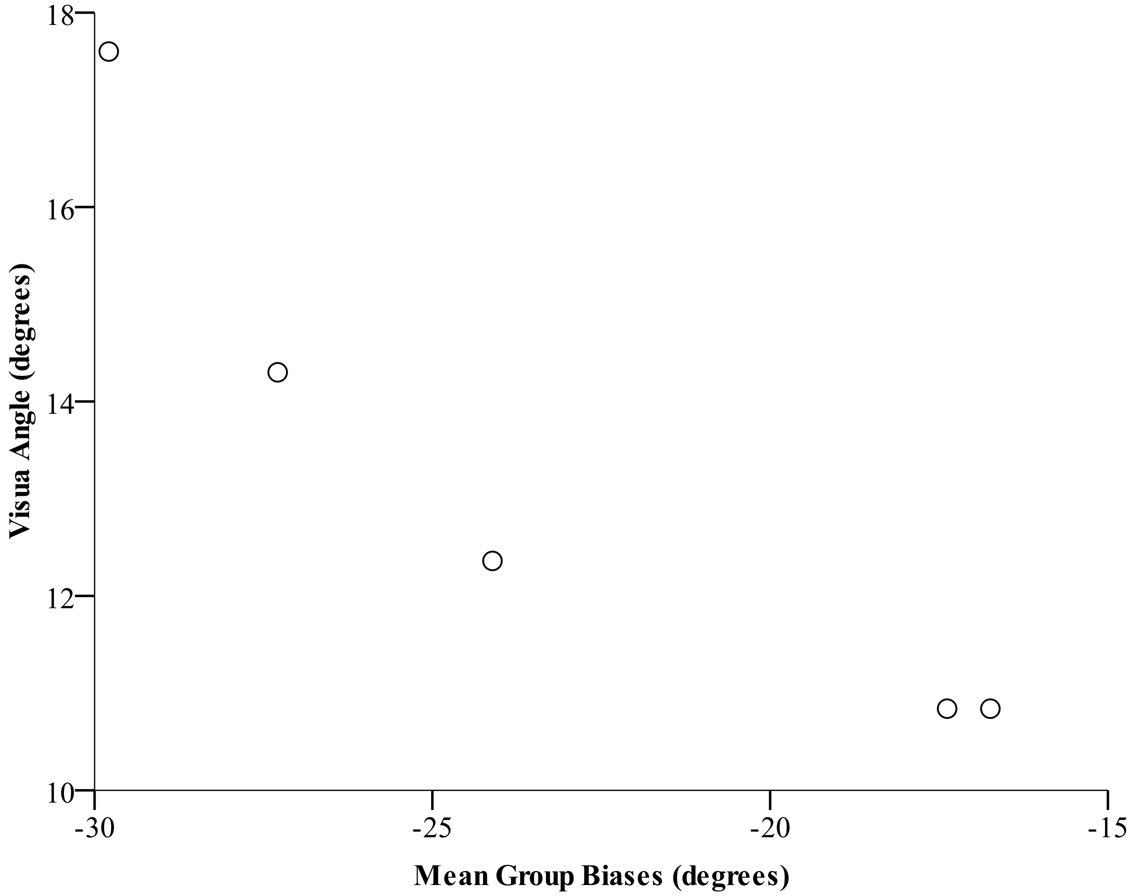


Figure 4.7: Scatter plot displaying the mean biases across experiments and the relationship with visual angle.

General Discussion

The current chapter intended to use interventions to induce lateralised attentional deficits and shift the mental representation of the left side of space in healthy participants.

However there is little evidence that a shift was successfully induced and as such the initial aims were not met.

Literature on the specific effects of PA is mixed, with some research showing an influence on visual perception and mental imagery tasks (Girardi et al., 2004; Loftus et al., 2008; Rode et al., 2001) and contrasting reports suggesting that predominantly motor behaviours are effected (Goedert et al., 2013; Striemer & Danckert, 2010). Therefore although after effects of the intervention were measured by open loop pointing, the extent to which these pointing errors reflect changes in visual perception is unclear. PA was used as a technique because the experiment began in 2011, before the majority of evidence suggesting only motor behaviours are affected was published. In Experiments Two and Three the tDCS did not cause a rightward shift in line bisection errors or quicker reaction times for targets on the right of the screen, suggesting an attentional shift to the right was not induced.

In summary, this chapter failed to induce HN like attentional deficits in healthy participants. As such, conclusions cannot be made regarding the effect of attentional shift on lighting bias.

Chapter 5. Effects of Ageing.

Chapter Overview

Chapter Three measured the assumed light source direction in stroke patients and age matched controls. The control group (mean age 62) showed a reduced lighting bias compared to the younger participants tested in other chapters. However due to different procedures and experimental equipment a direct comparison cannot be made. The current chapter recruited undergraduate students and measured their lighting biases using exactly the same procedure and apparatus as Chapter Three. Additional older participants were also recruited to replace the age matched controls who were younger than 60. There was a significant effect of age group and a significant correlation, with the older participants showing a significantly rightward lighting bias compared to the young participants. This is attributed to the change in hemispheric asymmetry that occurs with ageing, as the right hemisphere degenerates faster than the left, leading to a rightward shift in visual processing biases.

Chapter Three measured the assumed light source direction in three groups of patients and a fourth group of healthy age matched controls. The control group (mean age 62) showed a mean lighting bias of 5.9˚ to the left. This is small and close to 0˚ in comparison to the younger participants tested using the same stimulus in Chapters Two (English group) and Four (pre-prism adaptation and pre-tDCS) who showed biases of -26.86˚, -24.11˚, and -16.59˚ respectively. The reason for this apparent difference in age groups could be solely due to experience with light source manipulations. It seems unlikely, however, that observers drastically alter their light and object manipulations as they age. The difference could also be attributed to the experimental parameters which were different between chapters.

As mentioned in previous chapters, a non-experiential factor previously implicated in the left lighting bias is hemispheric asymmetry, that is, the right hemisphere advantage in processing visual information (de Montalembert et al., 2010; Mamassian & Goutcher, 2001). Furthermore Chapter Three showed a shift in lighting bias after right hemisphere disruption, although this shift was in the opposite direction to predictions.

Research has investigated the decline of hemispheric asymmetry with age using tasks which typically involve lateralised hemispheric specialisation. For example Goldstein and Shelly (1981) recruited 1,247 males and assigned them to one of 6 age groups from 20s to 70s. Participants completed a battery of tests which are capable of predicting lateralised brain damage, such as tests of verbal fluency, spatial judgements, and speeded tapping with each hand. It was found that performance declined linearly with age for all tasks. However this decline was significant only for the tasks which indicate right hemisphere damage, leading to the conclusion that the right and left hemispheres age differently. While this experiment has a large number of participants a disadvantage is that they were all male. However the same pattern of results has been found in a comparison of 32 adults (aged 18-77; Jenkins, Myerson, Joerding, & Hale, 2000) and 131 participants aged 18-90 (Lawrence, Myerson & Hale, 1998) of both sexes. A further complication of Goldstein and Shelly's results is that the participants were all medical patients. However they do attempt to address this complication by assessing only those without any evidence of structural brain damage and the pattern of results remained the same.

There is also evidence of greater bilateral processing, for instance, older participants show greater bilateral activations in verbal working memory tasks which are left lateralised in younger participants (Cabeza et al., 1997; Reuter-Lorenz et al., 2000). Reuter-Lorenz et al. (2000) attribute this change in activation to a compensatory mechanism, recruiting additional brain areas in order to combat age related neural decline. This is supported by Reuter-Lorenz, Stanczak, and Miller's (1999) study, where older and younger participants performed letter matching tasks with varying levels of complexity. Letters were matched to targets either in the same or the opposite visual field, thus the stimuli were either projected to one hemisphere or bilaterally, encouraging bilateral processing. The older participants performed quicker and more accurately with bilateral presentations regardless of task difficulty whereas the younger participants only benefitted from bilateral presentation during the complex task. This shows bilateral recruitment aids the processing of demanding tasks for all age groups. Reuter-Loranz et al. argue this shows that for older adults, in less demanding tasks bilateral activation compensates for age related decline in neural processing. Furthermore Grady et al. (1994) administered a face matching task to younger and older adults; during face matching prefrontal cortex activity was right lateralised in the young group and bilateral in the old group. This shows age-related changes in lateralisation occurs not only for higher cognitive functions such as working memory but also for simple cognitive processes.

These patterns of behavioural decline suggest different effects of ageing in the two hemispheres and viewed as evidence that the right hemisphere degenerating faster than the left. However structural imaging in healthy adults does not always support this. Terry, DeTeresa, and Hansen (1987) examined the brains of 51 adults aged 24-100 who had died without any evidence of neurological or cognitive abnormality. Findings suggested a decline in brain weight begins around the age 55 with a loss of large neurons developing with age in all cortical regions. In contrast, small neurons and glia cells increased with age in some areas, including the frontal cortex and superior temporal areas. However there was no evidence of different patterns of neuronal loss in each hemisphere. Similarly Resnick, Pham, Kraut, Zonderman, and Davatzikos (2003) measures tissue loss in 92 healthy older adults aged 59-85 over a period of four years. The greatest amount of cortical atrophy was seen in the frontal and parietal regions. There was a greater right lateralised loss of grey matter in the inferior frontal and anterior temporal regions; however this pattern was reversed in the inferior parietal region and there was greater white matter loss in the temporal lobe.

Subcortical areas have also been assessed; Gunning-Dixon, Head, McQuain, Acker, and Raz (1998) assessed the volume of the caudate nucleus, putamen, and the globus pallidus in 148 healthy participants. There was a greater level of age related shrinkage for the right side of the putamen compared to the left. However there were also gender differences; age related shrinkage of the caudate was greater on the left in males and on the right in females. These data raise the question of why decline in right compared to left hemisphere functions are consistently reported when evidence for degeneration of right hemisphere structure is mixed. Jenkins et al. (2000) suggest that neuronal losses in the brain are diffuse, but the verbal and visuospatial domains are supported by different neural networks which are differentially sensitive to these losses.

Cerella and Hale (1994) illustrated potential connectivity differences in a neural network model. Within this model there were unimedial and bimedial which do not differ in number of neurons but in patterns of connections between neurons, with the unimedial networks having a higher connectivity density. As such both network types could suffer the same amount of neuronal loss but the bimedial networks would be more sensitive to this damage. It has been posited that the degree of connectivity in the underlying verbal and visuospatial neural networks differs and as such the networks are differentially vulnerable to ageing.

The only other study to measure lighting assumptions in an “older” group of healthy participants (not the traditional undergraduate student age) was de Montalembert et al. (2010). In that study the age matched controls (mean age 57.6) showed a mean bias of 5.2˚ left of vertical. Interestingly this is much closer to 0˚ compared to another experiment which used exactly the same stimulus and task and produced a mean bias of 22.5˚ to the left (Gerardin et al., 2010). However it is difficult to make inferences from this regarding potential age differences for two reasons. Firstly, Gerardin et al. (2010) state that the participants were university students but do not give any information about the ages of the students. Secondly, although the task was the same between experiments, parameters such as presentation time and visual angle differed.

Similarly, a direct comparison of the data collected so far in different age populations is not possible because the control participants in Chapter Three were tested in a modified procedure in line with the patients. This involved a longer stimulus presentation time and a different method of response; the younger participants pressed buttons indicating their response whereas the older control group stated their response verbally. The effects of these changes on perceptions of the “honeycomb” stimulus are unknown and therefore a young group should be tested using these parameters. If the reduced light bias shown in the older controls is due to age then the younger participants will show a left bias similar to the biases in previous chapters. Alternatively, if the stimulus presentation time and response method modifies the bias then the younger participants will show a reduced bias similar to the older controls.

The older participants recruited in Chapter Three were chosen to closely match the stroke patients in age. This resulted in an age range of 45-81 and a mean of 62.64. As such, additional older participants should be recruited so there is a larger age range and a greater proportion of elderly participants in the "older" group.

Method

Participants

Fifteen Undergraduate students from Bangor University (mean age 21.13; range = 18-33) were recruited for the young group and received course credit for their participation.

Seven participants aged over 65 were and added to the data from Chapter Three, recruited through Bangor University's Participation Panel (mean age 64.2; range = 45-81) and were paid for their participation. All participants had normal or corrected to normal vision.

Apparatus and stimuli

Apparatus and stimuli were the same as in Chapter Three.

Procedure

Participants completed one practice block containing 15 trials, to familiarise the participants with the stimuli and responses. This was followed by two blocks of 120 trials for the older group and four blocks for the young group. As in Chapter Three participants verbally stated their responses and the experimenter, who could not view the screen, pressed the corresponding button. Each stimulus was presented for up to 3000ms with the next trial beginning upon the experimenter key press. If there was no response within 300ms of the stimulus ending a prompt appeared on screen saying “is it in or out?”.

Results

Data were analysed using the procedure described in Chapter Two. Two participants in the younger group were excluded because their responses were not significantly modulated by the orientation of the stimulus, p=.54 and p=.48. One participant in the older group did not complete the task as she exclusively saw the central hexagon as pushed in. Therefore 13 young adults and 20 older adults were included in the analysis.

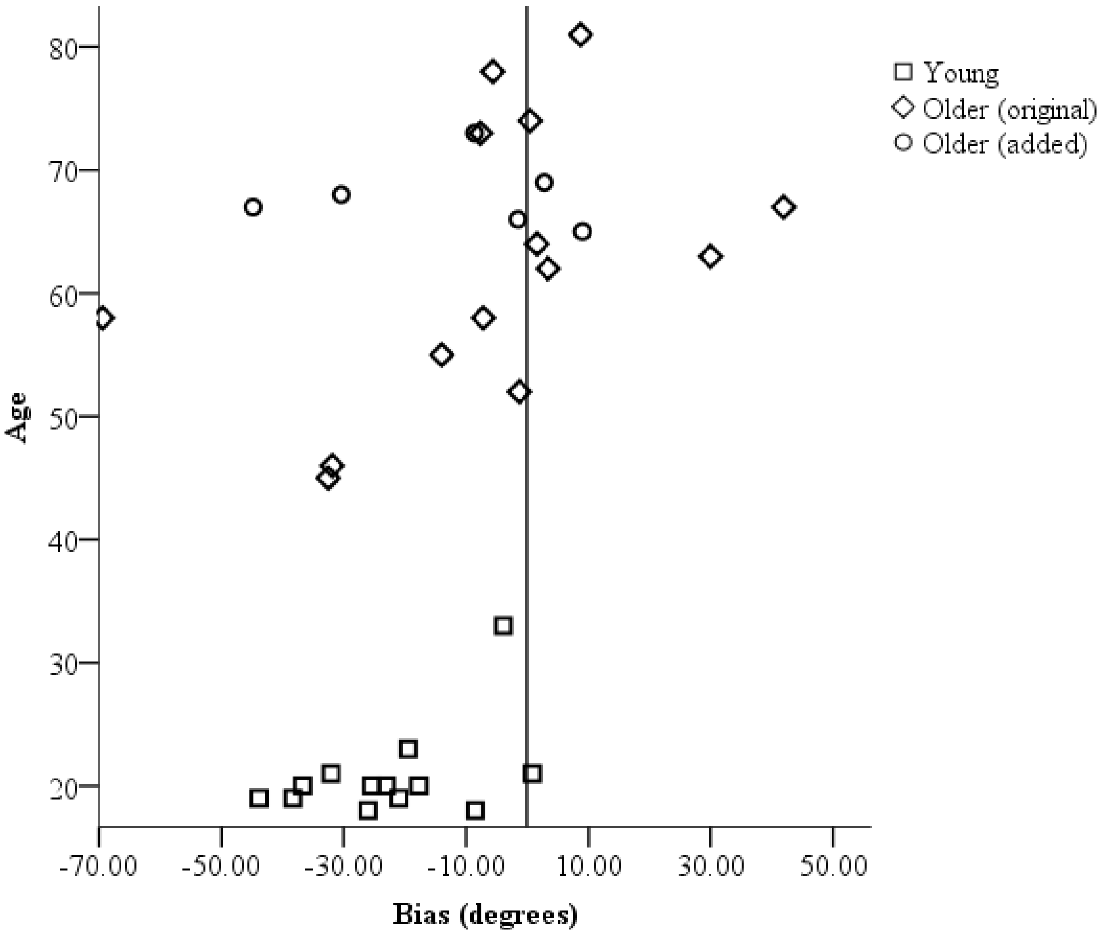


Figure 5.1: Graph displaying the age and bias of each participant, grouped by age and recruitment session. Reference line indicates zero degrees.

Figure 5.1 shows the age and lighting bias of each participant. All but one of the participants in the young group showed a leftward lighting bias (mean= -22.69˚ SE=3.7), resulting in a sample which was significantly different from zero $t(12)= -6.13$, $p<.001$. Conversely eight participants in the older group had a rightward bias; although they showed a larger range of results, this was caused by some more extreme left and right biases, with the majority of the group clustering around zero (mean= -7.85˚ SE=5.58). As a group they did not have a bias significantly different from zero $t(19)= -1.41$, $p=.18$.

The bias was significantly more leftward for the young group than the older group $t(31)= 1.96$, $p=.03$ showing that the left bias in light source assumptions are different in older compared to younger observers.

These effects of age cannot be accounted for by differences in stimulus exposure time, because there is no significant difference in reaction time between the age groups $t(31)= -.28$, $p=.78$. This is not the ideal measure of participant reaction time as it is taken from the experimenter key press rather than the time at which the participant stated their answer. However it can be assumed that the experimenter response time was consistent across participants.

Discussion

The results show firstly that the left lighting bias reduces with age, and secondly, confirm that the honeycomb stimulus is a robust and reliable stimulus that is not affected by stimulus presentation time. The reasons why age may affect the lighting bias are discussed.

This is in line with findings that tasks usually associated with right hemisphere function such as visuo-spatial tasks are more susceptible to decline with age than other tasks (Goldstein & Shelly, 1981; Jenkins et al., 2000; Lawrence et al., 1998). These age related deficits are not easily attributed to hemisphere specific decline, such as neuronal loss (Gunning-Dixon et al., 1998; Terry et al., 1987).

Levy (1976) argues that hemispheric asymmetry affects visual processing judgments because viewing pictures causes greater activation in the right hemisphere which leads to an attentional bias in the contralateral direction, toward the left visual field. As a result greater perceptual weight is placed upon stimuli in the left visual field. This suggests, in agreement with the conclusions of Mamassian and Goutcher (2001), that when young participants view a shaded shape, such as the honeycomb, greater perceptual weight is placed upon the left side of the stimuli and therefore the light is also internally represented on the left, to highlight this preferred side. However in the older adults the right hemisphere activation is reduced and thus the perceptual weight is no longer placed predominantly in the left visual field, reducing the leftward shift in light source biases.

One question arising from these findings is the relation to the results of Chapter Three. If degeneration of the right hemisphere can affect observers' lighting biases, it would make sense to predict that natural ageing and right hemisphere lesions would have a similar effect. Indeed, Kilsz (1978) reported that in the Halstead-Reitan Neuropsychological Test Battery (HRB) designed to test lateralised brain injury, the elderly control participants showed the same patterns of performance as the right hemisphere patients and not the left hemisphere patients. However this was not the case in the light source task, in fact the older controls' performance more closely resembled the left hemisphere patients. One possible reason for the difference in performance is that compensatory behaviour is different between the groups. The healthy older participants and the right hemisphere patients both have reduced activity in the right hemisphere, which is the explanation for their similar performances in the HRB (Kilsz, 1978). However both groups also employ compensatory mechanisms. Healthy ageing adults show growth of new synapses (Ivy, MacLeod, Petit, & Markus, 1992) and a reorganisation of brain circuitry (Pradhan, 1980). Similarly, a re-organisation of circuitry is seen in chronic stroke patients within both the damaged and the undamaged hemisphere in order to compensate for the lost functions (Rossini et al., 1998; Weiller, Chollet, Friston, Wise, & Frackowiak, 1992). As such, when comparing the right hemisphere stroke patients to the age matched controls there is not only the known damage or degeneration of the right hemisphere but also the unknown compensatory mechanisms within the brain circuitry, which may cause differences in performance of behavioural tasks.

An alternative possibility is that the two age groups are using different cognitive strategies to complete the task meaning that the difference between the age groups may not represent the development of lighting assumptions with age. Kleffner and Ramachandran (1992) found that reaction times for detecting a target sphere with the opposite shading to the distracters did not increase linearly with the number of distracters. Similarly, Adams (2007) showed that the light prior is correlated in individuals across a visual search task with multiple items, a shape processing task requiring judgment of a selected target, and reflectance judgements. This indicates there is a single process responsible for perceived shape across the different tasks, suggesting perceived shape from shading may be a pre-attentive feature.

Some studies have shown a deficit in preattentive processing in older participants (Ball, Beard, Roenker, Miller, & Griggs, 1988; Tales, Troscianko, Wilcock, Newton, & Butler, 2002), although other findings show no difference between older and younger groups (Foster, Behrmann & Stuss, 1995; Plude & Doussard-Roosevelt, 1989). A deficit in perceiving “pop out” features in the older participants would require the older participants to use more explicit cognitive strategies to complete the task, for instance using explicit knowledge of lighting cues to deduce the most likely solution. However this alternative explanation is unlikely because using reasoning to determine shape would take a longer time than perceiving the shape as a pop out feature, and there was no significant difference in reaction time between the two age groups. Furthermore, evidence suggests that preattentive processing deficits in older participants are more pronounced for targets presented in the periphery (Owsley, Burton-Danner, & Jackson, 2000) and during tasks with higher cognitive demands (Ball et al., 1988; Burton-Danner, Owsley, Jackson, 2001). The present study used a central presentation only and a simple shape processing task, suggesting the older participants were not likely to suffer preattentive deficits in this task. As such it is more likely that the difference between the two groups reflects changes in the ageing brain.

The current study used a combination of data previously collected (in Chapter Three) and additional data to confirm a hypothesis with was generated in part based on the results of Chapter Three. As such, it would have been more appropriate if an entirely new sample was recruited. In the future it would also be interesting to conduct a large cross-sectional experiment and recruit participants from throughout the lifespan, including throughout child development. As there was no apparent effect of presentation time or response method, age is analysed further in a multiple regression in Chapter 6 using all data collected throughout the thesis.

In summary, there is a significant correlation of age and light source assumptions, with the light bias shifting to the right as observers age. This may be due to changes in hemispheric asymmetry in the ageing brain. These changes alter the perceptual value placed on visual stimuli, so the left bias recorded in younger observers reduces with age. This results in different manipulations of light sources in the observers’ environment and thus alters their assumptions about normal lighting when viewing shaded stimuli.

Chapter Six. General Discussion

The aim of the current thesis was to explain why observers assume that light originates from the above left when viewing a shaded stimulus. Chapter Two shows that reading direction modifies the left lighting bias. First language Hebrew speakers, who read and write from right to left showed a significantly reduced lighting bias compared to first language English speakers. Chapter Three found that living with HN for up to 33 months does not result in a rightward shift of lighting assumptions; rather, the right hemisphere patients showed biases which were more leftward than the age matched controls, independent of attentional deficit. Chapter Four intended to add to the conclusions of Chapter Three by using interventions to induce lateralised attentional deficits in healthy participants. The interventions did not cause rightward shifts in light source biases, however this conclusion should be taken with caution for there was no evidence that the interventions successfully induced a rightward shift of attention. Finally, Chapter Five measured significant age effects, with the lighting bias shifting to the right with age.

Several factors have previously been implicated in the left lighting bias such as handedness (Sun & Perona, 1998), neural correlates (de Montalembert et al., 2010; Gerardin et al., 2010; Mamassian et al., 2003), visual field preferences (Mamassian & Goutcher, 2001), and experience (Adams et al., 2004; Thomas et al., 2010). The implications of the findings in this thesis are discussed below, with reference to these posited theories in the literature, as well as further findings which have arisen.

Multiple Regression Analysis

A multiple regression analysis was performed using the variables discussed in the thesis in order to test which of them significantly predict the variable of lighting bias. The predictors included were age, visual angle, gender, handedness, language (English or

Hebrew), HN (present or absent), left hemisphere damage (present or absent) and right hemisphere damage (present or absent). Data were used from all experiments reported in the thesis as well as the additional participants recruited for the published version of Chapter Two. As such data from 162 participants were included in the analysis. For experiments with repeated measures designs only data from the first session was used. The results of the regression indicated the eight predictors explained 25% of the variance (R=.5, R^2=.25 $F(8,153)=6.38$, $p<.001$. Table 6.1 shows the beta weights and significance levels for each of the individual predictors.

Table 6.1. Predictors of the variable lighting bias.

Predictor	β	*t*	*p*
Age	-.32	3.73	<.001**
Visual Angle	-.19	-2.03	.044*
Gender	-.04	-.56	.58
Handedness	-.01	-.18	.86
Language	-.30	-3.45	.001**
HN	-.19	-2.68	.008*
Left Hemisphere Damage	.13	1.66	.100
Right Hemisphere Damage	-.32	-4.24	<.001**

**p* values significant to .05 level

***p* values significant to .001 level

Age, visual angle, language, HN, and right hemisphere damage significantly predicted lighting bias and will be discussed in further detail.

Physical properties of the stimuli

An unexpected finding within this thesis is the effect of stimuli size. Chapter Two concluded that the left lighting bias was not modulated by properties of the stimulus because there was no difference in biases measured using different levels of blur. However, although similar procedures were used throughout the experiments, the size of the honeycomb stimulus differed slightly due to different experimental equipment. As reported in Chapter Four there was a significant correlation between the visual angle of the honeycomb stimulus and lighting bias, with larger stimulus presentations leading to more extreme left biases. This finding was confirmed by the multiple regression analysis which showed that visual angle is a significant predictor of bias.

There is evidence of other visual processing biases becoming more lateralised with larger stimulus presentations, for instance line bisection tasks, in which larger lines result in larger errors (Chokron & Imbert, 1993; Varnava & Halligan, 2007; see Jewell & McCourt, 2000 for review). This has been attributed to the entire line being processed during the task (Halligan, 1995) and task demands producing a systematic misperception of the line length (Varnava & Halligan, 2007).

The effect of stimulus size on light biases has not been explored within the literature, and could explain some of the variance across studies.

Handedness

Sun and Perona (1998) reported a correlation between light source biases and handedness, with left handed participants demonstrating a weaker leftward bias than right handed participants (7.9˚ and 23.3˚ to the left respectively). The authors concluded that this is caused by different light relative to object manipulations, with right handed observers showing a stronger preference for manipulating light sources in order to highlight the left side of objects. However this handedness difference has not been replicated by subsequent studies (Adams, 2007, Mamassian & Goutcher, 2001; McManus et al., 2004). Chapter Two confirms the left lighting bias is not modulated by handedness. Neither the first language English group, nor the first language Hebrew group showed an effect of handedness. This suggests that light sources are not manipulated differently in left and right handed observers. Mamassian and Goutcher (2001) suggest that there may have been several participants with atypical cerebral dominance among Sun and Perona’s left handed population, which could explain why they found such a strong effect of handedness which has not been found since.

The cerebral dominance of the participants recruited in Chapter Two is unknown. There is evidence that right hemisphere language dominance is more likely to occur in left handed individuals (Isaacs et al. 2006; Knecht et al., 2000); there is less consistent evidence for atypical cerebral dominance in attention and visuospatial tasks. Masure and Benton (1983) recruited non-right handed stroke patients and found that visuospatial functions are mediated primarily in the right hemisphere in both handedness groups, even when the right hemisphere is also dominant for language. However Borod et al. (1985) used a larger number of left hemisphere patients (21 left handed and 57 right handed) and more comprehensive visuospatial tasks and found that the left handed patients were significantly more impaired, particularly on tests requiring visuo-perceptual and spatial organisational skills. This suggests cerebral dominance for visuospatial processing can differ in left and right handed individuals because the left handed patients had more left hemisphere representation of non-verbal functions. However it is not evidence of a completely switched cerebral dominance in these left handed patients; simply that it is more bilateral in some left handed people.

Similarly Sun and Perona (1998) measured a range of handedness strength rather than exclusively strongly left and right handed participants. Therefore the likelihood that Sun and Perona would have a larger than average proportion of participants with atypical cerebral dominance is similar to the sample in Chapter Two, suggesting atypical cerebral dominance is not the reason for their conflicting results.

Neural Correlates

de Montalembert et al. (2010) investigated the effect of attentional deficits in HN patients upon the mental representation of light sources, but failed to find a correlation between severity of attentional deficit and shift in light source bias. Instead, of the right hemisphere patients, three of the patients showed a light bias which was right of vertical, one patient showed a bias of overhead lighting, and the remaining two patients showed left light source biases slightly more extreme than the control participants. The three patients who assumed the light sources were right of vertical had lesions within the frontal, temporal, and parietal areas of the cortex, whereas the remaining patients had subcortical lesions. The authors concluded that the fronto-temporo-parietal network modulates the lighting bias, with damage to this area resulting in an inability to mentally represent light sources in the contralesional space, thus the light sources are assumed to be right of vertical.

The results of Chapter Three contrast the results of de Montalembert et al. (2010) because the three HN patients who had cortical lesions encompassing areas of the frontal, temporal, and parietal lobes showed left biases more extreme than the age matched controls. Furthermore these biases were the same as the right hemisphere patients without HN. Therefore lesions to the fronto-temporo-parietal network do not appear to disrupt patients' abilities to mentally represent light sources on the left, even when there is a co-occurrence of chronic HN.

One possibility for this difference in performance is that it could be indicative of different recovery rates for representational neglect compared to perceptual neglect. HN for imagined space has been observed independently of other manifestations of HN (Beschin et al., 1997; Coslett, 1997; Guariglia et al., 1993). Therefore it is possible that although the HN patients demonstrated deficits in detecting external stimuli, their HN for imagined space had begun to recover. To address this in further experiments, recall tests for imagined space should be included in the neuropsychological assessments battery.

Chapter three did however report an effect of hemisphere, with all right hemisphere patients showing light biases significantly leftward compared to the left hemisphere patients, who showed biases similar to the age matched control group. This difference cannot be attributed to a specific lesion location or cortical network because within each hemisphere group there were patients with a range of cortical and subcortical lesions, all of whom showed the same pattern. Furthermore, in the multiple regression analysis HN and right hemisphere lesion were both significant factors but left hemisphere lesion was not significant.

This finding is particularly interesting because it is not what would be expected based on the role of the right hemisphere in other measures of visual field biases. In healthy observers, the right hemisphere has been reported to be hyperactive compared to the left hemisphere in the presence of visual stimuli. This leads to an attentional bias in the contralateral direction, toward the left visual field and thus makes stimuli in the left hemispace appear more salient (Kinsbourne, 1970; Levy, 1976). Furthermore, Beaumont (1985) states that participants look to the right of the point of interest to ensure the majority of the picture falls within the left visual field and thus will be more easily processed by the right hemisphere. This rightward bias in gaze was consistently measured in an eye tracking experiment displaying one or multiple objects of interest. However the data is limited, giving only a mean fixation coordinate for the entire set of trials in each condition. Additional information, such as analysis of first saccades, would be more informative.

The honeycomb stimulus used in this thesis was always presented centrally and central fixation was encouraged with a central fixation cross. As such, it is unlikely that the stimulus was processed predominantly by the right hemisphere during the task. However, the left bias is seen in various tasks which used central fixation and central stimuli (Gerardin et al., 2010; Mamassian & Goutcher, 2001) as well as stimuli spread across the visual display (McManus et al., 2004; Sun & Perona, 1996). As such, the left lighting assumption cannot be entirely due to the amount of stimuli visible in each hemifield.

Based on the above evidence it would be predicted that right hemisphere damage would lead to a rightward shift in attention. The fact that the right hemisphere patients showed a bias significantly to the left compared to the left hemisphere patients, who performed similarly to the control group, suggests that a shape from shading task is fundamentally different to other visual processing tasks. Perhaps due to the fact that during a shape from shading task participants are perceiving depth in a two dimensional picture, rather than forming judgements on physically visible properties of the stimulus. However why this would cause a shift to the left in all the right hemisphere patients with a range of cortical and subcortical lesions is unclear.

Chapter Four was designed to contribute to these conclusions. It was predicted that cathodal stimulation over the right and anodal stimulation over the left parietal lobes would simulate a lesion to the right parietal lobe in healthy participants. However stimulation had no effect on performance in the light source task or in a standard test of HN, despite previous research reporting effects after stimulation over the posterior parietal cortices using lower stimulation over a shorter amount of time (Giglia et al., 2007). As such, Chapter Four does not confirm that the right parietal lobe modulates the lighting bias.

In contrast, Chapter Five does support the prediction that degeneration of the right hemisphere results in a rightward shift in the lighting bias. A significant age effect was found, with the lighting bias shifting to the right with age, similar to previous findings that other visual processing biases shift to the right with age (Falia et al., 2003; Fujii et al., 1995; Jewell & McCourt; 2000; Stam & Bakker, 1990). This shift has been attributed to the right hemisphere degenerating more than the left with ageing (Ellis & Oscar-Berman, 1989; Gunning-Dixon, et al., 1998; Meudell & Greenhalgh, 1987) and to compensate for these ageing effects, processing that would be unilateral in younger individuals becomes more bilateral (Cabeza et al. 1997; Reuter-Lorenz et al., 2000).

It is possible that that the two age groups were using different cognitive strategies to complete the task meaning that the difference between the age groups may not represent the development of lighting assumptions with age. Some research has shown that shape from shading occurs preattentively (Adams et al., 2007; Kleffner & Ramachandran, 1982). Some studies have shown a deficit in preattentive processing in older participants (Ball et al., 1988; Tales et al., 2002), although other findings show no difference between older and younger groups (Foster et al.,1995; Plude & Doussard-Roosevelt, 1989). A deficit in perceiving "pop out" features in the older participants would require the older participants to use more explicit cognitive strategies to complete the task, for instance using explicit knowledge of lighting cues to deduce the most likely solution. However this alternative explanation is unlikely because using reasoning to determine shape would take a longer time than perceiving the shape as a pop out feature, and there was no significant difference in reaction time between the two age groups. As such it is more likely that the difference between the two groups reflects changes in the ageing brain.

The current thesis provides some evidence that hemispheric asymmetry modulates the lighting bias. However evidence is conflicting as to the specific role of the right hemisphere, with Chapter Three showing a leftward shift in the lighting bias after right hemisphere disruption and Chapter Five showing a rightward shift after right hemisphere degeneration. The reason for this is unclear; one possibility is that although both groups have reduced right hemispheric activity compared to young healthy observers that does not mean activity is similar in both groups. Healthy older participants and right hemisphere stroke patients both also employ compensatory mechanisms through a re-organisation of circuitry (Chollet et al., 1992; Ivy et al., 1992; Pradhan, 1980; Rossini et al., 1998; Weiller et al., 1992). As such, when comparing the right hemisphere stroke patients to the age matched controls there is not only the known damage or degeneration of the right hemisphere but also the unknown compensatory mechanisms within the brain circuitry, which may cause differences in performance of behavioural tasks.

Experience

Previous research has shown that both long term (Thomas et al., 2010) and short term (Adams et al., 2004) experience can modify light biases. Chapter Two shows that cultural experience, specifically the experience of reading direction, also affects observers' lighting bias. First language Hebrew readers showed a significantly reduced bias compared to first language English participants. Chokron and De Agostini (2000) posit that reading direction affects observers' direction of attention, resulting in observers directing attention toward the side on which they begin reading. This is compatible with Mamassian and Goutcher's (2001) suggestion that the lighting bias reflects a visual field bias. According to this theory, a preference for attending to one side of objects causes a preference in illumination which highlights that preferred side. Therefore Hebrew readers may direct their attention toward the right side of stimuli and place higher perceptual value on the right side of objects. This would result in different object and light manipulations within their environment and subsequently affect their lighting preferences.

Rather than showing an opposite rightward bias, the first language Hebrew participants showed a smaller leftward bias. This is in line with Vaid and Singh (1982) who found differences between left to right and right to left readers in a chimeric faces task and yet the rightward bias in the right to left reading group was not as strongly rightward as the leftward bias in the left to right reading group. First, Hebrew readers are not pure right to left readers because numbers, unlike words, are written from left to right. Also, the Hebrew participants were University students, with some exposure to English. Visual processing biases can be altered not only by the reading direction observers have learned from an early age, but also any other reading directions the observer is exposed to (Maas & Russo, 2003). Therefore, the reduced left bias may be due to the mixture of left and right writing directions experienced by the participants.

Conversely, it is possible that the default assumed direction of light is left but it can be modified by scanning habits related to reading direction. This latter suggestion appears the more likely as Vaid and Singh (1982) recruited Arabic readers for their right to left reading population and found a similar pattern of results. Unlike Hebrew, Arabic is written exclusively from right to left. Furthermore, Vaid and Singh only included participants with a low comprehension of English. The authors attributed the results to the mediating effect of both hemispheric interaction and reading direction on non-linguistic spatial tasks. This suggests that the hyper-attention of the right hemisphere is the cause of the left lighting bias, but our experience of consistently highlighting our preferred side of stimuli can modify or enhance that bias.

Chapter Three measured lighting biases in another population who habitually scan from, and attend to, the right. Three chronic HN patients with 16-33 months since lesion onset did not show a rightward lighting bias. In fact, all three patients showed a bias farther to the left than the age matched controls. It may be that up to 33 months is not long enough to modify the left lighting bias and the patients need to have experienced a preference for right sided stimuli for many years before a shift occurs. Indeed, 33 months is not long compared to the lifelong habit of scanning from the right as seen in Chapter Two. However, Adams et al. (2004) showed that light biases can be quickly modified by haptic information.

Although HN patients and first language Hebrew observers share the experience of preferentially attending to, and scanning from, the right side of stimuli the effect on assumed lighting direction is not the same in each group. This could indicate an interaction between preference driven experience with lighting and hemispheric damage.

Inter-observer variance

Across experiments a large range of biases was consistently measured between individual participants. Chapter Two shows that this variance is not caused by handedness; furthermore McManus et al. (2004) assessed lateralisation in more detail and found no correlation with participants' light bias. Additionally a chin rest was used at all times so the cause cannot be spontaneous head tilt as McManus et al. suggested.

Although Chapter Five shows that the lighting bias changes with age, this fails to explain much of the within group variance in other experiments as age was similar within each group in Chapters Two and Four. Sex is an obvious potential factor which could cause variance within a group. As mentioned above hemispheric asymmetry has been implicated in the lighting bias, and it has been shown that hemispheric asymmetry is different in males and females. Gender effects are seen in lateralised tasks such as higher scores of verbal reasoning in women, and greater performance in visuospatial tasks in men (Hellige, 2001; Voyer, 1996). Evidence for an effect of sex in visual processing tasks is mixed. Many studies have found no difference in performance between males and females in line bisection tasks (Chokron & Imbert, 1993; Luh, 1995; Milner, Brechmann, & Pagliarini, 1992; Scarisbrick et al., 1987; Shuren, Wertman, & Heilman, 1994) or chimeric faces tasks (Levine & Levy, 1986). Reported effects are also contradictory; Roig and Cicero (1994) reported greater leftward bisection errors in males whereas Wolfe (1923) reported greater leftward errors in females. Hausmann, Ergun, Yazgan, and Gunturkun (2002) reported an interaction between sex and the hand used to bisect lines; females showed similar biases with either hand whereas males predominantly showed a left deviation when bisecting using the left hand. Furthermore, Varnava and Halligan (2007) found effects of sex, age, and line length on bisection errors; these confounding effects may partly explain the inconsistent findings in other studies for not all of the experiments accounted for age, line length or handedness.

All the experiments in this thesis which recruited healthy young participants reflect the psychology undergraduate population at Bangor University, which is predominantly female. When participants are grouped by sex in each experiment that recruited healthy first language English participants (Chapters Two, Four, and Five), the female group consistently showed a more extreme, though not statistically significant, leftward bias than the male group. However, gender was not a significant predictor when all the data (60 males, 102 females) were entered into a multiple regression, suggesting gender cannot explain some of the inter-observer variance.

Additionally, Adams (2007) also reported high variance across participants and posited that it is unlikely the participants experience an environment of such highly different lighting directions over the long term; therefore the variance in biases must be caused by recent environmental experience. Adams et al. (2004) showed that light biases can be modified quickly by relevant information. Therefore it makes sense that individual’s light biases would be based not only on long term environmental experience but also updated by any relevant recent experience. As this cannot be accounted for and may be very different between participants it could well explain the inter-observer variance measured in previous chapters.

Object manipulation and internal representations

When discussing the factors affecting light source biases within this thesis, they are often described as affecting the left lighting bias in two different ways, by observers' experience of object manipulation and by their internal representation of the light source. Object manipulation is the accumulation of knowledge about light through interactions with objects relative to light sources. The position at which observers most often view light sources then becomes the normal lighting position for them. When asked to assume the light position in a shape from shading task observers assume the position which is the most likely based on their experience. If the left lighting bias seen in most observers was caused only by object manipulation then there would have to be one or several factors shared by most of the population which cause object manipulations to be similar across observers. As Chapter Two shows, habitual scanning caused by reading direction, a factor shared by most people, affects the lighting bias. Thomas et al. (2010) measured the light biases of a group of young children before they had achieved complete literacy and showed that the left lighting bias is not present at that stage. However this does not confirm that reading from left to right is the cause of the left lighting bias in left to right reading populations. Testing illiterate adults would help to identify the amount of influence habitual scanning has. If it is a primary influence in the left lighting bias then an illiterate group would show a greatly reduced, or no left bias.

Alternatively, this thesis has often described internal representations of the light source. This involves the participants imagining the location of the light while completing the shape from shading task. While this can be associated with object manipulation, for example observers internally representing the light source in the position that they are most commonly exposed to, it can also be dissociated. For instance de Montalembert et al. (2010) state that lesions to the fronto-temporo-parietal network disrupt patients' abilities to imagine light sources in the contralesional space. Chapter Four aimed to test whether disrupting the representation of the left side of space in healthy observers would lead to an inability to internally represent the light source on the left. This was not the case, participants continued to show a leftward bias after both PA and tDCS. However, this does not necessarily contradict de Montalembert et al. because it is unclear how effectively these interventions disrupted participants' representation of the left side of space. Some evidence suggests PA affects predominantly dorsal areas implicated in vision for action rather than perception (Fortis et al., 2011; Striemer & Danckert, 2010). As the light source task was perceptual this means that although pointing errors were measured these could be the only affect of PA and there is no way to know how each participant's representation of space was affected. Furthermore in Experiment Three a sensitive measure of HN showed that participant's reactions times to targets in different locations were not modified by the tDCS, suggesting participants' representation of the left side of space was not effectively disrupted.

The significant difference between age groups and the significant predictor of age suggests that older observers internally represent light sources farther to the right compared to young adults due to the degeneration of the right hemisphere with age. This would mean that in young adults the hyperactive right hemisphere causes a lateralised bias when viewing a shaded stimulus, so that the light is internally represented left of directly above. However if hemispheric dominance were the only factor causing the left lighting bias then the Hebrew speakers in Chapter Two would have shown a left bias to the same extent as the English speakers.

Therefore, it appears that the left lighting bias is mediated by hemispheric dominance and also reinforced by observers' experience. The two could also interact, with hemispheric dominance contributing to the lateralised preference of objects, this in turn would influence observers' light and object manipulations. As such, the left lighting bias is likely a combination of multiple experiential and neurological factors.

Limitations and Further Work

A limitation with many of the experiments in the current thesis is power, particularly when a specific population was sought. For example left handed participants in Chapter Two, patients in Chapter Three, and healthy ageing participants in Chapter Five.

A large cross sectional ageing study with a representative sample of a wider range of age groups would reveal more about the strong ageing effect measured in Chapter Five. Although this effect was confirmed with age as a significant predictor of bias using all the available data, few participants fell into the age range of mid twenties to late fifties. As such it is not clear whether there is a linear relationship between age and bias, or whether the effect of age measured so far is due to age related decline only seen in older populations of 60 and above.

The unexpected effect of visual angle requires further investigation using a within participants design. A larger range of visual angles can also be used. The current set of data contains four visual angles with a range of 10.84˚ to 17.6˚. A further experiment would be able to test the extent to which participants' responses can be modified by visual angle alone.

Another potential set of further experiments involves direct manipulation of spatial attention. Chapters Three and Four attempted to assess the effects of cerebral disruption and the subsequent effects on spatial attention and participants' lighting assumptions. It is possible to directly manipulate spatial attention without the confound of cerebral disruption through the use of cues. The Posner cueing paradigm (Posner, Nissen, & Ogden, 1978) shows that spatial attention can be directed to the left or right side of the display using an arrow as a central cue. In this paradigm participants are faster to detect targets which appear on the cued side compared to a neutral cue with no spatial information. Participants' response times were also poorer when the cue was invalid and the target appeared in the opposite location. This type of cue is an endogenous cue, whereby the information it provides informs top down orienting intentions. This may not be the best type of cue to use in a shape from shading task, particularly one which requires the shape discrimination of a central stimulus. This is because endogenous cues are used to inform participants in order to help them reach the task goals, and participants can ignore them if they are not informative (e.g. Berlucci, Chelazzi, & Tassinari, 2000; Jonides, 1981; Prinzmetal, Zvinyatskovskiy, Gutierrez, & Dilem, 2009). In the case of a central shape discrimination task an endogenous cue would not help the participants to complete the task so it is unlikely that the participants will choose to use it. Conversely, exogenous cues are automatic and stimulus driven, for instance a sudden stimulus onset in the periphery, and they cannot be ignored (Jonides, 1981). As such, exogenous cues would be appropriate for the manipulation of spatial attention in a shape from shading task.

Concluding remarks

The current thesis contributes substantially to our knowledge of light source biases. The lighting bias is affected by experience with language. There is also evidence for an effect of hemispheric asymmetry, although this relationship is less clear. Environmental experience is determined by a desire to highlight the left side of stimuli which informs observers' knowledge of normal lighting in their environment. The desire to highlight the left side of objects is not modulated by handedness or attentional deficits; it is however, affected by habitual scanning direction as a result of reading direction. It may also be exacerbated by hemispheric asymmetry, which itself effects judgements during a shape from shading task, as seen in the effects of ageing and right hemisphere lesions.

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