DOCTOR OF PHILOSOPHY

The Development of Visual Priors Across the Lifespan

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Award date:
2023

Awarding institution:
Bangor University

The Development of Visual Priors Across the Lifespan

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A thesis submitted to Bangor University in partial fulfilment of the degree of Doctor of Philosophy, 2022.

Declaration

‘I hereby declare that this thesis is the results of my own investigations, except where otherwise stated. All other sources are acknowledged by bibliographic references. This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree unless, as agreed by the University, for approved dual awards.

I confirm that I am submitting this work with the agreement of my Supervisor(s).’

Beverley Pickard-Jones

‘Yr wyf drwy hyn yn datgan mai canlyniad fy ymchwil fy hun yw’r thesis hwn, ac eithrio lle nodir yn wahanol. Caiff ffynonellau eraill eu cydnabod gan droednodiadau yn rhoi cyfeiriadau eglur. Nid yw sylwedd y gwaith hwn wedi cael ei dderbyn o’r blaen ar gyfer unrhyw radd, ac nid yw’n cael ei gyflwyno ar yr un pryd mewn ymgeisiaeth am unrhyw radd oni bai ei fod, fel y cytunwyd gan y Brifysgol, am gymwysterau deuol cymeradwy.

Rwy'n cadarnhau fy mod yn cyflwyno'r gwaith hwn gyda chytundeb fy Ngoruchwyliwr (Goruchwylwyr)

Beverley Pickard-Jones

Acknowledgements

They say it takes a village to raise a child, and the same is true of a PhD student. I've been so lucky to find such a supportive and scientifically rigorous village on my journey, which I consider having begun on the day I was accepted for undergraduate study at Bangor. My first thanks go, therefore, to Dr Caroline Bowman, who took a risk on a non-traditional student and facilitated a monumental change in my trajectory.

I'd like to express my gratitude to the many students who have helped with data collection along the way: Kimberley Stanford, Ronya Someschan, Jade Fenney, Caspar Wynne, Rebecca Philips, Tarab Khan, Amelia Oliver, and Marjola Peça, who I have no doubt will be an impressive researcher in her own right. Jakub Cieslak deserves a special mention for being a motivated and conscientious intern, who programmed the first version of the LAMP task. Thank you to Shir Presser, who tested many children in Israel on the Spheres Game. Also, I thank the British Academy, whose generous grant funded the development of the Spheres Game.

Nothing in this thesis would exist without willing participants and I was extremely fortunate to have been able to test hundreds of people who took the time to participate in this research. So, to my participants, the Soroptimists, Rotary Clubs, and U3A branches, who invited me to share my research and were generous with their time and insight: Thank you! There were also 160 children from various schools and nurseries across North Wales and Israel who were a delight to spend time with and a credit to themselves, their schools, and their parents. I am grateful for their willingness to complete these tasks (which were sometimes boring, but which they still endured with good spirits and impressive politeness!) and to the schools for facilitating our sessions and making space for us. I also appreciate the students who took part in my LAMP task and tried their best to complete a difficult task. I've also had many supportive colleagues and workplaces along the way, and I appreciate their willingness to listen to me about my research and for giving me time, where needed, to complete my activities.

It goes without saying, but I am deeply and eternally thankful for my supervisors, Dr Ayelet Sapir and Dr Giovanni d'Avossa, and my chair, Professor Paul Downing. As a *bona fide* psychologist now, I feel qualified to assert that every experience shapes your brain and I'm grateful to have had this team moulding my thoughts and guiding my development. I could not have wished for a more supportive and incisive supervisor than Ayelet, who was always willing to offer assistance and advice, and was always patient, even when I was stupid (which was often). I think Ayelet might be the most fiercely open-minded researcher I have ever met; I hope one day I can appreciate the merits and pitfalls of ideas as acutely as she can and explain them so clearly! Thank you, also, for always pushing me forward, making me do my best, and for sharing your brilliant ideas. Giovanni provided so much insight across the process, particularly with stats, and I learned such a lot (and realised how much I have still to learn). I wish that TMS experiment had worked out!

I've loved every minute of my PhD, and that wouldn't have been possible without being surrounded by the people with whom I've had the enormous privilege of sharing my journey. I have two personal thanks to give: to Emma Carr, my hype-woman, who never allowed me to believe I was anything other than a rockstar and genius – you're the best motivator and friend I could ever wish for! And my family, who provided inspiration, motivation, and supported me in a million different ways. If I wrote them all down, it would be an environmental disaster. Save the trees!

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Abstract

The efficient and accurate resolution of a three-dimensional percept from a two-dimensional retinal image is a computational problem that depends upon the conjunction of sensory information with prior knowledge. A tendency to assume that light comes from above and to the left of the apex in typical testing cohorts of young, Western adults, is a well-documented visual prior governing the resolution of three-dimensional shape from the patterns of light and shading on the surface of objects. Though the existence of the light-from-above prior and the leftward bias has been described extensively in previous literature, their origins remain unclear. Two primary theories have been posited for the light-from-above prior: that it develops in response to the visual experience of light coming from above, or that it is a developmental default. The left bias is more complicated. In addition to theories of visual experience, the roles of culturally proscribed reading habits and of innate hemispheric asymmetry may explain why a greater amount of attention is preferentially allocated to the left side of space. Chapter 1 discusses the primary theories posited on the origins of the light-from-above prior and the leftward bias by reviewing literature from developmental and ageing populations and from studies of pseudoneglect. In Chapter 2, these theories were investigated experimentally in a cross-sectional sample of 95 Welsh (left-to-right readers) and 64 Israeli (right-to-left readers) children, aged 3-10 years. From the earliest age at which children could engage with the visual search game, they exhibited a clear light-from-above prior that closely resembled adults' and did not change with age. Chapter 2 concludes that the light-from-above prior is likely fully mature by three years of age. Chapter 3 explores how priors change in later life by testing 67 adults aged 60+ on a shape judgement task. In this task, older adults judged the three-dimensional shape of geometric images in which the placement of light and dark lines yields an impression of depth. Group-level variability increased among older adults, reducing the consistent leftward bias typically observed at

group-level in young, Western adults. Interestingly, sex-specific effects were observed, with women exhibiting greater reductions in the left bias than men and better performance on cognitive tests. In particular, there were statistically significant differences between the cognitive test scores of women who did, and did not, successfully engage with the experimental paradigm. Such changes suggest that later-life reductions in behavioural asymmetry reflect reductions in hemispheric asymmetry and, as such, are a positive compensatory mechanism for neural losses. In Chapter 4, I present three iterations of a new paradigm to test the ability to perceive shape-from-shading. This test demonstrates that shading gradients offer a perceptual advantage over the direction of luminance polarity, but also that a common control stimulus for shaded spheres might contain conflicting cues to orientation that makes it an inappropriate control, and furthermore suggests that opposing orientation biases exist for shaded versus non-shaded stimuli. Chapter 5 concludes the thesis, drawing together the evidence presented to argue for the role of innate hemispheric asymmetry in the development of light priors and for the role of biological factors in the degeneration of directional biases.

Chapter 1: Literature review

Depth perception is an inverse problem in which the perception of three-dimensional depth must be resolved from a two-dimensional retinal image (Pizlo, 2001). Photons reflected off the surface of objects in the visual field are projected two-dimensionally onto the retina, replicating the concentration of photons on the object's surface. Many environmental conditions may lead to a given pattern of light on the retina; for example, a small tree nearby might produce the same image size on the retina as a large tree farther away (Hochberg & Hochberg, 1952). For this reason, the retinal image is considered to be ambiguous and the observer viewing the tree must estimate the conditions that gave rise to that retinal information.

Statistical models of perception have demonstrated that observers resolve the ambiguity inherent in interpreting a three-dimensional percept from a two-dimensional retinal image by recruiting visual cues learned from prior experience to encode the shape and position of objects in the visual field (Tassinari et al., 2006). *A priori* assumptions about the properties of light and its interactions with the objects and surfaces in our environment are termed "light priors", and they facilitate the swift identification of shapes (Mamassian, 1998), textures, and the orientation and shading of surfaces (Knill, 1998). For example, the *a priori* assumption that light comes from above corresponds with the statistical regularity of light placement in the environment, in which electric and natural light sources tend to be located above observers and objects (Ramachandran, 1988), and is termed the "light-from-above" prior. The light-from-above prior is a critical prerequisite to the perception of shape from the monocular depth cue of shading, which allows observers to resolve an object's three-dimensional shape from the pattern of shading on its surface (Metzger, 1936; Ramachandran, 1988). For example, most people perceive two-dimensional objects that are lighter at the top and darker at the bottom as convexities (see example in Figure 1.1), replicating the shading pattern exhibited by convex objects when lit from above (Berbaum et al., 1983; Kobayashi & Morikawa, 2019; Ramachandran, 1988).

The light-from-above prior can be illustrated using the shape-from-shading illusion, produced by shading two-dimensional circles from different angles (see example in Figure 1.1). Convex objects lit from above appear lighter toward the top (Papin et al., 2005) because their unobstructed surfaces, which are closer to the light source, reflect more light than sections that are farther away or obstructed. As a result, in Figure 1.1, observers are more likely to perceive the sphere that is lighter at the top as convex because they anticipate an overhead light source. The right image, on the other hand, is darker at the top, replicating how the geometry of a concave sphere interacts with photons travelling from an overhead light source: the sphere's upper curvature obstructs the light, whilst the lower curvature would catch it (see Figure 1.2 for an example). That observers tend to perceive this object as concave again reveals that they expect light to originate from above, and therefore the perception of depth produced by shading reveals the light-from-above prior.

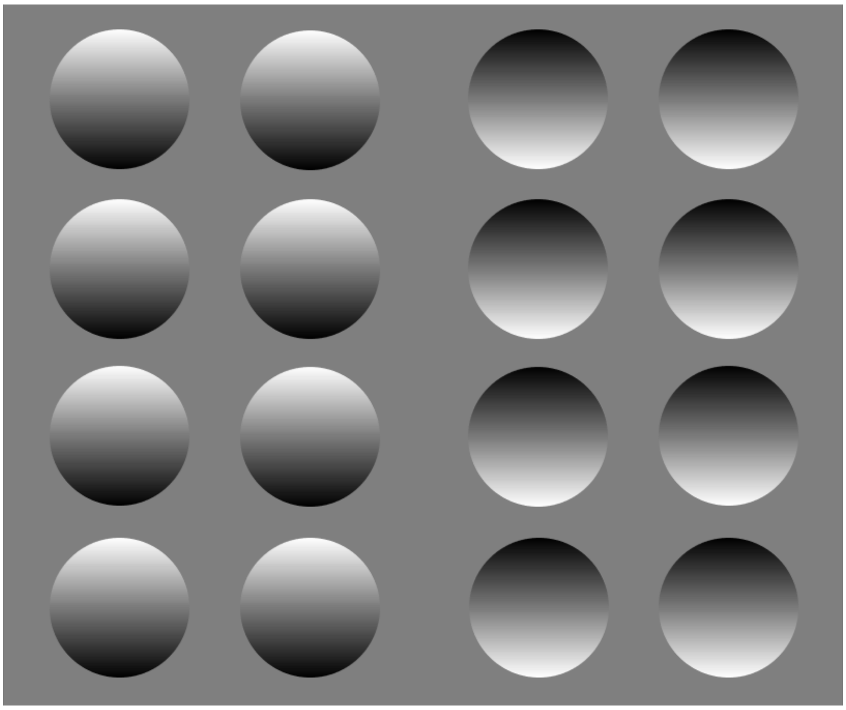


Figure 1.1. Shaded circles. Those on the left are usually interpreted as convex, whilst the right are usually perceived to be concave.

Figure 1.2. An object with a convex and concave face, illuminated by an overhead light source. The upper portion of the convex contour faces the light source and obscures the lower half. In contrast, the upper portion of the concave contour faces away from the light source, while the lower half is oriented towards it.

How do light priors develop?

It has been suggested that light priors are learned from the statistical regularities of the environment (Adams et al., 2004; Ramachandran, 1988; Sun & Perona, 1998); that is, that people learn to expect an overhead light placement because light is typically located overhead. If this were the case, we would expect that most people would have similar priors because experiencing light-from-above is a universal human experience. Indeed, the light-from-above prior, first described by Rittenhouse in 1786, seems to be a universal finding with no studies challenging the existence of a systematic overhead prior in a majority of subjects, though wide inter-individual differences in the precise direction of the assumed light direction are reported in most studies (e.g., Adams, 2007; Andrews et al., 2013; Andrews, et al., 2017; Croydon et al., 2017).

There is some evidence that the light-from-above prior, or its importance relative to other visual cues, develops throughout childhood. For example, in a study exploring the interaction between light-from-above and convexity priors in children's shape judgements, Thomas et al. (2010) found that the light-from-above prior dominated convexity priors in older children (aged 6 to 12 years), and the reverse in younger children (aged 4-5 years). Stone (2011) also observed an extended period of development for shape-from-shading, with younger children only able to make consistent shape judgements using shading cues after six years of age.

In contrast with the evidence from explicit shape judgement tasks (Pickard-Jones et al., 2020; Stone, 2011; Thomas et al., 2010), evidence from tasks requiring implicit judgements, such as preferential looking or reaching behaviours, suggest that the light-from-above prior is present much earlier in development. For example, three separate studies have established that very young children (aged three years and above in Benson & Yonas, 1973, and Yonas et al., 1979; and aged just seven months in Granrud et al., 1985) use the light-from-above prior to resolve shape-from-shading in two-dimensional shaded stimuli. Similarly, there is evidence to suggest the light-from-above prior is an evolutionary default: Chickens raised in an environment in which light came from below also assumed light came from above when pecking shaded stimuli (Hershberger, 1970). Taken together, these findings suggest that the ability to use the light-from-above prior develops after extended visual experience, but do not imply that the prior itself changes during childhood.

The leftward bias for the assumed light direction

A significant body of evidence has revealed a leftward bias in the light-from-above prior in Western adults. For example, behavioural data have shown that individuals more readily report objects as convex when their brightest edges are placed to the left of the uppermost portion of the object (Andrews et al., 2013; Andrews et al., 2017; Elias & Robinson, 2005; Gerardin et al., 2007; Mamassian & Goutcher, 2001; Pickard-Jones et al., 2020; Sun & Perona, 1998). Most studies of the light-from-above prior (in Western cohorts) report a leftward bias of between -30° and -10° for the assumed light direction (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020; Ramachandran, 1988; Smith et al., 2015; Sun & Perona, 1998; however, see McManus et al., 2004, for an example of an experiment that did not detect a left bias in a shape judgement task), illustrated by observers more readily perceiving an object as convex if it is shaded from above and to the left. The amplified perceptual value of leftward shading patterns has not only been observed in psychophysical experiments: the relief-inversion effect in cartography is known to be influenced by lighting direction, and a recent article by Biland and Çöltekin (2017) found the accuracy of categorising landforms as valleys or ridges in shaded relief maps was optimal when they were shaded with the lightest parts facing 23° left of the apex; a bias that is strikingly similar to those observed in conventional controlled lab-based experiments (e.g., Andrews et al., 2013).

Other leftward biases, similar to the left bias in shape-from-shading in that they are characterised by a greater allocation of attention to the left hemispace, have been observed in neurologically intact individuals in other visuospatial paradigms. For example, neurologically intact adults make leftward errors when marking the centre of a horizontal line in the line bisection task (e.g., Jewell & McCourt, 2000; Macdonald-Nethercott et al., 2000). Similarly, leftward errors are made in the landmark task, where the position of a bisecting line is judged by an observer (Çiçek et al., 2009; Jewell & McCourt, 2000). In the chimeric face test, a left bias has been established through the preferential processing of facial expressions presented on the left side of the face (Innes et al., 2016). A leftward bias for luminance has been observed in the greyscales task (Mattingley et al., 2004), in which observers judge shading gradients with equal luminance as lighter if the lighter part is on the left, and for leftward lighting conditions in advertisements (Hutchison et al., 2011). Spatial frequency judgements also show a left bias, with participants typically estimating that gratings have a higher spatial frequency when presented on the left (e.g., grating-scales task; Chen et al., 2019; Niemeier et al., 2007). Therefore, the leftward bias in the assumed light direction mimics other biases in spatial attention.

The left bias: visual experience

Whilst the idea that the light-from-above prior is derived from environmental regularities makes intuitive sense, there is no ecological reason to believe that people have more experience with light coming from the left in the natural world. Together with the lack of direct evidence that people experience more light coming from the left, one cannot conclude that the leftward bias for the assumed light direction originates from the same mechanism as the light-from-above prior. In their germinal study of shape-from-shading, Sun and Perona (1998) suggested that observers may adjust their surroundings to account for the shadow cast by their dominant hand, causing the right-handed majority to have a left bias and the left-handed minority to have a right bias. However, no studies have replicated the effect of handedness observed by Sun and Perona (e.g., Andrews et al., 2013; Mamassian & Goutcher, 2001).

If the left bias resulted from visual experience, some changes over childhood would be expected. Consistent with this view, Thomas et al. (2010) found that the tendency to interpret left-lit stimuli as convexities and right-lit stimuli as concavities only became evident between 9-12 years of age. However, Thomas et al.'s task was not designed to detect directional biases and instead computed the relative weight assigned to convexity and light priors, and as such offers only indirect evidence for the development of the left bias. Studies designed to explicitly probe the directional biases, instead, reveal a stable leftward bias that does not change with age (Croydon et al., 2017; Pickard-Jones et al., 2020). For example, using a paradigm designed to measure the assumed light direction in shaded stimuli, which has been used extensively and has a high degree of specificity in adult participants (e.g., Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017), Pickard-Jones et al. (2020) found that a leftward bias resembling that of adults was present at age seven and did not change through childhood. Using the same experimental paradigm, Croydon et al. (2017) also observed a strong leftward bias, indistinguishable from adult performance, in autistic and typically developing children aged seven to 14 years. This finding is inconsistent with an extended maturation period for the leftward bias and may indicate a developmental default.

The most robust evidence for the influence of statistical regularities on the assumed light direction comes from a behavioural paradigm by Adams et al. (2004), who demonstrated that the direction of the assumed light source could be shifted through cross-modal training in which visual and haptic depth cues conflicted. Their experiment demonstrated that new context-dependent light priors could be learned and generalised across different tasks (Adams et al., 2004). Later work revealed that the new priors persisted for several weeks when participants returned to the experimental environment (Kerrigan & Adams, 2013). That context-dependent priors can be established over a limited time is unsurprising, given that the human brain is extensively shaped by its environment (Gómez-Robles et al., 2013; Zohary et al., 1994). However, given that there is no direct evidence that people experience more light coming from the left, the presence of a leftward bias is not adequately explained by visual experience. Should a pervasive leftward predominance in lighting conditions exist in natural or constructed environments, the distribution of assumed light directions would be similar across populations. This is not the case as, for example, differences in the direction and magnitude of biases exist between right-to-left and left-to-right reading populations (Andrews et al., 2013).

Hemispheric asymmetry: A mechanistic explanation for the left bias

Rather than visual experience, light priors may result from biologically mediated processes such as innate hemispheric asymmetry. In this context, "biologically mediated" refers to processes that are programmed to achieve specific objectives independently of experience (Strober et al., 2019); gene expression to regulate cell function and identity is an example of a biological process (Mohn & Schübeler, 2009). Nevertheless, priors acquired through experience still rely on biological processes such as Hebbian plasticity (e.g., Abraham & Williams, 2003).

The theory of hemispheric rivalry (Kinsbourne, 1977) posits that both cerebral hemispheres direct attention contralaterally whilst mutually inhibiting the other. The presence of directional biases in certain tasks suggests that the contralateral hemisphere is dominant for the cognitive processes governing performance on those tasks; therefore, right hemisphere dominance presents an alternative explanation for leftward biases. There is a wealth of evidence to support this theory. For example, neuroimaging experiments have shown greater activation in the right parietal lobe, and some bilateral parietal activation, in response to shaded images in shape judgement tasks (Taira et al., 2001) and line bisection tasks (Fink et al., 2001). Furthermore, whilst neurotypical participants tend to have a left bias on tasks such as the line bisection test, performance on this task moves rightward in patients with a right hemisphere parietal lesion (Halligan et al., 2003; Sperber & Karnath, 2016). The same is true of the assumed light direction when assessed in a shape-from-shading shape judgement task (de Montalembert et al., 2010). Left hemisphere lesions, however, do not yield contralesional neglect symptoms to the same extent as right hemisphere lesions, with left hemisphere lesions usually, but not always, producing little-to-no differences in spatial attention (Stone et al., 1993).

The imbalance in the volume of hemineglect patients produced by right and left hemisphere lesions suggests that the right hemisphere is dominant in orienting visuospatial attention, with the left hemisphere serving a minor role (Bartolomeo & Chokron, 1999). Notably, though right-hemisphere patients do not exhibit the left bias expected of their neurologically intact peers, they do not lose their ability to perform these tasks. Their intact ability to perform shape-from-shading and line bisection tasks (among others), together with a left bias in neurologically intact individuals and systematically opposite biases in right-hemisphere patients, indicates that both hemispheres are involved in orienting visuospatial attention, with the left hemisphere able to compensate if the dominant right hemisphere is damaged.

Attention affects spatial biases: reading from left-to-right or right-to-left

Several differences in spatial biases between populations with different reading directions have been described (Andrews et al., 2013; Chokron et al., 2009; Morikawa & McBeath, 1992; Rinaldi et al., 2014; Smith et al., 2015; Speedie et al., 2002), suggesting that one's culturally proscribed habits may influence spatial attention, and thus directional biases. However, the biases of right-to-left readers do not present as opposite biases of equal magnitude to those of left-to-right readers, as would be expected from a behaviour that is entirely dependent on visual experience, but often as a diminished leftward bias. For example, when right-to-left readers are compared with left-to-right readers, the following results have been observed: a diminished leftward bias in the assumed light direction was found in Andrews et al. (2013); smaller rightward biases in cancellation and line bisection tasks in Rinaldi et al. (2014); and only left-to-right readers showed a significantly lateralised bias when judging left- and right-lit advertisements in Smith et al. (2015). Therefore, it is possible that the right-hemisphere dominance for visual attention (e.g., Bowers & Heilman, 1980; Heilman & Van Den Abell, 1980; Jewell & McCourt, 2000; Umiltà et al., 2009), and thus the leftward bias for the assumed light direction, represents typical brain development. This would imply that the variable effects of habitual reading direction observed in right-to-left readers indicates that visual experience modulates lateralised processes by training the locus of visual attention away from the developmental default.

Chapter two explores the development of light priors cross-sectionally in left-to-right and right-to-left reading children aged 3 to 10 years. By assessing children before and during reading acquisition, we aimed to determine whether directional biases are present earlier in development than previously shown, and to establish whether the developmental trajectory of directional biases interacts with reading direction. We sought to describe the developmental trajectory of directional biases cross-sectionally and, supposing that a left bias is a developmental regularity originating from hemispheric asymmetry, quantify how much visual experience is required to alter this bias to replicate the directional biases seen in right-to-left readers.

The left bias, pseudoneglect, and ageing

Previous works (e.g., Andrews et al., 2017; de Montalembert et al., 2010) have revealed age-related changes in the assumed light direction. For example, a group of healthy older adults in de Montalembert et al.'s (2010) study had a leftward bias of approximately 5°, smaller than the bias typically found in the literature on young adults, even when compared to studies that used the same paradigm. Andrews et al. (2017) observed significant variability at the group level in older adults aged 60-81, finding that although some adults showed a strong leftward bias in later life, many revealed an opposite bias of equal magnitude, and others an overhead bias that did not veer to the left or right, in stark contrast to the consistently leftward bias of approximately -10° to -30° seen in younger adults. An age-related decrease in pseudoneglect, as measured by the line bisection test, mimicked the reduced left bias in older persons: Andrews et al. (2017) found that the assumed light direction was correlated with errors on the line bisection task in both young and older adults, with older adults having a diminished left bias compared with young adults.

Studies of line bisection in older adults support the finding that left biases diminish with age; for example, Barrett and Craver-Lemley (2008) found that older adults exhibited no bias in line bisection compared with young adults. Using the landmark task, Schmitz and Peigneux (2011) also found evidence of a diminished left bias and, in some cases, a rightward bias in adults aged 60-81. Similarly, Benwell et al. (2014) observed a rightward shift in healthy ageing. However, it should be noted that performance on tasks measuring pseudoneglect among older adults is highly variable, both between and within studies. Corroborating Jewell and McCourt's (2000) findings following a qualitative review of the literature, Friedrich et al. (2018) noted inconsistent findings in a systematic review of the trajectory of pseudoneglect in adults: out of 37 studies reviewed, 21 found a diminished leftward bias in older adults (several tasks were reviewed; for a summary see Friedrich et al., table 6), whilst just two studies found an enhanced left bias. Four studies supported a left bias, and ten reported results comparable to young adults. These differences may reflect the substantial methodological differences between the studies.

Sex differences in ageing

Sex differences have been observed in healthy and pathological ageing processes (Bloomberg et al., 2021; Hatta et al., 2015; McCarrey et al., 2016); for example, women are more likely to develop Alzheimer's disease (Bloomberg et al., 2021), but conversely, when no disease pathology has been identified, show fewer cognitive and biological markers of ageing than men (McCarrey et al., 2016; Vinke et al., 2018). Additionally, sex differences have been seen on behavioural lateralisation assessments such as the line bisection test, with older women making significantly larger leftward errors (Varnava & Halligan, 2007), signifying intact right-hemisphere function, contrasting with men's more rightward errors on the same tasks (Chen et al., 2011). A more leftward bias suggests that the right hemisphere remains dominant in orienting visuospatial attention in women, while cortical and behavioural asymmetry is reduced in men.

Whilst many studies have described changes in the trajectory of pseudoneglect in healthy ageing populations, relatively few studies have sex-disaggregated their data (Friedrich et al., 2018), and no studies have explored the relationship between leftward biases and cognitive function, despite several studies of age-related changes in leftward biases (see Friedrich et al., 2018, and Learmonth & Papadatou-Pastou, 2021, for reviews). This is a surprising omission, given the wealth of evidence concerning functional and structural changes in the right hemisphere (Cabeza, 2002) that have been found in cohorts in which measurable cognitive decline is often detected (Bloomberg et al., 2021; McCarrey et al., 2016; Reas et al., 2017), and which also appears to coincide with the age at which left biases are less consistently observed (e.g., Learmonth & Papadatou-Pastou, 2021). Indeed, Cabeza suggested in his 2002 paper that sex and cognitive performance may offer significant power to generalise findings across a heterogeneous population. Given that tasks such as shape-from-shading and the landmark task can detect subtle individual differences, they are well suited to investigate whether the lateralisation of sensory processes, or the integration between top-down priors and bottom-up sensory processes, are subject to sexually dimorphic age-related changes.

In Chapter 3, men and women sampled principally from the semi-rural and coastal communities in North Wales, between the ages of 60 and 87, performed a shape judgement test on a geometric shape in which the position of light and dark lines suggested three-dimensional depth (the Honeycomb Task; Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020), and the Landmark Task (e.g., Harvey et al., 1995). We assessed the effects of age, sex, and cognitive function on their performance. We expected to observe a stronger left bias in women, consistent with previous findings (Chen et al., 2011; Varnava & Halligan, 2007); however, this was not the case: men had a stronger left bias than women, though the difference was not significant. We also evaluated whether age, sex, and cognitive function affected participants' sensitivity to the effects of the implied shading on the Honeycomb Task. Interestingly, whilst women who were not sensitive to the stimulus when making shape judgements had significantly lower MoCA scores than women who were, men who were, or were not, sensitive to the stimulus did not differ in cognitive function. This suggests sex differences in age-related changes in the cognitive processes associated with resolving 3-D depth from shaded stimuli.

Variability in light priors

A high degree of variability has been observed within and between studies of light priors, particularly in their directional components (Adams, 2007; Andrews et al., 2017; Friedrich et al., 2018; see Figure 1.3). Previous studies have typically shown a left bias of -10° and -30° for the assumed light direction, yet individuals within these studies often have an assumed light direction much farther from the mean of the testing cohort. For example, Pickard-Jones et al. (2020) show an overall standard deviation of 14.48° among typically developing children in a shape judgment task; Croydon et al. (2017), using the same experimental paradigm, observed a standard deviation of 12.51° in autistic children, 7.87° in typically developing children, and 16.72° in adults. Adams (2007) reported a standard deviation of 37.9° in a shape judgement task using shaded spheres.

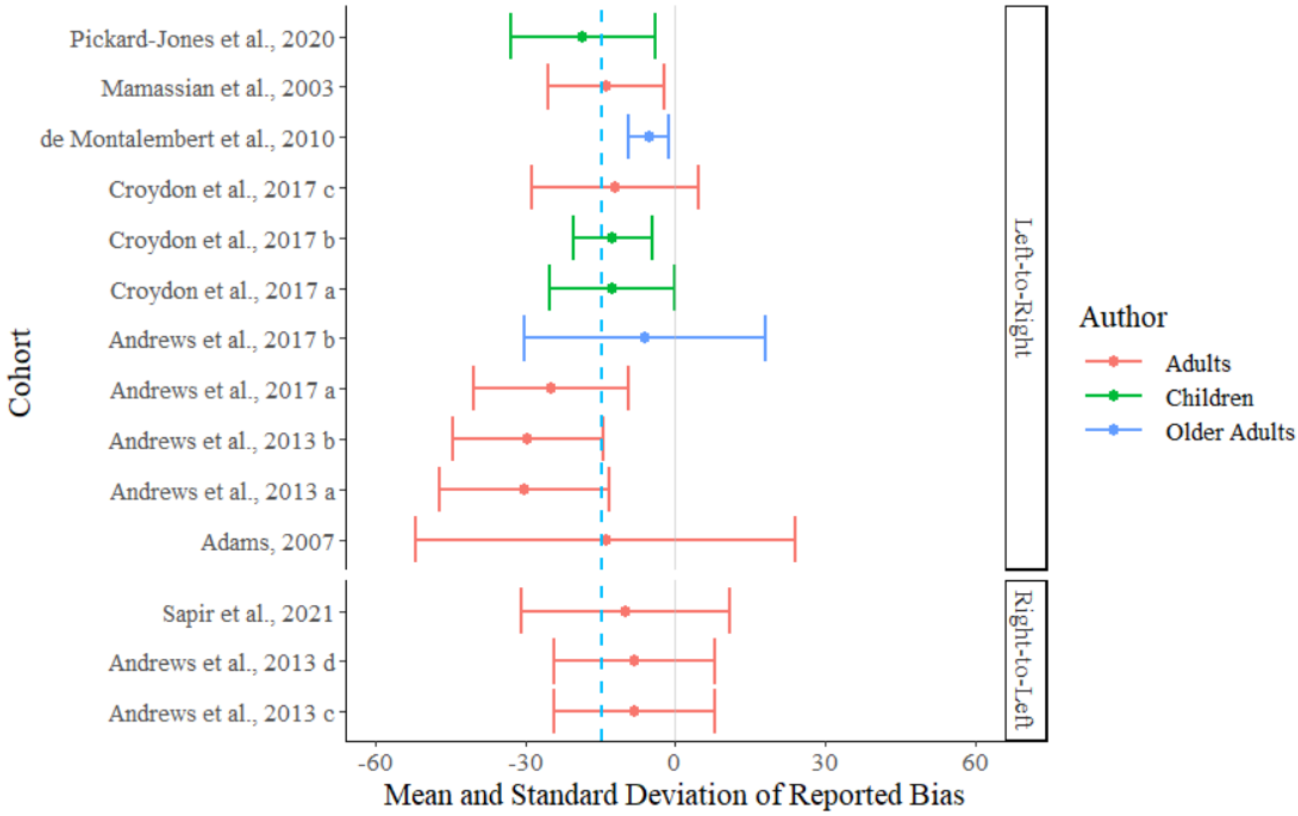


Figure 1.3. The reported mean and standard deviation of directional biases in shape-from-shading shape judgement tasks. The dashed blue line represents the mean of all included studies and the cohorts are grouped by reading group (left-to-right and right-to-left) and author. Authors are represented more than once when more than one cohort was included in their study. Studies were included if they reported a standard deviation (or a standard deviation could be calculated retrospectively from their reported results) in a shape judgement task that used shading as the primary cue to shape.

Variability in the ability to perceive shape-from-shading

There is also variability in participants' ability to perceive shape-from-shading. In studies where observers' shape judgements were established to have been significantly modulated by alternative presentations of the experimental stimulus (typically the rotation or orientation of the brightest part of the stimulus), some participants have been found to exhibit less sensitivity than others. Lower sensitivity may manifest as perceiving either convexity or concavity consistently regardless of the orientation of the stimulus or that they perform near to chance levels at most orientations (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017). Such participants are considered insensitive to the stimuli used and their suitability for inclusion in further analyses should be carefully considered. For example, in Andrews et al. (2013), three participants were removed because their results suggested they were not sensitive to the orientation of the honeycomb stimulus. In Andrews et al. (2017), two out of 22 young and three out of 24 older participants were removed using the same statistical methodology and experimental paradigm. One adult was removed for the same reason and using the same methodology in Croydon et al. (2017). Though some individuals exhibit low sensitivity to shading information on shape judgement tasks, this does not necessarily imply that they cannot perceive shape-from-shading. Instead, their perception may be more dynamically bistable than others, or the sequential effects of previous stimulus presentation may influence them to a greater degree as has been observed in other visual tasks that are bistable (Maloney et al., 2005; Soetens et al., 1985); alternatively, their perception of depth might be less dynamic than others, leading to a consistent impression of depth regardless of the rotation of the stimulus.

Tasks used to assess the light-from-above prior and left bias

Differences in experimental paradigms could explain some of the variability in the findings of shape-from-shading tasks. Two of the principal experimental methods used in shape-from-shading are visual search and shape judgement tasks. In an early study assessing the influence of prior knowledge of the illumination position on the judgement of shape from shading gradients, Berbaum et al. (1983) manipulated the external light source illuminating a muffin tin - an object that contained physical 12 concavities - and asked participants to judge its three-dimensional shape. Though the light source was presented and then removed before the experimental trial, Berbaum et al. found that participants accounted for the light source’s position when interpreting the stimulus’s three-dimensional shape. Successive researchers have replicated the effect of external lighting position on the interpretation of shading gradients when the light source has been removed and taken this as evidence for a dynamic, Bayesian reweighting of visual cues in response to new sensory information (e.g., Adams, 2007; Proulx, 2014), suggesting that the light-from-above prior is not an innate internal representation of lighting direction, but is derived purely from statistical learning (Proulx, 2014).

Later, Ramachandran (1988), Kleffner and Ramachandran (1992), Braun (1993), Symons et al. (2000), and Wolfe and Horowitz (2004) used arrays of shaded spheres to probe light source assumptions in shape judgement tasks and discovered several foundational elements of our understanding of light priors: namely, that shape-from-shading depends on the assumption of a single light source (Ramachandran, 1988; Kleffner & Ramachandran, 1992); that the position of one's head influences the perception of convexity by altering the frames of reference used to gain a sense of verticality (Kleffner & Ramachandran, 1992). Horizontal lighting conditions were found to produce inconsistent shape judgements compared with vertical (Kleffner & Ramachandran, 1992; Ramachandran, 1988), and concave targets were more effective amongst a convex distractor array than convex targets among concave distractors (Kleffner & Ramachandran, 1992; Symons et al., 2000). Most importantly, shape-from-shading was established as a visual texton, processed in parallel with other stimuli in the visual field and having a 'pop-out' effect when presented among arrays of distractors (Braun, 1993; Wolfe & Horowitz, 2004). Braun's (1993) findings lay the foundations for the work of Sun and Perona's (1998) highly influential study on shape-from-shading, which employed a visual search paradigm with the now well-established shaded sphere stimulus. Sun and Perona varied stimulus-onset asynchrony to alter the task's difficulty for each participant and identified the minimum length of time required to extract the perception of three-dimensional depth from the two-dimensional stimulus, finding a strong left bias.

Building upon the work of Sun and Perona (1998) and Kleffner and Ramachandran (1992), McManus et al. (2004) also used shaded spheres in both a visual search and a shape judgement task. In both experiments, the observers' head position was unconstrained. McManus et al. found a left bias in the visual search task, but no left bias in their shape judgement task. This disparity is likely to result from a limitation of the shaded sphere stimulus, which does not offer a consistent and robust percept of depth when presented in isolation: when McManus et al. followed the methods used by Kleffner and Ramachandran (1992) and Sun and Perona (1998), presenting the target stimuli among an array of oppositely shaded distractors, the left bias they observed was broadly in agreement with previous studies. However, the shaded spheres were presented in isolation in the shape judgement task, in which a left bias was not detected. It is possible that a pronounced left bias was detected in the visual search task, but not in the shape judgement task, because a bias to assume objects are convex (Chacón, 2004; Symons et al., 2000) influenced the perception of shaded spheres. This ambiguity in the interpretation of shaded spheres was illustrated by Chacón (2004), who found that circles shaded with the dark parts uppermost (usually perceived as concave) and presented in isolation were perceived as convex in 55.5% of shape judgements; however, they were perceived as convex just 22.2% of the time when presented amongst an oppositely shaded distractor.

Mamassian and Goutcher (2001) designed a shape judgement experiment using undulating sinusoidal strips to explore the effect of illumination position on the perception of an object's three-dimensional shape more directly, highlighting that visual search methods are an indirect way to investigate shape perception. Unlike McManus et al. (2004), who did not find a left bias in their later shaded spheres experiment, Mamassian and Goutcher (2001) found a significant bias to assume left-lit objects were convex. The disparity in their findings may be due to undulating strips containing more salient depth information than shaded spheres presented in isolation.

Gerardin et al. (2007) discovered that some naive participants could not perceive depth in Mamassian and Goutcher's (2001) undulating strips and proposed a new geometric stimulus (the polo mint; Gerardin et al., 2007) with enclosed borders and the impression of depth implied by the placement of black and white lines against a grey background. Their assessment of this figure showed that it was more reliably perceived as having the impression of three-dimensional depth by observers. They also manipulated the stimulus further by altering the impression of depth in distinct sections of the stimulus, enabling them to manipulate lighting and convexity cues simultaneously. Gerardin et al.'s new polo mint stimulus produced more reliable and sensitive measurements of the assumed light direction. The stimulus has been used in young adults and children (Thomas et al., 2010).

An alternative to Gerardin et al.'s (2007) polo mint stimulus, termed the honeycomb, was developed in 2013 by Andrews et al. and comprised six hexagons arranged around a central hexagon, with light and dark lines arranged to suggest areas of light and shadow. This stimulus, or variations thereof, has been used in several publications (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020; Sapir et al., 2021; Mainster et al., 2022) and different participant groups, including left-to-right and right-to-left readers, young adults, older adults, and in typically developing and autistic children. The honeycomb stimulus has been shown to reliably produce an impression of depth in all cohort groups and a sensitive measure of lateralised biases. However, the honeycomb and polo mint stimuli are not well tolerated by children under five (Pickard-Jones et al., 2020; Thomas et al., 2010), and most published studies using these stimuli report having to exclude some participants. For example, some individuals perform inconsistently, suggesting that altering the orientation of the light and dark edges by rotating the stimulus does not augment their perception of depth (e.g., Adams et al., 2004; Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020).

Addressing the limitations of shape judgement tasks

Most shape judgement tasks follow a two-alternative forced choice paradigm, asking participants to judge whether a shape is convex or concave and offering no opportunity for participants to record an ambiguous or unsure answer. It is also possible that some participants might respond intuitively without consciously perceiving depth in the images. Furthermore, some participants demonstrate that they cannot perceive any changes in depth across different stimulus orientations by responding consistently across many different stimulus rotations, and still others respond at chance levels across all stimulus rotations. It is conceivable, therefore, that some judgements may not reflect the observer's true perception and that some performance on shape judgement tasks could be attributed to other perceptual strategies. For instance, in visual search tasks in which an oddball must be detected from an array of shaded objects, an observer may notice two light or dark parts facing each other, and thus may infer that one is an oddball without perceiving any depth in the stimulus. It is therefore imperative that tests are devised to assess shape-from-shading ability objectively.

Objective measures of visual perception do exist; for example, Ishihara's (1962) polychromatic charts for the detection of colour blindness (see example in Figure 1.4), which people of different ages and abilities tolerate well, have a high degree of sensitivity and specificity and are considered sufficient for clinical use (NHS.uk, 2019). The Ishihara plates are free of any cues to the character rendered other than by colour (Hardy et al., 1945). They rely on the observer being able to differentiate between the different colours, perceptually group the circles that form the target character, read the target character, and communicate the character to the person administering the test.

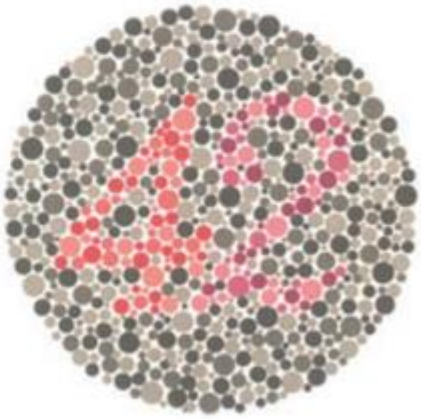


Figure 1.4 An example plate to test for colour blindness (reproduced from Ishihara, 1962).

Shape judgement tasks are highly suited to measuring subtle differences in the angle of rotation that offers an individual the greatest perceptual advantage. However, they are not able to identify people who struggle to perceive shape-from-shading, or those whose ability to perceive shape-from-shading is suboptimal. In typically developing populations, no clinical deficits in shape-from-shading have been detected; however, evidence from children with early-onset complete bilateral cataracts has shown that the ability to perceive shape-from-shading can be permanently impaired if the observer is deprived of visual experience during critical developmental periods (McKyton et al., 2015), even if vision has been restored when cataracts were surgically removed years later. Shape-from-shading deficits have also been found in patients with posterior cortical atrophy, accompanied by grey matter losses in the right posterior inferior temporal cortex (Gillebert et al., 2015). Though no subclinical populations have presented with shape-from-shading deficits, it is possible that the ability to perceive shape-from-shading exists on a spectrum, or that other shape and distance cues can compensate for the lack of shape-from-shading so effectively that a deficiency is not noticed.

Chapter 4 explores whether a test similar to the Ishihara (1962) test could show utility in detecting or diagnosing the deficient perception of shape-from-shading. Without an objective diagnostic test, it is only possible to speculate on whether and how the ability to perceive shape-from-shading changes or deteriorates with age. An objective diagnostic test could also permit earlier non-invasive testing for rare conditions such as posterior cortical atrophy (Gillebert et al., 2015). We replicate the concept of the Ishihara test (taking the 1962 version as a model), using the orientation of shading gradients to define target and background circles rather than colour, to explore shading perception in young adults. Three iterations of the experiment were piloted in young adults that, subject to testing with appropriate clinical populations, may have some utility as a test for the ability to perceive shape-from-shading.

Summary

This thesis explores changes in light priors across the lifespan. Namely, how development from the ages of 3 to 10 years affects the acquisition of light priors and their directional components by evaluating the relative contributions of innate hemispheric asymmetry and changes in visuospatial attention that result from habitual reading direction. Previous studies in children are restricted to single-reading-direction cohorts only. As such, they cannot quantify the effects of different reading directions or indicate how they might alter biases resulting from developmental defaults, such as a bias resulting from hemispheric asymmetry. I also aim to identify directional biases at earlier ages than in previous experiments by employing more child-friendly experimental methods. This thesis also addresses a significant gap in the literature on age-related changes in directional biases: whether such changes are related to cognitive function, and whether such changes or their relation to cognitive function are sex-specific. Because women tend to live longer than men and show fewer biological markers of ageing (Vinke et al., 2018), it is imperative to sex-disaggregate data to inform sex-specific assumptions about normative performance across the lifespan, rather than generalising across all older adults. Finally, a new test to identify individuals with deficits in perceiving shape-from-shading is proposed in this thesis. This new test may offer an opportunity to understand why some people do not perform within typical ranges on shape judgement tasks and present a new means of assessing depth perception. A more sensitive and specific diagnostic test may permit the earlier identification of rare conditions such as posterior cortical atrophy or assess the extent of depth-from-shading that has been retained or regained following ophthalmological conditions affecting the resolution of shape-from-shading.

Chapter 2: Attention changes with age

Abstract

Visual priors and sensory information are combined to produce the perception of the visual scene. The light-from-above prior is illustrated by observers categorising objects that are lighter at the top as convex, and those that are lighter at the bottom as concave. However, left-to-right readers are more likely to categorise objects as convex if they are shaded when the brightest parts are approximately 30° to the left bias of the apex. Right-to-left readers tend to have a reduced left bias, suggesting that reading habits alter visual priors. To determine how priors develop and how much visual experience is required to create a directional bias, we tested 164 children in Israel and Wales before and during reading acquisition on a shape-from-shading visual search task. We used naturalistic settings and free viewing conditions to enhance the generalisability and ecological validity of our findings. We observed a light-from-above prior that did not change with age in both cohorts but did not detect a directional bias in either group. This may be because the left bias results from the deployment of attention and augments the light-from-above prior. A slight (non-significant) tendency to favour the left hemispace in English-reading children was encouraging and should prompt further investigation with alternative experimental methods that permit the measurement of directional biases in very young children. We validated our methods in adults and revealed that visual search tasks are suitable for measuring the light-from-above prior, but they are not a sensitive measure of directional biases.

**A version of this chapter is in preparation for publication.*

The light-from-above prior has been theorised to develop either from prolonged visual experience with light coming from above (Proulx, 2014; Adams, 2007) or instead from an innate developmental default (Pickard-Jones et al., 2020). The left bias observed in Western populations is more complex; it is unlikely that left biases result from visual experience because there is no ecological reason to suppose that observers experience more light coming from the left. Instead, innate hemispheric asymmetry might offer a better explanation for the left bias, as evidence has established a heightened role for the right hemisphere in orienting visual attention to the left side of space. Specifically, in an fMRI experiment, Taira et al. (2001) demonstrated greater activation in the right parietal lobe in shape judgement tasks. Furthermore, the leftward bias shown in other left-lateralised tasks, such as the line bisection test, shifts rightward in right-hemisphere patients (Halligan et al., 2003; Sperber & Karnath, 2016). More rightward performance is also seen in shape judgement tasks in right-hemisphere patients (de Montalembert et al., 2010), but few changes are observed in left-hemisphere patients (Stone et al., 1993). Increased activation in the right hemisphere in neurologically intact patients, together with atypical performance in right-hemisphere but not left-hemisphere patients, strongly suggests that directional biases result from innate hemispheric asymmetry orienting visual attention to the left side of space rather than visual experience.

However, a purely nativist account of directional biases is not borne out by the evidence: right-to-left readers do not exhibit the same left biases as left-to-right readers, as right-to-left readers do not have an opposite bias of equal magnitude to that of left-to-right readers. Instead, right-to-left readers show more variable inter-experimental performance, having either a smaller left bias than left-to-right readers (Andrews et al., 2013), rightward biases (Rinaldi et al., 2014), or no bias at all (Smith et al., 2015). For this reason, it is unlikely that either hemispheric asymmetry or habitual reading direction are responsible for the development of directional biases: the differences observed in right-to-left readers are more likely to indicate that the left bias is a developmental default caused by right-hemisphere dominance in orienting visuospatial attention, which is subsequently modulated by attentional shifts caused by habitual reading direction. If the left bias is a developmental default that can be modulated by scanning habits, it is not clear how much right-to-left reading experience is required to alter the default left bias.

To probe the development of light priors, the relative contributions of visual experience, attentional habits, and innate developmental defaults must be controlled; therefore, we tested young children before and during reading acquisition in left-to-right and right-to-left reading cultures. We recently suggested (Pickard-Jones et al., 2020) that findings previously observed in young children, namely a tendency that increased with age to interpret shapes shaded from the left as convex (Stone, 2011; Thomas et al., 2010), may have been confounded by variable task performance among very young children. It is interesting to note that both Thomas et al. (2010) and Stone (2011) used explicit shape judgement tasks in a very young cohort and observed near-chance performance in their youngest participants, with more consistent performance as their age increased. When inconsistent children were included in the results, children's ability to use the light-from-above prior appeared to improve with increasing age. However, the inconsistency in the younger children may illustrate their inability to maintain attention on repetitive experimental tasks rather than their propensity to make shape-from-shading judgements. In fact, Croydon et al. (2017) used geometric stimuli to measure an assumed light direction in an explicit shape judgement task and found that children's ability to use light priors did not change appreciably after seven years. In a similar experimental paradigm, Pickard-Jones et al. (2020) found no age-related differences after children who were unable to perform the task were removed from analyses, suggesting that it is not shape-from-shading that changes with age, but only the ability to engage with explicit shape judgement tasks continuously.

Removing participants from analyses is controversial, and their inclusion or exclusion can significantly affect how data are interpreted. Croydon et al. (2017) and Pickard-Jones et al. (2020), using the methodology published in Andrews et al. (2013) and Andrews et al. (2017) used a statistical method to exclude participants whose data indicated that their responses on a shape judgement task were not sufficiently modulated by the experimental stimulus. Pickard-Jones et al. (2020) suggested that the exclusion of such participants revealed a directional bias that was stable across development in those that remained. Supportive of the position that light priors are present earlier in development than posited by Thomas et al. (2010) and Stone (2011), Granrud et al. (1985) discovered that infants as young as five and seven months old tended to choose convexities over concavities in a preferential reaching task. Infants aged seven months and over also preferentially reached for photographs of convexities, implying that a convexity bias is present at an early stage of development and that infants aged seven months and older can interpret shading gradients to perceive three-dimensional shape. Furthermore, children as young as three years were able to recognise shapes from shading in accordance with a light-from-above prior in Benson and Yonas (1973) and Yonas et al. (1979).

Given that younger children are less tolerant of traditional psychophysical tasks, developing a more age-appropriate way to measure the assumed light direction in both left-to-right and right-to-left readers aged 3-10 years was necessary. We chose to design a visual search paradigm because they are well tolerated by infants as young as three months of age. For example, visual search has been used in implicit kicking and looking tasks (e.g., in Gerhardstein & Rovee-Collier, 2002; Rovee-Collier et al., 1992; Rovee-Collier et al., 1996). Visual search was also selected because this method has been used successfully to explore directional priors (e.g., Braun, 1993; Kleffner & Ramachandran, 1992; Ramachandran, 1988; Sun & Perona, 1998; Symons et al., 2000; and Wolfe & Horowitz, 2004). We expected that children would identify vertically shaded targets faster than horizontally shaded targets, thus demonstrating a light-from-above prior comparable to that of adults (e.g., Adams, 2007). If the development of shape-from-shading requires visual experience, children's priors should gradually mature until they resemble adult-like light priors. However, if the light-from-above prior is developmentally stable, it should not change with age.

Because Adams (2007) found that visual search was the least sensitive way to measure the angle of directional biases compared with shape judgements and reflectance, we did not expect to detect biases of the same magnitude as seen in shape judgement tasks. Should directional biases be detectable, we expected a leftward bias in all of the youngest children. This would be consistent with previous studies (e.g., Croydon et al., 2017; Pickard-Jones et al., 2020), but in a younger cohort than previously tested. If, with increasing age and reading experience, leftward biases are observed in left-to-right reading children, and rightward or a diminished leftward bias in right-to-left reading children, this could be taken as evidence of the interaction between innate priors and acquired habits (e.g., Rinaldi et al., 2014). We would expect such changes to occur in right-to-left reading children after age seven, when children in Israel commence formal literacy education, and to increase in magnitude with age.

The perception of convexity is a known factor in figure-ground separation, which is integral to the perception and organisation of the visual scene (Peterson & Salvagio, 2008). To determine whether the ability to process the visual scene globally is necessary for performing a parallel visual search, we measured global processing preferences using a Navon (1977)-style match-to-sample task. We expected that shape-from-shading would depend on a precursory process of separating the local foreground of a visual display from its global background. We predicted an increase in the tendency to process stimuli globally with age and a relationship between the tendency to process stimuli globally and a relationship between global processing preferences and the degree of left bias on the Honeycomb Task and spheres game.

Experiment 1

Methods

Participants

There were ten experimental groups in this experiment, comprised of two reading groups (English and Hebrew) and five age groups that were aligned with British school years (Group 1, aged 3-4 years; Group 2, aged 4-5 years; Group 3, aged 5-6 years; Group 4, aged 7-8 years; and Group 5, aged 9-10 years. In previous work (Pickard-Jones et al., 2020), we determined that 18 participants per group would be required to detect an effect of age on children's assumed light directions, given a linear increase in their ability to engage with our task over time. This sample size would yield a power of 0.88. Information and consent forms were distributed to all children. Only children whose parents returned the signed consent form were included in the experiment; there were 164 participants in total (see Table 2.1 for the number of participants in each group).

Table 2.1. *The number of children in each age group in both English and Hebrew reading groups.*

Group name	Age Group	*n*	English	Hebrew
Group 1	3-4	20	18	2
Group 2	4-5	22	13	9
Group 3	5-6	44	20	24
Group 4	7-8	41	26	15
Group 5	9-10	37	18	19

English group

Ninety-five English-speaking children aged between 3 and 10 years were recruited from three local primary schools (children aged 3 to 11 years) and one nursery (children from 3 to 4 years of age) in Wales (see participant information form in Appendix 2.1). Children received a small token for participation, such as a small animal figure, stickers, or a coloured pen and a certificate of participation. The study was approved under Bangor University School of Psychology ethics application number: 2015-14987-A14415.

Hebrew group

Sixty-four Hebrew-speaking children, aged between 3 and 10 years, were recruited from three local schools and one nursery in Israel. Ethical approval was granted by the chief scientist in the Education Minister's Office; approval number 10302.

Stimuli and apparatus

All experiment were presented on a 6th generation iPad, with a 24.25cm (diagonal) LED-backlit screen, with a 2048-by-1536-pixel resolution at 264 ppi.

Spheres Game

The Spheres Game was developed locally and programmed in Unity (San Francisco, USA). Both Welsh and Israeli children completed this task. The stimuli comprised coloured (green, red, or blue) shaded circles arranged on a coloured background that matched the colour of the stimuli (see Figure 2.1). The display colour alternated randomly with each trial.

One target and seven distractor stimuli were presented randomly in any of the 15 possible stimulus locations, arranged in a 5 (horizontal) x 3 (vertical) grid. Each distractor sphere shared the same linear shading gradient, with the brightest parts either vertically (0°), horizontally (left: -90°, right: 90°), or at an oblique angle (left: -60° and -30°; right: 30° and 60°); see Figure 2.2 for an illustration of shading gradients. The target sphere displayed an exactly opposite shading gradient to the distractor. We chose to present concave targets from convex distractors because concavities offer more salient targets than convexities (Hulleman et al., 2000; Kleffner & Ramachandran, 1992) and to replicate Sun and Perona's (1998) experiment, which used the predominant lighting condition (e.g., the distractor orientation) as their experimental variable.

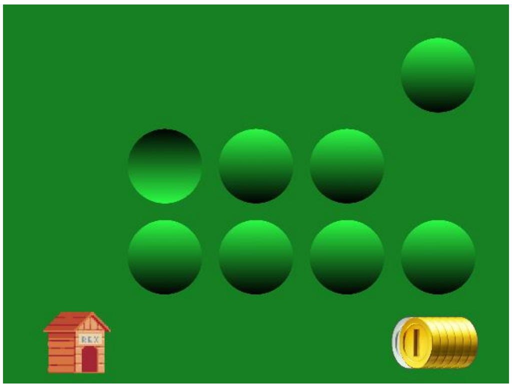


Figure 2.1. Example of Shaded Spheres Game. The target stimulus is shown on the middle line at the leftmost position.

The target and distractor stimuli measured 5cm in diameter and were viewed at approximately 30cm from the child's face, and thus covered a visual angle of approximately 9.53°. The visual angle of the iPad screen (comprising the background and all target and distractor stimuli) was approximately 44°.

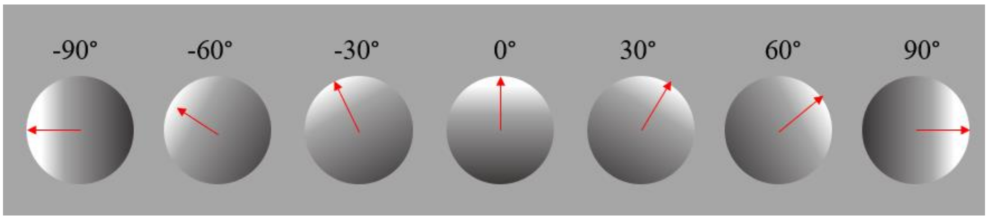


Figure 2.2. The seven shading gradients used in Spheres Game with arrows signifying the shading direction of the distractor stimuli.

Figure 2.1 illustrates seven randomly-located distractor stimuli with the brightest part of the stimulus located on their apices and a 180°-rotated target stimulus. The orientation was varied on a trial-by-trial basis. In each experimental block, each of the seven target orientations was presented once.

Participants were asked to tap the target stimulus to reveal an animal (a cat, dog, or fish) and drag the animal back to the 'home' icon in the bottom left-hand corner. When the screen was tapped, a 'popping' noise was played. The same sound was produced regardless of the location or the type of stimulus (target or distractor). The home icon varied according to the animal, showing a kennel for the dog, a pet bed for the cat, and a bowl of water for the fish. When the animal was taken home, an appropriate animal noise was played (e.g., a barking noise for a dog, a splash for a fish), and a coin appeared in the gauge in the bottom right-hand corner. Each time a block (seven trials) was completed, a congratulatory message was displayed, noting the level (block number) the participant had achieved, and the coin gauge was reset to zero.

Honeycomb Task

Only Welsh children over seven years of age were asked to complete this task. The Honeycomb Task was coded in Unity (San Francisco) and presented on an iPad. The stimuli comprised a grey hexagon surrounded by six identical hexagons, presented on a grey background, and depicted a light source direction via the arrangement of the brighter and darker edges. The brighter and darker edges were arranged such that an impression of depth could be perceived in the central hexagon. Twelve possible light source directions were presented from 0° to 330° in 30° increments (see examples in Figures 2.3A and 2.3B). The stimuli measured 7.8cm across and were viewed approximately 30cm from the child, presenting a visual angle of 11.13°.

A

B

Figure 2.3A and B. The Honeycomb Task. In Figure A, the orientation of the stimulus is 0°, and in figure B the orientation is 180°. Most people will perceive the central hexagon in Figure A as convex, and in Figure B as concave.

Global Local Task

Only Welsh children completed this task. Navon-style images (Navon, 1977) were presented to measure each participant's processing preference (Kimchi & Palmer, 1982). The stimuli were presented on an iPad and allowed participants to make a similarity judgement: A probe (for example, a large square made of small black squares; see description in Figure 2.4) was first presented in the middle of the screen on a grey background, followed by two targets, which appeared simultaneously on either side of the probe. The two targets were similar to the probe in either their global or local features. A fixation cross appeared between each of the 72 trials. The widest parts of the stimuli subtended a visual angle of 5.72° when held 30cm from the face.

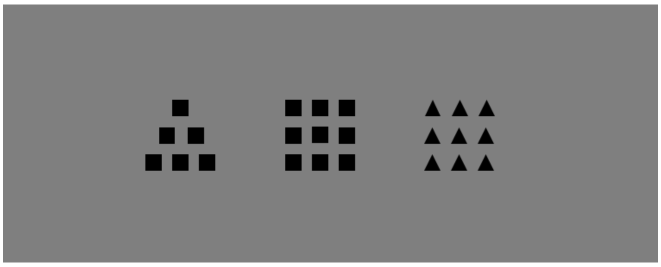


Figure 2.4. The target probe (centre) is a large square (global aspect) made of small squares (local aspect). The left target replicates the local aspect of the target but varies the global aspect, whilst the target on the right replicates the global aspect of the probe, varying the local aspect.

Procedure

Children were tested in several locations: three primary schools, one nursery in Wales, and three schools and one nursery in Israel. Children were taken from their class to a quiet classroom or office for the duration of the experiment. It was not possible to control the lighting in the rooms, but overhead lights were switched off. However, as the direction of external lighting has been found to have little effect on the perception of shape-from-shading (see Erens et al., 1993; Yonas et al., 1979), the light in the room is unlikely to have influenced shape judgements.

Children sat next to the researcher so that both could see the screen. The iPad was initially placed in line with the child's midline and supported in an upright position by a rugged case/protective cover. The children were permitted to move freely during the experiment, and their head position was not controlled. Some children held the iPad in their hands, and others left it on the table. The distance from the iPad to the eyes was approximately 30cm.

Individual tasks were discontinued if the participant showed signs of boredom, such as persistently looking away from the screen, ceasing to fixate on the screen, or pressing buttons randomly. Otherwise, tasks were allowed to continue until the predetermined endpoint (72 trials in the Global/Local task, 60 trials in the Honeycomb Task, and 10 blocks of seven trials in the Spheres Game).

The tasks were performed in random order. An additional Spheres Game task was performed at the end of the testing session when a child appeared to lose interest quickly but appeared receptive afterwards. In such cases, the two Spheres Game data files were combined and treated as one.

Spheres Game

The Spheres Game is a visual search task. Participants were given a standard verbal instruction: "You will see lots of shapes on the screen. One is different to all of the others. An animal is hiding behind the one that is different. If you tap the different one, you will find the animal and you can take it home". The instructions were not scripted, and some variations, depending on the age and the child's understanding, were permitted. Various prompts were used during the task, particularly with younger children who appeared to respond randomly or who appeared to employ a serial scanning strategy without looking at the whole screen, for example, “remember to look at the whole screen”, “Try to find the odd one out”, “Which one is different to all of the others?”, or “Try to tap the different one first”.

After each trial, a blank (coloured) screen was displayed until a ‘start’ icon was tapped. Children aged seven and under had unlimited time to detect the oddball stimulus. A timer was set to limit the time available to detect the target to maintain the interest of older children in this otherwise simple task. During the first block, the timer allowed 30 seconds to complete all seven trials in the block. The 30-second timer reset with each subsequent block. As the levels (blocks) increased, the available time decreased by five seconds to increase the difficulty of the game. For example, there were 25 seconds in which to complete all seven trials in block 2, and 20 seconds to complete all seven trials in block 3. Children were asked to find the oddball as quickly as possible.

Honeycomb Task

Participants over the age of seven, in Wales only, were asked to try this task. Stimuli were presented for 3 seconds, after which a prompt appeared, saying ‘is it in or out?’ for 3 seconds. A fixation cross appeared on the screen between trials for 1 second.

Each stimulus was presented up to five times, resulting in 60 possible trials. Participants indicated whether the central hexagon was convex or concave by pressing ‘In’ (concave) or ‘Out’ (convex) on the bottom left and right corners of the screen. The location of the ‘in’ and ‘out’ icons was counterbalanced.

Global Local Task

The Global Local Task is a match-to-sample Navon-style task (Navon, 1977), based on Kimchi and Palmer (1982). Children, in Wales only, were given an example on paper to ensure that they understood the task. The experiment then ran on the tablet. Children were asked to tap the target most similar to the central probe. The target stimuli appeared for up to 10 seconds unless a judgement was made earlier. Judgements were made by tapping the target stimulus. If a target stimulus was not tapped, the trial ended and the next began.

Verbal prompts were provided to children, particularly the youngest children, to ensure they understood the task. For example, when the probe stimuli appeared, the researcher asked, “Which of these is most like the one in the middle?”. One point was awarded to a global judgement, and zero to a local judgement.

Design

This mixed (between and within-groups) experiment comprised several within-subject factors. In the Spheres Game, accuracy and reaction times were dependent variables, and the orientation of the target stimulus was an independent variable. In the Honeycomb Task, convexity judgements were dependent variables, and the orientation of the stimulus was the independent variable. In the Global processing task, response types were the dependent variable.

There were two between-group factors: age (a child’s exact age and their categorical age group, based on their school class; see Methods, Participants), and reading group: English/left-to-right, or Hebrew/right-to-left.

Data Analysis

Spheres Game

A regression model was calculated to estimate the assumed light direction for each child, fitting the normalised reaction times for each of the seven target orientations. Reaction times were normalised using a reciprocal transformation (1/RT).

We assessed performance on the Spheres Game task by calculating each child’s accuracy, namely, the proportion of trials on which the child correctly identified the target circle on their first attempt. The proportion of accurate trials increased with age (r (162) =

.56, p < .001). Children whose accuracy fell below 50% (20 children), or who did not complete at least three blocks of seven trials (20 children), and those whose assumed light direction lay more than 2 *SD* from the mean of the assumed light direction in their age group were removed (14 children). In total, 54 children were excluded from analyses on the Spheres Game. Figure 2.5 shows the average age and the distribution of children's ages when excluded children were removed. The proportion of accurate trials increased with age after exclusion criteria were applied (r (108) = .21, p < .001; Figure 2.6).

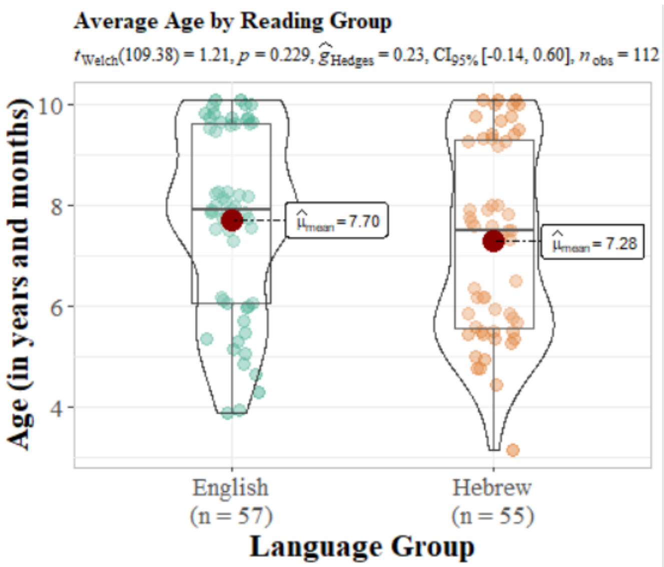


Figure 2.5. Violin plot to show age equivalence in English and Hebrew reading groups.

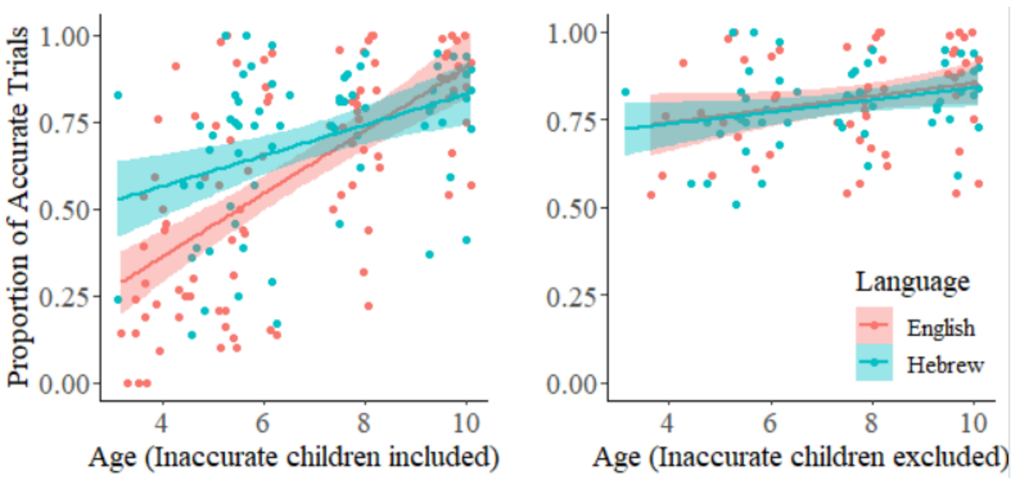


Figure 2.6. Scatterplots with linear trend (shaded area represents 95% confidence levels) to illustrate the proportion of accurate trials by age in children whose data included and excluded in this experiment.

Honeycomb Task

The proportion of convex responses for each stimulus orientation was analysed in a multivariate logistic regression to produce two measures; firstly, the degree to which participants' convexity judgements were modulated by the orientation of the stimulus (sensitivity). Participants whose logistic fits were not significant at the $p = .001$ level ($n = 3$) were considered insensitive to the stimulus and excluded from group-level analyses that included the honeycomb stimulus. Secondly, the angle of stimulus rotation most likely to produce a convex interpretation formed the estimate of the assumed light direction. Children ($n = 3$) who did not complete at least four out of five blocks (48 out of 60 trials) were excluded from the group-level analyses. Of the 38 children who attempted the Honeycomb Task, 32 were included after these exclusion criteria were applied.

Global/Local Task

The proportion of trials in which a global judgement was made, was used to determine whether a child exhibited a bias for global or local figure processing. Children who made fewer than 0.33 global judgements were categorised as local processors ($n = 19$), and those who made more than 0.66 were categorised as global processors ($n = 30$). Participants who made between 0.34 and 0.65 global judgements were categorised as ambivalent processors ($n = 24$). The group-level analysis did not include children who completed fewer than 18 trials (nine of the 62 children who attempted this task).

Results

To determine whether increasing age and habitual reading direction influences the development of the light-from-above prior or the left bias, we tested children before and during reading acquisition, aged between 3 and 10 years, in left-to-right and right-to-left reading group. We expected the light-from-above prior to be detected in all age groups and remain stable across the age groups. We predicted that if a left bias could be detected in a visual search task, that it would be present at the earliest ages in both age groups, remaining stable in the left-to-right reading group and diminishing in the right-to-left reading group with increasing age. We expected the left bias on the visual search task to correlate with the left bias on the Honeycomb shape judgement task in those children in whom the test was performed, and correlations between speed and accuracy on the Spheres Game with the propensity to make global vs local judgements in a global/local match-to-sample task.

Spheres Game

Reaction Times

Effect of Shading Direction

Children were fastest to respond to shading directions that were overhead (M = 2.35 seconds, SE = 0.13) or oblique (-60°: M = 2.9, SE = 0.16 ; -30°: M = 2.5, SE = 0.13; 30°: M = 2.5, SE = 0.14 ; 60°: M = 2.9, SE = 0.24), compared with horizontal shading directions (-90°: M = 3.73 seconds, SE = 0.18; 90°: M = 4.03 seconds, SE = 0.24). A three-way repeated-measures ANOVA suggested that shading direction significantly affected reaction times on the Spheres Game (F (2.89, 248.28) = 46.12, p < .001, η_p^2 = .35). Bonferroni-corrected post-hoc tests revealed that there were no significant differences between the three most-overhead shading directions (e.g., between -30°, 0°, and 30°; ps > .05), and neither were the comparisons made between symmetric shading directions (e.g., -90° and 90°, -60° and 60°, or -30° and 30°). However, the more-horizontal symmetric pairs (positive and negative 60° and 90° orientations) were significantly slower than more-overhead orientations (ps < .001). All orientations between -60° and 60° were significantly faster than horizontal conditions (-90° and 90°; Figure 2.8A).

Effect of Age, Reading Direction, and Shading Direction

Age-related decreases in mean reaction times were observed on the Spheres Game; age groups 1 (ages 3-4; M = 3.82 seconds, SE = 0.74), age group 2 (ages 5-6; M = 4.08, SE = 0.47), and age group 3 (ages 7-8; M = 3.93, SE = 0.26), were very similar. Reaction times decreased substantially in age group 4 (age 9-10; M = 2.93, SE = 0.21) and age group 5 (ages 10-11; M = 2.12, SE = 0.22). Each age group responded to overhead and oblique orientations faster than horizontal orientations (see Figure 2.7). A two-way ANOVA showed a main effect of age group (F (1, 104) = 24.80, p < .001, η_p^2 = .19), indicating that the increase in speed with age was statistically significant. There was a main effect of target orientation (F (2, 104) = 3.13, p = .048, η_p^2 = .02). However, the interaction between age and target orientation was not significant (statistics for non-significant results used as evidence against age-related changes can be seen in Appendix 2.2a), demonstrating that the response to different target orientations is stable with increasing age.

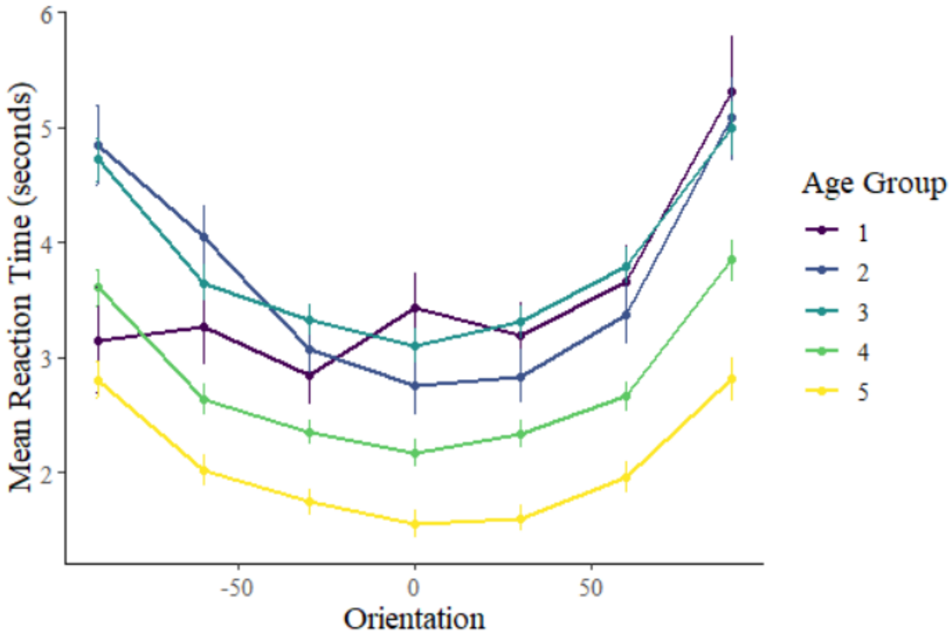


Figure 2.7. Line graph illustrating reaction times on the spheres game by age and stimulus orientation. Error bars represent the standard error.

Age by reading direction analyses were only undertaken on age groups 3, 4, and 5, as there were not enough participants in groups 1 and 2 in the Hebrew reading group. Performance on the Spheres Game was similar in English- and Hebrew-reading children; mean reaction times to detect target stimuli are shown in Table 2.2 and are displayed according to the shading direction in Figure 2.8C.

Table 2.2. *Mean reaction times to detect targets in accurate trials, by age group and reading group.*

Age Group	Age	English	Hebrew
Group 3	5-6	3.67	4.06
		(0.80)	(0.46)
Group 4	7-8	2.91	3.08
		(0.33)	(0.42)
Group 5	9-10	2.12	2.12
		(0.34)	(0.16)

* Standard deviations expressed in parentheses below means.

A three-way mixed ANOVA was calculated to determine whether children's reaction times to detect oddballs shaded at different orientations were significantly modulated by their reading direction or age. As expected, the difference in reaction times across age groups was statistically significant: (F (2, 86) = 15.11, p < .001, η_p^2 = .26). Bonferroni-corrected post-hoc tests demonstrated that each of the age groups included in this analysis (age groups 3, 4, and 5) were significantly different from each other. The mean difference between groups 3 and 4 was 1.01 seconds (SE = 0.31, p = .006); between groups 3 and 5 was 1.81 seconds (SE = 0.32, p < .001); and between groups 4 and 5 was 0.81 seconds (SE = 0.31, p = .006).

There was no significant interaction between age group and target orientation (p > .05), demonstrating that the light-from-above prior does not change with age. Likewise, there was no significant difference between reading groups, and no interaction between reading direction, age, and target orientation (all *ps* > .05), suggesting that there are no differences between English and Hebrew-reading children. All statistics for non-significant results used as evidence against age-related changes in reaction times can be seen in Appendix 2.2a.

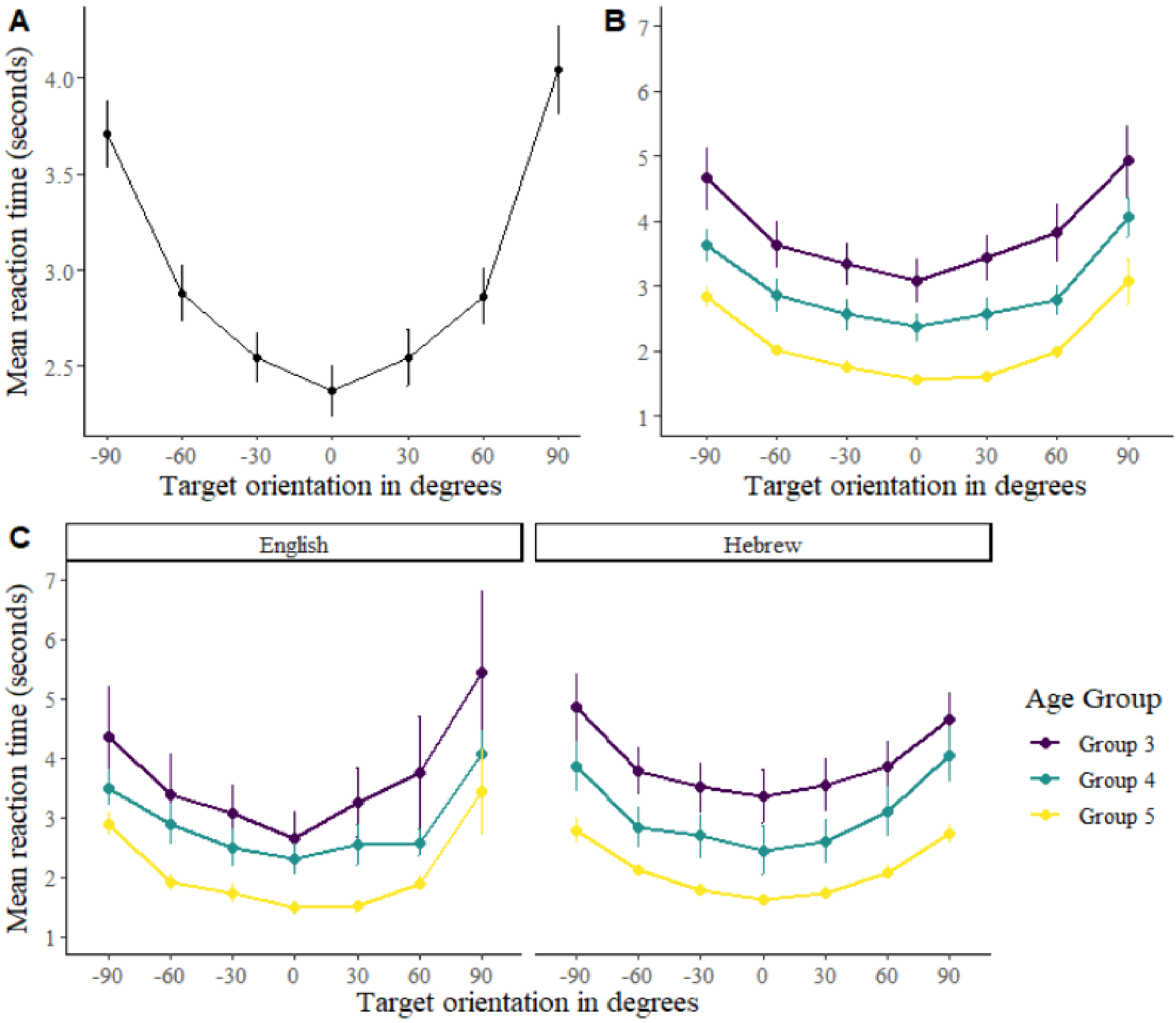


Figure 2.8. **A**: Mean reaction time in seconds by target orientation in degrees for English and Hebrew-reading children in all age groups. **B**: Mean reaction time in seconds by target orientation in degrees for both English and Hebrew-reading children in age groups 3, 4, and 5. **C**: Mean reaction time in seconds by target orientation in degrees, for English and Hebrew-reading children respectively, in age groups 3, 4, and 5. Error bars represent the standard error.

Accuracy

Effect of Shading Direction

A pattern of responses resembling that of reaction times was observed in the number of errors (selecting the wrong stimulus before the target) made to each target orientation, with overhead and oblique orientations (ranging from -60° to 60°) generating more accurate responses (M = 0.42, *SD* = 0.82) than horizontal orientations (-90°: *M* = 1.78, *SD* = 1.67, and 90°: *M* = 1.57, *SD* = 1.65).

A three-way repeated measures ANOVA revealed a significant effect of shading direction on accuracy (F (3.70, 332.05) = 28.17, $p < .001$, $\eta_p^2 = 0.39$). Bonferroni-corrected post-hoc tests showed that there were no significant differences between the more overhead shading directions (e.g., from -30° to 30°), and neither were the comparisons made between symmetric shading directions (i.e., -90° and 90°, -60° and 60°, or -30° and 30°; all *p*s > .05). However, participants were significantly more accurate at the -60° and 60° shading directions than they were at both horizontal conditions (-90° and 90°; *p*s < .001), and the leftmost and rightmost conditions (-90° and 90°) generated significantly more errors than all other shading directions (*p*s < .001). The overhead orientations (-30°, 0°, and 30°) were significantly more accurate than all other orientations, but were not different to each other, clearly demonstrating a general advantage for overhead shading directions (see Figure 2.8 A, which illustrates the pattern of errors generated by each shading direction).

Effect of Age, Reading Direction, and Shading Direction

Accuracy increased linearly with age (age Group 1: Mean number of errors = 1.21, *SE* = 0.16; age group 2: *M* = 1.93, *SE* = 1.82; age group 3: *M* = 1.31, *SE* = 1.34; age group 4: *M* = 0.56, *SD* = 0.87; age group 5: *M* = 0.47, *SE* = 0.85); a pattern that replicated across each shading direction (see Figure 2.9). A two-way ANOVA showed a main effect of age group (F (1, 104) = 9.12, $p < .001$, $\eta_p^2 = .08$), indicating that the increase in accuracy with age was statistically significant. There was a very small main effect of target orientation (F (2, 104) = 3.13, p = .048, η_p^2 = .001) but no interaction between age and target orientation (p > .05; statistics for non-significant results used as evidence against age-related changes can be seen in Appendix 2.2b), demonstrating that the response to different target orientations does not change with age. The two youngest groups are excluded from further analyses.

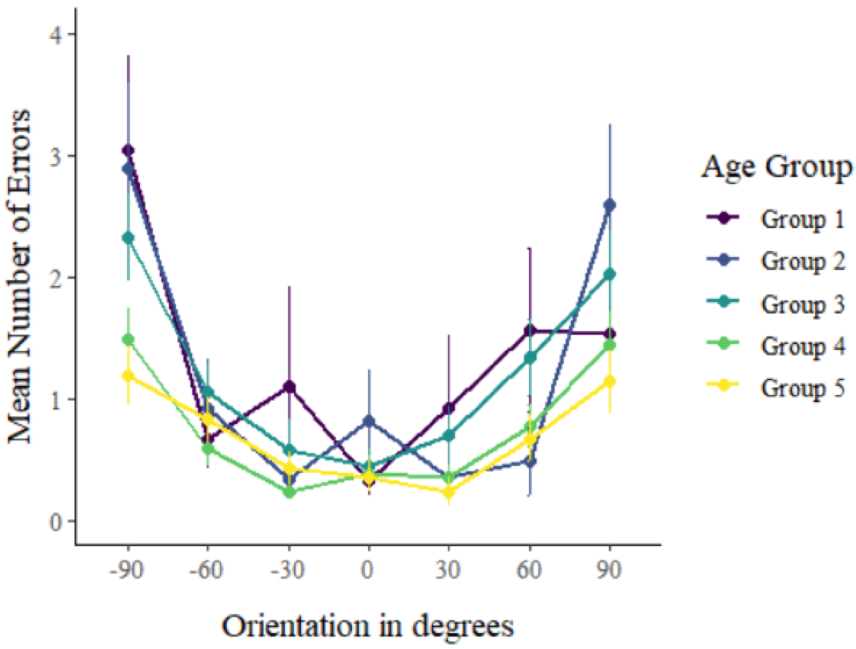


Figure 2.9. Line graph illustrating the mean number of errors on the spheres game by age and stimulus orientation. Error bars represent the standard error.

A three-way mixed ANOVA was calculated across age groups 3, 4, and 5 to determine whether age or reading direction significantly affected accuracy, or whether the shading direction interacted with age to affect the accuracy of target detection on the Spheres Game (see Figure 2.10 A). As expected, age affected accuracy, with older children able to detect targets with significantly fewer errors than younger groups, though with a very small effect size (F (2, 89) = 3.23, p = .044, η_p^2 = .07). Bonferroni-corrected post-hoc tests indicated that the age-related increases in accuracy were not statistically significant. There was no interaction between age group and the shading direction (p > .05), indicating that light priors do not change with age. Accuracy on the Spheres Game was similar in English and

Hebrew reading children ($p > .05$) and there was no interaction between age group, reading direction, and target orientation on accuracy ($p > .05$). This suggests that there were no differences between English and Hebrew-reading children, regardless of their age.

Table 2.3. *Mean number of errors made before selecting a target stimulus, by age group and reading group.*

Age Group	Age	English	Hebrew
Group 3	5-6	1.10	1.23
		(0.26)	(0.20)
Group 4	7-8	0.87	0.66
		(0.16)	(0.21)
Group 5	9-10	0.69	0.71
		(0.87)	(0.18)

* Standard error expressed in parentheses below means.

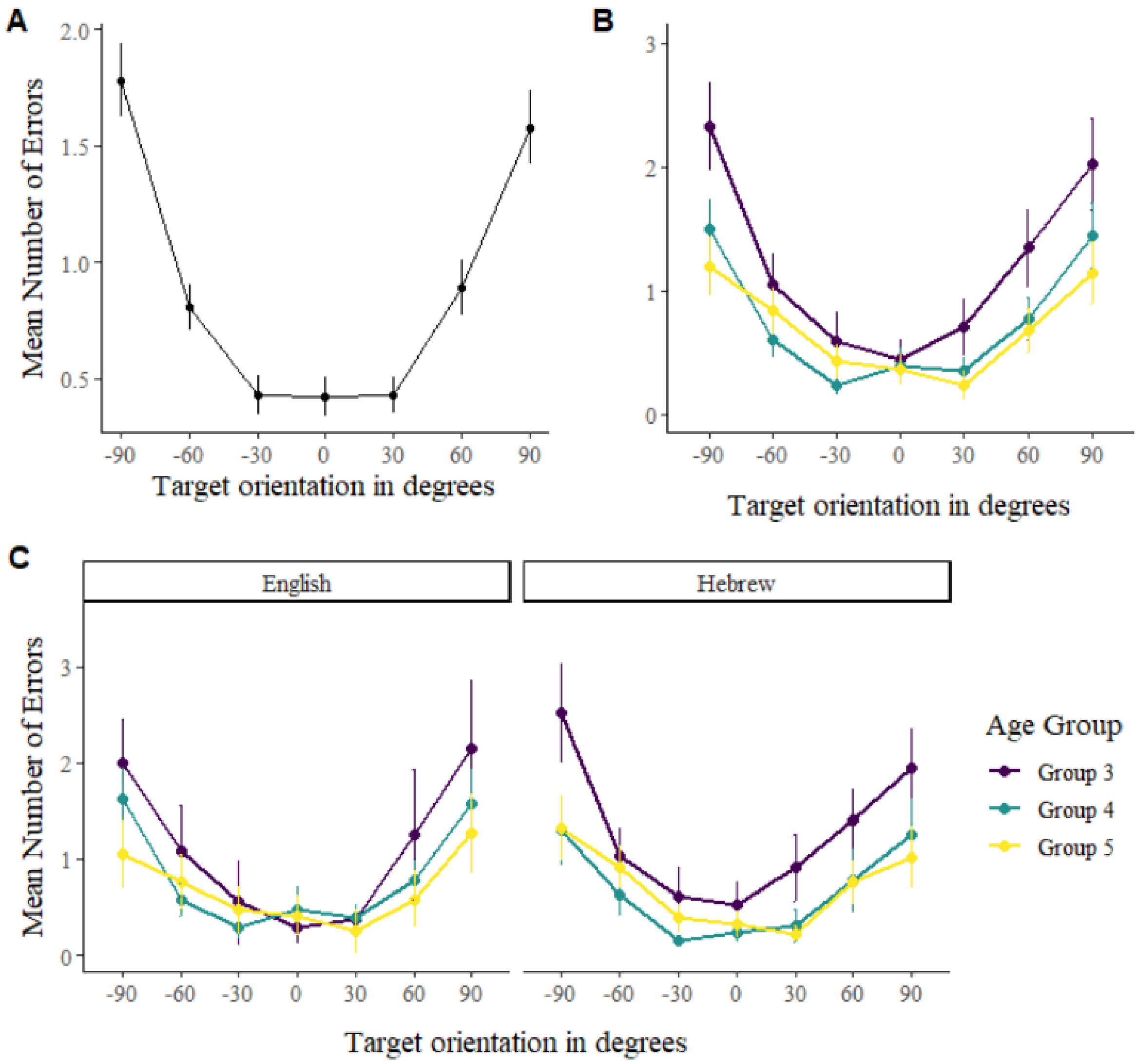


Figure 2.10. **A**: Mean number of errors by target orientation in degrees for English and Hebrew-reading children. **B**: Mean number of errors by target orientation in degrees for both English and Hebrew-reading children in age groups 3, 4, and 5. **C**: Mean number of errors by target orientation in degrees, for English and Hebrew-reading children respectively, in age groups 3, 4, and 5. Error bars represent the standard error.

Accuracy by Screen Position

Accuracy was analysed as a function of screen position to determine whether the location of the target stimulus on the screen affected accuracy (see Figure 2.11). Summary statistics were calculated to compare each row. Row 1 (bottom; M = 0.75, SD = 0.01) attracted more accurate responses than rows 2 (middle; M = 0.74, SD = 0.03) and 3 (top; M =

0.72, *SD* = 0.02). The columns (A-E) were also compared; column A attracted the lowest accuracy (*M* = 0.72, *SD* = 0.04), followed by columns B (*M* = 0.72, *SD* = 0.03), C (*M* = 0.72, *SD* = 0.02), D (*M* = 0.72, *SD* = 0.03), and E (*M* = 0.72, *SD* = 0.01). The differences between rows (1-3) or columns (A-E) did not reach the classical cut-off for statistical significance (p > .05), suggesting that screen position did not influence accuracy on this task.

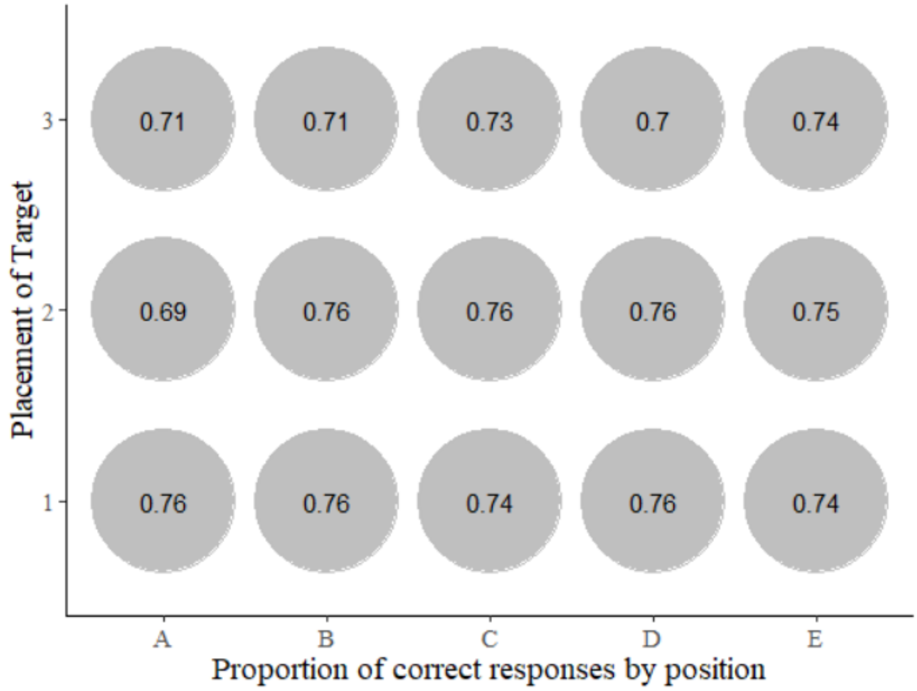


Figure 2.11. Proportion of correct responses to target stimulus as a function of screen position. Circles represent the 15 possible locations in the task.

Assumed Light Direction from Reaction Time Model on the Spheres Game

A regression model was calculated to generate an estimate of the assumed light direction for each child, fitting the normalised reaction times for each of the seven target orientations. Reaction times were normalised using a reciprocal transformation (1/RT). Figure 2.12 shows the pattern of responses when children whose overall accuracy fell below .5 were removed from the analysis. Table 2.4 shows the means and standard deviations of the assumed light direction, calculated from the reaction time model of performance on the

Spheres Game, for each age and reading group. This table only includes the assumed light direction of accurate children.

Table 2.4. *Means (μ) and standard deviations (σ; expressed in parentheses adjacent to means) of the assumed light direction derived from the reaction time model on the Spheres Game, in degrees, according to each age group.*

Age Group	*n*	μ (σ)
1	4	20.7 (51.1)
2	7	-22.3 (20.6)
3	28	-11.2 (8.16)
4	36	0.77 (1.68)
5	35	2.62 (1.17)

Given the low number of children who performed an adequate number of trials (see Data Analysis) in the youngest age groups, inferential analyses were undertaken with only age groups 3, 4, and 5 (number of participants per age group shown in Table 2.4).

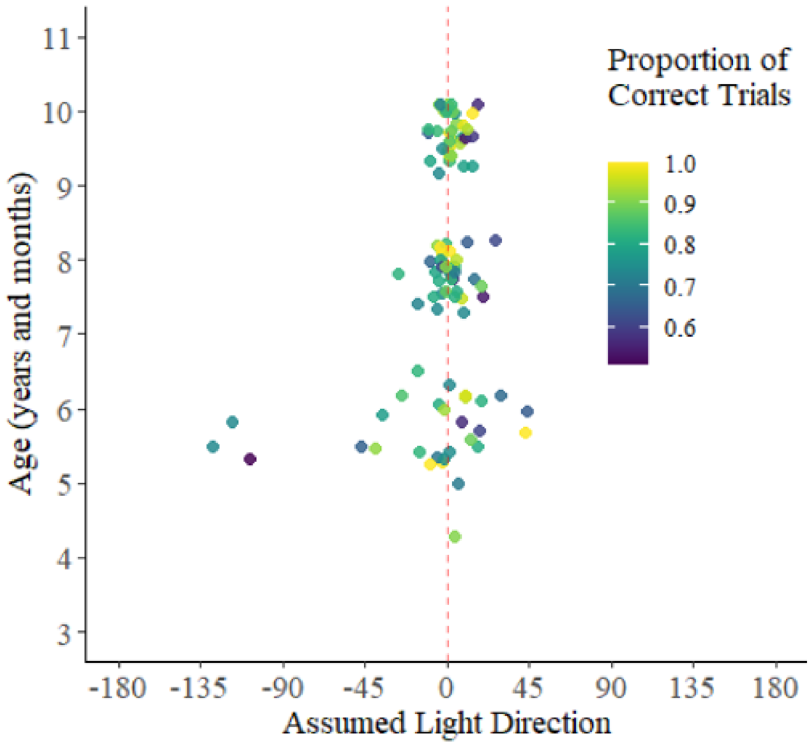


Figure 2.12. The distribution of assumed light directions by age on the Spheres Game. This figure shows only age groups 3, 4, and 5.

A multiple linear regression was calculated to determine whether a child's age, reading direction, or accuracy on the Spheres Game could significantly predict their assumed light direction. The results of the regression indicated that the model was a significant predictor (F (3, 94) = 3.89, p = .006), explaining 14% of the variance in assumed light directions. Both age (β = 24.03, t = 2.60, p = .011) and accuracy (β = 212.71, t = 2.41, p = .018) were significant predictors, and there was a significant interaction between age and accuracy (β = -25.57, t = -2.30, p = .024). Reading direction did not significantly predict the assumed light direction. The pattern of data suggests that increasing age leads to an advantage for shapes shaded from above, and that more accurate children tended to have a more overhead assumed light source direction.

Honeycomb Task

The Honeycomb experiment was only performed on English-reading children (n = 32). We predicted a left bias on the Honeycomb Task that was related to the degree of bias (the assumed light direction from the reaction time model) on the Spheres Game. A leftward bias was detected on this task: the mean assumed light direction from the Honeycomb task was -8.27° (SD = 53.61). However, there was no correlation between the assumed light direction derived from the Honeycomb task and age, or the Honeycomb task and the assumed light direction derived from the Spheres Game (ps > .05). There were no correlations between the assumed light direction derived from the Honeycomb Task and either age, sensitivity to the task (see Data Analysis), or the assumed light direction derived from the Spheres Game.

Global Processing

These analyses were undertaken on English-reading children only (n = 73). Nineteen favoured a local processing style, making fewer than 33% global judgements. A further 31 children were global processors, making more than 66% global judgements. Twenty-three participants were ambivalent processors, making between 34% and 65% global judgements. See individual data points plotted by age in Figure 2.13.

There was a significant Pearson's correlation between global processing and age (r (71) = .39, p < .001, R^2 = .15), with the likelihood of a child processing stimuli globally increasing with age (see Figure 2.13). Spearman's correlational analyses determined that no significant relationship existed between global processing preferences and either the bias derived from the Honeycomb task (p > .05); the bias derived from the Spheres Game (p > .05); or sensitivity to stimulus orientation on the Honeycomb task (p > .05), indicating that performance on these tasks was not mediated by a child's tendency to process stimuli globally.

We performed nested linear regression models to assess whether global processing preference predicted either the speed or accuracy to detect targets shaded at different orientations on the Spheres Game. When corrected for multiple comparisons, no significant predictors were identified, suggesting that global processing preference is not related to performance on the Spheres Game.

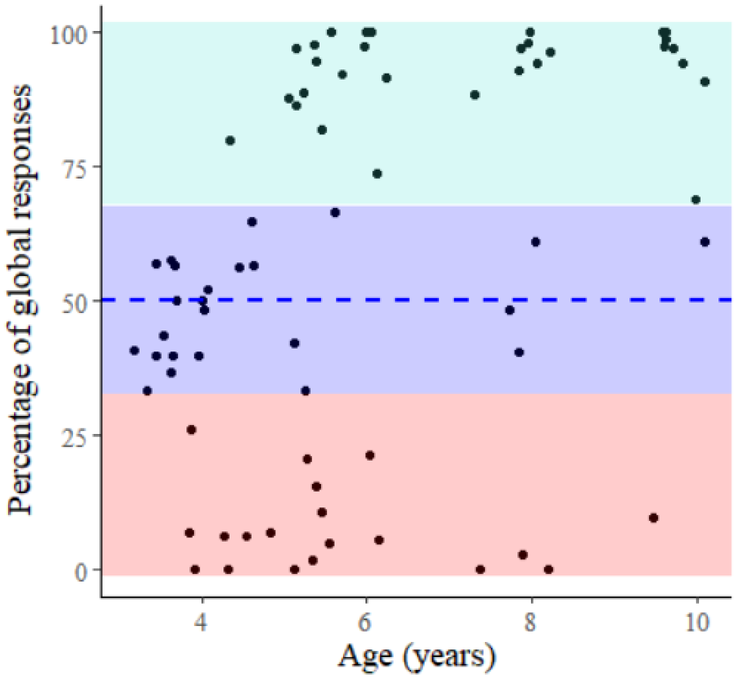


Figure 2.13. Scatter plot to illustrate the percentage of global responses by age group. The blue dashed line represents 50% global judgements, and the coloured sections represent the boundaries into which children were classified – as most global, mostly local, or ambivalent processors.

Experiment 2: Validation Task

Children exhibited no lateralised bias in the Spheres Game and a smaller left bias on the Honeycomb Task than reported in previous studies. We therefore conducted an experiment to validate our methods using young adults, who consistently demonstrate a left bias of 20°-30° in lab-based experiments (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017). We replicated the Honeycomb Task experimental paradigm as published in several papers (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020), and then performed the Honeycomb Task and the Spheres Game on the iPad to determine whether the results in Experiment 1 were specific to children.

Methods

Participants

Ten young adults aged 18-21 (9 female, all right-handed) from Bangor University's School of Psychology participated in the experiment to gain course credits.

Stimuli and apparatus

Honeycomb Task: PC Paradigm

The experiment was conducted in a dark room using a 24-inch NEC MultiSync P242w screen. The stimuli replicated the Honeycomb Task in Experiment 1, but were rotated across 24 orientations in 15° increments to reproduce the experimental conditions used in previously published studies that use this paradigm (e.g., in adults in Andrews et al., 2013, and Andrews et al., 2017; and in adults and children in Croydon et al., 2017). In a previous study of the Honeycomb Task in children, Pickard-Jones et al. (2020) used a condensed 15-orientation, 120-trial version of the experiment and found results comparable to adults and children in previously published studies using the 24-orientation version. Participants completed 240 trials, seeing each stimulus orientation ten times. Head position and the distance from the screen were maintained using a chin rest.

Honeycomb Task: iPad

The Honeycomb Task (iPad version) was completed on an iPad as described in Experiment 1.

Spheres Game: iPad

The Honeycomb task was completed on an iPad as described in Experiment 1. No time limit was set, but participants were asked to detect the oddball as fast as they could, and all participants were instructed to finish after block 10.

Procedure

The order in which participants completed the three tasks was counterbalanced to prevent order effects from affecting results. Participants' head position was maintained at a constant distance of 57cm from the screen using a chin rest during the PC version of the

Honeycomb Task. In the Honeycomb Task (PC version), participants were instructed to indicate whether the central honeycomb was convex or concave via a key press.

The procedure for the iPad version of the Honeycomb Task and the Spheres Game was the same as for Experiment 1.

Design

The validation task was a within-subject experiment. In the Spheres Game, reaction times were dependent variables, and the orientation of the target stimulus was an independent variable. In both versions of the Honeycomb Task, convexity judgements were dependent variables, and the orientation of the stimulus was the independent variable.

Data Analysis

Data analysis parameters matched those in experiment 1. There were no outliers, and no participants failed to complete any of the three experimental tasks. Data from all ten participants were included in this experiment. A total of 49 trials were discarded because the reaction time lay outside 2.5 *SD* of the mean reaction time.

Results

Honeycomb Task

Participants on the PC version of the Honeycomb task had a strong left bias of -29.3° (*SD* = 14.8°). On the iPad version, the mean bias was slightly smaller at -21.4° (*SD* = 15.7°). A paired t-test revealed that this difference was significant (t (8) = 3, p = .03, Δ = 0.52), suggesting the two versions of the task do not measure the extent of directional biases equally. However, there was a positive linear relationship between participants' performance on the two versions of the Honeycomb task, with most participants being more leftward on the PC version (see Figure 2.14). A linear regression analysis showed that the model was a good fit for the data (F (1,8) = 13.34, p = .006) and that performance on the PC version explained 63% of the variance on the iPad version of the Honeycomb Task.

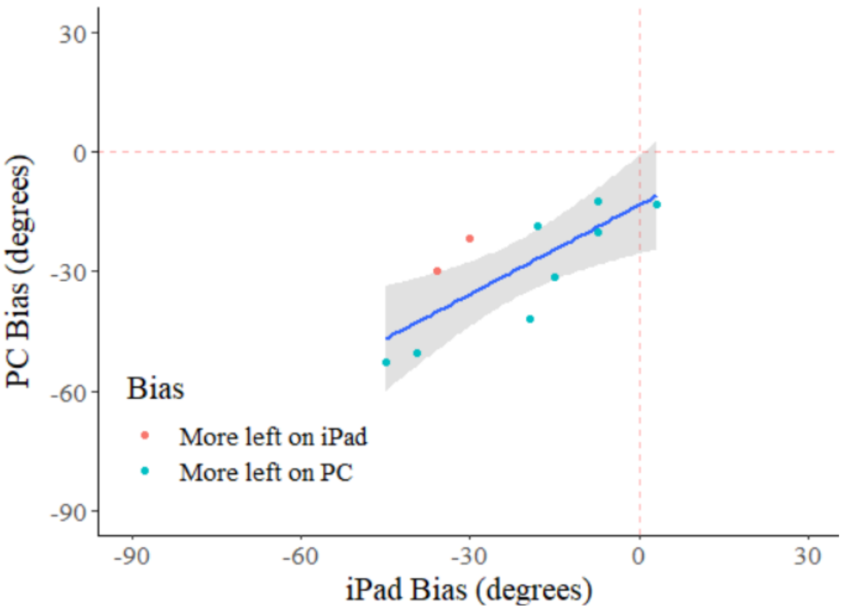


Figure 2.14. Scatterplot to illustrate linear relationship between the bias measured on the PC and iPad versions of the Honeycomb Task.

Spheres Game

Participants on the Spheres Game were generally fast (mean reaction time = 2.16 seconds, *SD* = 2.41 seconds) and accurate (92.61%). Participants were slightly faster at -60°, -30°, 0°, 30°, and 60° orientations than to -90° and 90° orientations (see Figure 2.15); however, a one-way ANOVA did not reveal a statistically significant effect of orientation on reaction times ($p > .05$). Similarly, a one-way ANOVA did not reveal a significant effect of orientation on accuracy ($p > .05$).

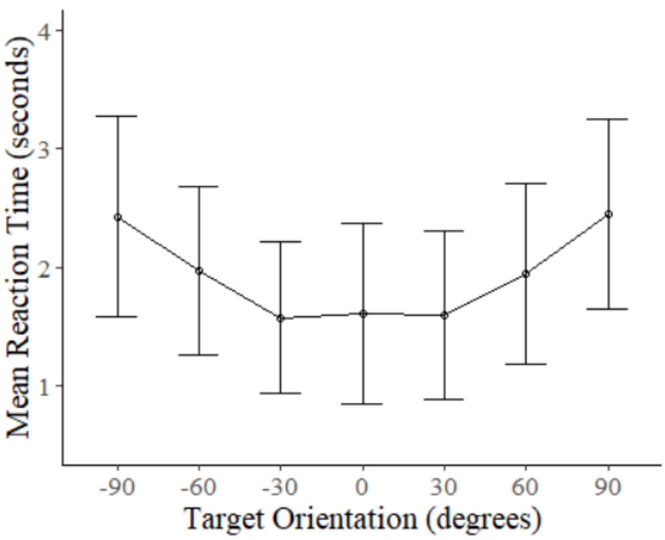


Figure 2.15. Line graph to show reaction times in seconds by target orientation. Error bars represent the standard deviation.

Discussion

The present study investigated the development of light priors in children aged between 3 and 10 years. We designed a visual search game to explore light priors in younger children, who are less able than older children to tolerate traditional experimental tasks. We tested children before and during reading acquisition in left-to-right and right-to-left reading cultures to probe the contribution of habitual reading direction to the development of directional biases. We validated our methods by testing young adults on the Spheres Game and Honeycomb Task. We established that the Honeycomb Task on the iPad reliably produced smaller leftward estimates of the assumed light direction than typical highly-controlled versions of the task in which head position is maintained (e.g., Andrews et al., 2013) and that an overhead light source bias was present on the Spheres Game with no discernible lateral bias.

Children displayed an unambiguous light-from-above prior by detecting vertically shaded stimuli faster and more consistently than horizontally shaded targets in each age group, in a pattern that did not change with age. Though the light-from-above prior has previously been demonstrated in younger children than in the present study (e.g., infants in Granrud et al., 1985), our findings challenge the notion that age-related changes occur in the magnitude of the light-from-above prior. Previously, Thomas et al. (2010) and Stone (2011) suggested that either the light-from-above prior, or children's ability to use the light-from-above prior, may change with age. We do not dispute the possibility that children may prioritise certain visual cues to different degrees over the course of their development; however, by testing the light-from-above prior in isolation (e.g., without comparing it to other depth cues), we show that it is not the prior that changes. Coupled with the evidence that the light-from-above prior exists in children as young as five months, this stable pattern of responses across age groups indicates that light priors are an innate developmental regularity.

Though it was not statistically significant, we did detect a modest tendency to respond faster to left-shaded targets: English-reading children systematically detected targets shaded with their brightest parts at -90° faster than those with the brightest parts oriented to 90° (see Figure 2.7 C in English-reading children). This pattern was true in all age groups, including the youngest children whose data were excluded from some group-level analyses due to overly small group sizes. This suggests that the left bias may be present as early in development as the light-from-above prior. Interestingly, this pattern of responses was not present in the Hebrew-reading children, implying that early reading experience affects the direction of innate biases. That reading experience strongly affects the direction and magnitude of biases in adults is well-established (Andrews et al., 2017; Chokron & De Agostini, 2000; Friedrich & Elias, 2016; Rinaldi et al., 2014), but differences between right-to-left and left-to-right reading young children might indicate that comparatively little experience is required to invoke or change the bias. Woods et al. (2013) previously demonstrated that just two years of formal reading experience is sufficient to evoke significant changes in children's search organisation, with left-to-right reading children increasingly beginning visual searches from an upper-leftward position. Nevertheless, given the lack of statistically significant results for the left bias in this experiment, more work is needed to find a test that is not only well-tolerated by young children, but also sensitive enough to detect subtle biases.

We did not anticipate that we would detect a strong leftward bias, given that previous research has shown that visual search is a less sensitive way to measure directional biases (Adams, 2007), in contrast to Sun and Perona's (1998) earlier observation of a strong leftward bias in visual search tasks. Like Adams, we did not detect a statistically significant difference between left and right shading patterns in the visual search game. The discrepancy between findings on different visual search tasks could be attributed to differences in experimental design: whilst the visual search task in Adams' (2007) and the present study allowed participants ample time to detect oddballs, Sun and Perona instead employed a variable presentation time, adjusting the difficulty on a per-participant basis and thus increasing the demands on their attention. The strong left bias found by Sun and Perona might therefore reflect the increased requirements on visual attention and, consequently, right hemisphere activation (Heilman & Van Den Abell, 1980), leading to an augmented left bias.

Supportive of this view, our validation task (Experiment 2) suggests that the deployment of attention may affect the expression of the left bias. We observed that the performance of adults and children was remarkably similar on the Spheres Game, with reaction times following the same pattern in both groups. There were age-related increases in accuracy and decreases in reaction times, as would be expected of a visual search task among this age range (Enns & Cameron, 1987). However, adults were faster and more accurate than even the oldest children in our sample and, unlike children, did not exhibit the slight tendency to respond faster to left-shaded stimuli. Adults' enhanced performance on this task suggests that it was easier for them. Therefore, we speculate that observing a trend towards responding faster on targets shaded from the left in children, who found the task more difficult, and no such trend in adults, who found the task easier, suggests that an advantage for left-shaded stimuli might emerge from greater demands on attention.

It is possible that our choice of testing methods reduced our ability to detect a directional bias. We used an iPad held freely at variable distances from the face with the head position unconstrained, according to the child's comfort. In psychophysical experiments, head position is typically controlled via a chin rest or by encouraging participants to maintain a stable head position, and screens are placed at a fixed height and distance. Changes in head and iPad position will result in a disparity between the shading direction of the stimulus relative to the top of the iPad screen (the reported stimulus orientation) and the shading direction of the stimulus projected onto the retina (see Howard et al., 1990; Kleffner & Ramachandran, 1992, for a discussion of retinal vs gravitational reference frames in shape-from-shading). It is also possible that head or tool movements might be made to compensate for left biases – observers might interact with the world in a way that accounts for their internal biases, thus offsetting their effect under natural viewing conditions.

Given the young age of the children in our experiment, we took a gentle approach to testing and discontinued if any signs of fatigue or boredom were detected. Although this approach certainly garnered fewer trials than we might have collected for some children (and subsequently prompted the exclusion of any child who completed too few trials to permit reasonable confidence in their results), we question the usefulness and validity of collecting data when a child is not fully engaged. Though our conservative choice increases the likelihood of making a Type II error, having fewer high-quality trials increases our confidence in our statistically significant results.

The Honeycomb Task was subject to the same limitation as the Spheres Game: a lack of control over head and screen position. The task was performed with a small number of children to compare against previous results (e.g., Croydon et al., 2017; Pickard-Jones et al., 2020) and ensure that it was possible to measure the assumed light direction under our experimental conditions. Due to time constraints imposed by the ethics board in Israel, it was only possible to perform this task in Wales. As previous experiments have demonstrated that young children often perform inconsistently on this task, it was only attempted with children who were still engaged after the primary tasks were complete. We observed a slightly smaller left bias than typically reported (e.g., Croydon et al.; Pickard-Jones et al.) but in line with other estimates of the bias (e.g., Adams, 2007). Our validation task supported this finding:

adults performing the Honeycomb Task both on the iPad and in a typical lab setting showed a smaller bias on the iPad version, which was well-correlated with the strong leftward bias detected on the lab version. That we found a left bias of a lesser magnitude under our experimental conditions in the Honeycomb Task, but no bias in the Spheres Game, supports the position that uncontrolled head and screen position is likely to decrease our power to detect subtle biases in any experimental paradigm, and that visual search is a less sensitive measure of directional biases.

Figure-ground separation is intrinsic to the perception and organisation of the visual scene, and the perception of convexity is a known factor in figure-ground separation (Peterson & Salvagio, 2008). We measured global processing preferences using a Navon (1977)-style match-to-sample task to explore whether the ability to perform a parallel visual search relies on the ability to process the visual scene globally, implying that shape-from-shading relies on a precursory process of segregating the local foreground of a visual display from its global background. We did observe the expected increase in the tendency to process stimuli globally; however, global processing preference did not significantly predict either speed or accuracy to any shading direction on the spheres game, and neither was global processing preference related to the assumed light direction.

Conclusion

This study presents new evidence from younger populations than have previously been tested, demonstrating that the light-from-above prior is present early in development. we concluded that the light-from-above prior does not change with age, as we observed a strong light-from-above that did not change from ages 3-10 and exactly matched the pattern of adult responses in the validation task, despite participants' spontaneous head tilt possibly conflicting with the object-centred cues to the orientation in the experimental stimuli. The Spheres Game successfully addressed some of the previous limitations of psychophysical tasks: it was more acceptable to younger children and an effective measure of the light-from-above prior in ages three years and above. We also applied robust inclusion criteria to prevent those who performed at chance levels from altering results. However, we did not detect a directional bias in English- or Hebrew-reading children and established that visual search is unsuitable for detecting directional biases in children, regardless of the additional cognitive effort that children must expend to engage with psychophysical tasks. Although we could not detect a directional bias, a slight tendency to favour the left hemispace in English-reading children only was encouraging and should prompt further investigation with alternative experimental methods that permit the measurement of directional biases in very young children. We suspect left bias is present earlier in development than current methods can detect, but we require more definitive evidence to substantiate this claim.

Chapter 3: Do changes in lateralised light assumptions index cognitive function? Evidence for sex-specific effects.

Abstract

Young, Western observers typically assume light originates from an above-left location in shaded stimuli in which a light source is not explicitly depicted. This left bias is thought to reflect hemispheric asymmetry. Like certain cognitive functions, behavioural markers of hemispheric asymmetry reduce with age and are often sex-specific, yet the relationship between cognitive function, sex, and hemispheric asymmetry have not been assessed. This study assesses the relative contributions of age, sex, and cognitive function on performance in two typically left-biased behavioural tasks: the Honeycomb measure of the assumed light direction and the Landmark Task. Sixty-seven older adults (41 women) aged 60-87 years judged whether geometric shapes, shaded to convey 3-D depth, were convex or concave. The stimulus was rotated across 24 orientations (ranging from 0° to 330° in 15° increments), and the proportion of convex judgements to each orientation was used to generate an estimate of their assumed light direction. We also assessed whether participants' responses to the Honeycomb stimuli were significantly modulated by the orientation of the stimulus, providing a measure of sensitivity to shading information and categorised them as SfS-sensitive or SfS-insensitive. Cognitive function was assessed using the Montreal Cognitive Assessment (MoCA; Nasreddine et al., 2005). Though men exhibited a more leftward bias than women, this difference was not significant. However, whilst SfS-insensitive women had significantly lower MoCA scores than SfS-sensitive women, there was no difference in cognitive function between SfS-sensitive and SfS-insensitive men, suggesting that age-related changes in the cognitive processes associated with resolving 3-D depth from shaded stimuli are sex-specific.

**A version of this chapter is in preparation for publication.*

Whilst many studies have described changes in the trajectory of pseudoneglect in healthy ageing populations, relatively few studies have sex-disaggregated their data (Friedrich et al., 2018), and no studies have explored the relationship between leftward biases and cognitive function, despite several studies of age-related changes in leftward biases (see Friedrich et al., 2018, for a review, and Learmonth & Papadatou-Pastou, 2021, for a meta-analysis, which both highlight the need to include sex and measures of cognitive ageing in future studies).

This is a surprising omission, given the wealth of evidence concerning functional and structural changes in the right hemisphere (Cabeza, 2002) that have been found in cohorts in which measurable cognitive decline is often detected (Bloomberg et al., 2021; McCarrey et al., 2016; Reas et al., 2017), and which also appears to coincide with the age at which left biases are less consistently observed (e.g., Learmonth & Papadatou-Pastou, 2021). Indeed, Cabeza suggested in his 2002 paper that sex and cognitive performance may offer significant power to generalise findings across a heterogeneous population. Given that tasks such as shape-from-shading and the landmark task can detect subtle individual differences, they are well suited to investigate whether the lateralisation of sensory processes, or the integration between top-down priors and bottom-up sensory processes, are subject to sexually dimorphic age-related changes.

In addition to a plethora of behavioural studies documenting the leftward bias observed in the light-from-above prior (Adams, 2007; Andrews et al., 2013; Andrews et al., 2017; Ramachandran, 1988; Sun & Perona, 1998), neuropsychological (de Montalembert et al., 2010; Stone et al., 1993), neurophysiological (Mamassian et al., 2003), and neuroimaging (Fink et al., 2001; Gerardin et al., 2010; Taira et al., 2001) evidence has converged to detail its neural correlates: the leftward bias reliably occurs within the context of increased right hemisphere activity in the dorsal stream, particularly in the right intraparietal sulcus (Fink et al., 2001). Given the right hemisphere's well-established role in orienting visual attention and resolving shape-from-shading, it is possible that age-related changes in the assumed light direction and other left-biased tasks (Barrett & Craver-Lemley, 2008) may index structural or functional changes in the right hemisphere.

A reduction in hemispheric asymmetry in older adults is well-established within psychological and imaging literature (see Cabeza, 2002, for a review of literature related to hemispheric asymmetry reductions in the pre-frontal cortex). Cabeza's (2002) germinal hemispheric asymmetry reduction in older adults (HAROLD) model posits that the reductions in hemispheric asymmetry observed in older adults may result from a plastic reorganisation of neurocognitive networks across the cortex, which may compensate for cognitive decline by recruiting additional neural populations during tasks that incur a higher cognitive load. Patterns of overactivation have been observed synergistically with underactivation; for example, in a memory task, older adults with reduced hippocampal activation recruited additional frontal regions relative to younger adults (Gutchess et al., 2005). Gutchess and colleagues found that the degree of frontal activation was negatively correlated with hippocampal activation, providing strong evidence that overactivation occurs in response to a reduction of typical activation patterns. Compensatory overactivation may signify optimal activation patterns in the ageing brain, as older adults with a bilateral activation pattern exhibit better performance on memory tasks than those with unilateral activation patterns (Cabeza et al., 2002 b), suggesting that reductions in hemispheric asymmetry reflect healthy ageing processes.

Alternatively, neural dedifferentiation, or the finding that neural processing becomes less selective with age (Koen & Rugg, 2019), may contribute to less lateralised performance on cognitive tests. Research in non-human primates has shown that receptive fields for single neurons widen in older primates (Li et al., 2001); for example, Schmolesky et al. (2000)

studied awake in-vivo neural responses from cells in V1 in young adult and very old rhesus monkeys. Schmolesky et al. found that the cells of old monkeys exhibited significantly less selectivity to orientation than young monkeys, finding that the cells sampled were more responsive and less orientation-specific than those of young adult monkeys. Several studies have attempted to quantify the relationship between neural dedifferentiation and cognitive performance in a variety of cognitive tasks in humans (see Koen et al., 2020, for a review), and whilst the available evidence suggests that dedifferentiation co-occurs with ageing and contributes to worse performance on cognitive tests (Li et al., 2001), the selectivity of neural populations confers benefits on cognitive task performance regardless of age. Ultimately, should reduced behavioural asymmetry result from increased levels of neural dedifferentiation, this would indicate worse ageing, in contrast to the successful compensatory mechanisms posited in the HAROLD model.

There are substantial sex differences in patterns of both healthy and pathological ageing (Bloomberg et al., 2021; Hatta et al., 2015; McCarrey et al., 2016). Although women are at a 50% greater risk of developing Alzheimer's disease (Bloomberg et al., 2021), they may also be more resistant to normative cognitive decline (McCarrey et al., 2016). In healthy older adults, biomarkers of ageing such as microbleeds and cortical or lacunar infarcts are present earlier in the MRI scans of men (Vinke et al., 2018), who have also been shown to experience steeper declines in several aspects of cognition, including visuospatial ability (McCarrey et al., 2016). It is possible that decrements in visuospatial ability could be explained by increased cortical atrophy in parieto-occipital regions that have been observed predominantly in men (Coffey et al., 1998). Several studies have found a steeper trajectory in men for elements of cognitive decline such as mental status and memory (Bloomberg et al., 2021; McCarrey et al., 2016) and global function (Reas et al., 2017), and in women for executive function (Reas et al., 2017). Sex differences have also been found in performance trajectories on tests of lateralisation such as the line bisection test, with older women making larger leftward errors on longer lines (Varnava & Halligan, 2007), consistent with intact right-hemisphere function. Similarly, Chen et al. (2011) found that women retained a leftward bias in line bisection, whilst men's errors became more rightward. A more leftward bias suggests that the right hemisphere remains dominant in orienting visuospatial attention in women, while cortical and behavioural asymmetry is reduced in men.

The aims of the present study were twofold: firstly, to assess whether a reduced left bias reflects a successful compensation process or indicates either pathological or suboptimal ageing. Consistent with previous results in older adults (Andrews et al., 2017; de Montalembert et al., 2010), we predicted that older adults in this study would show an overhead or a leftward bias at the group level that was smaller than typically observed in younger adults (Adams, 2007; Andrews et al., 2017; Smith/Elias?). To explore this question, we tested the assumed light source direction in older adults aged 60 to 87 years, using a shape-from-shading paradigm alongside measures of cognitive ability and, because Andrews et al. (2017) found a correlation between the assumed light direction and line bisection in older adults, we also assessed hemispheric asymmetry using the Landmark Task. Because reductions in hemispheric asymmetry coincide with the age at which cognitive decline begins, we predicted that the degree of hemispheric asymmetry in older adults would index their cognitive health. If individuals with better cognitive ability (measured using the Montreal Cognitive Assessment; MoCA, Nasreddine et al., 2005) exhibit a reduced leftward bias in the assumed light direction, we would conclude that reduced asymmetry reflects a successful compensation strategy, with regions in the left hemisphere being recruited to address shortcomings in the right hemisphere. Alternatively, if individuals with worse cognitive ability have a reduced left bias, this will imply that reduced asymmetry reflects neural dedifferentiation (Koen et al., 2020), which is not suggestive of any protective or compensatory functions.

Secondly, we aimed to measure sex-related differences in the assumed light direction and cognitive functions. Because Varnava and Halligan (2007) found more left-lateralised performance in line bisection in women with increasing age and Chen et al. (2011) observed significant age-related reductions in right-hemisphere dorsal spatial activity in men, we predicted that women would retain a more leftward bias than men. Given that men's cognitive abilities may decline earlier and that men experience earlier structural brain changes than women (Bloomberg et al., 2021; McCarrey et al., 2016; Reas et al., 2017), we also predicted that men would attain lower MoCA scores than women. Given our prediction of a more leftward bias and better MoCA scores in women, we expected that a more leftward bias would be related to better cognitive function and thus provide support for the HAROLD model of hemispheric ageing (Cabeza et al., 2002).

Methods

Participants

In total, 67 older adults aged between 60 and 87 years of age participated in this experiment, including 41 females (mean age = 71.83, *SD* = 5.7) and 26 males (mean age = 74, *SD* = 6.81). Participants were recruited from Bangor University's participant panel and from the community after attending outreach sessions designed to engage older adults with research.

Participants were tested in a Bangor university laboratory or an external facility closer to their homes. Consent was obtained in line with Bangor University School of Psychology's ethical guidelines (ethics application number: 2019-16550; see Appendix 3.1). Participants were allowed to opt-out of tests and were compensated with £7.

Measures

Honeycomb Task

The Honeycomb Task has been used extensively in adults (e.g., Andrews et al., 2013; Andrews et al., 2017) and children (Croydon et al., 2017; Pickard-Jones et al., 2020) to test the assumed light source direction. The stimuli comprised a grey hexagon surrounded by six identical hexagons, presented on a grey background, and depicted a light source direction via the arrangement of the brighter and darker edges. The brighter and darker edges were arranged such that an impression of depth could be perceived in the central hexagon. Twenty-four possible orientations were presented from 0° to 345° in 15° increments (see examples in Figures 3.1A and 3.1B).

The Honeycomb Task was coded in E-prime and presented in the laboratory on a PC (24-inch NEC MultiSync P242w screen) or a laptop (Samsung 400B laptop with a 32cm screen).

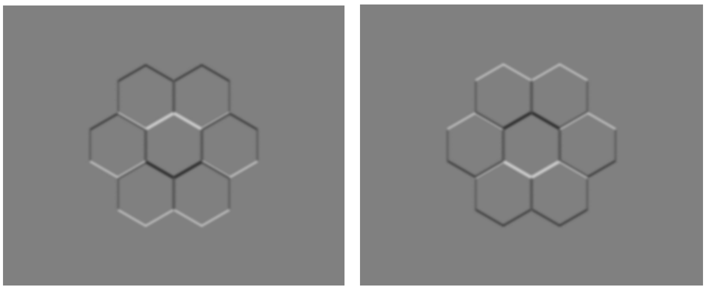


Figure 3.1 A and B. honeycomb stimulus oriented at 0° (A) and 180° (B).

Landmark Task

The Landmark Task (based on Çiçek et al., 2009) was coded in PsychoPy2 (Peirce et al., 2019). In the laboratory setting, stimuli were presented on a PC (24-inch NEC MultiSync P242w screen). White lines measuring 20cm horizontally and 2mm vertically were presented on a black background. Stimuli were randomly presented in the centre and each of the four quadrants of the screen. Lines subtended a visual angle of 20°. Participants tested in the community viewed the stimuli on a Samsung 400B laptop with a 32cm (diagonal) screen. Horizontal lines were 12cm across, 35cm away, and covered a 19.5º visual angle.

Lines divided at the veridical centre comprised 40% of trials. Lines divided to the left or right of the veridical centre were categorised as small deviations (0.5cm; 2.5% of the line length), medium deviations (1cm; 5% of line length), or large deviations (1.5cm; 7.5% of line length). Each deviation was represented in 10% of the total number of trials. Stimuli were presented for 1500ms, with a 500ms pause (black screen) between trials. There were two blocks of 105 trials each, and a pre-programmed rest break between the blocks.

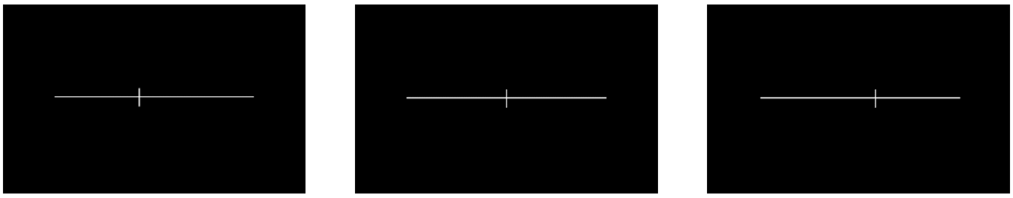


Figure 3.2. Landmark task trial, displaying a large left deviation (left image), a central bisection (centre image), and a large right deviation (right image). All examples are shown in the centre of the screen.

Montreal Cognitive Assessment (MoCA)

Cognitive functioning was assessed using the MoCA (Nasreddine et al., 2005). This paper-based task takes ten minutes to administer and assesses six cognitive domains: working memory, visuospatial abilities, executive functions, attention, language, and orientation to time and place (see example in Appendix 3.2). Scores range from zero to 30. The traditional cut-off for the diagnosis of cognitive impairment is <26. The number of years of education individuals attained was also collected on the MoCA form.

Procedure

All tasks were delivered in counterbalanced order to prevent order effects. Participants were tested in a laboratory setting and in the community. For computer-based tasks, participants tested in the laboratory sat in front of the monitor, which was placed 57cm away. In the community setting, participants sat at a table facing a laptop that was placed 35cm away. In both testing environments, head position was maintained using a chin rest unless the participant was uncomfortable; in such cases, the importance of maintaining a stable head position and distance from the monitor was emphasised and the researcher monitored head position during the task. In both settings, overhead lights were switched off during computer tasks and windows were obscured.

Honeycomb Task

Each stimulus was presented ten times, in random order, resulting in 240 trials. A rest break was pre-programmed to occur after 120 trials. Participants indicated whether the central hexagon seemed convex or concave by pressing ‘In’ (concave) or ‘Out’ (convex) using the D and L keys on a keyboard. Trials were preceded by a 1000ms fixation cross, followed by the test stimulus for 500ms. The Honeycomb Task lasted 15 minutes.

Landmark Task

A trial began with a blank screen for 500ms, followed by a bisected line for 1,500ms. The bisected line appeared centrally or at one of the four quadrants of the computer screen and was either bisected in the middle or with a small or large deviation to the right or the left. Participants pressed “Q” or “P” to indicate whether they thought the intersecting line was placed to the left or the right of the veridical centre. This task took ten minutes to complete.

MoCA

The MoCA test was administered on paper according to the published guidelines (Nasreddine et al., 2005) Our consent procedure emphasised that researchers were not clinically trained and that any concerns with memory must be directed to the participants' family doctor. Participants could choose not to be informed about potentially abnormal scores. If they did not opt-out, a clinician assessed low-scoring tests, and participants were invited to attend an in-depth assessment or have their results sent to their family doctor. The MoCA test takes ten minutes to administer.

Design

This mixed design included several within- and between-subject factors. Age, Sex, and individual scores on each of the experimental measures were used as between-subject variables. In tests of association, individual scores on each of the experimental measures were used as within-subject variables.

In the Honeycomb Task, the estimate of each participant's assumed light direction was a dependent variable. In the Landmark Task, dependent variables were the accuracy on left and right deviations and the proportion of left guesses to central bisections.

Data Analysis

Honeycomb Task

The proportion of convex responses to each of the 24 stimulus orientations was analysed in a multivariate logistic regression that estimated the orientation most likely to generate a convex response in each participant. Sensitivity to the stimulus was classified as the extent to which the orientation of the stimulus influenced individuals' convexity judgements (see Figures 3.3 A-D for examples). Participants whose logistic fits were not significant at the $p = .001$ level were deemed insensitive. Z-scores were used to identify outliers; participants with a bias of more than two standard deviations from the mean were excluded. Of the 38 participants classed as sensitive, five were removed as outliers and one participant was excluded from analyses on this task because they tested below Carson et al.'s (2018) threshold for normal cognitive performance on the MoCA test (see Data Analysis, MoCA section, for explanation).

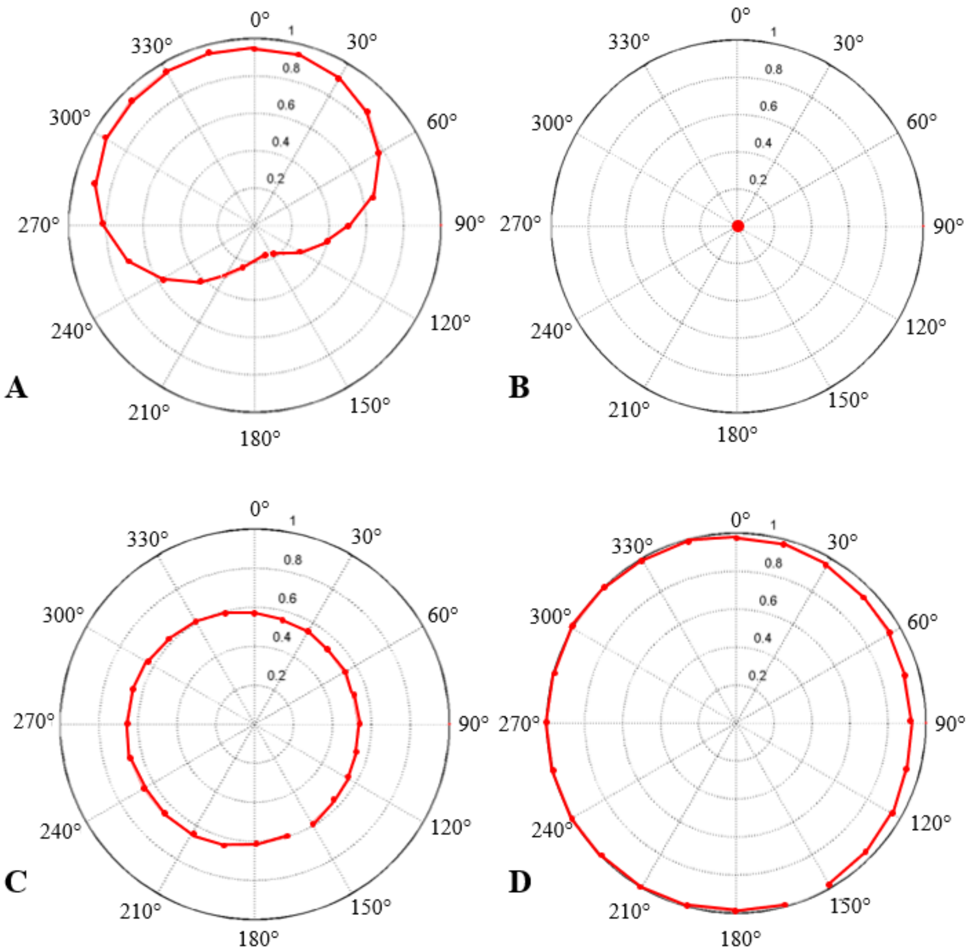


Figure 3.3 A: Fitted radar plot for Participant 157, who showed high sensitivity and a left bias of -18.13°. B shows data from Participant 158, who made no convex judgements regardless of the orientation of the stimulus. C shows data from Participant 139, who performed at near chance levels at all stimulus orientations. D shows data from Participant 141, who made exclusively convex judgements regardless of the orientation of the stimulus. Figures B, C, and D demonstrate low sensitivity to the orientation of the stimulus when making shape judgements.

Landmark Task

Missed trials (trials that were not responded to before the next trial began) were discarded from analyses and not classified as incorrect guesses in accuracy analyses.

MoCA

The MoCA has been validated clinically as a measure of cognitive function. Though Nasreddine et al.'s (2005) paper describes scores lower than 26 as indicative of cognitive impairment, recent meta-analyses have demonstrated a high false positive rate when using this cut-off (Carson et al., 2018). Instead, a cut-off of 23 has been shown to correctly identify a similar number of cognitive impairments whilst reducing the number of false positive results (Carson et al., 2018). Five participants were removed in total using this criterion.

Results

Assumed Light Direction

Only participants who were sensitive to the Honeycomb stimulus (see Data Analysis; n = 32) were included in analyses of the assumed light direction. A group-level leftward bias of -15.30° (SD = 33.51) for the assumed light direction was detected, which a one-sample t-test confirmed was significantly leftward of an overhead (e.g., 0°) lighting condition (t (31) = -2.58, p = .015, Δ = 0.46). Men exhibited a larger bias to the left (n = 9, M = -34.01°, SD = 33.60°) than women (n = 23, M = -7.99°, SD = 31.19°). A Welch's t-test for unequal group sizes indicated that this difference did not reach the classical threshold for statistical significance (p > .05). There was no correlation between age and the assumed light direction at the group level, or in men and women as individual groups (all ps > .05; see Figure 3.4).

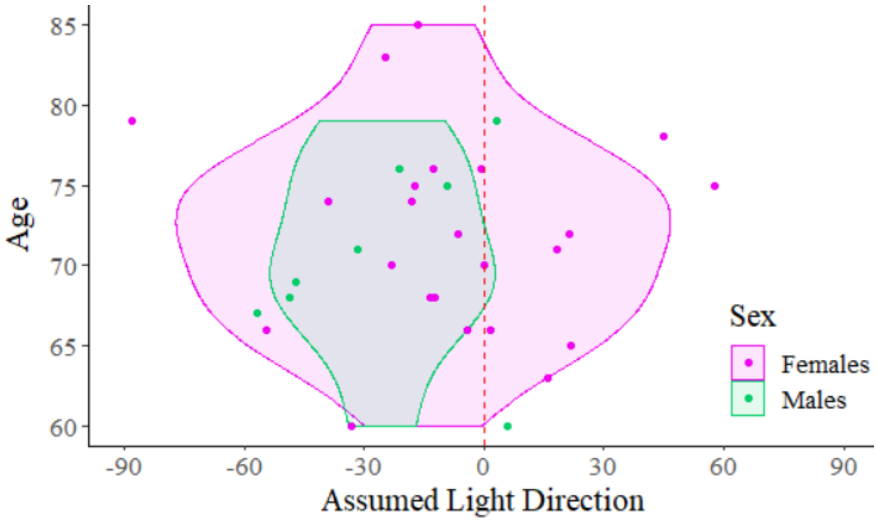


Figure 3.4. Violin plot with individual datapoints to display the relationship between the assumed light direction in men and women on the Honeycomb task.

Age and SfS-Sensitivity

Participants were categorised according to their sensitivity to the honeycomb stimulus (see Data Analysis) as Shape-from-Shading (SfS)-sensitive (n = 32) or SfS-insensitive (n = 29). The distribution of ages in each of the SfS-sensitivity categories suggested that participants who were SfS-insensitive were older (mean age = 73.64, SE = 1.23) than those who were SfS-sensitive (mean age = 71.97, SE = 0.97); however, a two-way ANOVA (Age ~ Sex * SfS-Sensitivity) showed that the age difference between the SfS-sensitive and SfS-insensitive groups was not significant ($p > .05$). Likewise, the age of men and women in this task did not significantly differ, and there was no interaction between sex and SfS-sensitivity ($ps > .05$).

Montreal Cognitive Assessment Scores

Scores on the MoCA test ranged from 20 to the maximum-available 30 points. Women garnered slightly higher MoCA scores than men (women: M = 27.00, SD = 2.46; men: M = 26.50, SD = 2.77), though an independent samples t-test indicated that this difference was not statistically significant ($p > .05$). There was a small but significant negative correlation between age and the MOCA score at the whole-group level (r (66) = -.26, p = .039, R^2 = .007), indicating that cognitive functioning declined with age.

MoCA and the Assumed Light Direction

A Pearson's correlation was computed to assess the relationship between the MoCA score and the assumed light direction in SfS-sensitive adults. Though an equivalent positive trend was observed in men and women (Figure 3.5), suggesting a reduction in left-sided lateralisation in individuals with higher MoCA scores, this relationship was not statistically significant at the whole group level, in men only, or women only ($ps > .05$).

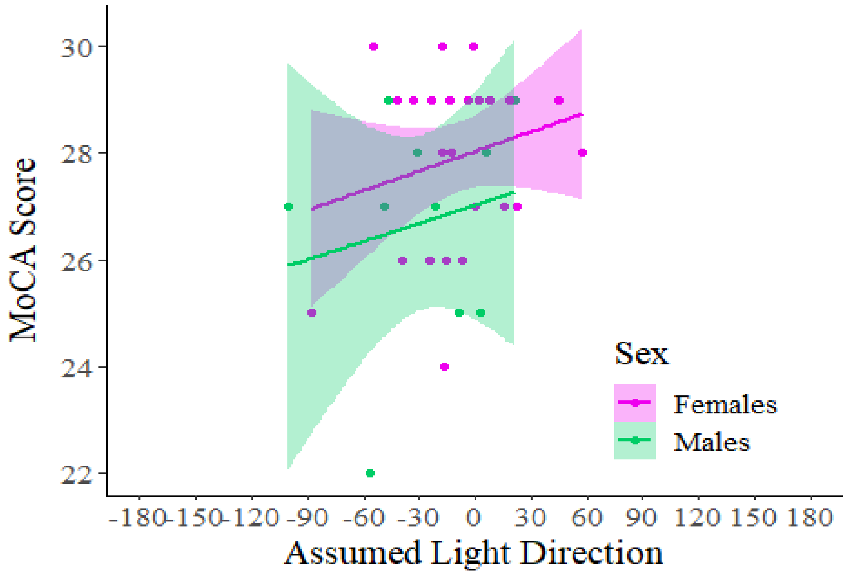


Figure 3.5. Scatterplot illustrating the association between increasing MoCA scores and a more overhead assumed light direction.

MoCA and Sensitivity

A mixed factorial ANCOVA revealed significant differences in MoCA scores according to an individual's sensitivity to the Honeycomb Task and their sex (see Figure 3.6). Age was used as a covariate in this model to control for the decrements in MoCA scores that are associated with increasing age. SfS-sensitive participants had significantly higher MoCA scores (M = 27.6, SD = 1.80) than SfS-insensitive individuals (M = 25.6, SD = 3.06; F (1,58) = 10.40, p = .002, η_p^2 = .15). There was no main effect of sex, but there was a significant interaction between sex and SfS-sensitivity (F (1,58) = 4.63, p = .036, η_p^2 = .07), with SfS-insensitive women having significantly lower MoCA scores (M = 25.00, SD = 2.83) than SfS-sensitive women (M = 27.9, SD = 1.60; t (15.82) = -3.43, p = .0035, Δ = 1.26). There was no significant difference between SfS-sensitive (M = 26.8, SD = 2.09) and SfS-insensitive men (M = 26.2, SD = 3.23; p > 05). This analysis included participants whose assumed light directions were considered outliers (and were thus excluded from other Honeycomb Task analyses) because this analysis does not include the measurement of the assumed light direction.

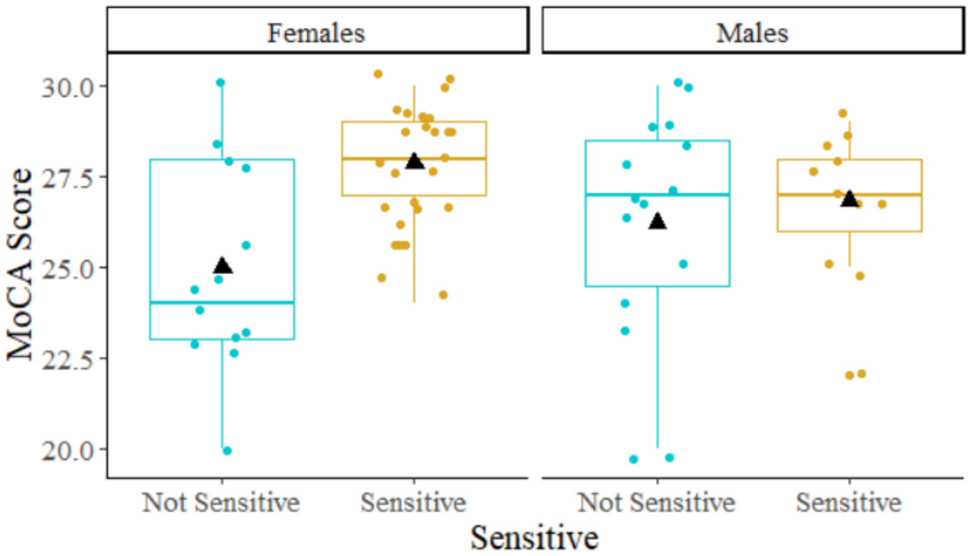


Figure 3.6. MoCA scores by sex and sensitivity to the honeycomb stimulus.

We calculated a logistic regression to determine whether an individual's MoCA score could predict whether they would be sensitive to the orientation of the Honeycomb stimulus when making shape judgements. This model significantly predicted MoCA scores for every unit increase in MoCA scores, the likelihood of being SfS-sensitive increased by 10.89% (β = 0.33, *SE* = 0.12, *p* = .005). The model correctly predicted the likelihood of a person being sensitive to the honeycomb stimulus with 70% accuracy and was highly sensitive to changes in MoCA scores when predicting sensitivity to the honeycomb stimulus (87%). The model was less specific, only correctly predicting SfS-insensitive participants 46% of the time.

Landmark task results

We assessed the effects of age, cognitive performance, the assumed light direction, and sex on Landmark task performance. Men made more leftward judgements to centrally bisected lines (*n* = 26, 53.85%) than women (*n* = 41, 49.37%). Those who were not sensitive to the orientation of the honeycomb stimulus when making shape-from-shading judgements made more rightward guesses on the Landmark task (*n* = 35, 47.5% leftward judgements to centrally bisected lines). Those who were sensitive to the honeycomb stimulus made more leftward judgements to centrally bisected trials (*n* = 32, 53.3% leftward judgements). A

Pearson's correlation indicated that the percentage of central trials judged as leftward deviations did not differ as a function of age in men or women, or at the whole group level (*p*s > .05).

A two-way ANOVA was calculated to determine whether the likelihood of a person categorising centrally bisected trials as leftward deviations differed between men and women or those who were sensitive or insensitive to the honeycomb stimulus. There was no main effect of sex or sensitivity, and no interaction between the two (all *p*s > .05), suggesting that the processes governing sensitivity to the orientation of the honeycomb stimulus when making shape judgements are distinct from the lateralised attentional processes measured via the Landmark task.

We also assessed accuracy in deviated trials - those in which the vertical line was placed to the left or right of the veridical centre. Women were slightly more accurate than men (women: 94.21% accuracy, *SD* = 8.69; men: 92.38% accuracy, *SD* = 15.46). Those who were sensitive to the honeycomb stimulus were most accurate (96.82%, *SD* = 3.41%) with SfS-sensitive participants being 9.12% more accurate on deviated trials than SfS-insensitive participants (87.7% accuracy on left deviated trials, *SD* = 17.8). There was a significant main effect of SfS-sensitivity on accuracy in left- and right-deviated trials (left trials: F (1,49) = 8.19, p = .006, η_p^2 = .14; right trials: F (1,49) = 11.38, p = .002, η_p^2 = .19), but no main effect of sex (*p*s > .05). There was no interaction between sex and SfS-sensitivity on accuracy on either left- or right-deviated trials (p > .05).

At a group level, MoCA scores were positively correlated with accuracy on right- (r (52) = .50, p < .001, R^2 = .25) and left-transacted lines (r (50) = .41, p = .003, R^2 = .17), indicating that increased accuracy was related to better cognitive function. Interestingly, these relationships differed between men and women: in women, only accuracy on right-deviated lines was significantly related to MoCA scores (r (29) = .49, p = .005, R^2 = .24), whereas in men, accuracy on both left- and right-deviated lines was related to MoCA scores (on right-deviated lines: *r* (19) = .49, *p* = .025, R^2 = .24; and on left-deviated lines, the relationship just reached the classical cut-off for statistical significance: *r* (19) = .43, *p* = .049, R^2 = .18). In SfS-sensitive adults, neither left nor right accuracy was related to scores on the MoCA test (*p*s > .05); however, the there was a significant positive correlation between accuracy on right-deviated trials only in SfS-insensitive participants (*r* (17) = .55, *p* = .016, R^2 = .30). Figure 3.7 illustrates the difference in accuracy between those sensitive or insensitive to the honeycomb stimulus, and is coloured according to sex to illustrate the similarity between the two groups.

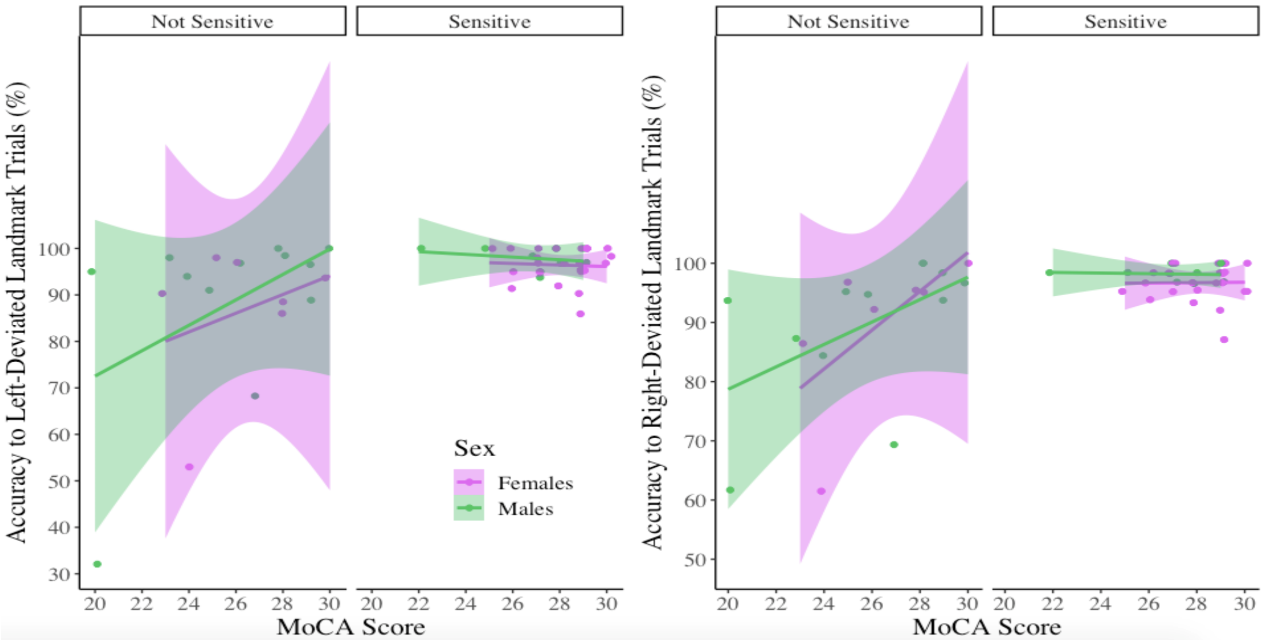


Figure 3.7. Scatterplots showing individual accuracy scores to left-deviated trials (left image) and right-deviated trials (right image) and MoCA scores in SfS-sensitive and SfS-insensitive men and women.

The assumed light direction did not correlate with either accuracy on rightward deviation trials, accuracy on leftward deviation trials, or the proportion of central trials judged as leftward deviations (all *p*s > .05). This was true at the group level, in men only, and in women only (Figure 3.8).

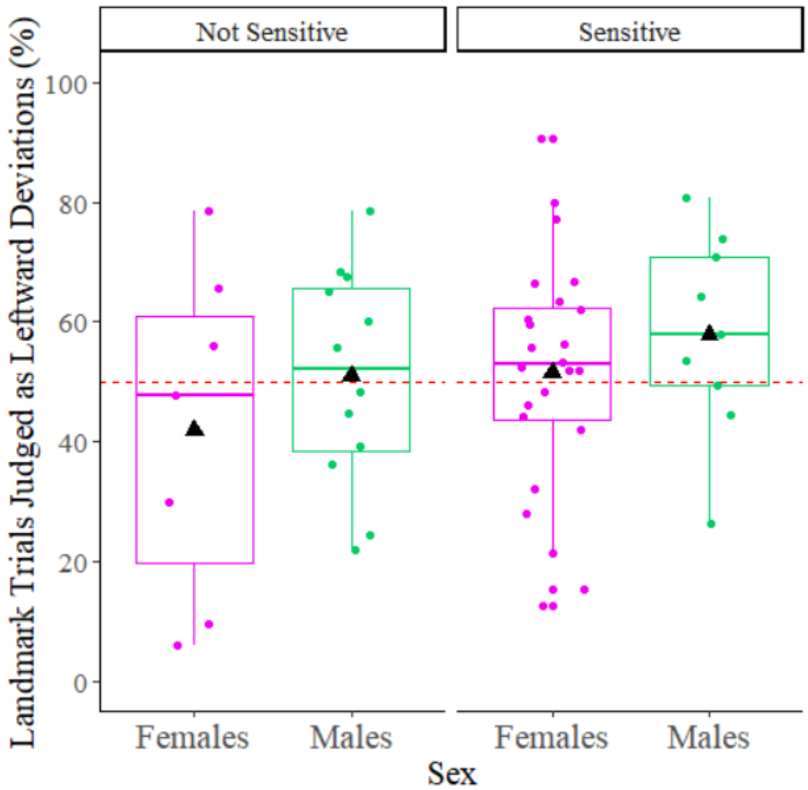


Figure 3.8. Boxplot showing the median and interquartile ranges of the number of centrally-bisected Landmark task trials judged as leftward deviations in SfS-sensitive men and women, and SfS-insensitive men and women. The mean of each group is indicated with a black triangle. Individual participants' accuracy scores are plotted within the boxplot range.

Years of Education

The mean number of years of education completed was 16.3 (*SD* = 3.46, min = 9, max = 25; in women: *M* = 16.9, *SD* = 3.53; in men *M* = 15.3, *SD* = 3.18). There was no correlation at the group level between the assumed light direction and years of education, suggesting that the assumed light direction is not associated with years of education in older adults ($p > .05$). We calculated this correlation in men and women separately, but there was no association in either group ($p > .05$).

Longitudinal Assessment of Assumed Light Direction and MoCA Scores

A small number of participants ($n = 7$; five women) returned after one year to repeat the Honeycomb Task and MoCA (Nasreddine et al., 2005). In this small sample, the mean assumed light direction at the first sampling point was -8.56° (*SD* = 32.9°), and after one year was -25.01° (*SD* = 28.3°), a difference of 16.5° (*SD* = 20.80). MoCA scores decreased by less than 1 point, from 28.6 (*SD* = 1.72) to 27.9 (*SD* = 1.86), a difference of -0.71 (*SD* = 0.95). Given the small sample, a one-sample t-test was calculated to determine whether the assumed light direction in either session differed significantly from 0. At time point 1, the difference from zero was not statistically significant; at time point 2, the difference just missed the significance threshold (*ps* > .05).

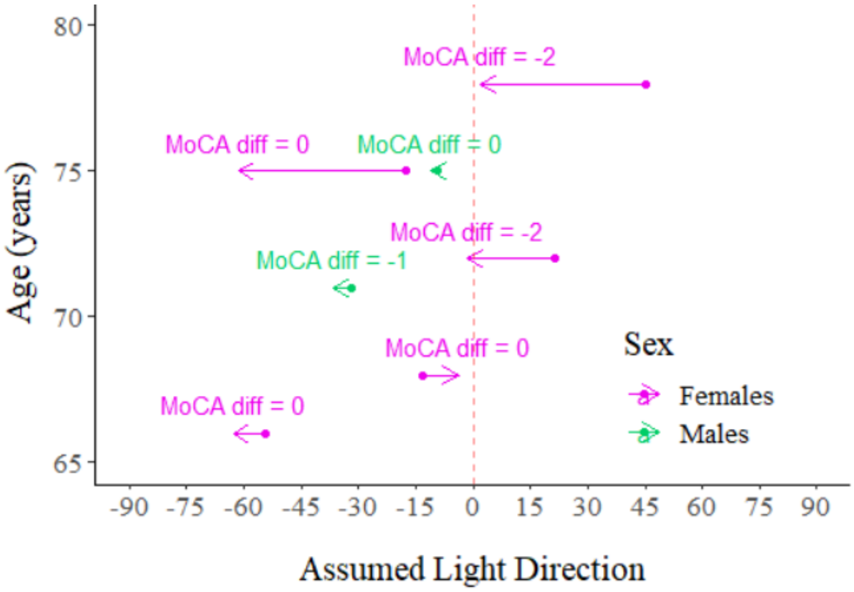


Figure 3.9. The assumed light direction in seven participants, taken one year apart. The beginning of the arrow (no arrowhead) represents their assumed light direction on their first session, and the end of the arrow (arrowhead) represents their assumed light direction after one year. The difference in MoCA scores is show above each arrow (negative scores indicate reductions in MoCA scores after one year).

Discussion

Young adults typically exhibit a leftward bias in several measures of lateralised visuospatial perception, such as the assumed light direction in ambiguous shaded images and the landmark task. A wealth of research has shown that leftward biases decrease with age (see Friedrich et al., 2018; Learmonth & Papadatou-Pastou, 2021), but no studies have assessed whether cognitive decline is associated with these changes. The present study explored age-related changes in the assumed light direction and its relation to the potential mediating factors of cognitive function. Because several studies of lateralised biases have shown different patterns of responses in older men and women, we sex-disaggregated our data to determine whether sex influenced the pattern of responses in shape-from-shading.

There are considerable interindividual differences in the assumed light direction in many shape-from-shading tasks in young adults and children (e.g., Adams, 2007; Croydon et al., 2017; Mamassian et al., 2003). Because previous literature has shown an increased leftward bias in women compared with men in other directionally biased visual tasks (Chen et al., 2011; Varnava & Halligan, 2007), we predicted that we would also detect a more leftward bias in women on the Honeycomb Task. However, men who were sensitive to the orientation of the honeycomb stimulus had a stronger leftward bias (-34.01°) that more closely resembled the typical bias of young adults than that of women (-7.99°). A larger leftward bias implies that the right hemisphere continues to dominate in orienting visuospatial attention, which could lead to the conjecture that the retention of a leftward bias signifies optimal ageing processes. However though the mean assumed light direction in older men in this sample was similar to what is found in the literature in younger adults, their variability at the group level was more pronounced. Greater variability suggests that other factors influence changes in the assumed light direction and therefore make it implausible to suggest their results are more equivalent to those typically seen in younger adults (e.g., Adams, 2007; Andrews et al., 2013; Croydon et al., 2017) than women's, particularly given that older adult men's cognitive function, measured via the MoCA (Nasreddine et al., 2005), was lower than women's. Taken together, these factors preclude the conclusion that older adult men in this sample have retained a youthful cognitive processing style.

At the group level, older women had a diminished left bias in the assumed light direction, which was more aligned with previous group-level findings in older adults (Andrews et al., 2017; de Montalembert et al., 2010). This result was surprising, given that previous research suggested that women made more leftward errors than men in tasks such as the line bisection test (Chen et al., 2011; Varnava & Halligan, 2007). Chen et al. (2011) suggested that reduced right dorsal activity may occur in ageing males but not females, citing women's leftward errors and men's increasing rightward errors in line bisection tasks. However, this study analysed very few participants and tested adults aged 22-93 years. Given the considerable differences observed both within and between younger and older adults, a larger sample is required to account for the large variability one would expect to observe at the group level across the age ranges. Nevertheless, the large difference between men and women in our sample was surprising. If reduced behavioural asymmetry indexes less-lateralised cognitive processes, our data suggest that women either employ a successful compensatory strategy or experience increased neural dedifferentiation compared with men. Given that women received higher MoCA scores than men, the HAROLD model (Cabeza, 2002) better accounts for women's reduced bias in the assumed light direction as it suggests that a successful compensatory strategy is being employed. We recommend that future studies deploy a more comprehensive assessment of cognitive function and hemispheric lateralisation to provide more explicit evidence for this claim.

The Honeycomb Task has been shown to produce consistent results in several populations and is sensitive to subtle differences in perception; however, previous studies have noted that a small number of participants' data indicates that they are not sensitive to the orientation of the Honeycomb stimulus when making shape judgements. In the present study, we noted that a large proportion of participants (35 out of 67) were not sensitive to the Honeycomb stimulus. The number of excluded participants was far more than in previous experiments. For example, in Andrews et al. (2013), three participants were removed because their results suggested they were not sensitive to the orientation of the Honeycomb stimulus. In Andrews et al. (2017), only two out of 22 young, and three out of 24 older, participants were removed using the same statistical methodology and experimental paradigm. One adult was removed for the same reason, and using the same methodology, in Croydon et al. (2017). Though the large number of SfS-insensitive participants in the present study was unexpected, an important difference between this study and others, in particular Andrews et al. (2017), was our sampling methodology. In Andrews et al., participants were recruited exclusively from a panel of older adults who had elected to be invited to studies within the School of Psychology. In the present study, in addition to a small number of older adults recruited from the participant panel, we recruited older adults by word of mouth and through their participation in social groups aimed toward older adults, such as the University of the Third Age, The Soroptimists, and Rotary Clubs. It is possible that the older adults who are part of a participant panel are those who find it easy to travel independently and are more familiar with computer-based tasks. The present sample may therefore be more reflective of the general older adult population in the UK.

Previous literature on light priors in shape judgements have understandably focused on the primary measure: the assumed light direction or the angle of rotation required to produce the most reliable (Adams, 2007; Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Mamassian et al., 2003) or efficient (Kleffner & Ramachandran, 1992; Sun & Perona, 1998) shape judgements. Some previous studies have assessed SfS-sensitivity in shape judgement tasks as an exclusion criterion (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017). However, only one other paper has assessed SfS-sensitivity as an independent variable: Pickard-Jones et al. (2020) showed that children's sensitivity to shading information increased significantly with age and suggested that the ability to perform the task could account for task performance in a shape judgement task. In Pickard-Jones et al. (2020), age-related increases in SfS-sensitivity were not related to the assumed light direction, but instead correlated weakly with global processing preference, suggesting the ability to segregate the foreground from the background in visual scenes influences the ability to make shape judgements. A preference towards global processing develops over childhood, is consistently observed in neurotypical young adults (Kimchi & Palmer, 1982), and is known to decline in older adults (e.g., Staudinger et al., 2011). Global and local processing are highly lateralised processes (Gable et al., 2013), with global processing being a right-parietal function and local a left-parietal function (Hübner & Volberg, 2005). As such, a link between declining global processing abilities and the capacity to perform shape judgement tasks that require the foreground to be segregated from the background makes intuitive sense when considered through the lens of the reductions in hemispheric asymmetry proposed by Cabeza et al. (2002). We recommend exploring SfS-sensitivity alongside global processing in future tasks to probe further the elements of visual processing that contribute to the ability to make shape-from-shading judgements, independently of the assumed light direction.

We observed the predicted age-related decrements in MoCA scores (Nasreddine et al., 2005) with a small correlation that was well-aligned with previously reported research (e.g., Bruijnen et al., 2020). The men in our sample tended to have lower MoCA scores than women, replicating findings in previous literature (e.g., Engedal et al., 2021), though this difference was not statistically significant. Whilst our data did not reveal a correlation between the MoCA score and the assumed light direction, the pattern of data suggested a positive trend, implying a reduction in left-sided lateralisation in individuals with higher MoCA scores. It is possible that our sample was too small to detect a statistically significant result, but it merits further investigation with more people and a more comprehensive age range. We would particularly recommend sampling older adults with a broader range of cognitive abilities to better reflect population-level metrics.

Seven participants returned to complete the MoCA and Honeycomb Tasks after one year to indicate whether longitudinal changes could be observed in MoCA scores and the assumed light direction. The low number of participants constrained the analyses and implications that could be drawn from their data. However, there was a small decline in MoCA scores, as would be expected from an ageing sample (Bruijnen et al., 2020). We had expected the bias to become less leftward with ageing; therefore, a marked leftward shift in the assumed light direction was unexpected. However, the leftward shift is consistent with our main finding that more leftward assumed light directions are associated with lower MoCA scores.

A logistic regression revealed that an individual's MoCA score could predict whether they would be sensitive to the orientation of the honeycomb stimulus when making shape judgements, with the likelihood of being SfS-sensitive increasing by 10.89% for every unit increase in MoCA scores. Whilst the association between assumed light direction and MoCA scores was not statistically significant, and thus it is not possible to use the direction of the light bias to make assumptions about the relationship between cognitive function and behavioural lateralisation, it is interesting that more cognitively healthy people were much more likely to be able to resolve depth from shading in a consistent manner. This experiment was not designed to test the reverse of this scenario: in other words, to use the measure of a participant's sensitivity to the stimulus to predict their MoCA scores. However, we recommend designing future experiments to allow for this possibility; the MoCA test has been suggested to be unreliable in non-clinical populations and more sensitive in clinical populations (Bernstein et al., 2011) and therefore if sensitivity to the Honeycomb Task could reliably predict MoCA scores, it would imply that the Honeycomb Task (or similar tasks) might offer an efficient way to assess cognitive health. Currently, the MoCA test is usually performed in person, and although remote tests are available, it still requires a trained individual to administer the test (mocatest.org). An online language-free test to quickly screen individuals could deliver the opportunity to screen for cognitive impairment more widely than currently (e.g., Dias & Patel, 2009; Kagstrom et al., 2019; Morgan et al., 2019; Musyimi et al., 2021; Patel et al., 2016) and improve access to early interventions to improve quality of life for people with cognitive impairments (Brayne et al., 2007; Elliot et al., 2021).

Interestingly, sensitivity to the honeycomb stimulus interacted significantly with participants' sex to predict MoCA scores. SfS-insensitive women had significantly lower MoCA scores than SfS-sensitive women, but the difference between SfS-sensitive and SfS-insensitive men was not significant. There were fewer men than women in this study, which could explain the difference between men and women: a qualitative appraisal of the pattern of data shows that men generated a similar pattern of responses to women in both SfS-sensitivity categories; in particular, that SfS-insensitive men shared the same wide variability in MoCA scores as women. As an unplanned analysis, we share these results with caution and recommend that further work be undertaken to establish whether and how the ability to perceive shape-from-shading in our task relates to other cognitive functions.

Though men made more leftward judgements on centrally bisected trials than women, the difference between men and women was not significant. The number of central trials judged as leftward deviations did not differ as a function of age in men or women, or at the whole group level. We explored whether sensitivity to the honeycomb stimulus was related to lateralised spatial processing as measured in the Landmark Task; although SfS-insensitive participants made slightly more rightward judgements than left, this difference was not significant. This suggests that the processes governing sensitivity to the orientation of the honeycomb stimulus when making shape judgements are distinct from the lateralised attentional processes measured via the Landmark Task. This finding is contrary to Andrews et al. (2017), who found a correlation between the assumed light direction and the degree of error in line bisection in old and young participants; however, measures of spatial attention do not always correlate well (Learmonth et al., 2015) and it is possible that the principal difference between these tasks – the motor component required of the line bisection task – could interfere with the perception of line length, or could entail different strategies to either estimate the length of the line.

Though the standard measure of behavioural asymmetry on the Landmark Task – the likelihood that a person would say left or right to a centrally bisected line – did not differ as a function of sex, SfS-sensitivity, or MoCA score, accuracy on right- and left-deviated lines did. Women were slightly more accurate than men, but those who were sensitive to the honeycomb stimulus were 9.48% more accurate on the Landmark task than SfS-insensitive participants. This accuracy seemed to be related to MoCA scores, which were positively correlated with accuracy on both right and left trials, but with a stronger correlation that was more significant on right-deviated trials. Intriguingly, women’s MoCA scores were only significantly correlated with accuracy on right-deviated trials, but men’s MoCA scores were correlated with accuracy on both left and right-deviated trials. However, the correlation between men’s accuracy in right-deviated trials and MoCA scores was stronger and more significant than in left-deviated trials. A similar pattern was found when the correlation between MoCA and landmark accuracy was explored in SfS-sensitive vs SfS-insensitive older adults. In SfS-sensitive adults, scores on the MoCA test were not related to accuracy on either left-deviated or right-deviated landmark trials; however, in SfS-insensitive participants there was a significant positive correlation between MoCA scores and accuracy on right-deviated trials only. The stronger and more significant relationship between right-deviated trials and MoCA scores indicates that increased accuracy on right-deviated lines is related to better cognitive function. Previously, Benwell et al. (2014) performed the Landmark Task in healthy younger and older adults and found the subjective midpoint shifted rightwards. Though they did not test cognitive function, Benwell et al. suggested the tendency for attention to shift rightward was a feature of healthy ageing, given that the elderly sample reported no known neurological disorders. If better MoCA scores are related to greater accuracy in rightward trials, this could imply that the default left advantage observed in young people reverses with age and indexes better cognitive function.

In older adults, the reorganisation of neural networks coincides with neural losses (Cespón et al., 2018), which are an unavoidable part of typical and atypical ageing. Similarly, reductions in grey matter volume have been observed with increasing age (Ziegler et al., 2012) in regions often activated during shape-from-shading tasks (e.g., Georgieva et al., 2008; Gerardin et al., 2010; Peuskens et al., 2004; Taira et al., 2001), particularly within the superior parietal cortex (Driscoll et al., 2009). Functional changes have also been observed in EEG studies of pseudoneglect, with apparent reductions in right-lateralised activity during the Landmark task in older adults (Learmonth et al., 2017). Taken together, evidence of neural losses in the right dorsal stream, reduced activity in the right hemisphere during tasks measuring pseudoneglect, and reduced or altered pseudoneglect in behavioural tasks broadly supports a neurogenic account of the HAROLD model of ageing (Cabeza, 2002). In the present study, higher MoCA scores and less lateralised behaviour were observed in women, and extremely variable biases and lower MoCA scores in men. Both groups demonstrated that the consistent lateralisation of automatic perceptual processes and behaviours observed in younger adults reduces with age and seems to follow different trajectories in men and women. However, given that the relationship between MoCA scores and the assumed light direction was not significant, more work is needed to determine whether the changes in the assumed light direction index either cognitive function or offer evidence in support of the HAROLD model.

It is also possible that two processes are implicated in our behavioural paradigms: coordinate spatial processing and categorical spatial processing (Hellige & Cumberland, 2001). Coordinate spatial processing, or coordinate representation, refers to the measurement of locations, distances, and sizes very precisely in a coordinate system. Categorical spatial processing involves categorising spatial perceptions – e.g., in vs out, or closer vs farther away. Studies have shown that the right hemisphere is dominant in coordinate spatial processing and the left hemisphere in categorical spatial processing (Meadmore et al., 2009) – a logical separation, since the categorisation of sensory stimuli fundamentally involves language processes (Sapir, 1929; Whorf, 1940), which are located in the left hemisphere (Papçun et al., 1974). It is possible that adults at different stages of cognitive ability preferentially adopt either coordinate or categorical spatial processing strategies: some participants may have maintained a verbal working memory of "left is in, right is out" to remember their responding hand. The idea that some participants might have used cognitive strategies to engage with the task supports the Compensation-Related Utilisation of Neural Circuits Hypothesis (CRUNCH; Reuter-Lorenz & Cappell, 2008). Though the Honeycomb task itself is not difficult, participants are expected to quickly perceive a stimulus and remember which hand should be used for each response. This does place a demand on executive function and working memory, which are subject to resource limits that are reached under less task demand in older than younger people (Cappell et al., 2010).

The CRUNCH hypothesis purports that, at any age, the amount of brain activity can alter depending on the task difficulty (Reuter-Lorenz & Cappell, 2008). In contrast, the HAROLD model (Cabeza, 2002) suggests that a pattern of bilateral prefrontal activation observed in older adults deviates from the typically unilateral pattern observed in younger persons. It is possible that there are two streams of ageing; first, recruiting one compensatory mechanism, and then another. More evidence is required to understand whether reduced asymmetry characterises optimal ageing processes, or whether it instead implies an underlying pathology, and to definitively establish whether the behavioural findings observed in Chapter 3 suggest either the HAROLD or the CRUNCH hypothesis, or an alternative or interactive model of neurocognitive ageing.

Age-related reductions in cognitive performance and other aspects of sensory perception are expected in ageing. However, the interaction between cognitive performance and perceptual processes, such as the resolution of shape-from-shading information and other lateralised behavioural measures, such as the Landmark task, have been neglected. Ontological changes to otherwise remarkably consistent processes in early adulthood may offer insight into normal or pathological ageing processes and merit further investigation, particularly if such changes occur systematically across cohorts. Despite the many sex differences observed in ageing studies of several lateralisation measures in older adulthood, most studies are not disaggregated by sex. This study established that the ability to perceive shape-from-shading is related to cognitive performance in women only, and demonstrated that, given the broad inter-individual differences in performance observed across and within cohorts, measures used in psychophysical tasks and neuropsychological assessments should be age- and sex-normed before being generalised across all older adults.

Chapter 4: Light Assumptions Measurement of Perception (LAMP): Towards a New Test of the Ability to Perceive Shape-from-Shading.

Abstract

Traditional shape judgements tasks can measure very subtle differences in individuals' light source direction assumptions and can distinguish between people whose impressions of convexity are modulated by the position of light and dark areas on geometric shapes, and those whose impressions of convexity are less affected by the rotation of the stimulus. However, some shape judgements on traditional tasks can be made without the observer perceiving any depth in the stimulus. An objective test is therefore required to differentiate between people who can and cannot perceive shape-from-shading. This pilot comprises three experiments that explore the parameters of a new test for shape-from-shading, modelled on the Ishihara (1962) colour blindness test. Experiment 1 validated the fundamental elements of the experimental paradigm by establishing that shading offered a perceptual advantage over non-shaded control circles with an equivalent luminance polarity. Experiment 2 probed the effect of different stimulus presentation durations, manipulating task difficulty to establish whether directional biases are enhanced when attentional demands are more pronounced. Experiment 3 deployed the most informative experimental parameters from the previous experiments to probe the effects of shading direction on participants' ability to detect target characters. We anticipated that shaded trials would generate more accurate performance than non-shaded trials and that targets defined by overhead shading gradients—particularly those with the brightest parts orientated towards the above-left—would be identified faster and more accurately than other orientations. We found an effect of shading, indicating that shading gradients provide a perceptual advantage over control stimuli with the same luminance polarity and some evidence of a left bias. Further work is needed to assess the

paradigm among populations with shape-from-shading deficits or other conditions resulting in poor depth perception.

Since shading was formally described as a cue to three-dimensional shape by Rittenhouse (1786), many studies have probed the ability of the human visual system to perceive shape-from-shading (Adams et al., 2004; Adams, 2007; Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Gerardin et al., 2007; Granrud et al., 1985; Hartle et al., 2022; Mamassian et al., 2003; Pickard-Jones et al., 2020; Thomas et al., 2010). Researchers have quantified not only subtle individual differences in the assumed light direction (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020), but also the relative weight assigned to shape-from-shading when other cues conflict or are combined with it (Hartle et al., 2022; Thomas et al., 2010). The ability to use shading as a depth cue is present in infancy (from age seven months in Granrud et al., 1985) through to older age (Andrews et al., 2017; de Montalembert et al., 2010), in typically developing (Pickard-Jones et al., 2020) and autistic children (Croydon et al., 2017), and in right-to-left and left-to-right reading populations (Andrews et al., 2013; Smith et al., 2015).

Several tasks have been used to probe how light priors influence the ability to perceive shape-from-shading. For example, by manipulating the direction of light illuminating physical arrays of convexities and concavities, Berbaum et al. (1983) extricated the influence of placing a light above or below an object on the observer's perception of three-dimensional shape. By photographing such arrays and presenting them at upright or inverted angles (Granrud et al., 1985), researchers determined that an assumption of the illumination position affects the interpretation of depth. These simple experiments permitted a fundamental understanding of the influence of shading on the perception of three-dimensional shape.

Visual search tasks rely upon the ability to segregate target objects from background distractors and have been used to explore shape-from-shading by many researchers (e.g., Braun, 1993; Kleffner & Ramachandran, 1992; McManus et al., 2004; Ramachandran, 1988;

Sun & Perona, 1998; Symons et al., 2000; Wolfe & Horowitz, 2004). Given the relative ease with which shaded stimuli can be segregated from the background in visual search (e.g., Braun, 1993; Enns & Rensink, 1990; Kleffner & Ramachandran, 1992; Sun & Perona, 1998), shading information, and consequently the direction of light, may be processed pre-attentively and therefore provides an efficient search feature according to the feature-integration theory of attention (Treisman & Gelade, 1980). Efficient visual searches are those in which the searched-for features are processed in parallel regardless of the size of the distractor array, emerging effortlessly from background noise. There is evidence that shading information is processed in parallel, with some studies showing a pop-out effect for shaded stimuli (e.g., Braun, 1993; Enns & Rensink, 1990; Kleffner & Ramachandran, 1992; Sun & Perona, 1998).

However, shading is a less efficient guide than many pre-attentive features (Wolfe & Horowitz, 2004): shading direction may affect search efficiency, with vertically shaded objects being processed more efficiently than those shaded horizontally (see Chapter 2 and Adams, 2007). An advantage for certain shading directions over others suggests that shading alone is not processed as a visual feature. Instead, an object's three-dimensional shape, inferred from its shading direction, may be processed automatically. It is also possible that participants may use alternative strategies to detect oddballs in visual search tasks using shaded stimuli. For example, participants may attend to areas where the direction of luminance polarity converges (for example, looking for areas where two light or dark edges face each other, which can only happen when a target is placed next to an oppositely shaded distractor). It is, therefore, difficult to isolate the effect of shading direction from luminance polarity, shape perception, and other strategies participants may use to detect oddballs in visual search using shaded circles.

Shape judgement tasks also fail to perfectly isolate the ability to resolve shape from shading cues. A significant minority of participants have had to be excluded from analyses in shape-from-shading experiments because their responses do not appear to be modulated by the orientation or degree of rotation in experimental stimuli (e.g., see Experiment 2; Adams et al., 2004; Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020). Individuals may respond at chance levels to all stimulus orientations, suggesting that no single orientation or shading direction reliably influences their perception or that visual after-effects from previous stimulus presentations impact their perception more dynamically than typical participants (Maloney et al., 2005; Soetens et al., 1985). Other participants exhibit an invariant impression of depth regardless of the orientation of the stimulus. Because shape judgement tasks tend to employ a 2AFC paradigm, it is possible that some participants might have atypical depth perception, but their ability to guess a shape affects the experimenter's assessment of their perceptual idiosyncrasies.

Deficits in shape-from-shading perception have been observed in specific clinical populations, such as patients with posterior cortical atrophy (Gillebert et al., 2013; 2015). Furthermore, the ability to perceive shape-from-shading can be permanently compromised if an individual is deprived of visual experience during critical developmental phases (McKyton et al., 2015). However, this aspect of vision is not routinely tested, so the incidence of atypical shading perception cannot be estimated in the typically developing population. Considering the significant proportion of participants must be excluded from analyses due to atypical performance, it is surprising that no studies have yet assessed whether the ability to perceive shape-from-shading is uniformly available to typically developing observers.

The Ishihara test (e.g., Figure 1.4; Ishihara, 1962) is notable for its specificity and sensitivity to detect protanopic and deuteranopic colour-blindness, using arrays of coloured circles arranged into the shape of a number. No other cues are used to group the circles.

Using the Ishihara colour blindness testing plates as a model, we developed a test for deficits in the ability to perceive shape-from-shading. Rather than using coloured target and background circles, we grouped circles with shading gradients to define a target alphanumeric character to be identified by participants. Like the Ishihara test, we assumed that participants must be able to perceptually group (Treisman, 1982) the target circles to identify the character. We also assumed that participants would be able to automatically recognise the alphanumeric character represented by the target circles if they were able to perceptually group target circles accurately. Automatic word recognition involves processing whole words (each letter in parallel rather than serially) without conscious awareness (Blomert, 2011; Logan, 1997). Though not pre-attentive, reading is an extremely swift and automatic function: once a person develops the skills required to facilitate automatic word recognition (Kuhn et al., 2010), those who recognise the word have no choice but to read it (Megherbi et al., 2018). Stroop (1935) interference tasks run with children during reading acquisition shows that the interference caused by the Stroop effect increases with reading skills (Megherbi et al., 2018).

We ensured that the spatial placement of the target and background circles was uniform and did not suggest any alphanumeric character. Because our participants were university students who were required to have normal or corrected-to-normal vision, we assumed that they might deploy a range of strategies to perform perceptual grouping on visual features other than shading (Wagemans et al., 2012). For example, a person might not be able to perceive depth from shading but might be able to group the circles based on their luminance polarity. To extract the effects of grouping and luminance polarity from the ability to perceive shape-from-shading, we introduced a control condition of half-black, half-white circles (as per Ramachandran, 1988), which replicated the luminance polarity of shaded circles without a shading gradient.

This experiment was intended to address a common limitation of some shape judgement experiments: the propensity of shapes to be bistable or ambiguous at certain orientations, and for chance performance to occur due to the two-alternative forced choice nature of shape judgement tasks. We therefore anticipated that requiring participants to detect an alphanumeric character would make it less likely for observers to guess a correct response by chance alone. We planned a series of tests to validate the stimuli and experimental parameters in this pilot; firstly, whether observers responded differently to shaded and non-shaded control circles; secondly, whether some experimental parameters (the characters suggested by the grouping of target vs background circles) were more effective than others; thirdly, whether the test can differentiate between people who can and cannot perceive shape-from-shading; and finally, whether the test offers another way to measure directional biases such as those seen in shape judgement tasks by assessing the response to different luminance polarities in shaded and non-shaded stimuli.

We expected to observe better performance for shaded vs control trials, indicating that shading gradients offer a perceptual advance over non-shaded stimuli with the same luminance polarity. We also predicted an advantage in speed and accuracy to overhead shading directions, particularly stimuli shaded from the above-left, in accordance with evidence from shape judgement tasks (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Mamassian et al., 2003; Pickard-Jones et al., 2020). Given that shape judgement tasks often include a small number of participants whose responses indicate that they are not influenced by the orientation of shading gradients when making shape judgments, we expected that we might find some people whose performance fell significantly below the average of the testing cohort after the effects of perceptual grouping were controlled. There is no prediction for characters because they were an experimental parameter of no theoretical interest.

Experiment 1

Methods

Participants

Thirty-one participants (28 female) studying for an undergraduate psychology degree were recruited via Bangor University's online participant pool (SONA Systems). All had normal or corrected-to-normal vision and were aged between 18 and 25 years (mean age: 19.2, *SD* = 1.42). Participants earned course credit for their participation.

Stimuli

Stimuli were modelled on Ishihara's colour blindness test (Ishihara, 1962) and created in MS PowerPoint. They were comprised of 525 foreground circles, ranging in size from 2mm to 8mm, whose placement replicated the random placement of circles in Ishihara's colour blindness test within a grey background circle of 14cm in diameter (see example in Figure 4.3). No circles overlapped, and the gap between each circle was no greater than 3mm and no smaller than 1mm.

Circles were shaded on a gradient from white to black. Seven letters and numbers ("R", "8", "S", "9", "6", "3", and "P") with similar gradient shading were used as target characters (see example in Figure 4.1). Control stimuli replicated the characters and the angle of shading presented in the experimental stimuli, but omitted the shading gradient, appearing half-black and half-white (see Figure 4.2). Finally, one stimulus was defined with no shading (see Figure 4.4, for an example), to verify that the circles in the stimulus were randomly placed and elicited no systematic responses.

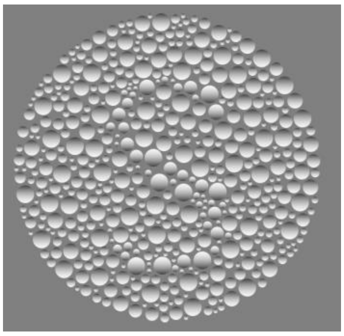


Figure 4.1. An example of a stimulus, representing the letter “S” shaded at 0° degrees (e.g., shaded from directly above).

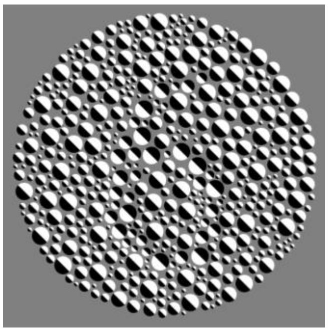


Figure 4.2. A half-black/half-white control stimulus, depicting the number “6” at a 45° shading direction.

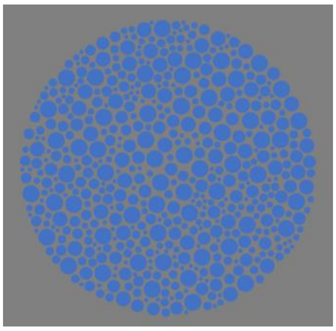


Figure 4.3. A non-shaded control stimulus.

Each stimulus was created by temporarily superimposing one character on the centre of the background circle in 300px Times New Roman to determine “target” and “distractor” foreground circles. Target circles that covered the character were shaded opposite to the distractor circles, and the superimposed character was removed. Each character was replicated with an altered shading gradient direction. Ten shading gradients were used in this experiment (0º, +/- 30º, +/- 45º, +/- 90º, +/- 135º, and 180º; see Figure 4.4). The vertical (0º and 180º) and horizontal (+/- 90º) shading directions were used to determine whether the light-from-above prior would influence responses, and the oblique orientations (+/- 30º and +/- 45º) were chosen to explore whether a directional bias, such as those typically observed in shape judgement tasks, influenced performance on this task. Background circles were always shaded at an angle of 180º from the shading direction of target circles. After the placement and orientation of circles were complete, the stimulus size was reduced to 12cm in diameter. As head position and distance from the screen were not controlled in this experiment (see Procedure), the estimated visual angle ranged between 9.15º (at an assumed viewing distance of 75cm) and 13.69º (at a viewing distance of 50cm), with differences in screen sizes introducing further variation in these visual angles.

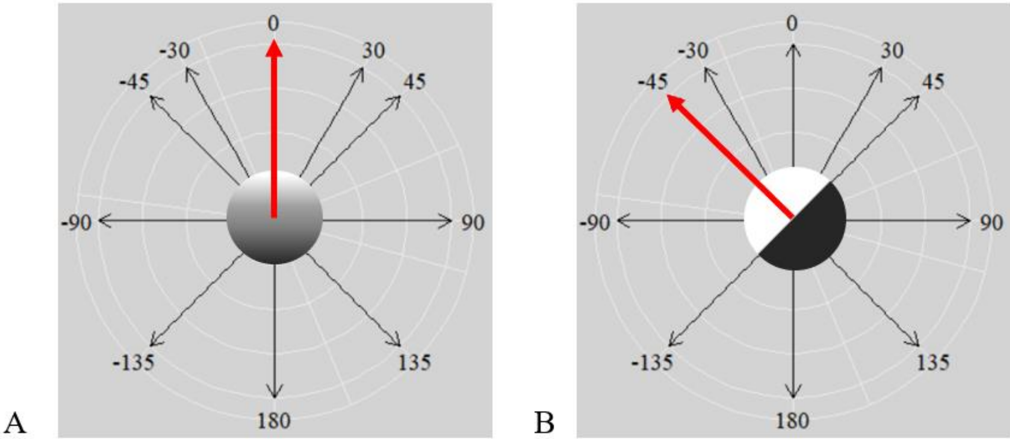


Figure 4.4. **A**: Shading directions of target stimuli used in Experiment 1. Arrow points to the brightest part of the stimulus (0° in pictured example). **B**: Shading directions of control stimuli used in Experiment 1. Arrow points to the brightest part of the stimulus (-45° in pictured example).

Questionnaire

A short questionnaire was issue to participants to collect demographic and eligibility data (see Appendix 4.1).

Procedure

The experiment was coded in PsychoPy3 (Peirce et al., 2019) and hosted online by Pavlovia (https://pavlovia.org/). Participants were given a link to a website and asked to complete the study on their own computers, and in their own time. The website included the experiment information, the demographic questionnaire, the links to the experiment, and the debriefing form. As participants completed the experiment on their own equipment, the monitor size and resolution, viewing distance, and head position were uncontrolled in this experiment. However, participants were asked to sit comfortably in a darkened room, avoid tilting their heads, and place their fingers on the “Z” or “M” keys on their keyboard. The stimulus duration was 1000ms, and stimuli were preceded by a 500ms fixation cross at the centre of the screen. After the stimulus was presented, a prompt offering two choices, one correct and one distractor, was presented for 3000ms. The two characters were chosen from the seven characters presented in the stimuli. Participants were required to press either "Z" or "M" to indicate which character was presented (example given in Figure 4.5); "Z" corresponded to the option on the left of the prompt and "M" to the option on the right. Each prompt-stimulus combination was presented twice, reversing the order of prompts on the second presentation to counterbalance any bias introduced by the responding hand. The subsequent trial began with a fixation cross once the previous choice was made or three seconds had elapsed.

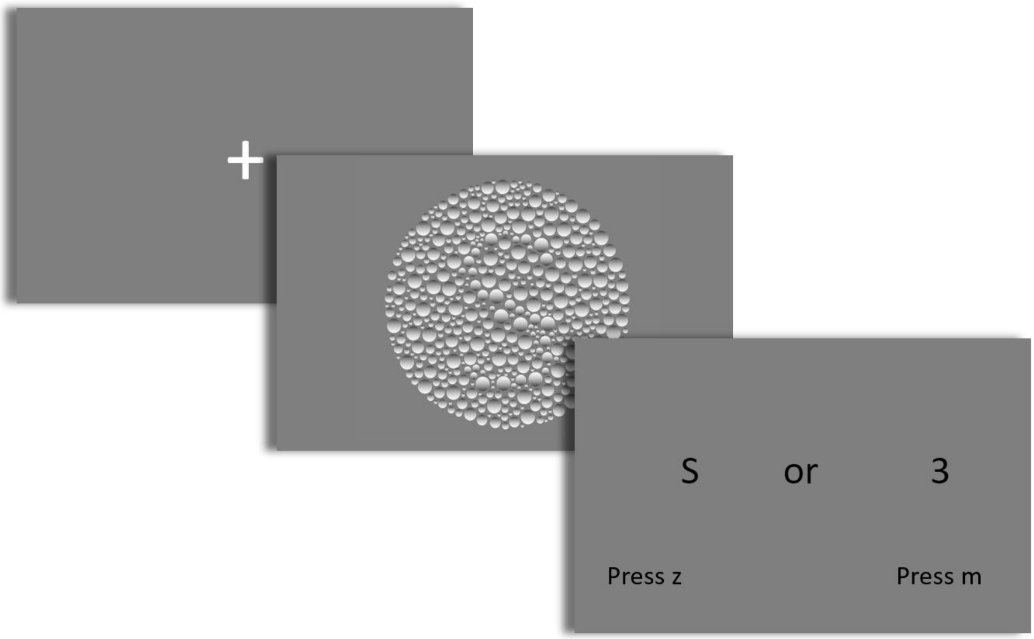


Figure 4.5. Example of procedure; a white fixation cross on a grey background, followed by an experimental stimulus, and then a prompt screen in which "S" corresponds to the "Z" key, and "3" corresponds to the "M" key.

Three blocks of 185 trials, totalling 565 trials, were presented. The trials comprised 420 experimental, 120 control, and 25 blue controls. All stimuli were presented twice to counterbalance the prompt following the stimulus presentation (e.g., "S or 6" was also presented as "6 or S"). Participants were provided with a rest break after each block. Rest breaks could last up to 10 minutes, but participants could choose to end the rest break at any time by pressing the space key. The experiment restarted automatically after 10 minutes.

Design

Experiment 1 included a within-subjects comparison of the effect of the ten shading directions (stimulus orientations) on the accuracy and time taken to identify the characters presented (reaction time) correctly. Additionally, a within-subjects comparison of trial type (experimental, shaded stimuli; or control, half black and half white circles) was included to assess the effects of shading on the accuracy and reaction times to identify the characters presented correctly.

We also assessed whether there were any effects of the alphanumeric target character used via a within-subjects comparison of the seven characters ("R", "8", "S", "9", "6", "3", and "P").

Data processing

All statistical analyses were undertaken in R. As a two-alternative forced-choice task, an accuracy rating of 50% indicates chance performance; to exclude participants performing at or near chance levels, an inclusion criterion of 70% accuracy on experimental trials was applied and resulted in the removal of 12 participants. Blue control trials were extracted and analysed separately (see “Solid blue control trials” section below) and were not included in any experimental analyses. After blue trials were extracted, data cleaning steps included the removal of reaction times of less than 150ms; of an initial 16735 experimental and half black, half white control trials, 15717 remained (n_{Removed} = 1018; 6.18% of trials). A further 956 trials (626 experimental and 330 control trials) were not responded to by participants and were thus not used in any analyses (see Table 4.1 for the proportion of non-responses per character). In total, 14761 trials were analysed, or 88.2% of the total possible trials. Only correct trials were used in reaction time analyses, and the distribution of reaction times revealed a positively skewed distribution (skewness 1.78).

Table 4.1. *The proportion of trials not responded to by character and trial type.*

	Proportion of non-responses	
Character	Experimental Trials	Control Trials
3	0.06	0.11
6	0.05	0.11
8	0.06	0.10
9	0.08	0.11
P	0.05	0.12
R	0.05	0.11
S	0.04	0.08

Solid blue control trials.

Twenty-five additional blue control trials were included per participant, with no character defined by grouping or shading. These trials were analysed to determine whether a systematic response was made, which could indicate an inadvertent grouping of the circles within the stimulus. Overall, participants responded with the "z" key in 32.4% of trials, the "m" key on 29.1% of trials, and failed to respond on 38.4% of trials. We accepted that there was no systematic tendency to respond with a particular character on blue trials, which were removed from each participant's results and not assessed further.

Results

Participant inclusion criteria

An arbitrary threshold of 70% accuracy on experimental trials was applied as an inclusion criterion. A post-hoc k-means clustering algorithm was used to assess whether this exclusion criterion was appropriate and found that the correct exclusion criterion was applied in 11 of the 12 excluded participants.

Effect of trial type and character

Reaction times

A critical objective of this study was to explore the parameters of the experiment to identify areas for improvement in future iterations. We therefore explored whether the type of stimulus (trial type; a shaded experimental stimulus, or a half black, half white control stimulus; blue control stimuli were assessed separately and not included in any further analyses) or the character affected the time taken to identify a target character correctly. Accurate trials were used in the reaction time analysis. The mean time to respond to experimental stimuli was 730ms (*SD* = 340ms), and to control stimuli was 810ms (*SD* = 350ms). Reaction times for each character, in experimental and control trials, are shown in Figure 4.6.

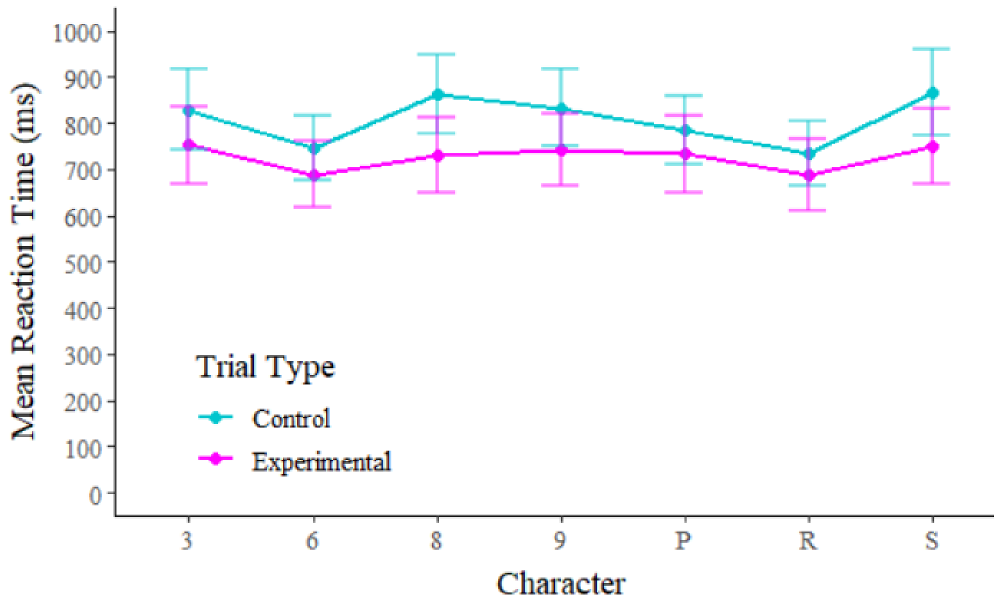
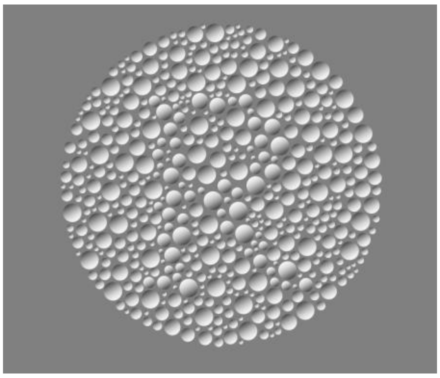


Figure 4.6. Line graph to illustrate the mean reaction time to control and experimental target characters. Error bars represent the standard error.

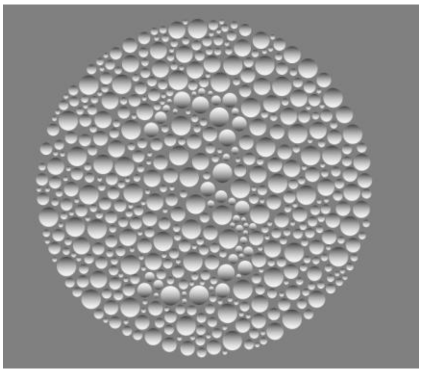
Reaction times followed a gamma distribution with positively skewed residuals; therefore, we fit a generalised linear mixed model by maximum likelihood (Laplace approximation), with a gamma error distribution and a log link function. The model revealed a significant effect of trial type, with participants responding faster to trials than to control stimuli (β = -0.12, *SE* = 0.01, *t* = -11.60, *p* < .01). There was also a significant effect of character, with participants responding faster on all characters used in the experiment compared with the reference character "3", which generated the slowest reaction times in this experiment. Only characters "6", "R" and "P" were significantly faster than the reference character (see Table 4.2 for comparisons between characters, and an example of these stimuli in Figure 4.7 A and B).

Table 4.2. *Results of a generalised linear mixed-effect model to explore the effect of experimental parameters on the experiment. All characters were compared to the number "3".*

Character	β estimate	Standard error	T value	P value
6	-0.1022	0.0155	-6.60	< .01
8	-0.0230	0.0157	-1.47	.142
9	-0.0198	0.0158	-1.26	.209
P	-0.0396	0.0156	-2.53	.011
R	-0.1065	0.0155	-6.88	< .01
S	-0.0130	0.0158	-0.82	.411



A



B

Figure 4.7. A) The target character with the fastest responses ("R"; shaded at -30°); B) the character with the slowest responses ("3", shaded at 0°).

Accuracy

To explore the relative efficacy of the parameters of the experiment to elicit accurate responses, we reviewed whether the type of stimulus (experimental or control) or the character (letters and numbers) affected how accurately participants identified a target character defined by the shading direction of the target circles in the stimulus. No trials were excluded from this dataset based on accuracy.

The mean accuracy on experimental stimuli was 81.5% (*SD* = 39%), and on control stimuli was 60.9% (*SD* = 49%). The accuracy of each target character in experimental and control trials is shown in Figure 4.8

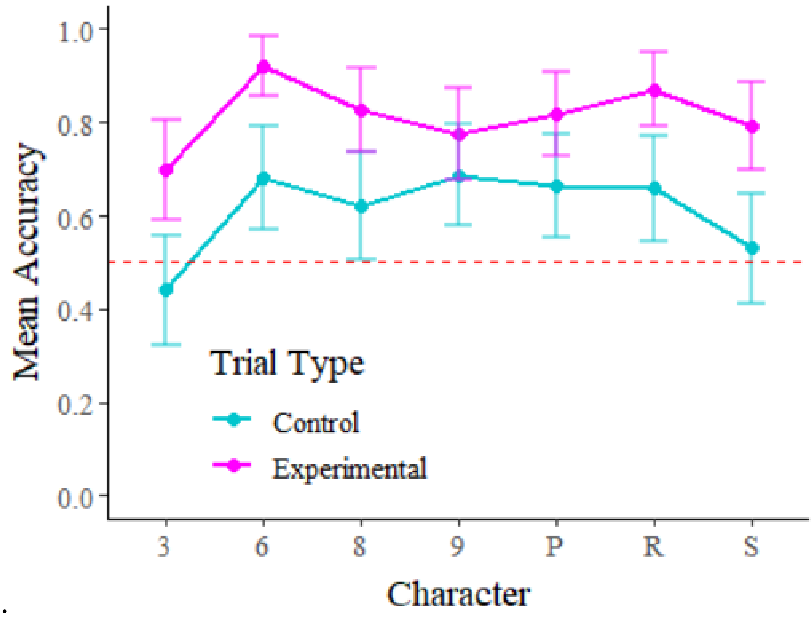


Figure 4.8. Line graph to illustrate the mean reaction times to control and experimental target characters. The red dashed line at 0.5 indicates chance performance levels. Error bars represent the standard error.

We fit a generalised linear mixed model by maximum likelihood with a logit function to analyse the binary outcome variable: accuracy. The model revealed a significant effect of trial type, with participants responding more accurately to trials than to control stimuli (β = 1.06, *SE* = 0.06, *t* = 18.74, *p* < .01). There was also a significant effect of character, with participants responding more or less accurately to certain characters (see Table 4.3).

Table 4.3. *Results of a generalised linear mixed-effect model to explore the relative effect of experimental parameters on the experiment. All characters were compared to the accuracy of the number "3", the character that generated the fewest accurate responses..*

Character	β estimate	Standard error	T value	P value
6	1.45	0.11	13.54	< .01
8	0.74	0.09	8.20	< .01
9	0.59	0.09	6.70	< .01
P	0.76	0.09	8.43	< .01
R	1.02	0.09	10.86	< .01
S	0.47	0.09	5.45	< .01

Effect of orientation

Reaction times

We explored whether the direction of shading on target stimuli affected participants' reaction times to detect the characters (see Figure 4.9). Only accurate trials were included in reaction time analyses.

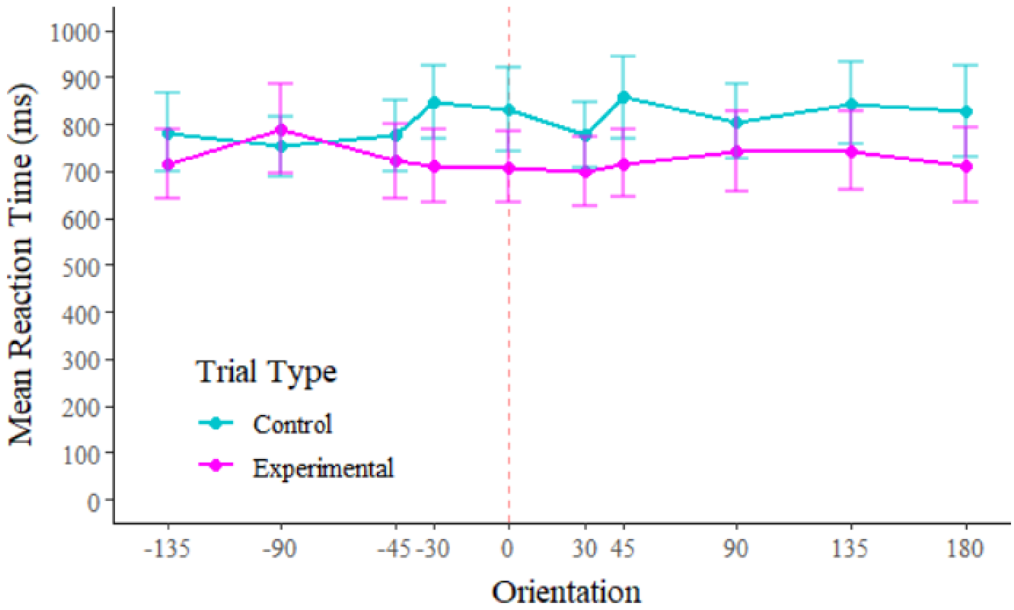


Figure 4.9. Reaction times to detected targets shaded from different directions. The magenta dashed line indicates the mean of experimental reaction times and the blue dashed line shows the mean of control trials. Error bars represent the standard error.

A repeated-measures ANOVA was calculated to assess whether the effects of orientation differed across trial types and showed that whilst reaction times to experimental trials were significantly faster than to controls (F (1, 321) = 62.76, $p < .001$, $\eta_p^2 = 0.16$), there was no significant effect of orientation (F (9, 321) = 0.54, p = .85). Furthermore, there was no interaction between orientation and trial type (F (9, 321) = 1.45, p = .16). This suggests that the direction of the shading gradient did not affect participants' speed to detect the target character in this experiment when compared with control stimuli.

A generalised mixed effects model was fit to assess the effect of orientation alone, removing trial type as a predictor and using experimental trials only. Because reaction times followed a gamma distribution with positively skewed residuals, the model was fit by maximum likelihood (Laplace approximation) with a gamma error distribution and a log link function. The model compared each orientation to the overhead (0°) orientation to reveal each orientation's relative perceptual value. The reaction times to the -90° orientation were significantly slower than the 0° reference category (β = 0.06, SE = 0.02, t = 3.24, $p < .01$) and reaction times to the 30° orientation were significantly faster than the 0° reference category (β = 0.04, SE = 0.02, t = -2.09, p = .036; Figure 4.10). No other orientations produced significant differences (ps > .05).

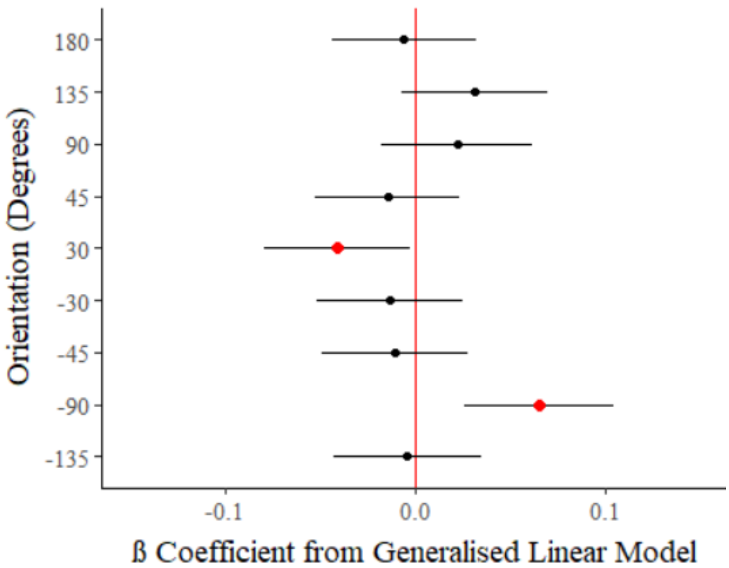


Figure 4.10. Plot showing the standardised coefficients of the model on the X axis, comparing reaction times at each orientation (shown on the Y axis) to the 0° reference category. The red dots highlight significant comparisons. Estimates to the left of the vertical line indicate faster reaction times.

Accuracy

We explored whether the direction of shading affected participants' ability to correctly identify a character defined by shaded circles. The mean and standard deviation of accuracy for each orientation is shown in Figure 4.11. A repeated-measures ANOVA was calculated to assess whether the effects of orientation differed across trial types. The ANOVA revealed significant main effects of both trial type (F (1, 339) = 176.11, p < .001, η_p^2 = 0.34) and orientation (F (1, 339) = 7.01, p = .008, η_p^2 = 0.02), and a significant interaction (F (1, 339) = 9.54, p = .002, η_p^2 = 0.03). This indicates that shaded stimuli offer a perceptual advantage over control stimuli and that the orientation of the shading gradient facilitates the detection of the target characters. However, the very small effect sizes for the effect of orientation and the interaction term suggest that orientation did not account for much of the variance in performance. Interestingly, accuracy to shaded and non-shaded stimuli diverged at overhead-oblique orientations (-/+ 45°, -/+30°), demonstrating that these orientations were the most informative for shaded stimuli and among the least informative orientations for non-shaded stimuli.

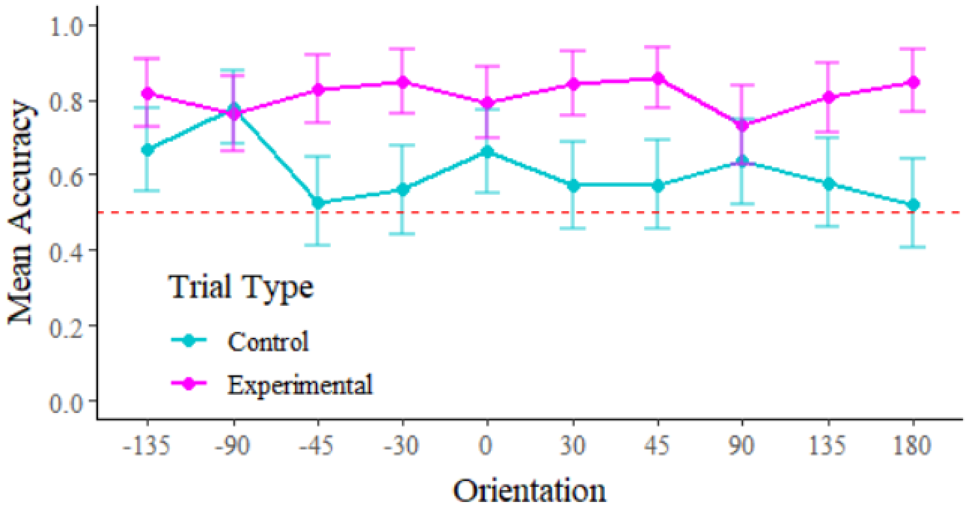


Figure 4.11. Line graph showing the mean and standard deviation of accuracy to each stimulus orientation for experimental and control trials. A dashed line at 0.5 represents chance performance level. Error bars represent the standard error.

A generalised linear mixed model was fit by maximum likelihood with a logit function. The model revealed a significant effect of trial type, with participants responding more accurately to experimental trials than to control stimuli ($\beta = 1.06$, $SE = 0.06$, $t = 18.74$, $p < .01$). There was also a significant effect of orientation, with participants responding faster or slower to certain orientations (see Figure 4.12). A further generalised mixed effects model was fit to assess the effect of orientation alone, removing trial type as a predictor. We fit a generalised linear mixed model by maximum likelihood with a logit function, using accuracy as the outcome variable. Only the 90° shading direction was significantly less accurate than the 0° reference character ($\beta = -0.29$, $SE = 0.11$, $t = -2.72$, $p < .01$). Significant comparisons are highlighted with a red circle in Figure 4.12).

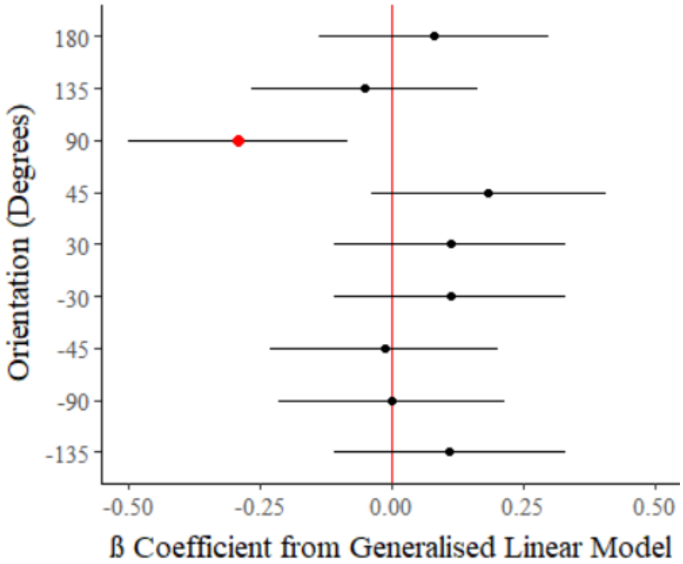


Figure 4.12. Plot showing the standardised coefficients of the model on the Y axis, comparing accuracy at each orientation to the 0° reference category. The red dot highlights the significant comparison.

Discussion

Experiment 1 comprised the first iteration of the LAMP study, which presents a new test of the ability to perceive shape-from-shading by measuring individuals' ability to perceive target characters, defined by their shading gradient, concealed within distractor circles. We predicted that stimuli shaded from overhead orientations, in particular those shaded from the above-left, would attract the fastest and most accurate responses, in accordance with evidence from shape judgement tasks, which clearly demonstrate a perceptual advantage for shading directions originating from the left of the apex of objects in the visual field.

We identified two possible confounds during the conceptual phase of this experiment and controlled them systematically. Firstly, the ability to perform perceptual grouping is essential to complete this task and can account for part of participants' performance. It is possible that participants might adopt other strategies to perceptually group the target circles other than shading, such as orientation (independent of shading), which is a well-known low-level characteristic of early visual processing (Christensen et al., 2019), which we considered equivalent to luminance polarity. We controlled for the effects of grouping by orientation or luminance polarity by including control trials grouped in the same way as shaded experimental trials, with equivalent luminance and luminance polarity, but without a shading gradient. Secondly, the characters used as target shapes were a feature of the experiment and not of practical importance. Nevertheless, a character's orientation, lines, and curves may interact with the shading direction or the placement of circles on the experimental stimulus to facilitate better performance than others, offering an additional perceptual grouping advantage. We analysed the performance of characters to determine whether some attracted better or worse performance than others to inform future development of the experiment rather than to specifically explore how characters interact with shading information to affect participants' ability to use shading information as a perceptual cue.

Despite strong evidence from shape judgement tasks, the orientation of the shading direction did not offer a robust model of performance; only stimuli shaded horizontally at -90° significantly increased the time taken to detect targets. Horizontal shading directions produce the least consistent shape judgements (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Mamassian et al., 2003; Pickard-Jones et al., 2020) and less efficient visual search performance (see Chapter 2; Kleffner & Ramachandran, 1992; Sun & Perona, 1998), so impaired performance at these orientations was expected and indicative of the reduced capacity of these orientations to produce a robust percept of 3-D depth. There was insufficient variability within the other orientations to permit a meaningful analysis. It is possible that the lack of variability in reaction times was partly due to the interaction between the different cognitive processes deployed to resolve the task: in addition to resolving the shape defined by the shading gradient in the target and distractor circles, participants had to perceptually group the target circles, recognise the character, read the on-screen prompt, decide which hand to respond with, and then move their hands.

Accuracy produced stronger and more significant effects than reaction times and therefore comprised a more informative measure of performance. It is interesting to note, however, that although the difference in accuracy between most shading directions was not statistically significant, Figure 4.11 illustrates a systematic and opposite pattern between control and experimental stimuli. Performance between the trial types converged at directly overhead (0°) and horizontal (90° and -90°) shading directions, with lower accuracy in shaded stimuli and greater accuracy in non-shaded controls than in other orientations. This suggests that shading information offered little-to-no perceptual advantage over perceptual grouping and orientation at these stimulus orientations. However, accuracy between trial types diverged at oblique stimulus orientations and 180°. We expected that oblique and overhead orientations would attract faster and more accurate responses because search tasks have shown that depth perception is an informative visual feature (Hulleman et al., 2000; Kleffner & Ramachandran, 1992; Wolfe & Horowitz, 2004), and as such are found faster in visual search tasks (Itti & Koch, 2000). Shape judgement tasks also reveal an advantage at these orientations, making it surprising that vertical (0°) orientations were comparatively less informative in this task. However, visual search tasks have shown that concave targets set against a background of convex distractors are more salient targets than convexities among concavities (Hulleman et al., 2000; Kleffner & Ramachandran, 1992; Sun & Perona, 1998). Therefore, the diverging pattern of responses at oblique orientations and 180°, and the converging pattern of responses at 0°, 90°, and -90°, strongly suggest that shading information is more informative when it produces a stronger sense of depth. As this is a 2AFC experiment, participants could feasibly correctly answer up to 50% of trials by guessing alone. As diagnostic tests require greater specificity, future versions of the experiment must reduce the likelihood of guessing the correct answer by chance alone and thus must require participants to select the corresponding character on the keyboard without providing a prompt. Nevertheless, the difference between trial types was highly significant, demonstrating that depth cues from shading offer a perceptual advantage over perceptual grouping and orientation in this task, suggesting that the test may be an appropriate way to assess the ability to use shape-from-shading as a depth cue. Experiment 2 presents a further iteration of this task, addressing some of the limitations identified in experiment 1.

Experiment 2

Experiment 1 of the LAMP task demonstrated that shading direction offered a perceptual advantage over the orientation of luminance polarity when identifying target characters from an array of distractors with an opposite luminance polarity, suggesting that shape-from-shading may be processed automatically. Furthermore, overhead and oblique orientations were processed faster and more accurately than horizontal orientations. An advantage for these orientations implies that attention was involved in participants' ability to recover the impression of depth from shading, in the same way as in other shape judgement (Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Mamassian et al., 2003; Pickard-Jones et al., 2020) and visual search tasks (Chapter 2; Kleffner & Ramachandran, 1992; Sun & Perona, 1998).

Experiment 1 revealed that reaction times were not an informative measure in the LAMP task, having less variability than accuracy. Reaction times were removed from further analyses in the next iteration of the task, and accuracy was chosen as the dependent variable. Answer prompts were removed to increase the explanatory power of the experiment by reducing the likelihood that participants could choose the correct response by chance. This change required participants to select the character they identified from the keyboard.

Sun and Perona's (1998) visual search study demonstrated that circles shaded from the above left could be detected under shorter presentation times than other shading directions and that directional biases were more pronounced under conditions that required a higher cognitive load. Sun and Perona suggested that directional biases in visuospatial attention might therefore occur in the early stages of visual processing, and that protracted viewing may obviate the effects of early visual attention. To establish whether shorter presentation times might facilitate the detection of a directional bias by engaging more visuospatial attention and, by extension, to determine whether left-shaded stimuli offered a perceptual advantage under shorter stimulus presentation times, we altered the stimulus presentation time in three separate blocks. We predicted that left-shaded stimuli would attract a higher degree of accuracy than other shading directions under shorter stimulus presentation times and speculated that an increased left bias would suggest an increase in right hemisphere activation in response to the increased demands on visuospatial attention. Because accuracy was relatively low in Experiment 1, we added a training block in Experiment 2.

Methods

Participants

Twenty participants, aged between 18 and 30 years, were recruited via Bangor University's participant panel, receiving course credits for participation. No participants reported any uncorrected vision problems or neurological conditions.

Stimuli

The questionnaire and stimuli were replicated from Experiment 1, except the stimuli that generated the slowest and least accurate responses ("3" and "S") were excluded, leaving five characters in this experiment: "6", "8", "9", "P" and "R". The same ten orientations were used (see Figure 4.2 A and B for an illustration of the orientations used in this experiment), and the blue control trials were omitted.

Procedure

Participants were asked to complete the short questionnaire and were then directed to the experiment via a web link. Participants completed the experiment in their own time, using their own computers; as such, environmental factors were not controlled. However, they were asked to sit at arm's length from the screen and to maintain a straight and stable head position, avoiding tilting their head to one side. The experiment included a short training block of ten trials, which were not used in analyses.

There were three experimental blocks, each with a variable presentation time: Block 1 presented the stimuli for 350ms, Block 2 for 500ms, and Block 3 for 650ms. A fixation cross preceded each trial and was presented in the centre of the screen for 500 milliseconds. Participants were asked to identify the character and select the corresponding key from their keyboard. Each of the ten stimulus orientations was presented five times in each block for both experimental and control trials; therefore, there were 100 trials in each block and 300 trials (150 experimental trials) in total. Participants were required to make a choice before the next trial began.

Data Analysis

The dependent variable in Experiment 2 was accuracy, which was analysed by ten orientations, two trial types (experimental trial and controls) and block (three blocks with a variable presentation time).

Overall accuracy in this experiment was low (see Figure 4.13). Participants were required to have greater than 20% accuracy in experimental trials for their results to be included in the experiment; this resulted in the exclusion of 14 out of 20 participants, leaving only six participants. This level (20%) was chosen to ensure that participants had at least 30 correct experimental trials to use in statistical analyses.

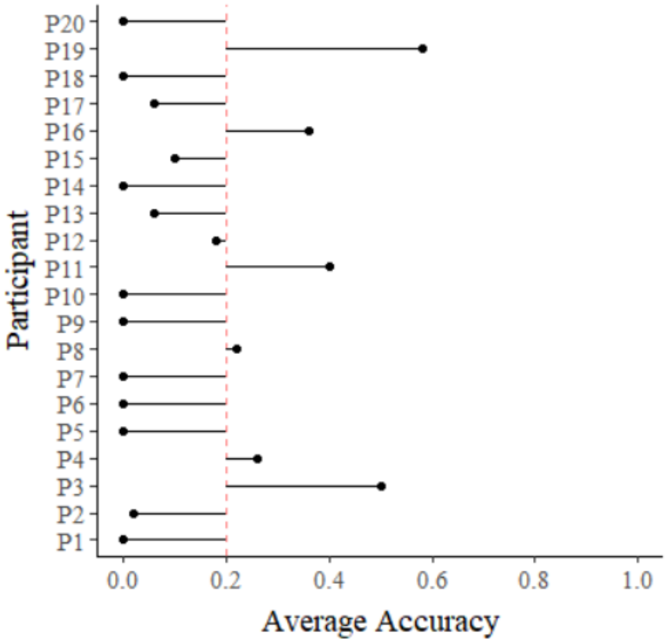


Figure 4.13. Accuracy in Experiment 2 of the LAMP task.

Results

We assessed the effects of the variable presentation time (350ms, 500ms, or 650ms) and trial type (experimental or control trial) on participants' ability to accurately detect characters defined by their shading gradient. Participants were more accurate on shaded (mean accuracy = 27.7%) vs control stimuli (19.9%) and more accurate in blocks with longer presentation times (Block 1: 15.8%; Block 2: 22.7%, Block 3: 32.3%; see Figure 4.14). A repeated measures ANOVA was calculated to determine whether these differences were statistically significant. Accuracy in experimental trials was significantly higher than in controls (F (1, 28) = 9.59, p = .004, $\eta_p^2 = 0.26$), though with a small effect size, suggesting that shading accounted for 26% of the variance in performance compared with perceptual grouping.

There was also a main effect of increasing the presentation time in each block (F (1, 28) 26.46, p < .001, $\eta_p^2 = 0.49$), which had a bigger impact on accuracy. The difference between Block 1 and Block 3 was statistically significant (M_{diff} = 0.39, SE = 0.06, p = .003), as well as between Block 2 and Block 3 (M_{diff} = 0.15, SE = 0.06, p = .013). There was no interaction between trial type and presentation time, suggesting that increasing the difficulty of the task did not increase the perceptual value of shading information.

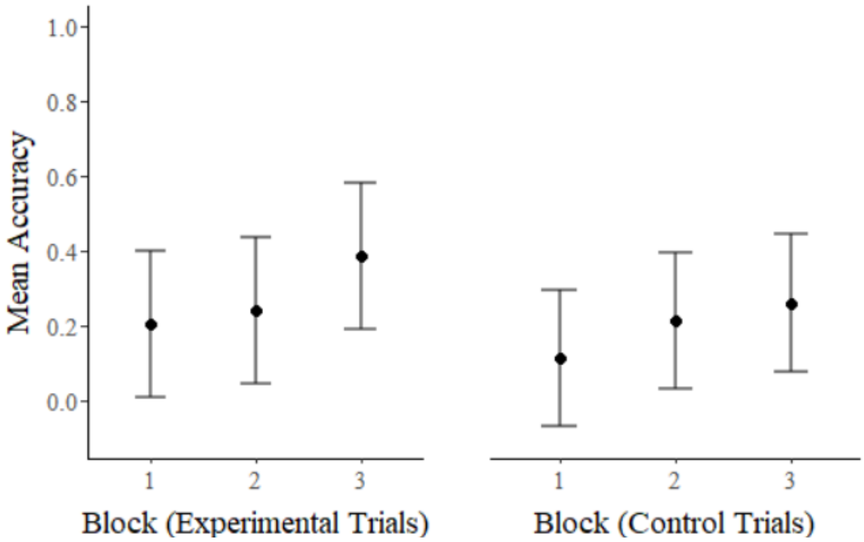


Figure 4.14. Mean accuracy by block in experimental and control trials Error bars represent the standard error.

To determine whether the orientation of the shading gradient offered an increased perceptual value, we assessed the accuracy to each orientation. We used responses from Block 3, which attracted the most accurate responses and therefore offered a more robust way to measure the effect of the shading gradient. We used experimental trials only in this analysis. The mean accuracy of experimental trials in Block 3 was 38.7% (*SD* = 0.48), ranging from 26.7% at 180° to 46.7% at -45° and 30° (see Figure 4.15). A repeated measures ANOVA was calculated to assess whether these differences were statistically significant. There was a main effect of orientation (F (9, 45) = 2.21, p = .039, η_p^2 = 0.31), but Bonferroni-corrected post-hoc tests did not reveal any significant comparisons between shading directions.

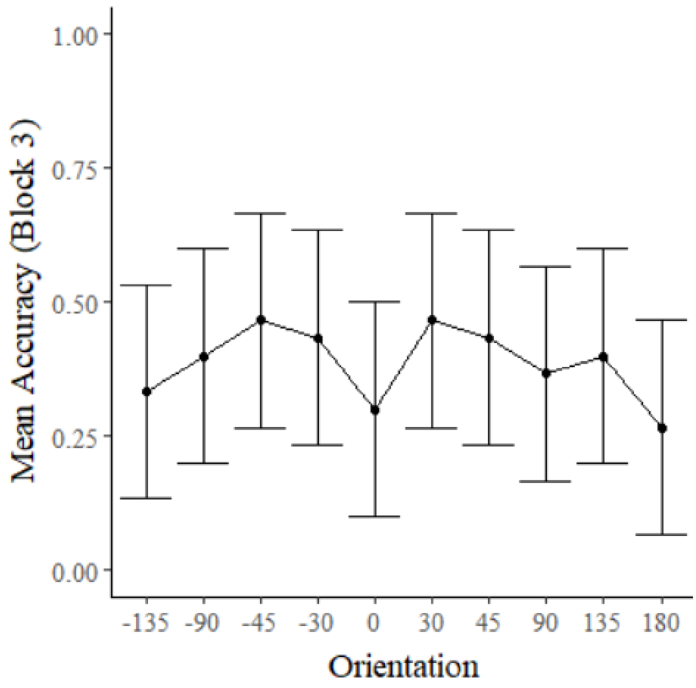


Figure 4.15. Mean accuracy by orientation in block three (experimental trials only). Error bars represent the standard error.

Discussion

As in Experiment 1, Experiment 2 confirmed that shading gradients offered a perceptual advantage over non-shaded controls by generating a higher degree of accuracy in experimental than control trials. We deployed a variable presentation time to evaluate the effect of increasing difficulty on accuracy to different shading directions; however, accuracy across the experiment was extremely low, and a large proportion of participants failed to engage with the task, repeating the same key, or using the same two keys sequentially across the entire experiment. In those participants we determined had engaged with the task, we were confident that correct guesses were genuine because answers were not prompted. We found a main effect of orientation when correct guesses from Block 3 were analysed; however, post-hoc tests did not reveal any significant comparisons. This experiment was likely underpowered, having only six participants after exclusion criteria were applied. However, this experiment still offered a valuable insight into the parameters required for participants to engage successfully with the task: the experiment demonstrated that short presentation times are too difficult and that more experimental specificity can be achieved through unprompted responses. The next iteration of this task will retain longer presentation times and decrease the number of orientations to reduce the length and difficulty of the experiment. Measures will also be implemented to increase engagement with participants to improve statistical power; however, it is important to note that the strong and significant finding that shaded circles offered a perceptual advantage over controls replicated the main finding from Experiment 1 in only six participants, indicating that this task merits further exploration as a measure of the ability to resolve shape-from-shading.

Experiment 3

Experiment 3 of the LAMP pilot tested incremental changes resulting from experiments 1 and 2. From Experiment 1, we identified that removing prompts would reduce the likelihood of correctly identifying the character by chance alone and determined the most effective stimuli to probe the differences between shaded and non-shaded controls. Experiment 2 showed that shorter presentation times resulted in floor effects and that longer presentation times were required to achieve an acceptable degree of accuracy. Experiment 3 addressed this limitation by only including 1000ms presentation times.

Because shading directions of -45° and 45° tend to generate the most accurate responses, and because in Experiment 2 these orientations generated the widest difference in accuracy from stimuli shaded directly overhead (0°), the number of shading directions was reduced to include only these three shading directions. This change also helped to address the most serious limitation of Experiment 2 –the lack of engagement from participants – by reducing the length of the experiment. We also sought to increase participant engagement by scheduling online meetings in which participants completed the task in the virtual presence of experimenters to reduce the likelihood of participants responding randomly. We expected that accuracy would increase as a result of these changes, the experimental trials would continue to attract greater levels of accuracy than controls, and that by including more trials at the most informative shading directions (-45° and 45°, relative to 0°), that our within-experiment statistical power would increase to allow us to detect differences in accuracy between left and right shading directions. We predicted that characters defined by an above-left shading gradient would attract higher accuracy than those shaded from the above right.

Methods

Participants

Twenty-six participants, aged between 18 and 25, were recruited via Bangor's SONA participant panel and received two course credits as compensation. No uncorrected vision problems were reported.

A power analysis (G*Power 3.1.9.2) suggested that the minimum sample size required to detect an effect of shading on accuracy in a repeated-measures test, based on the previous effect size for the effect of shading ($\eta_p^2 = 0.34$), given an alpha level of 0.05 and a beta level of 0.95, was 24 participants.

Stimuli

The stimuli were replicated from Experiment 2, except that only three shading directions were used: -45°, 0°, and 45°; and a single stimulus presentation time of 1000ms.

Procedure

Participants were asked to complete the short questionnaire and were then directed to the experiment via a web link. Participants completed the experiment using their own computers but attended an online video call with the experimenter at a pre-arranged time and date. Participants were asked to sit at arm's length from the screen and to maintain a straight and stable head position, avoiding tilting their head to either side. The experiment included a short training block of ten trials, which were not used in analyses. There were four blocks of

60 trials, of which 45 were experimental, and 15 were controls. There was a training block of 15 stimuli (10 trials and five controls), which were not included in any analyses.

Data Analysis

The average accuracy in experimental trials was 69% (*SE* = 4.22%). We therefore defined an exclusion threshold of 60% accuracy on experimental trials. Six participants fell below this threshold, leaving 20 participants (see Figure 4.16).

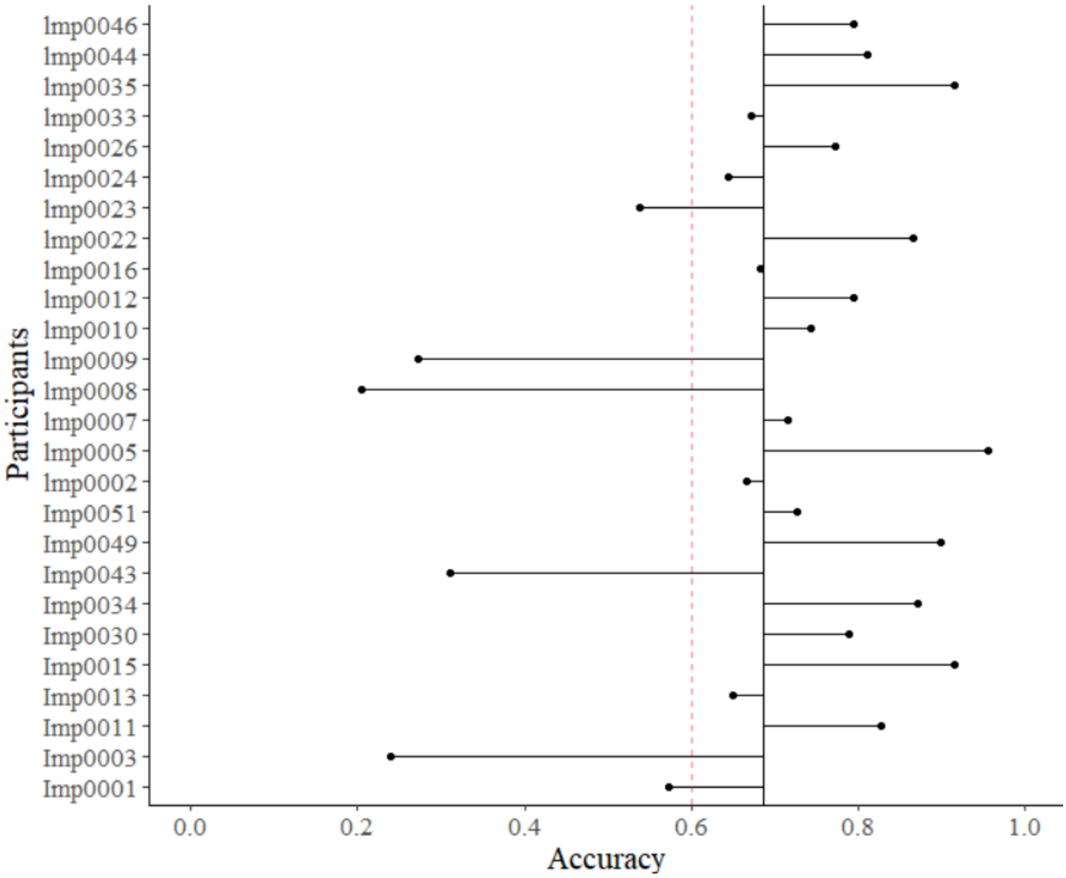


Figure 4.16. Plot to show each participant's accuracy on experimental trials. The solid vertical line represents the average accuracy, and the left side of dashed line represents the exclusion threshold.

Results

Participant inclusion criteria

A threshold of 60% accuracy on experimental trials was applied as an inclusion criterion. A post-hoc k-means clustering algorithm was used to assess whether this exclusion criterion was appropriate and found that the correct exclusion criterion was applied in all of the excluded participants, but that an additional two participants could have been included.

Accuracy by trial type

Experimental trials attracted greater accuracy than controls (mean accuracy on experimental trials: 78.2%, SD = 0.41; mean accuracy on control trials = 49.7%, SD = 0.50; see Figure 4.17). A t-test showed that this difference was statistically significant (t (22.82) = 4.66, $p < .001$) with a moderately large effect size ($\Delta = 0.62$), suggesting that shaded spheres were more informative cues to shape than perceptual grouping.

The greatest accuracy in experimental trials was at -45° (M = 82.8, SD = 0.38), suggesting that shading information was more perceptually informative at this shading direction. Overhead (0°) shading directions attained 80.3% (SD = 0.40) accuracy. The least informative shading direction was 45°, which received 73.6% accurate guesses (SD = 0.44).

A linear mixed-effect model fit by maximum likelihood was calculated with a Laplace approximation, including shading direction and trial types as fixed effects with an interaction term. There was no interaction between shading direction and trial type, and the model including an interaction term was not significant ($p > .05$). We therefore fit a further linear mixed-effect model including shading direction as a fixed effect, which showed that some shading directions significantly affected accuracy. Compared with the 0° shading direction, circles shaded from -45° were, on average, 2.5% more accurate, suggesting a 0.17% increase in accuracy for each degree left of the apex; however, this difference was not significant ($p > .05$). Circles shaded at 45° were significantly less accurate than 0°, with an approximately 0.40% decrease in accuracy for each degree right of the apex ($\beta = -0.40$, $SE = 0.10$, $t = -3.90$, $p < .001$), confirming that objects shaded from the above-right are less informative cues to shape those shaded from above or above-left.

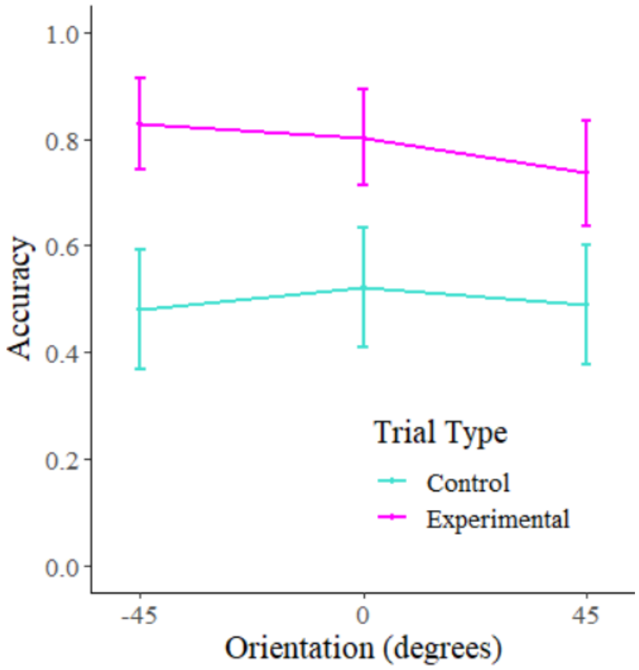


Figure 4.17. Line graph showing accuracy by orientation (in degrees) on experimental and control trials.

Discussion

Experiment 3 of the LAMP experiment addressed some limitations demonstrated by Experiment 1; specifically, that reaction times were not a strong predictor of performance, and that providing prompts for answers reduced confidence in the specificity of the responses obtained. Iteration 3 also addressed the limitations identified in Experiment 2: firstly, that briefer presentation times made the experiment too difficult; and secondly, that engagement was low. It is possible that engagement was low, in part, due to the difficulty of the experiment. We addressed this by reducing task difficulty and decreasing the length of the experiment. Furthermore, several participants pressed two keys sequentially or randomly, regardless of the stimulus presentation duration or any other experimental factors. We assumed that some participants were not motivated to engage with the experiment regardless of its difficulty and therefore predicted that the presence of a researcher would encourage them to participate in the study by exploiting demand characteristics (McCambridge et al., 2012; Orne, 1962). By increasing presentation times and arranging a virtual meeting in which researchers and participants were present, the average accuracy of the task increased substantially. We attribute the success of this approach principally to the virtual meeting because, in Experiment 2, the longest presentation time of 650ms generated an average accuracy of just 32.3% after 14 out of 20 participants whose accuracy fell below 20% were excluded, despite some participants generating much higher accuracy. In Experiment 3, the presentation time was 1000ms, and only six participants fell below 60% accuracy in experimental trials.

Because Experiment 2 generated few useable trials, our within-participant statistical power was low, and there was insufficient variability between different shading directions to perform a meaningful statistical analysis. In addition to increasing participant engagement and reducing task difficulty, we also reduced the length of the experiment to 15 minutes. We focused on three shading directions, increasing the number of trials per orientation for the shading directions of interest, permitting a more robust statistical analysis.

As predicted, we observed a left bias: characters defined by circles shaded with the brightest parts oriented to the left of the apex (-45°), amongst a background of distractor circles shaded with the darkest parts at 45°, generated the highest accuracy scores. The difference in accuracy for left-shaded vs stimuli shaded from directly overhead was not significant.

Although the interaction between trial type and shading direction was not statistically significant, both Experiment 1 and Experiment 3 showed that the difference in accuracy between experimental and control trials increased and decreased systematically (see Figures 4.11 and 4.17), with experimental trial accuracy decreasing proportionally to increases in accuracy on control trials, and vice-versa. Because all stimuli were free of any means of perceptually grouping target characters other than their luminance polarity, this suggests that an orientation of -45° is more informative only when the orientation is defined by a shading gradient and thus is an effect specific to the resolution of shape-from-shading rather than an effect of orientation. However, the luminance polarity in half-black and half-white control circles may not offer the same cues to orientation as shading gradients. For example, a circle shaded with the brightest point at -45° may direct attention to the above left, but half-black and half-white control circles with the brightest point at -45° (see Figure 4.18 A), typically considered an equivalent control for luminance polarity to a -45° shaded circle (e.g., Ramachandran, 1988), might actually contain above-right or lower-left orientation cues because of the orientation of the line generated by the intersection of the black and white halves (illustrated in Figure 4.18 B).

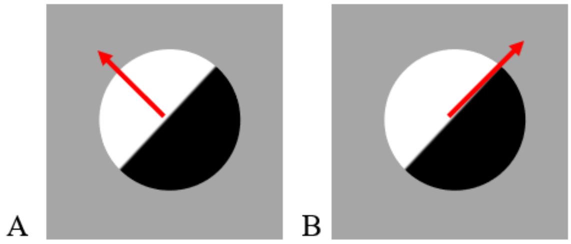


Figure 4.18. A and B show a half-black, half-white control stimulus, with an equivalent luminance, and luminance polarity, to a shading gradient with the brightest part at -45°. In A, the red arrow points to the midpoint of the white portion. B shows an alternative interpretation of the orientation of the stimulus, with the red arrow following the line created by the placement of the two halves.

It is, therefore, possible that conflicting orientation cues exist within half-black, half-white controls. Further work must be done to establish whether these are suitable as a control for this experiment or if alternative or additional controls should be included. For example, grated circles with an equivalent luminance to shaded circles and clear orientation cues but no luminance polarity (see Figure 4.19 for an example) may be appropriate as an additional control to assess the effects of orientation, distinct from luminance polarity.

Figure 4.19. An example half-black, half-white grated control stimulus, with an equivalent luminance to a shaded circle and orientated at -45°/135°.

Should luminance polarity and orientation cues conflict in our control stimulus and exert different effects on the locus of visuospatial attention, this might explain the converging/diverging pattern of responses observed in Experiment 3 and reveal that directional light priors are distinct from other known orientation biases. Finally, although we identified some participants with low accuracy in the final iteration of the LAMP tasks, the test for the ability to perceive shape-from-shading did not identify individuals who could not complete the task, and we therefore consider that we have established a baseline level of performance in normal populations. Future iterations of this experiment should include testing cohorts with visual deficits, such as patients with PCA; if its utility as a test measure can be established among populations with actual deficits in the ability to perceive shape-from-shading, the LAMP task might then be used as part of a test battery in those populations.

Chapter 5: General discussion

Prior assumptions reduce the cognitive load associated with processing enormous quantities of sensory information, helping observers to rapidly interpret the visual world. The origin of light priors has attracted much research and debate, with three distinct hypotheses being presented to explain how humans develop these prior assumptions. The role of acquired experience with light has been argued by several researchers, including Adams (2007), Proulx (2014), Thomas et al. (2010), and Stone (2011), and the plasticity of light priors under certain conditions does provide strong evidence for this claim. Other studies have noted the importance of attentional habits, such as the direction of one's habitual scanning direction, which has been shown to modulate priors in a range of experimental paradigms (Andrews et al., 2013; Chokron & De Agostini, 2000; Friedrich & Elias, 2016; Rinaldi et al., 2014; Smith et al., 2015). Finally, given the many sources that have demonstrated the involvement of specific brain regions in resolving shape-from-shading (de Montalembert et al., 2010; Gerardin et al., 2010; Mamassian et al., 2003; Taira et al., 2001), and because priors are present even in infants with limited visual experience (Benson & Yonas, 1973; Granrud et al., 1985; Yonas et al., 1979), light priors have been argued to be innate (Pickard-Jones et al., 2020). As such, light priors may develop in a standard pattern in most observers and be adjusted by experience over the lifetime. Assessing how these factors affect the formation of light priors is best achieved by investigating how priors develop and change across the lifespan.

This thesis examined changes in light priors acquired during early childhood and literacy development (Chapter 2) using child-friendly experimental techniques, and aimed to detect directional biases at younger ages than in past studies, determine the amount of reading experience required to modulate directional biases, and assess whether light priors changed with increasing age and experience with light. This thesis also represented the first attempt to correlate changes in shape-from-shading with cognitive abilities in older adults and explored whether changes in light priors suggest healthy or pathological ageing processes (Chapter 3). An important gap in the literature on age-related changes in directional biases was also addressed: whether or not these changes are sex-specific and related to cognitive function, to facilitate the formation of sex-specific assumptions about normative performance over the lifespan. Finally, a new test (the LAMP task; Chapter 4), modelled on the Ishihara (1962) colour blindness test, was proposed to identify people who cannot perceive shape-from-shading or perform outside the expected ranges on shape-from-shading tasks. The LAMP task was also designed to address some of the limitations of other paradigms investigating shape-from-shading.

The development of light priors

If light priors are innate, they must be present very early in life and not develop with visual experience. Therefore, the answers to two critical questions were sought in Chapter 2: firstly, whether there is an extended developmental trajectory for the light-from-above prior; and secondly, whether directional biases in light priors emerge or change as a function of visual experience or habitual reading direction. The presence of light priors in infants has been assessed in previous literature; Benson and Yonas (1973) trained 3–7-year-olds to point to convexities in a physical stimulus that contained a convexity and a concavity, and established that the children could perceive shape-from-shading when they were able to point to a two-dimensional image that suggested a concavity through its shading gradient. Later, Yonas et al. (1979) found that sensitivity to shading information, operationalised as the ability to point towards apparent convexities, did not change between 3 and 8 years. Subsequently, Granrud et al. (1985) demonstrated a very early ability to perceive shape-from-shading, showing that 7-month-old infants preferentially reached for images of convexities defined by their shading gradients. Supportive of these findings, a very clear light-from-above prior was observed in all age groups in Chapter 2, with a pattern that showed that the three most-overhead shading directions garnered the fastest responses and highest accuracy. Chapter 2 adds an important finding to the previous literature: that the light-from-above prior does not depend upon the ability to judge the three-dimensional shape of a shaded image explicitly. It is possible that some of the children tested in Chapter 2 did not perceive the illusory three-dimensional shape of the stimulus and instead relied upon other visual attributes to identify the oddball, such as its luminance polarity. Nevertheless, objects shaded with the brightest parts near the apex of the image attained an additional perceptual value that enabled children to detect oppositely shaded oddballs faster and more accurately than in other shading directions. This finding clearly shows an orientation-specific effect of shading directions, but more work is required to understand whether this effect is distinct from the ability to perceive depth in a shaded image or instead reflects that some aspects of shape-from-shading are processed pre-attentively.

To assess whether light priors are truly innate, an experimental paradigm suitable for infants must be devised. Chapter 2 provided a more comprehensive appraisal of the light-from-above prior than previous literature, quantifying the perceptual value of different shading directions using a different task. Though some children aged three to four years were excluded from experimental analyses because they could not maintain their attention on the task, we suspect some adaptation may render this task suitable for even younger children. For example, if the time-based element of the task and requirement to touch the oddball was removed, this task could be adapted for eye-tracking with infants, who are known to preferentially look at oddballs (Houston-Price & Nakai, 2004). Infants as young as three days old have been shown to preferentially look at oddballs (Snyder et al., 2008), and novelty preferences for orientation in visual search tasks have been shown in infants as young as five months of age (Rieth & Sireteanu, 1994). Adapting this experiment for infants using this method would combine the fine detail of the perceptual value of different stimulus orientations that our modern and child-friendly methods have attained, at ages potentially even younger than those tested by Granrud et al. (1985). We would predict that the light-from-above prior would be present at the earliest age at which it can be measured, providing compelling evidence that the light-from-above prior is innate.

Directional biases and the suitability of the experimental paradigms

The second important contribution of Chapter 2 was the investigation into directional biases in light priors, for which previous literature has provided mixed evidence. Thomas et al. (2010) observed a leftward light source bias that manifested between 6 and 8 years of age, becoming more pronounced between the ages of 9 and 12. However, Thomas et al.'s task was not designed to detect directional biases, instead placing light source and convexity priors in conflict to determine which priors provided the strongest cues to shape when the shape was ambiguous. Thomas et al.'s findings were supported by Stone (2011), who found inconsistent performance in children younger than six. Interestingly, Stone suggested (based on a re-analysis of Granrud et al. and Yonas et al.'s experimental data and subsequent comparison with regression slopes reported in his own and Thomas et al.'s study) that children were expected to have a neutral light-from-above prior for pictorial stimuli from 1.7 years of age, and for symbol stimuli from 3.8 years. While Stone acknowledged that developmental data might not always be linear, being subject to variable rates of development at critical developmental periods, the very youngest children in Chapter 2 were under three years of age and were able to complete our shape-from-shading visual search task. They showed no difference from older children other than in the number of trials they were willing to perform, strongly implying that light priors are formed far earlier than predicted by the Bayesian inference methods used by Thomas et al. and Stone.

The earliest evidence of a clear leftward light source bias in children (e.g., ages seven and above in Croydon et al., 2017, and Pickard-Jones et al., 2020) coincides with the age at which children's reading proficiency increases dramatically for most typically developing children (Nation et al., 2010) and therefore suggests that habitual reading direction might direct visuospatial attention to the left side of space. In fact, leftward biases have been shown to be influenced by an individual's habitual reading direction: left-to-right readers have a leftward processing bias in tasks such as line bisection, number line processing, and the light source bias; however, right-to-left readers show greater variability in their biases, with some studies showing rightward biases of the same or greater magnitude than the left biases observed in Western populations (Chokron & De Agostini, 2000). Other studies show a diminished leftward bias (Andrews et al., 2013; Rinaldi et al., 2014), and still others show no bias at all (Friedrich & Elias, 2016; Smith et al., 2015). Though compelling, the fact that right-to-left readers show variable biases whereas left-to-right readers reliably show leftward biases may indicate that an individual's habitual reading direction is not the origin of the leftward bias. It may imply that the leftward bias is a developmental default, which is then modified by habitual scanning direction.

In previous shape judgement tasks, both Croydon et al. (2017) and Pickard-Jones et al. (2020) demonstrated that children could explicitly make three-dimensional shape judgments, in a manner that did not differ from adults' performance, on a two-dimensional stimulus in which shading information was conveyed by the placement of light and dark lines. In Croydon et al., the youngest children tested were aged seven years, and in Pickard-Jones et al., the youngest children tested were five years old. In these studies, and in Stone (2011) and Thomas et al. (2010), many young children performed at near-chance levels. Rather than suggesting that near-chance performance means that children cannot perceive depth from shading or that it reflects an immature ability to use shading cues, this may simply indicate that these methods are not suited to young children. Nevertheless, these studies have the advantage of being designed to probe directional biases in light priors explicitly, making them more sensitive to detect directional priors than other methods (e.g., see Adams, 2007). Because reading direction has been shown to influence directional biases, it was imperative to test children before and during reading acquisition in different reading cohorts, which necessitates testing very young children. However, previous studies (Croydon et al., 2017; Pickard-Jones et al., 2020) have shown that traditional shape judgement tasks are ineffective in very young children. Although Adams (2007) showed that visual search was not a sensitive measure of directional biases in adults, we anticipated that it would be appropriate for children for two reasons: firstly, visual search has been shown to be eminently suited to small children (Houston-Price & Nakai, 2004; Rieth & Sireteanu, 1994; Rovee-Collier et al., 1996). Secondly, due to their slower reaction times than adults in a variety of cognitive tasks (Bisanz et al., 1979; Hale, 1990; Luna et al., 2004; Manis et al., 1980), we assumed that children might perform more with variability than adults and that this method might therefore reveal subtle differences in children more effectively. Our validation task revealed that children generated slower reaction times and lower accuracy than adults, but with a response pattern that precisely matched that of adults.

Unfortunately, the Spheres Game did not provide any evidence for directional biases, and neither did it reveal a difference between Welsh and Israeli children. We consider two possible reasons for this. Firstly, Chapter 2 demonstrates that, as in adults, visual search tasks are not sensitive enough to measure directional biases in children, regardless of children’s reduced performance overall. Secondly, the uncontrolled viewing conditions that were prioritised to maintain the suitability of this task for children may have reduced the task’s ability to measure directional biases. The results of the validation task support both arguments and strengthen the evidence that the light-from-above prior exists in a mature state in young children: adults, who maintained the strong leftward bias typically observed in adult populations under controlled viewing conditions, showed no directional biases in the Spheres Game.

Null results, or results that do not show a significant effect or relationship, can be used as evidence in research to rule out specific hypotheses or theories. However, it is essential to consider the context under which the null results were obtained and interpret them carefully. Null results can be challenging to interpret; for example, if a study is not designed or powered adequately to detect a difference or relationship, then any null results may require further analysis or additional studies to determine their statistical significance. It is also important to consider whether the null results are in line with other findings in the field. Ultimately, whether null results can be used as evidence in research will depend on the specific context and the research question being investigated. In Chapter 2, the absence of statistically significant differences between age groups was used as evidence that the light-from-above prior does not change with age. This finding aligned with the *a priori* predictions that age-related changes would be observed if visual experience was the origin of light priors and that no such changes would be observed if they were not, and the power analysis determined that the study's power was sufficient to detect a significant age-related change should one have been observable in the data. Statistical tests to confirm that the differences between groups were not significant are required to reach more definitive conclusions on the contribution of visual experience to the development of light priors.

Reference planes and experimental control

In the developmental experiments and the validation task (both Chapter 2), and in the LAMP task (Chapter 4), free-viewing conditions were used to enhance our findings' generalisability and ecological validity. Previously, McManus et al. (2004) demonstrated that observers spontaneously tilted their heads when their head position was not controlled and suggested that directional biases might result from this feature and thus disappear under free-viewing conditions. As a potential cause of directional biases and a probable limitation of free viewing experiments, spontaneous head tilt deserves further discussion.

In the visual system, a reference frame is an abstract, metaphorical construct through which the location of any object can be expressed through its distance from a unit of origin on the three planes: the abscissa, ordinate, and applicate. There are many possible points of origin; for example, the observer is the point of origin in the egocentric reference plane. In the object-centred reference plane, it is the object. Gravitational reference planes, in which the point of origin is the sense of verticality, rely on somatic and sensory cues, such as information from the vestibular system (Lacquaniti et al., 2015). Kleffner and Ramachandran (1992) systematically changed the perception of shape-from-shading by altering the angle of head tilt in their participants: when the orientation of light in the stimulus corresponded with the angle of the participant's head tilt rather than the gravitational apex of the stimulus, the reaction times to detect a shaded oddball from an array of distractors suggested that participants emphasised the information provided by the retinal, rather than gravitational, reference plane. Other studies have found contradictory results: Jenkin et al. (2004) assessed the relative weightings given by the visual system to visual, gravitational, and body-centred reference frames. Using the York Tilted Room facility to manipulate visual cues, Jenkin et al. found that the visual system combined reference frames to create a sense of verticality and alternated the weight allocated to either the retinal or gravitational reference frames depending on the task at hand. Adams (2007) also observed that the emphasis on different reference frames was task-dependent; in visual search tasks, retinal coordinates superseded gravitational, and in shape judgement tasks, gravitational coordinate systems were emphasised and compensated for conflicting retinal information (Adams, 2007). Therefore, the uncontrolled head position coupled with the freely-held iPad may explain why some directional biases may have been minimised–or obviated entirely–in the present study.

Directional biases also seem to be reduced when the stimuli are presented in the lower visual field (Thomas & Elias, 2012), which could represent a further limitation of our free-viewing conditions. In the Spheres Game, one-third of the stimuli were presented in the lower half of the screen, which might have impacted the ability to measure a directional bias in those stimuli. Our analyses did not reveal an effect of screen location in the Spheres Game; however, this factor could be explored under more tightly controlled conditions using a static-mounted monitor and chin rest. We recommend exploring this approach in adults only; the overriding motivations for using free viewing conditions in Chapter 2 were to enhance ecological validity and be more suitable for children. Reductions in the magnitude of biases to stimuli presented in the lower half of the screen are unlikely to have affected performance on the LAMP task, given that target spheres were distributed across the stimulus and not concentrated in any area of the screen.

Supporting the proposition that our emphasis on natural viewing conditions made the Spheres Game less sensitive, a smaller left bias was found in the Honeycomb experiment in the validation task than is typically observed (e.g., Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Pickard-Jones et al., 2020). In the validation task, two versions of the Honeycomb Task were performed; one under controlled viewing conditions, producing the typical left bias seen in young adult populations; and the other on the iPad, producing a smaller left bias that correlated well with the lab-based version. For this reason, and because a left bias was not observed in the Spheres Game in adults, the validation task can provide confidence in the assertion that the reason a left bias was not observed in children is not that younger children do not have a left bias, but rather that visual search tasks are unlikely to offer sufficient sensitivity to measure this feature in any testing cohort. Although it is impossible to make any claims about the development of the left bias from these findings, we can assert that children showed no development in their priors and performed as adults did. This implies that children will have the same priors and biases as adults, but also necessitates further exploration into methods that will permit the testing of children at younger ages.

Evidence for age-related changes in light priors

Numerous studies have documented that the strength and direction of directional biases vary widely across individuals during gerontological development. For instance, Andrews et al. (2017) discovered an extensive range of variability in light priors, demonstrating that while some older adults retained a strong leftward bias in later life, some had an opposite bias of comparable magnitude, and others an overhead bias. Using various tasks, de Montalembert et al. (2010), Schmitz and Peigneux (2011), and Barrett and Craver-Lemley (2008) found that older persons had a reduced leftward bias. In a comprehensive review of the progression of pseudoneglect in adults, Friedrich et al. (2018) reported contradictory results across studies. However, there is no evidence that older adults experience less light, or systematically experience light coming from different directions than younger adults. To facilitate the formation of sex-specific assumptions about normative performance in tests of directional biases over the lifespan, Chapter 3 addressed three important gaps in the literature on age-related changes in directional biases: whether these changes are related to cognitive function, suggest healthy or pathological ageing processes, or are sex-specific.

Few other researchers have noted sex-based disparities in their findings, but some notable examples include Varnava and Halligan (2007), who showed that older women made larger leftward errors on longer lines in a line bisection task, and Chen et al. (2011), who found that women retained a leftward bias in line bisection, with men’s errors becoming more rightward. Sex-specific changes in directional biases are echoed by studies into structural and functional brain health, with men tending to have more biological ageing markers than women (Vinke et al., 2018). For these reasons, we expected that women would show a more leftward bias in Chapter 3 and retain better cognitive function.

Though men exhibited a more leftward bias than women in Chapter 3, this difference was not significant. The primary difference between men and women in this study was interaction between cognitive function and sensitivity to the orientation of the Honeycomb stimulus in the Honeycomb Task: whilst SfS-insensitive women had significantly lower MoCA scores than SfS-sensitive women, there was no difference in cognitive function between SfS-sensitive and SfS-insensitive men. This finding suggests that age-related changes in the cognitive processes associated with resolving 3-D depth from shaded stimuli are sex-specific and, as such, are biologically mediated.

Chapter 3 also demonstrated that men did not experience a different probability than women of classifying centrally bisected trials on the Landmark Task as leftward deviations, but people who were sensitive or insensitive to the honeycomb stimulus did. This finding broadly supports the work of other studies in this area. For example, a sex-specific relationship was detected between performance on sensory tasks and cognitive function in a multisensory integration task: Hernández et al. (2019) revealed that higher MoCA scores were related to lower sensitivity to an audio-visual illusion that relies upon slower multisensory integration, demonstrating that people with higher MoCA scores processed visual and auditory stimuli faster. In this task, men were less susceptible to the illusion than women at longer stimulus onset asynchronies. Their reduced susceptibility to the illusion was thought to be unrelated to unisensory processing abilities, instead revealing a mechanistic difference in cognitive-sensory processing between the sexes. Although we require more evidence to conclusively state the nature of the relationship between performance on the Honeycomb Task, brain lateralisation, and cognitive function, these results confirm the value of disaggregating psychophysical measures by sex and measures that may indicate cognitive function.

In Chapter 3, we concluded that the processes governing sensitivity to the orientation of the honeycomb stimulus when making shape judgments are likely different from the lateralised attentional processes measured via the Landmark task, given that neither sex, nor an interaction between sex and sensitivity to the honeycomb stimulus, was observed on the probability of classifying centrally bisected trials as leftward deviations.

Relation of age-related changes to biologically mediated processes

In Chapter 3, we observed a left bias in the assumed light direction in men and a smaller left bias in women. We had expected the opposite pattern of results because of the research suggesting that women exhibit more leftward performance in lateralised tests in older age (e.g., Chen et al., 2011; Varnava & Halligan, 2007). We did expect that women would have better MoCA scores than men because same-aged women tend to score slightly higher on the MoCA than men (Al-Yawer et al., 2019; Engedal et al., 2021; Thomann et al., 2018). To assess whether better performance on the MoCA and the direction of the light source bias are related to brain health, future experiments should deploy brain imaging methods alongside the behavioural paradigm. For example, structural magnetic resonance imaging would be appropriate to establish the presence of lesions and assess the integrity and volume of areas along visual pathways (Fjell & Walhovd, 2010). Diffusion tensor imaging (DTI) has shown clear linear declines in white matter fractional anisotropy with increasing age (Sullivan & Pfefferbaum, 2006) and would therefore be suited to explore the microstructure of white matter circuitry and the health of anatomical connections. We would expect to see indications of biomarkers of ageing such as lesions, reduced cortical volume and reduced anisotropy that correlate with worse MoCA scores and performance on this task. Because the research shows that women have fewer biological markers of ageing in their brains than same-aged men (Vinke et al., 2018), we would assume that women would have fewer biological markers of ageing and better MoCA scores. If future versions of this experiment replicate the reduced left bias in women, alongside better MoCA scores and fewer brain abnormalities than men, this would suggest that age-related reductions in the left bias indexes healthier ageing processes.

We invited participants to return and repeat the MoCA and Honeycomb Task after one year had passed, hoping to show longitudinal changes in MoCA scores and within-participant changes in the bias. Only seven participants returned to repeat the experiment, limiting the scope of analyses that could be undertaken and the conclusions that could be reached from their data. A slight decrement in MoCA scores was observed. Surprisingly, given the original prediction that the bias would become less leftward with increasing age, a substantial leftward shift in the assumed light direction was also observed. Nevertheless, the sizeable leftward shift agrees with the overarching finding from Chapter 3: that lower MoCA scores correlate with a more leftward assumed light direction.

Some, but not all, age-related increases in brain abnormalities, such as periventricular hyperintensities (Matsubayashi et al., 1992) and white matter abnormalities (Gunning-Dixon & Raz, 2000), have been found to correlate with declines in neuropsychological function scores. However, many older adults have asymptomatic brain abnormalities, such as infarcts, cerebral aneurysms, and benign tumours (Vernooij et al., 2007), and exhibit typical behaviours or cognitive performance lying below the symptomatic detection threshold (Cole & Franke, 2017). Women are more likely to have metabolic disease phenotypes due to illnesses such as diabetes or cardiovascular disease (Dubno et al., 2013), which are two other illnesses that can raise the risk of cognitive impairment (Calvo-Ochoa & Arias, 2015) and vascular pathologic changes in the brain. Therefore, screening for hormone levels and metabolic diseases in future iterations of these tests is vital to quantify the relationship between age, sex, health, and brain lateralisation.

Lower oestradiol levels in postmenopausal women have been connected to worse cognitive function, and postmenopausal hormone alterations have been related to a higher risk of Alzheimer’s disease in women (Ryan et al., 2012). In addition to affecting later-life disease susceptibility and progression, hormones may have another role in cognition. Many body tissues, including the brain, are sexually dimorphic because of the effects of gonadal steroid hormones, which shape tissues in foetal development, during puberty, and in adulthood (Cahill, 2006). Visual perception is an example of a non-reproductive behaviour that is subject to sex-specific cellular and morphological alterations in the brain due to changes in circulating steroid hormones over the lifetime (Handa & McGivern, 2015). One example of a sex difference in vision is protanopia and deuteranopia colour blindness, which is inherited differently in men and women (Rodríguez-Carmona et al., 2008). Some sex differences in visual perception have been shown to be caused by the arrangement of gonadal steroid hormone receptors on cortical pathways that process objects and movement (Goldman et al., 1974; Handa & McGivern, 2015), which could explain the common finding that, on average, women are better with object discrimination and men are better at spatial processing (Jones & Healy, 2006; Overman, 2004; Silverman et al., 2007). There is cross-species evidence for sex differences in elements of visual perception: studies using artificial hormones on monkeys show that early androgen exposure is necessary to develop sex-related patterns (Overman et al., 1996). For example, castrated male monkeys do equally well on the object discrimination task as uncastrated female monkeys but perform worse on object position tasks. In object position tasks, castrated and androgen-treated females function on par with males, but perform worse than untreated females in object discrimination (Overman et al., 1996). Cross-species evidence for aspects of behaviour that we consider sexually dimorphic supports a biological view of sexually dimorphic differences in the developmental trajectory of visual perception abilities observed in Chapter 3 and reinforces the need to sex-disaggregate data. In conjunction with this research, more investigation into hormone levels is required. If it is possible to explain the relationship between lateralisation and cognitive performance more explicitly and accurately, then measures of lateralisation may show more clinical utility as an index of one's biological brain age rather than chronological age (Ahadi et al., 2020).

There are other animal models for vision that support a nativist account of priors, including the ability to perceive shape-from-shading. Hess (1950) raised chicks from birth in an environment in which light was perpetually placed below the chick, offering no experience of light coming from above within the chicks' lifetimes. He examined pecking responses to images of grains, some of which had shadows above them and others which had shadows below them. Experimental chicks and regularly reared control chicks revealed no differences in pecking at the two types of grains photographed in the first week of life. However, as they grew older, their responses changed: experimental chicks preferred to peck grains with shadows above them, while control chicks preferred grains with shadows below them. This finding revealed that the position of the presumed light source might be acquired via practise. Building upon this work, Hershberger (1970) used a discrimination test with photos of shaded objects and the actual objects to try to reproduce Hess's study. Regardless of their prior experiences, two groups of hens raised in different light situations both demonstrated good transfer from actual to apparent convexity. Hershberger concluded that the assumption that light originates from above is innate (Rowland, 2009). This suggests that light priors may be innate or learned evolutionarily rather than ontologically.

There does not seem to be a valid ecological or behavioural explanation for differences in performance between men and women: it is unlikely that men would have developed different attentional habits than women, and there is no evidence that men and women's sensory processing ability is different in ageing (Ueno et al., 2019). The amount of light that can reach the retinae does decrease with age (Weale, 1961), but this accords with general, rather than sex-specific, declines; therefore, the difference in performance between men and women supports a biological determinant of degeneration in directional biases and light priors.

Variable findings are common in studies of lateralisation among older adults (e.g., see line bisection in De Agostini et al., 1999; Failla et al., 2003; Fujii et al., 1995) and this heterogeneity is problematic for research into the biologically mediated processes driving brain lateralisation. If the relationship between brain health and lateralisation measures can be explained, accounting for sex-specific differences in performance, the Honeycomb Task could become a simple, cheap, and efficient way to screen for cognitive health impairments. More efficient screening tests are vital to address the treatment gap in dementia diagnoses, which is a particular problem in rural communities in the UK and worldwide (e.g., Kagstrom et al., 2019; Morgan et al., 2019), and countries in the Global South, which experience significant diagnostic gaps in dementia and in which up to 90% of people living with dementia remain undiagnosed (Dias & Patel, 2009; Musyimi et al., 2021; Patel et al., 2016). Closing diagnosis and treatment gaps are crucial to enable people with dementia to maintain a higher quality of life for longer (Elliot et al., 2021), whilst they are still capable of making crucial decisions about their care and support requirements, as well as legal and financial issues. Many people living with dementia are undiagnosed and, therefore, cannot access treatments that will maintain their quality of life and cognitive health for longer (Brayne et al., 2007). Delayed diagnoses also cause people to miss the opportunity to access interventions to extend their ability to live independently; for example, pharmaceutical therapies in people with dementia provide more significant benefits to the patients when applied earlier in the disease process, before extensive degeneration has occurred (Cummings et al., 2007; Tanaka et al., 2020). As such, people with delayed dementia diagnoses enter care facilities earlier, increasing costs to individuals and taxpayers (Green et al., 2019).

The principal contribution of Chapter 3 was the relationship between cognitive function and the ability to perceive shape-from-shading in the Honeycomb Task in women only, suggesting that the processes governing shape-from-shading deteriorate in a sex-specific way. These data indicate that women either use an effective compensation technique or exhibit more brain dedifferentiation relative to men, which is consistent with the hypothesis that reduced behavioural asymmetry correlates with less-lateralised cognitive processes. Because women scored higher on the MoCA than men, the HAROLD model (Cabeza, 2002) provides a better explanation for women's reduced bias in the supposed light direction than the CRUNCH (Reuter-Lorenz & Cappell, 2008) because it implies that compensatory mechanisms are being utilised successfully. Like Chapter 2’s findings in children, these data support a biological account of directional biases.

Future research should include a more thorough evaluation of cognitive function and hemispheric lateralisation to provide more concrete support for this assertion. Changes in hormone-related brain health might drive declines in brain lateralisation; however, more work is needed to definitively establish the origin of these changes, and particularly to assess the contribution of factors such as metabolic health and hormone levels to performance on tests of lateralisation and light priors. Future research should also explore when age-related changes begin to appear by examining adults aged between 30 and 60 years. We predict increasing variability and a diminished left bias with increasing age and recommend sex-disaggregating data from all age groups to facilitate a better understanding of how and when the consistent left bias observed in young adults begins to dissipate.

The LAMP task: A new test for shape-from-shading abilities?

Chapter 4 outlined a new test for the ability to perceive shape-from-shading based on the Ishihara (1962) tests for deuteranopia and protanopia. Deficits in the ability to perceive shape-from-shading have been observed in a limited number of cohorts, such as people with posterior cortical atrophy (PCA; Gillebert et al., 2013; 2015); a relatively rare condition (Schott & Crutch, 2019), often characterised as a subtype of Alzheimer's Disease (Tang-Wai & Mapstone, 2006). Deficits in shape-from-shading perception have also been observed in children whose congenital cataracts were surgically removed past critical periods for the development of visual perception (Cattaneo et al., 2011).

Although deficits have been shown to exist in these clinical groups, none have been observed in typically developing, neurologically intact populations. However, a substantial minority of participants in shape judgement tasks do not perform consistently, suggesting either bistable perception at all orientations or that the orientation of the stimuli does not systematically modulate their perception of depth from shading. In Chapter 3, a large proportion of participants fell into this category. As we screened participants using the MoCA test (Nasreddine et al., 2005), it is unlikely that we inadvertently tested people with PCA. Participants who perform atypically in shape judgement tasks do not report problems with depth perception in their daily lives. The discrepancy between their performance and lived experience might result from other depth cues compensating for deficits in their ability to perceive shape-from-shading. It is also possible that 2AFC paradigms are not appropriate for people whose ability to perceive shape-from-shading is atypical, given the likelihood of obtaining chance performance simply by guessing.

Previous work has shown that shading offers a pop-out effect (Braun, 1993; Kleffner & Ramachandran, 1992; Wolfe & Horowitz, 2004), resembling the pop-out effect for colour, though at a lower level of efficiency (Wolfe & Horowitz, 2004). Therefore, we expected that shading would offer a perceptual advantage, with shaded circles popping out from the background array of oppositely shaded circles to facilitate the swift and accurate detection of target characters. We also saw an effect of orientation in Chapter 2 in children, who detected oddball targets faster at vertical and oblique orientations; however, in Chapter 2 we suggested that it was possible that children used other cues to identify oddballs or that shape was processed pre-attentively, rather than consciously perceiving depth in the stimuli. Likewise, because the participants in the LAMP task were university students, who were required to have normal or corrected-to-normal vision, we assumed they might deploy a range of strategies to perceptually group the target circles other than shading. For example, a person might not perceive depth from shading but might be able to group the circles based on their luminance polarity. To extract the effects of grouping by luminance polarity from the ability to perceive shape-from-shading, we introduced a control stimulus comprising half-black, half-white circles (as per Ramachandran, 1988), which replicated the luminance polarity of shaded circles without a shading gradient. As expected, we observed a highly significant difference between the experimental and control trial types, indicating that shading offered a distinct perceptual advantage over non-shaded controls with an equivalent luminance polarity, suggesting an orientation effect specific to shape-from-shading.

Interestingly, both Experiment 1 and Experiment 3 showed that the difference in accuracy between experimental and control trials increased and decreased systematically (see Figures 4.11 and 4.17), with experimental trial accuracy decreasing proportionally to increases in control trial accuracy. Because all stimuli were considered free of any means of perceptually grouping target characters other than their shading gradient and luminance polarity, this suggests that an orientation of -45° is more informative only when the orientation is defined by a shading gradient and thus is an effect specific to the resolution of shape-from-shading rather than an effect of orientation. Nevertheless, the luminance polarity in half-black and half-white control circles may not offer the same cues to orientation as shading gradients.

In Experiments 1 and 3 of the LAMP study, vertically shaded circles attracted lower accuracy and slower reaction times than circles shaded at oblique orientations. This pattern of results contradicts the findings from the visual search task in Chapter 2 (and previous visual search tasks with shaded stimuli, e.g., Adams, 2007), in which a clear overhead bias was detected. It is also subtly different from the results observed in shape judgement tasks, which generate better performance at overhead and leftward, rather than oblique, orientations (see Chapter 3). Adams (2007) suggested that *perceived shape* is likely responsible for differing performance on shape-from-shading vs visual search tasks rather than orientation; however, given that the orientation of the brightest parts of stimuli is known to influence the perception of the shape (e.g., Adams 2007; Andrews et al., 2013; Andrews et al., 2017; Croydon et al., 2017; Mamassian et al., 2003; Pickard-Jones et al., 2020), the cause of systematically different performance across different tasks remains unclear.

Different orientation biases in different tasks

Various biases have been observed for orientation under different conditions. For example, human observers have previously been shown to favour cardinal (vertical and horizontal) rather than oblique orientations (Appelle, 1972), a bias thought to result from environmental regularities (Coppola et al., 1998) and driven by orientation-selective cells in the primary visual cortex (Nasr & Tootell, 2012). However, the oblique effect, or poorer performance at oblique angles, may be confined to viewing natural scenes – a view supported by imaging research showing greater activation in the parahippocampal place area when viewing cardinal orientations in natural scenes (Nasr & Tootell, 2012). However, evidence in this area is inconsistent: Hansen and Essock (2004) showed that performance was best at oblique angles in natural scenes and worse at horizontal angles. The data from this thesis supports the view that orientation biases are task-dependent: in Chapter 2, faster and more accurate oddball detection was observed at overhead, followed by oblique, stimulus orientations. In Chapter 3, the left bias observed in both groups showed an advantage for above-left orientations. Experiment 1 and 2 in Chapter 4 revealed a slight preference for stimuli shaded from oblique angles – both left and right of the apex – over vertically shaded stimuli; however, the orientations that attracted the best performance in shaded stimuli generated the worst performance in non-shaded stimuli. This discrepancy could result from conflicts between luminance polarity and an alternative orientation cue generated by the line intersecting the light and dark areas of the control stimulus. Experimenting with different control stimuli is imperative to understand why these results were observed and whether different orientation biases exist for lines versus shading. Experiment 3 in the LAMP task showed a small left bias. In all experiments in this thesis, horizontally shaded stimuli generated the worst performance.

As expected, we observed a left bias in Experiment 3 in the LAMP task: characters made from circles shaded with the lightest sections orientated to the left of the apex produced the highest accuracy scores, and the accuracy scores were significantly different to those shaded from the right. However, there was no statistically significant difference between the accuracy of left-shaded stimuli versus stimuli shaded from directly overhead. This finding agrees with shape judgement tasks, which also show a bias to the overhead and left shading directions. However, these differences were not large; it is unlikely that this task would be sensitive enough to detect slight variations in groups that do not experience difficulties with shape-from-shading perception. Also, congenitally blind people have been shown to have a robust left bias in haptic bisection tests, comparable to the visual bias of sighted participants (Cattaneo et al., 2011) and to the haptic bias of sighted people in representational pseudoneglect (Brooks et al., 2014). Chapter 4, therefore, replicated the finding that stimuli shaded from the above-left offer a perceptual advantage over other orientations in people with normal vision, which should be noted when establishing norms for future iterations of this task.

Sun and Perona (1998) suggested that left biases might result from where one prefers the sun to appear. For example, Sun and Perona found a strong correlation between what they described as the “preferred” light source direction and handedness. Right-handers were shown to have a more substantial left bias than left-handers, suggesting that right-handers might orient themselves towards the sun to avoid having their dominant hand cast a shadow over their work. They also demonstrated that most historical paintings depicting light and shadow were left-lit, suggesting that people prefer leftward lighting conditions. This finding was substantiated in a more modern context by Hutchison et al. (2011), who established that left-lit advertisements attracted a higher preference rating and greater intention to purchase than those lit from the right. However, characterising this behaviour as a “preference” might obscure a more accurate interpretation of the left bias: a preference represents a desire to have something a certain way, yet the predisposition to categorise left-lit objects as convex might be more appropriately categorised as an expectation. But rather than preferring left-lit objects, observers may find them more salient. Humans and their preferences are infinitely variable, but Western adults have a very predictable left bias when it comes to lighting, and it would be implausible to suggest that they overwhelmingly preferred the left side of space.

Although more work is required to increase the sensitivity and specificity of the LAMP task before it can be used to establish whether an observer can perceive shape-from-shading, or whether an individual's ability to perceive shape-from-shading depends upon a narrower window of shading angles than others, we did create a test with an acceptable baseline level of performance. To develop a test that offers clinical utility, the LAMP task must be made easier. Like the Ishihara Test, people with normal vision must be able to see the character effortlessly, whilst people with deficient shape-from-shading perception must either find it impossible, or impossible only at specific orientations. Additionally, we recommend exploring the control stimuli further to continue to develop the LAMP task as a test of shape-from-shading abilities in normal populations. If a control stimulus can be devised that offers greater explanatory power, this could reveal that distinct orientation biases exist for different elements of visual perception.

General conclusion

Three primary explanations exist for the left bias in the assumed light direction: visual experience, innate hemispheric asymmetry, and visual attention. The visual experience hypothesis has dominated much of the literature (Murray & Adams, 2019) for several years. However, whilst visual experience is a compelling explanation for the light-from-above prior, particularly because it is possible to change the prior temporarily through training, it is not a convincing explanation for the left bias because there is no evidence that observers experience more light coming from the left than the right. Moreover, I argue that the bias is innate for two reasons: in Chapter 2, the experimental findings clearly demonstrated that children have a light-from-above prior from the earliest age at which they could be tested, corroborating evidence from implicit tasks, such as preferential reaching (e.g., Benson & Yonas, 1973; Granrud et al., 1985; Yonas et al., 1979). Because the light-from-above prior did not change with age, it reduces the likelihood that it is formed through extended visual experience and supports an innate or evolutionary account of light priors. Previous work showing that reading direction influences directional priors (Rinaldi et al., 2014) further supports an innate account; though left-to-right readers have a consistent left bias that is consistent with their habitual reading direction, right-to-left readers are more variable. Child-friendly experiments are required to quantify the effect of reading direction on directional biases, but visual search is not a sensitive enough method to reveal directional priors.

Chapter 3 replicated the previously found wide variance in light priors in older adults, but showed that the ability to perceive shape-from-shading was correlated with cognitive function in women only. It is unlikely that women have systematically different visual experiences from men, yet the influence of sex hormones on ageing and visual pathways is well established. Therefore, visual experience is less likely to have caused the left bias or induced age-related change in the bias than innate hemispheric asymmetry and sex differences in right-hemisphere ageing. Repeating this study in right-to-left and left-to-right reading cohorts, and including additional measures such as metabolic disease screening, hormone levels, and brain imaging, would contribute to establishing age, sex, and cultural norms for measures of lateralisation, and thus provide context to understand atypical performance and greater insight into how healthy and pathological ageing processes affect the visual system.

Chapter 4’s LAMP study indicates that orientation biases in shading are different to those for luminance polarity, highlighting the need for appropriate control stimuli and suggesting different streams of processing for the orientation of different stimuli. Chapter 4 also established a baseline level of performance on a new task and identified recommendations for future task development. With further development, the LAMP Task could identify people whose ability to perceive shape-from-shading is atypical, providing additional context to the results of 2AFC tasks.

Traditional lab-based experiments offer the opportunity to control the environment and human behaviour to a greater degree than one might experience outside the laboratory. This approach leads to precise and repeatable results. However, when placed precisely 57cm in front of a screen with their head position maintained by a chinrest, participants' perceptions may not necessarily reflect their sensory experience of the world. Furthermore, when over 90% of research participants are drawn from a sample representing just 12% of the world's population – Western, educated, industrialised, rich, and democratic ('WEIRD') university students (Henrich et al., 2010) – the precise and repeatable results obtained cannot always be used to inform a generalised understanding of perception and cognition. A particular strength of this thesis is its strong emphasis on testing populations outside of typical university student cohorts. An extensive range of participants, aged from 3 to 87 years and in Wales and Israel, was sought to increase the generalisability of the observations made to the people we hoped to understand, and to enhance the ecological validity of the inferences we drew.

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Appendices

List of appendices

Appendix 2.1 Consent form for children

School of Psychology, Bangor University
Information Sheet and Consent Form

Title of Research: Investigation of the development of the depth perception in children.

Names and Positions of Investigators:

Principle Investigator: Dr Ayelet Sapir (Lecturer, Director of Masters Studies)

PhD Researcher: Beverley Pickard-Jones

BSc Researcher: Jade Fenney

Invitation:

Your child is being invited to take part in a study about depth perception. In the study children will be asked to look at a stimulus on a computer screen and search for the stimulus with a different depth. Before consenting for your child to take part in this research, it is important that you understand why this research is being carried out, and what it involves.

We are interested in understanding how 3-11 year olds respond to stimulus shading with the hope that this research will extend our current understanding of development of depth perception in children. Please feel free to contact Dr Ayelet Sapir by telephone (01248 38 8734) or by email (a.sapir@bangor.ac.uk) at any point, should you have any questions regarding this research.

What is the purpose of the study?

The main purpose of this study is to track the development of depth perception. Literature suggests that the ability to use cues, such as light and shades, in order to see depth, is acquired in different times during development.

Task:

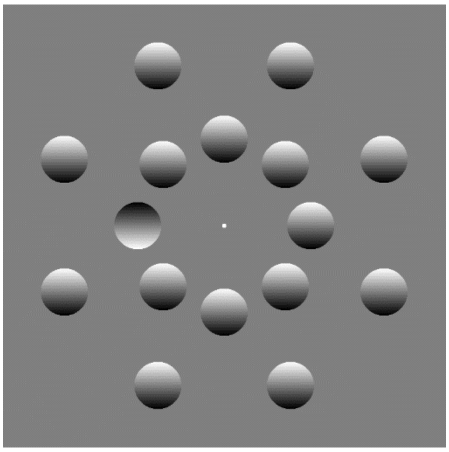
We would like to collect data from children aged 3-11 years old.

Children will be asked to take part in shaded-stimulus games like the example below. They may also be asked to create a picture using magnet figures, match pictures composed of shapes to similar shapes, and read a few lines of text.

The tasks will take place in a room provided by the school and will take no longer than 20 minutes including breaks. Children will be taken out of class for this short period of time in agreement with their teacher. In each session there will be two ‘grown-up helpers’ (the Experimenters) who will show the child the visual stimulus on the computer screen.

Visual Stimulus sample

Here the child will be asked to decide if there is a circle that looks different from the others. Some of the pictures will contain an odd circle and some will not.



Does my child have to take part?

Whether or not you wish your child to take part in this study is entirely your choice. Your child may withdraw from the study at any point, and should they show any signs of discomfort or tiredness, we will immediately end the testing session. Moreover, if you change your mind and prefer that your child’s results should not to be part of the study after their participation, just contact the principle investigator (a.sapir@bangor.ac.uk) stating the results of your child to be excluded from our study.

What are the possible disadvantages and risks of taking part in this study?

There are no risks associated with participation in this study.

What are the possible benefits from taking part?

There are no direct benefits associated with participating in this study, however the data collected could benefit our understanding of development of depth perception in children.

Will my child’s data be confidential?

Yes absolutely. All data collected will be anonymous and the recorded response will be coded with a participant number. The results will be analysed in ways as to make the connection between your child and their data impossible.

Will my child receive compensation for his or her time in taking part in this study?

Your child will be given a small token of participation (such as stickers or crayons) and a certificate for participation.

Contact for further information

We welcome any questions that you may have about any aspect of this study or your child's participation in it. Please contact the Principle Investigator of this research, Dr Ayelet Sapir on 01248-388734 or by email (a.sapir@bangor.ac.uk)

Complaints

If any complaints arise concerning the conduct of research or practices of the researchers, these should be addressed to Mr. Hefin Francis School of Psychology, Brigantia Building, Bangor University, Bangor, Gwynedd, LL57 2AS.

Please retain this information sheet for your records.

Thank you for your consideration.

****Please fill out the consent form for the participation of your child****

Appendix 2.2a. Statistics for non-significant findings in Chapter 2 (reaction times)

Table 2.2a: Statistics for non-significant comparisons between conditions on the Spheres Game (dependent variable: reaction times in seconds), including the page where the non-significant result was reported.

Comparison	Statistic	Page
Age group * target orientation (all age groups)	F (2, 104) = 0.79, p = .457	50
Age group * target orientation (age groups 3-5)	F (2, 86) = 0.12, p = .899	52
Reading groups	F (1, 86) = 0.12, p = .726	52
Reading direction * age * target orientation	F (2, 86) = 0.47, p = .625	52

Appendix 2.2b. Statistics for non-significant findings in Chapter 2 (accuracy)

Table 2.2b: Statistics for non-significant comparisons between conditions on the Spheres Game (dependent variable: accuracy), including the page where the non-significant result was reported.

Comparison	Statistic	Page
Age * orientation (all age groups)	F (2, 89) = 1.34, p = .723	54
Age * orientation (age groups 3-5)	F (12, 89) = 1.34, p = .192	55
Reading groups	F (1, 89) = 0.01, p = .924	55
Age group * reading direction * orientation	F (6, 89) = 0.01, p = .995	56

Appendix 3.1. Consent form for older adults

Title of Research: Investigation into the assumed light source.
Ethics study number: 2010-1102-A14155

Names and Positions of Investigators:
Ayelet Sapir, PhD. Lecturer
Beverley Pickard-Jones, PhD student

The nature of the research project
You are being asked to participate in a research study. It is being conducted by Dr. Ayelet Sapir, a lecturer in the School of Psychology at Bangor University, and is run by Beverley Pickard-Jones. Our goal is to better understand perceptual processes and discover how people perceive the light source in ambiguous stimuli.

Procedures of the study
If you decide to volunteer, we will present some visual stimuli on the computer screen and ask you to press a key in response to these stimuli. For example, you will need to judge whether the shape of the object is concave (hollowed inward) or convex (bulging outward). In addition, you may be asked to complete some paper and pencil tasks. The test may take up to an hour and you will have breaks every 5-10 minutes. No language is involved in the test but the instructions will be given in English.

Benefits and harms of procedures
Risks: These tests are neither painful nor dangerous in any way. They do not involve any drugs, surgery or experimental treatment. They will in no way interfere with any medication or other therapy. None of the equipment used is in any way dangerous.
You may find some of the tests to be fatiguing, boring or frustrating: If so the testing will be stopped at any time you request.

Benefits: It is unlikely that you will benefit directly from your participation.

Compensation: If you should decide to participate, you will receive 2 SONA credits or £7 for your participation.

Incidental Findings:

The tests in this study are being performed to answer research questions and are not designed as diagnostic instruments. However, people who suffer from memory or thinking problems have a greater chance of having difficulties performing the tests. Therefore, a physician affiliated with the research team will review the results if these indicate that there may be an issue relevant to your health. If the physician concludes that it may be useful to share the findings with you, you will be given the opportunity to meet the physician, discuss the findings and what medical follow-up may be indicated. The disclosure of an abnormal result may cause you emotional distress. If you do not wish to be contacted, even in the case of an abnormal result, you have the option to let us know this is so.

Confidentiality and anonymity

The scientific information obtained from these experiments may be published in scientific papers, but your name will not appear in any public document, nor will the results be published in a form which would make it possible for you to be identified.

Further information

If you have further questions you can contact Dr. Ayelet Sapir (a.sapir@bangor.ac.uk 01248-388734).

Right to Refuse or Withdraw

Participation in the study is entirely voluntary, and participants are free to refuse to take part or withdraw at any time without penalty.

Complaints

In the case of any complaints concerning the conduct of research, these should be addressed to Mr Huw Ellis College Manager, Brigantia, Penrallt Road Bangor University, Gwynedd, LL57 2DG

Consent

☐ I agree to participate in this study. I have been given a copy of this form and had a chance to read it.

☐ I DO NOT want to be contacted in the event of an abnormal result.

Signature: ____

Date: ____

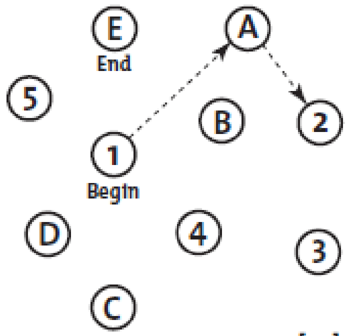
Signature of Investigator: _______________________________

Appendix 3.2. The MoCA Test (Nasreddine et al., 2005)

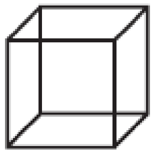
MONTREAL COGNITIVE ASSESSMENT (MOCA)

NAME :
Education : Date of birth :
Sex : DATE :

VISUOSPATIAL / EXECUTIVE



[ ]



Copy cube

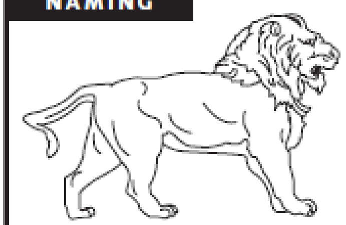
[ ]

Draw CLOCK (Ten past eleven)
(3 points)

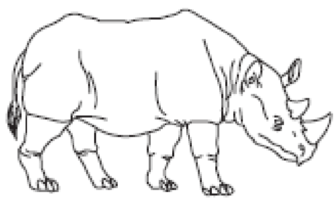
[ ] Contour [ ] Numbers [ ] Hands

POINTS ___/5

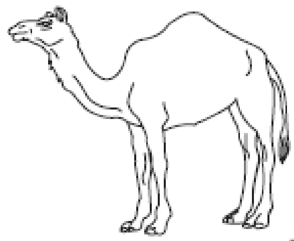
NAMING



[ ]



[ ]



[ ]

___/3

MEMORY

Read list of words, subject must repeat them. Do 2 trials. Do a recall after 5 minutes.

	FACE	VELVET	CHURCH	DAISY	RED
1st trial					
2nd trial					

No points

ATTENTION

Read list of digits (1 digit/ sec.). Subject has to repeat them in the forward order [ ] 2 1 8 5 4
Subject has to repeat them in the backward order [ ] 7 4 2 ___/2

Read list of letters. The subject must tap with his hand at each letter A. No points if ≥ 2 errors
[ ] F B A C M N A A J K L B A F A K D E A A A J A M O F A A B ___/1

Serial 7 subtraction starting at 100 [ ] 93 [ ] 86 [ ] 79 [ ] 72 [ ] 65
4 or 5 correct subtractions: **3 pts**, 2 or 3 correct: **2 pts**, 1 correct: **1 pt**, 0 correct: **0 pt** ___/3

LANGUAGE

Repeat : I only know that John is the one to help today. [ ]
The cat always hid under the couch when dogs were in the room. [ ] ___/2

Fluency / Name maximum number of words in one minute that begin with the letter F [ ] ____ (N ≥ 11 words) ___/1

ABSTRACTION

Similarity between e.g. banana - orange = fruit [ ] train – bicycle [ ] watch - ruler ___/2

DELAYED RECALL

		FACE	VELVET	CHURCH	DAISY	RED	
	Has to recall words WITH NO CUE	[ ]	[ ]	[ ]	[ ]	[ ]	Points for UNCUED recall only
Optional	Category cue						
	Multiple choice cue						

___/5

ORIENTATION

[ ] Date [ ] Month [ ] Year [ ] Day [ ] Place [ ] City ___/6

www.mocatest.org

Normal ≥ 26 / 30 TOTAL ___/30
Add 1 point if ≤ 12 yr edu

Appendix 4.1 Questionnaire on website to collect demographic and eligibility data.

Choose ID

Email

Age

Sex/gender

- ☐ Female
- ☐ Male
- ☐ Transwoman
- ☐ Transman
- ☐ Non-binary

First language

Second language

Do you have any known neurological conditions?

Education

- ☐ Left school at or before age 11
- ☐ Completed some or all of high school
- ☐ Undergraduate qualifications (e.g. Bachelors)
- ☐ Postgraduate qualifications

Are you mainly:

- ☐ Left handed
- ☐ Right handed

Do you have any problems with your vision?