



Behavioural and electrophysiological correlates of lightness contrast and assimilation

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**Behavioural and Electrophysiological Correlates of Lightness Contrast and
Assimilation**

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Abstract

Lightness contrast and lightness assimilation are examples of the perception of a surface being influenced by surrounding areas. In contrast, a grey target is perceived lighter when neighbouring a dark surface, and darker when neighbouring a light surface. The reverse is true for assimilation. The general aims of this thesis were to investigate contrast and assimilation in parallel, using behavioural and electrophysiological methods to examine the responses. The first part of the project used a matching-chart method to assess the effect of depth separation on the perception of stimuli shown to elicit either contrast or assimilation, making a direct comparison between the effect on contrast and on assimilation. The second part of the project developed a forced-choice (lighter/darker) task to investigate the electrophysiological (ERP) responses associated with contrast and assimilation, thus investigating the time course of the associated neural processing, and whether contrast and assimilation result from different underlying processing.

Throughout the studies, contrast effects were stronger with white inducers, whereas assimilation effects were stronger with black inducers. Both contrast and assimilation effects were disrupted when the target and inducer were separated by depth. When comparing contrast and assimilation responses, there was a difference in N1 amplitude in the left occipital area, but this was only apparent in one condition. Within other conditions, the P1 amplitude decreased as the strength of contrast effects increased and increased as the strength of assimilation increased. When comparing between conditions, a stronger contrast effect (white inducers) resulted in smaller amplitude than a weaker contrast effect (black inducers). The observation that both effects change after depth separation despite the 2D retinal image remaining equivalent, and the ERP activity throughout occipital and parietal areas suggest that contrast and assimilation require processing at the cortical level, rather than retinal processing alone.

Dedication

To those who helped this come to be;

To old friends, lost along the way;

And to new friends, who found me.

Acknowledgements

I would like to thank my supervisors, Naira, Alessandro, and John, for their time, feedback, and for each bringing their own expertise to this project. I have learnt from each of them in different ways, both specifically relating to this work, and things to apply more generally.

I would also like to thank my colleagues in the PhD office for various elements of practical and moral support over the last 4+ years. Particular thanks go to Gary, for much-needed comradeship and guidance in getting to grips with the EEG lab.

There would be no data without the contribution made by my various research participants, so I'd like to express gratitude to them all (especially those who sat through long EEG sessions). I'd also like to thank Lee and Dan for providing technical support – and sometimes moral support too!

My family deserve special thanks for continued support throughout the time I have spent on this project. I'd particularly like to thank my dad, Ian, for being an essential voice of reason, for proofreading tricky paragraphs; and for making sure I always had space for time away.

I would also like to thank James, for teaching me to tame a dragon and reminding me of the rewards of perseverance.

Finally, I would like to give thanks to Linda, who helped me to get started in psychology and perception, and who would have been so proud to see this come together.

Candidate's Statement

The work presented in this theses is solely my own work, and has not been submitted for any other award. A complete list of references to material cited, and acknowledgements of those contributing to the progress of the project have been included.

Table of Contents

Abstract	2
Dedication	3
Acknowledgements	4
Candidate's Statement.....	5
Table of Contents	6
Table of Figures	11
Chapter 1: Introduction	14
1.1. Defining Contrast and Assimilation.....	15
1.2. Theoretical Accounts of Contrast and Assimilation	18
1.2.1. Low-level physiological explanations.....	19
1.2.2. Attributing contrast and assimilation to different levels of processing.....	21
1.2.3. Higher-level explanations.	24
1.3. Behavioural and Psychophysical Investigations of Contrast and Assimilation	32
1.3.1. The effects of the luminance of surfaces.....	32
1.3.2. The effects of surface size.....	38
1.3.3. The effects of depth and distance.....	41
1.4. Neurophysiology of Lightness Perception	43
1.4.1. Findings from neuroimaging studies.....	48
1.4.2. Findings from electrophysiological studies.	50
1.4.3. ERP investigations of lightness effects	52
1.5. Aims and Scope of the Project	55

Chapter 2: The Effects of Depth Separation on Lightness Contrast and Lightness

Assimilation	58
2.1. Method.....	60
2.1.1. Participants.....	60
2.1.2. Design and stimuli.	60
2.1.3. Procedure.	63
2.2. Results.....	64
2.3. Summary and Discussion.....	66
2.3.1. The effects of depth separation.	68
2.3.2. Asymmetries associated with colour of inducers.....	69
2.3.3. Perceptual grouping and figure-ground segmentation	70
2.4. Conclusion.....	72
Chapter 3: Considerations for the ERP Task and Methodological Studies	73
3.1. Brief Overview of ERPs.....	73
3.2. Participants.....	74
3.3. Task Design.....	75
3.4. Stimulus Design – Methodological Studies	76
3.4.1. ‘Contrast’ stimuli – large inducer.	78
3.4.2. ‘Assimilation’ stimuli – small inducers.	79
3.4.3. Fixation.	80

3.4.4. Control stimuli and practice trials.....	81
3.5. Task Procedure and Inter-Stimulus Interval	82
3.6. Stimulus Presentation and EEG Recording Equipment	83
3.7. ERP Analysis Methodology	84
3.8. Quantification of ERP Measurements.....	86
3.8.1. Amplitude.	86
3.8.2. Latency.....	87
3.9. Statistical Considerations and the Jackknife Approach	87
3.10. Methodology Summary.....	89
Chapter 4: ERP Study	90
4.1. Method.....	91
4.1.1. Participants.....	91
4.1.2. Design and stimuli.	91
4.1.3. Procedure.	93
4.1.4. Electrophysiological methods.	94
4.2. Results: Behavioural Data.....	96
4.2.1. Response Type	96
4.2.2. Categorical representation of response type data.....	98
4.2.3. Response time (RT) data.....	100
4.3. ERP Data.....	104
4.3.1. Making comparisons between pairs of conditions.....	104
4.3.2. Contrast versus assimilation responses within the ‘Black Large’ condition	108

4.3.3. Contrast versus assimilation within the ‘White Small’ condition	112
4.3.4. Contrast responses in the ‘Black Large’ condition and the ‘White Large’ condition.....	117
4.3.5. Assimilation responses in the ‘Black Small’ condition and the ‘White Small’ condition.....	121
4.3.6. Assimilation responses in the ‘Black Large’ condition and the ‘Black Small’ condition.....	124
4.3.7. Contrast responses in the ‘White Large’ condition and the ‘White Small’ condition.....	127
4.3.8. Overall comparison of contrast versus assimilation responses	129
4.4. Correlations between Behavioural and ERP Measures.....	129
4.5. Summary.....	131
Chapter 5: General Discussion.....	133
5.1. Overview of Key Findings	133
5.2. Direction and Magnitude of Contrast and Assimilation Effects (Behavioural/Psychophysical Data)	135
5.3. Speed of Contrast and Assimilation Responses	139
5.4. ERP Responses when specifically comparing Contrast and Assimilation.....	141
5.4.1. Effects of electrode cluster, independent of response type.....	143
5.5. ERP Responses concerning the Inducer Colour.....	144
5.6. ERP Responses concerning the Stimulus Configuration	145
5.7. Brain-Behaviour Correlations	146

5.8. Theoretical Implications and Future Directions.....	148
5.8.1. P1 amplitude as a possible marker of the strength of the contrast/assimilation effect. 149	
5.8.2. Different patterns of responses in the ‘Black Large’ and ‘White Small’ conditions.	149
5.9. Limitations of the Current Work.....	150
5.10. Concluding Comments.....	152
References	154
Appendix 1 – Ethical Approval and Associated Documents	172
Appendix 2 – Distribution of Responses per Condition in the ERP Study.....	183

Table of Figures

Figure 1.1. Examples of lightness contrast and lightness assimilation.	16
Figure 1.2. Descriptions of lightness effects in ‘absolute’ and ‘relative’ terms.	17
Figure 1.3. An example of Adelson's (1993) stimulus.....	21
Figure 1.4. A representation of the anchoring explanation of the simultaneous lightness contrast effect.	23
Figure 1.5. Coren's reversible figure.....	25
Figure 1.6. A demonstration of the role of perceptual belongingness in lightness contrast.	27
Figure 1.7. The Benary cross.	28
Figure 1.8. ‘Pincushion’ display used by De Weert and van Kruysbergen (1997).....	29
Figure 1.9. An example of the checkerboard stimulus used by Maertens, Wichmann, & Shapley (2015).	30
Figure 1.10. The physical stimulus of the painted dome used by Li and Gilchrist (1999; and a representation of how this stimulus is perceived.....	33
Figure 1.11. An example of the type of stimulus used by Rudd and Zemach	34
Figure 1.12. An example of figure-ground segmentation affecting lightness.....	37
Figure 1.13. Boyaci et al. (2014)'s examples of 'contiguous' and 'non-contiguous' stimuli.....	40
Figure 1.14. Retinal cells from rod/cone receptor cells, up to retinal ganglion cells.....	45
Figure 1.15. The visual pathway from the retina, via the optic nerve, to the LGN and then visual cortex	46
Figure 1.16. Examples to show Craik-O'Brien-Cornsweet illusion; and White's illusion	48
Figure 1.17. Example ERP waveform.....	51

Figure 1.18. The variant of the Craik-O'Brien-Cornsweet stimulus and control stimuli used by Sulykos and Czigler	54
Figure 2.1. Conditions used in study 1	61
Figure 2.2. Photographs of the experimental set-up	62
Figure 2.3. Example matching chart.	63
Figure 2.4. Mean difference between baseline and perceived luminance of the target for each condition	65
Figure 3.1. The stimulus and comparison square, as presented in the tasks.	77
Figure 3.2. Inducer-surrounded-by-target and target-surrounded-by-inducer stimuli.	79
Figure 3.3. 'Assimilation' stimuli with and without lines added.	80
Figure 4.1. The four stimulus conditions: White Large and Black Large inducers, and White Small and Black Small inducers.	92
Figure 4.2. The stimulus and comparison square presented above and below the centre of the screen.	93
Figure 4.3. Electrode clusters in their relative positions.	95
Figure 4.4. Mean number of each type of response in each condition.	97
Figure 4.5. Mean RT for each type of response within each condition, separated according to whether a participant's response was consistent or inconsistent.	101
Figure 4.6. Overall mean RT for contrast and assimilation responses in each condition	102
Figure 4.7. ERP waveforms as averaged into clusters for contrast responses and assimilation responses in the 'Black Large' condition.	109
Figure 4.8. Mean amplitude and latency for contrast responses and assimilation responses in the 'Black Large' condition.	111

Figure 4.9. ERP waveforms as averaged into clusters for contrast responses and assimilation responses in the ‘White Small’ condition	114
Figure 4.10. Mean amplitude and latency p for contrast responses and assimilation responses in the ‘White Small’ condition	115
Figure 4.11. ERP waveforms as averaged into clusters for contrast responses to Black Large and White Large conditions.....	118
Figure 4.12. Mean amplitude per condition (Black Large; White Large), hemisphere, and cluster for the time periods of P1, N1, and N2.....	120
Figure 4.13. ERP waveforms as averaged into clusters for assimilation responses to Black Small and White Small conditions.....	122
Figure 4.14. Mean amplitude per condition (Black Small; White Small), hemisphere, and cluster for the time periods of P1, N1, and N2.....	124
Figure 4.15. ERP waveforms as averaged into clusters for assimilation responses to Black Large and Black Small conditions.....	126
Figure 4.16. ERP waveforms as averaged into clusters for contrast responses to White Large and White Small conditions.....	128

Chapter 1: Introduction

The ability to perceive objects and surfaces is central to the process by which individuals can interact with their environment. A significant proportion of the brain's structure is dedicated to processing visual input, which initially arrives as light either directly from a light source, or reflected from the surfaces in the environment. The perception of a surface does not always correlate with the physical properties of the surface. 'Lightness' is the perceptual correlate of the 'reflectance' (proportion of light reflected by a surface), and therefore relates to a property of the surface of an object, rather than the illumination under which the object appears. Lightness is a specific case within colour perception which describes situations where a surface reflects all wavelengths of light equally (i.e. achromatic surfaces that would be described as 'white', 'grey', or 'black') as opposed to those surfaces which reflect different proportions of each wavelength of light and result in chromatic perception (e.g. red being perceived for light with wavelengths of ~635-700 nm; green for 520-560nm). A surface does not appear in complete isolation, however, and may appear illuminated by light of any intensity (or indeed colour). The physical qualities of reflectance and illumination are amalgamated into 'luminance', which is the stimulus for lightness perception and can be measured in cd/m^2 (candela per square metre: the derived SI unit of luminance).

The retina is not able to separate reflectance from illumination in the raw stimulus (luminance) which it receives. In addition to the tangled contributions made by reflectance and illumination, perception is further complicated by the fact that the lightness of a particular surface can be influenced by the areas surrounding that surface, and by the context within which the surface is perceived (e.g. Adelson, 1993; Agostini & Galmonte, 2002; Gilchrist, 1977; Kingdom, 2011; Koffka, 1935). Thus, the lightness value perceived for a surface can vary considerably, depending on

the context. This has led to many examples of 'illusions' which rely on demonstrating a discrepancy between a physical measurement and a perceived quality. The study of instances where the perceived quality of a surface does not exactly correlate with the physical measured properties of the surface can lead to a more detailed understanding of the mechanisms by which lightness perception occurs.

1.1. Defining Contrast and Assimilation

Lightness contrast and lightness assimilation are examples of phenomena in which the lightness of a surface is influenced by the context within which that surface is perceived. The contrast phenomena is well-known and is perhaps one of the oldest and most studied phenomena in visual perception, having been described and investigated for over two millennia (Kingdom, 1999; see also Wade, 1996). In lightness contrast, the perceptual quality of a surface appears to shift away from that of its neighbouring surface: a grey surface appears darker when it borders a light surface and lighter when bordering a dark surface (see Figure 1, top row). Conversely, in lightness assimilation, the perceptual quality of a surface appears to shift towards that of its neighbouring surface: a grey surface appears lighter when bordering a light surface and darker when bordering a dark surface (Figure 1.1, bottom row shows an example of an assimilation effect known as the 'von Bezold effect'). Given that assimilation can be thought of as an effect which operates in the opposite direction to that of contrast, the relationship between contrast and assimilation presents an intriguing paradox in visual perception, whereby surfaces of the same luminance can produce different percepts under different conditions.

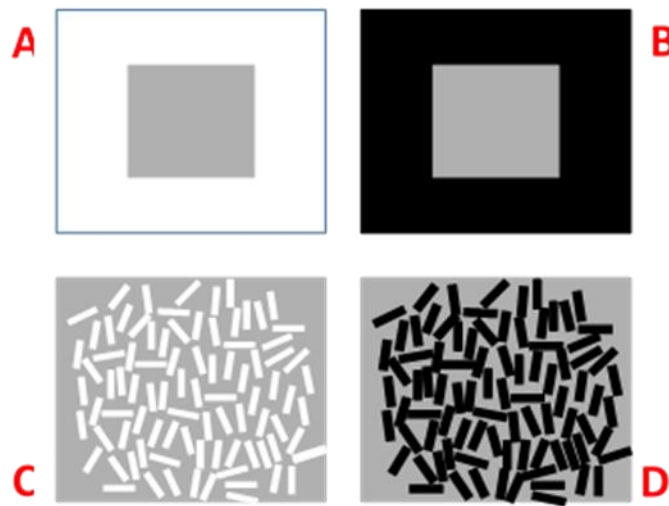


Figure 1.1. Examples of lightness contrast and lightness assimilation. Top row: An example of lightness contrast, in which the grey surrounded by white (A) is perceived to be darker than a physically equivalent grey surrounded by black (B). Bottom row: An example of lightness assimilation, in which the grey square is perceived to be darker with the black (D) inducers than with the white inducers (C).

In discussing these lightness effects, it is also important to define the use of the terms ‘direction’ and ‘strength’ to describe the effects. The term ‘direction’ of effect will be used to refer to whether a lightness effect is categorised as a contrast or an assimilation effect. This is not to be confused with a target being perceived to be darker or lighter than its physical luminance or reflectance value. More intuitively perhaps, the terms ‘strength’ and/or ‘magnitude’ are used to describe the size of the over- or under-estimation of the difference in lightness between a target and inducer. The definitions outlined above reflect ‘absolute’ definitions, in that contrast and assimilation are defined in relation to the difference between the perceived lightness of a target and the physical properties of the stimulus. This is typically measured in terms of a difference between the luminance of the target (measured by a photometer) and the luminance chosen by an observer to match the target (as shown in the left example of Figure 1.2). Contrast and assimilation have also been defined and discussed in more ‘relative’ terms, for example, an effect defined in terms of the relative perceived difference between a target neighbouring black and a physically-identical target neighbouring white (thereby not referring to the physical luminance value of the

targets and making a measurement in terms of a difference between the luminance values chosen by an observer to match each of the two targets, as shown in the right example of Figure 1.2).

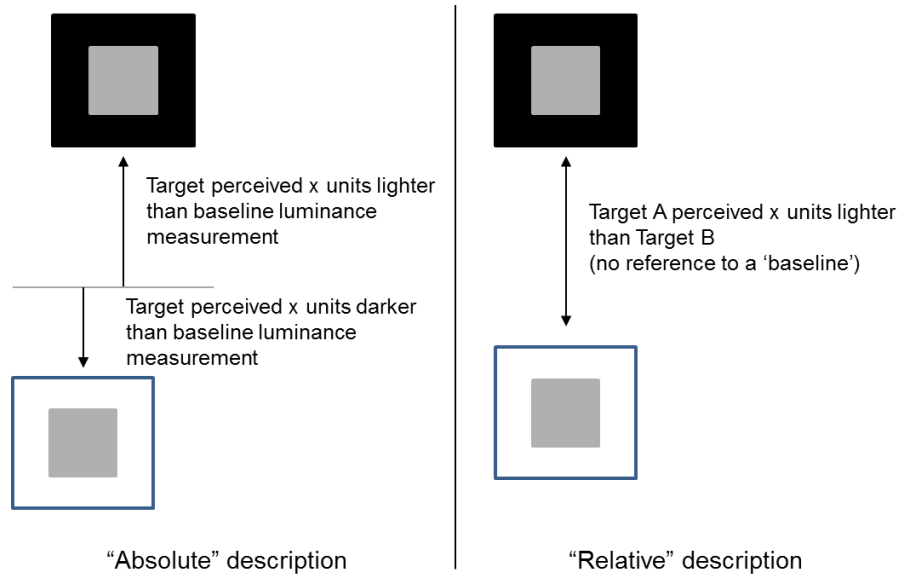


Figure 1.2. Descriptions of lightness effects in ‘absolute’ and ‘relative’ terms.

Although often described separately in the literature, Kingdom (2011) stated that ‘contrast’ and ‘assimilation’ can be regarded as descriptors for the direction of lightness effects rather than as concepts signalling entirely different underlying mechanisms. Previously Helson (1963) had raised a similar point, arguing that, rather than being entirely separate and opposite phenomena, contrast and assimilation may actually be parts of a ‘continuum’ of lightness phenomena, which includes a region in which neither contrast nor assimilation occurs. The question of whether there are two completely distinct processes – one of contrast and one of assimilation – or whether both are manifestations of a single underlying process was also raised by Kanizsa (1979), who made a paradoxical observation that, although in contrast the grey appears darker with white than with black ($A < B$; see corresponding stimuli in Figure 1.1), and in assimilation the grey appears lighter with white than with black ($C > D$), observers stated that the two greys neighbouring white were equal to one

another ($A=C$); likewise the two greys neighbouring black were equal to one another ($B=D$). This observation prompts the question of whether contrast and assimilation are distinct processes operating in opposing directions (i.e. in $A<B$ and $C>D$), or whether a single underlying process which operates differently, hence leading to different results, when the perceptual comparison is changed.

1.2. Theoretical Accounts of Contrast and Assimilation

A starting point towards an examination of the phenomena of contrast and assimilation is to establish the physical conditions under which they each occur. The examples shown in Figure 1.1 can be considered 'prototypical' examples of the contrast and assimilation effects which will be discussed throughout this work. A striking difference is the size, spatial frequency (in terms of the pattern, measured in cycles per spatial unit), or configuration of the black and the white inducers. In these cases, the large inducers (A and B) typically produce contrast; whilst smaller and more scattered or 'fragmented' inducers (C and D) typically produce assimilation. Kanizsa (1979) described the fragmentation, or 'dispersion', of the inducing elements as the necessary condition for assimilation to occur rather than contrast. Spatial frequency and size of the inducers placed on grey targets is a factor which, from a physical perspective (i.e. the properties of the stimulus itself), can produce a 'shift' from contrast to assimilation (Helson & Joy, 1962; Helson, 1963; Kanizsa, 1979; Smith, Jin & Pokorny, 2001).

However, the psychological factor(s), relating to perceptual processing rather than the physical properties of the stimulus, which underlie the occurrence of contrast and assimilation have not been widely agreed upon in the literature. Several branches of explanation exist which aim to account for the 'shift' between contrast and assimilation, spanning a range of 'low-level' physiological factors which take place at retinal level, to 'higher-level' perceptual/cognitive factors which take into account the wider context of

the image. These will be discussed in more detail in the following three sections, beginning with explanations of contrast and assimilation which rely on 'low' physiological/retinal levels of processing, before moving on to explanations featuring a mix of 'low' and 'high' level processing, and those depending on 'high' level neural processing.

1.2.1. Low-level physiological explanations.

Traditionally, illusory lightness phenomena such as contrast and assimilation have been explained in terms of low-level visual mechanisms such as lateral inhibition, and neuronal spatial integration within centre-surround receptive fields (DeValois & DeValois, 1975; Hurvich & Jameson, 1966; 1974; Jameson & Hurvich, 1975). For example, Jameson and Hurvich (1975) attributed both contrast and assimilation to interactions between the receptive fields of retinal ganglion cells. They describe a "physiological contrast mechanism" whereby differences between adjacent surfaces in the retinal image are enhanced as a result of spatial antagonism in centre-surround receptive fields, thereby producing an overestimation of the difference in lightness between the two surfaces. Assimilation, according to Jameson and Hurvich, results when surfaces of different colours lie within a receptive field in such a way that the cell responds as though the colours are superimposed, thereby making them appear more similar to one another. This is consistent with the observation that assimilation tends to occur in stimuli with higher spatial frequency as, in high spatial frequency displays, any given receptive field is more likely to contain parts of both the inducer and the target colour.

The Oriented Difference of Gaussians (ODOG) model (Blakeslee & McCourt, 1999, 2004; Blakeslee, Cope, & McCourt, 2016) aimed to account for brightness perception in terms of early visual processing, using spatial frequency selectivity,

orientation selectivity, and contrast gain control. The model consists of a series of filters, composed of a central excitatory region with outer inhibitory regions, which are tuned to particular stimulus features (i.e. spatial frequency and orientation). Lightness effects occur due to attenuation of low spatial frequencies (resulting in contrast effects) and contrast normalization, in which different outputs are equated (resulting in assimilation effects). This model suggests that lightness effects each fall on part of a continuum of stimuli (Blakeslee, Pasioka, & McCourt, 2005), which can be explained by the same set of principles, largely based on low-level physiological processing of the properties of the stimulus.

However, authors such as Adelson (1993), have observed that geometric modifications such as changing the shape, spacing, or orientation of the elements in a scene can produce dramatic changes in the lightness of surfaces within the scene. Figure 1.3 shows one such example, in which identical grey patches appear to undergo a lightness change when the luminance of those patches remains the same but the geometry of the stimulus is changed. When the local manipulation of a stimulus has not changed, such as the edge adjacencies and surface luminance, low-level mechanisms would be unaffected by the modifications made. In light of this, Adelson argued that some lightness changes cannot be explained by this type of model. Other studies have also provided evidence suggesting that peripheral, low-level theories, particularly which do not incorporate depth information, do not account for all instances of lightness contrast (e.g. Agostini & Galmonte, 2002; Agostini, Murgia, & Galmonte, 2014; de Weert & van Kruysbergen, 1997; Economou, Zdravković, & Gilchrist, 2015; Kingdom, 2011; Todorović & Zdravković, 2014).

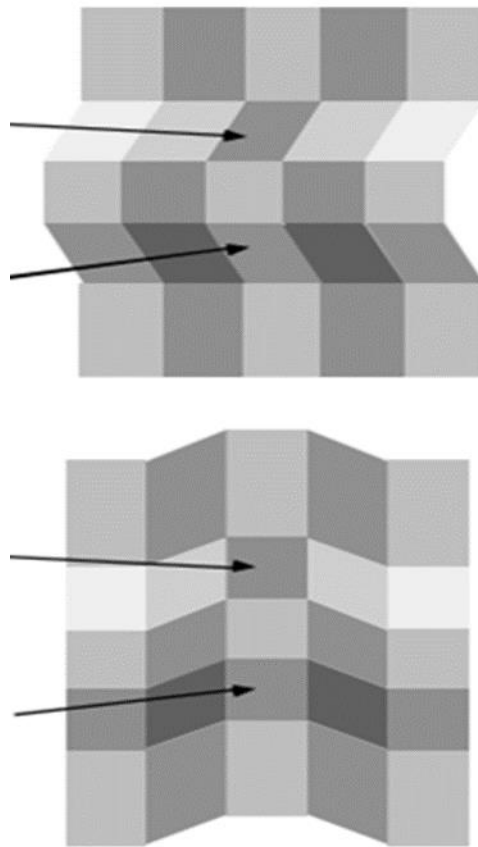


Figure 1.3. An example of Adelson's (1993) stimulus. The luminance of the identical targets (indicated by arrows) and their surrounding areas has not changed, but the change in the geometric arrangement results in a lightness change.

1.2.2. Attributing contrast and assimilation to different levels of processing

Evidence suggesting that low-level mechanisms could not account for lightness contrast accumulated before similar evidence for assimilation was reported. This has led some theories, such as Anchoring theory, which is the focus of this section, to suggest that lightness contrast and lightness assimilation can be attributed to different levels of processing. More specifically, contrast is attributed to higher-level processing mechanisms, and assimilation to lower-level processing mechanisms.

Anchoring theory (Gilchrist et al., 1999) gives an account of the way in which higher-level principles, including perceptual grouping-based frameworks, can contribute to an explanation for contrast, in the form of the simultaneous lightness contrast display. According to the anchoring theory, surface lightness can be predicted by a highest-

luminance rule and an area rule. The highest-luminance rule states that the surface with the highest luminance in a display will appear white, and the apparent lightness of other surfaces in the display depend on their relationship with the white region. This rule is modified for displays where the area rule is relevant, in which the surface with the largest area will take on the lightest appearance.

For more complex images, local and global 'frameworks' are essential in explaining lightness perception. 'Frameworks' in the original description of anchoring theory (Gilchrist et al., 1999) are defined in terms of Gestalt principles of perceptual grouping, and perhaps descended from Koffka's (1935, pp. 246) discussion of lightness, perceptual organisation, and belongingness or 'appurtenance'. Koffka stated that "The more [surface] x belongs to the field part y , the more will its whiteness be determined by the gradient xy ", and that the strength of belongingness depends on "factors of space organisation". Thus, the lightness of a surface is determined in relation to other surfaces, depending on the strength of belongingness between those surfaces. These ideas plant the seeds for the concept of frameworks based on perceptual organisation; and the strength of influence of an anchoring surface depending on the strength of the belongingness between the anchoring surface and the other surfaces in the frameworks. More recently, Zdravković, Economou and Gilchrist (2012) noted that frameworks can also be conceptualised as a region of the visual scene which is perceived as having a single, common level of illumination. Thus, surfaces, whether or not they are retinally adjacent to one another, can be grouped together on the basis of a shared single level of illumination or on the basis of perceptual grouping factors such as proximity and similarity.

Lightness anchoring does not take place solely within-frameworks, however - it is also dependent on interactions with other frameworks in the scene - as Gilchrist

(2014) describes it, a 'codetermination compromise' between frameworks. The way in which frameworks in this context operate can be thought of as a 'resurrection' of Kardos's (1934; in Gilchrist, 2014) codetermination principle (the lightness of a surface is determined by a combination of its immediate field of illumination and the adjacent field of illumination), with the modification that frameworks in the context of anchoring theory are organised in a hierarchical or embedded manner, such that the local framework(s) lie within a larger global framework. Within each framework, the apparent lightness of a surface can be computed using the previously-outlined highest-luminance and area rules. The anchoring theory proposes that the lightness of a given surface is predicted by a weighted average (in terms of the strength of each framework) of the lightness values predicted for that surface in each framework to which it belongs (an example is shown in Figure 1.4).

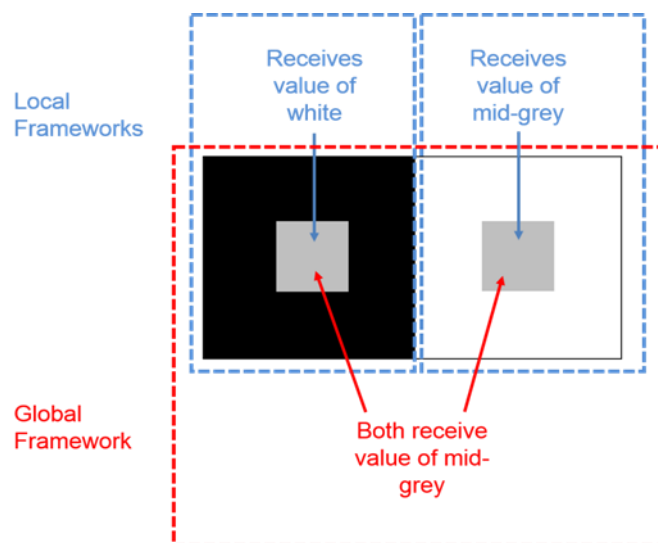


Figure 1.4. A representation of the anchoring explanation of the simultaneous lightness contrast effect. Lightness values are computed within local frameworks (blue) and the global framework (red) and a 'compromise' between the surface's values in each of these frameworks gives the perceived value.

This anchoring within- and between-frameworks is how Gilchrist et al. accounted for the occurrence of simultaneous lightness contrast – in terms of high-level processing which assigns a lightness value to a target surface by combining local and global anchoring of lightness values in the display. The perceived difference between

two physically-identical targets in the simultaneous contrast illusion is said to arise as a result of a weighted average of the targets' apparent luminance in the local framework, and that in the global framework (see Figure 1.4).

The anchoring theory is unable to account for assimilation in a comparable manner - instead assimilation is conceptualised as a result of peripheral processing, in the form of a 'relatively low-level kind of space-averaged luminance' mechanism (Gilchrist et al., 1999, p. 802), which hints at the involvement of retinal processes such as those outlined by Jameson and Hurvich (1975), described in the previous section. Thus, under this theory, contrast and assimilation are thereby attributed to different levels of visual processing.

1.2.3. Higher-level explanations.

The importance of higher-level processing has been increasingly recognised as more examples of lightness phenomena which cannot be accounted for by low-level mechanisms alone have been reported and investigated, for example 'reversed' contrast effects (Agostini, Murgia, & Galmonte, 2014). Thus, theories about the factors underlying contrast and assimilation have moved somewhat away from low-level physiological mechanisms, and instead take into account more global, contextual factors. Higher-level factors include figure-ground segmentation, perceptual grouping, and the effects of depth and three-dimensional context.

In a relatively early example, Coren (1969) showed that figure-ground segmentation can affect the perceived lightness in a given display. In a reversible stimulus (shown in Figure 1.5), contrast occurred to a stronger extent with a grey surface perceived as figure than when the same size and shape grey surface was perceived as ground, suggesting that the perception of a surface as 'figure' makes that surface's lightness more likely to undergo a stronger contrast effect relative to its

respective 'ground'.



Figure 1.5. Coren's reversible figure. When the 'rabbit' was perceived as figure, the grey underwent a greater contrast effect than when the image was rotated so that the 'faces' were perceived as figures and the grey as ground.

Further to this, allocation of attention to the different surfaces within a display has also been suggested to explain a shift from contrast to assimilation. In conditions where attention is explicitly directed to the grey surface (such as a lightness-matching task), contrast has been found to occur, even in response to stimulus displays which would give rise to an assimilation response in a forced-choice task (Festinger, Coren & Rivers, 1970). This suggests that, while contrast occurs when attention is directed to the grey surface, assimilation only occurs when attention is caught and held by the other surfaces (i.e. black/white inducers) in the display, and not directed to the grey surface. Festinger et al. suggested that the reason that Coren (1969) observed differences in the strength of contrast but did not observe any assimilation responses in his study was due to the methodology. Coren's participants were required to match the grey in the display with another grey, thereby directing attention towards the grey, and producing contrast, whereas assimilation may have occurred had attention not been directed to the grey. This is consistent with the observation that assimilation is facilitated by observing a stimulus without rigid fixation, such that attention is not specifically directed to the grey

(Burnham, 1953). These findings imply that the occurrence of contrast and assimilation is not independent of, and does not precede, the separation of figure and ground or in fact the allocation of attention to a particular surface within the image.

The influence of attention is acknowledged in ‘edge-integration’ theories, proposing that lightness perception occurs as a result of edge detection and edge integration. A ‘higher-level’ neural representation of the visual scene is produced by a physiological detection of local edge structure and spatial integration (Rudd, 2013; Rudd, 2010), and lightness values are computed from a weighted sum of the responses of edge detector neurons in visual cortex. Edges are detected early in visual processing, and weighted according to attentional influence, followed by spatial context influence, before edge integration occurs. Intermediate processing, between the weighting and integration aspects, includes additional factors such as figure-ground segmentation and perceptual grouping.

Perceptual grouping is another factor which contributes to lightness perception. This is not a new idea - almost a century ago, Fuchs (1923), in reference to chromatic (colour) assimilation, argued that assimilation is a sign that elements have been grouped as part of one perceptual unit. However, when two discrete surfaces or perceptual units are grouped (i.e. according to Gestalt grouping principles), the luminance of a surface is likely to contrast with the luminance of the other surfaces with which it is grouped. For example, Agostini and Proffitt (1993) reported that lightness contrast was elicited when surfaces were perceptually grouped by common fate and/or figural alignment, that is, a grey target circle belonging to a group of white circles was perceived as darker than a grey target circle belonging to a group of black circles. Thus, surfaces’ lightness contrasts with that of the surfaces with which they are perceptually grouped.



Figure 1.6. A demonstration of the role of perceptual belongingness in lightness contrast (Agostini & Galmonte, 2002). The grey squares in this figure undergo a contrast effect in relation to the corners of the cube rather than in relation to the background upon which they lie.

Contrast effects produced due to higher-level factors such as perceptual belongingness have been found to override the effects produced due to lower-level contrast between the edges of neighbouring surfaces. For example, Agostini and Galmonte (2002) demonstrated that perceptual belongingness prevails over local contrast in displays such as Figure 1.6, where the lightness of a target underwent a contrast effect with the elements with which it was perceptually grouped, rather than contrasting with the background on which it was presented. Using variants of the Benary cross (Figure 1.7, Benary, 1924), Vergeer and van Lier (2011) have also provided evidence to suggest that global and local perceptual organisation can mediate perceived differences in the lightness of surfaces.

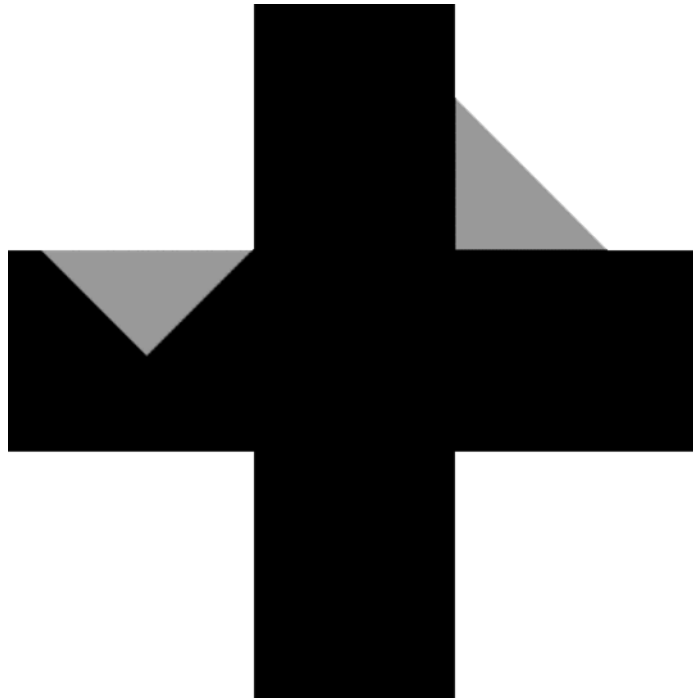


Figure 1.7. The Benary cross. The two grey triangles are equal in luminance and are surrounded by the same amount of black and white, but they appear different in lightness. Vergeer and van Li (2011) showed that changing the position of the triangles could affect the lightness of the triangles.

The effect of perceptual belongingness on the direction of lightness effects has also been found to depend on the intentionality (i.e. intentional vs non-intentional attentional focus on one part of the image) and grouping stability (i.e. stable belongingness vs multi-stable or reversible belongingness) of the display (Murgia, et al., 2016). Murgia et al. reported that contrast is more likely to occur when perceptual grouping is non-intentional and/or stable; whereas assimilation is more likely to occur when perceptual grouping is intentional and/or multi-stable. In addition, Murgia et al. reported that the perceptual outcome (i.e. contrast or assimilation) is also dependent on the luminance of inducers: white inducers favour contrast whereas black inducers favour assimilation. Conversely, contrast effects with black inducers, and assimilation effects with white inducers are more susceptible to being reversed by a change in the intentionality or stability of the perceptual grouping.

In addition to the two-dimensional arrangement of a stimulus, coplanarity (a shared depth plane between surfaces) in a display can also be used as a proximity-based

perceptual grouping mechanism. Depth separation has been used in investigations of the level of processing at which lightness effects occur. It has been suggested that if there is no difference between the lightness of a surface in a coplanar display, and the same surface in a retinally-equal, non-coplanar display, then lightness processing must occur at a lower level of processing, prior to the processing of depth (Gibbs and Lawson, 1974; Julesz, 1971). Conversely, when a lightness effect is altered or eliminated by separating surfaces into different depth planes, this has been argued to suggest the involvement of higher-level processing (Gilchrist, 1977; Gogel & Mershon, 1969; Mershon, 1972; Soranzo et al. 2010).

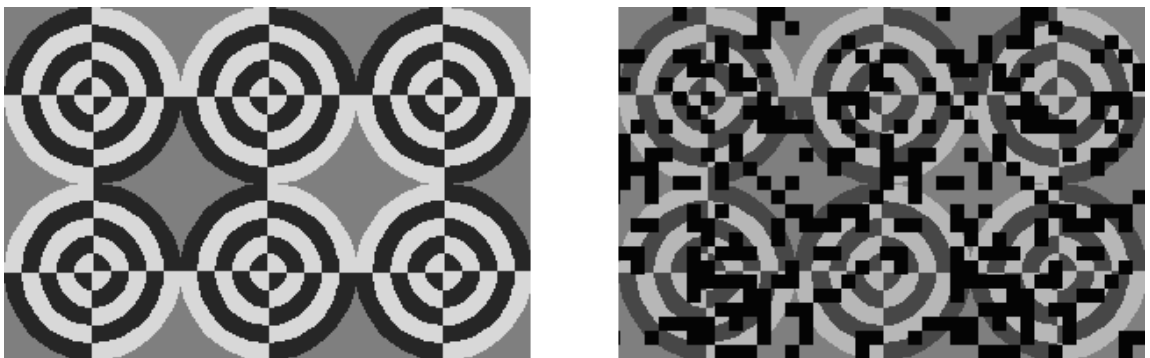


Figure 1.8. 'Pincushion' display used by De Weert and van Kruysbergen (1997). Left: An assimilation display (the pincushion surrounded by black appears darker than the pincushion surrounded by white). Right: Spatial noise added to the assimilation display (the assimilation effect is weakened).

One example of an effect of depth separation is that when spatial noise is added, coplanar with a display, it weakens the assimilation effect usually experienced, but that when the spatial noise is presented in a different depth plane to the pincushion display, the original strength of the assimilation effect is retained (De Weert & van Kruysbergen, 1997; see Figure 1.8). This provides further evidence to suggest that assimilation occurs later than the cognitive processes which separate surfaces in different depth planes, as the assimilation effect was only disrupted when spatial noise was added to the same depth plane. De Weert and van Kruysbergen also observed that when red and green discs are presented on a white background, the background appeared reddish when the

green inducers were perceived in a different plane, closer to the observer. Vice-versa, the background appeared greenish when the red discs appeared closer to the observer. This suggested that depth separation between surfaces may affect colour contrast and assimilation. In this display however, both the green and red inducers were presented at the same time. Therefore, it could be argued that the effect could have arisen from a contrast effect, from the segregated discs; or an assimilation effect, from the coplanar discs. To control for this, the two colours of inducers must be tested separately.

Following this, Soranzo, Galmonte and Agostini (2010) performed an experiment aimed at measuring separately the effects of two types of inducers (in this case black versus white inducers). Using a stereoscopic technique to manipulate the distance between inducers and the target, Soranzo et al. found that contrast effects occur in stimuli with high spatial-frequency inducers if they are non-coplanar with the target, and assimilation effects occur when the inducers and target are coplanar. This result strongly supports the importance of higher-level mechanisms for both contrast and assimilation because the retinal image would be equivalent in the coplanar and non-coplanar conditions.

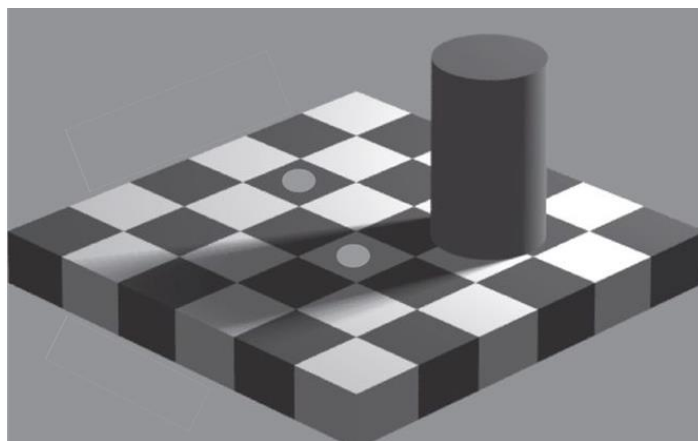


Figure 1.9. An example of the checkerboard stimulus used by Maertens, Wichmann, & Shapley (2015). The discs undergo an assimilation relative to the squares they lie on – even though those squares do not differ in terms of luminance, only in terms of lightness.

In addition to depth separation of surfaces, the wider three-dimensional context within which a surface is perceived can also impact lightness. Using the ‘checkerboard illusion’, Maertens, Wichmann & Shapley (2015) placed clear and blurred-edge discs on top of the equiluminant target squares, such that the discs were surrounded by surfaces that were equal in luminance (although the squares differ in lightness). The perceived difference between the two grey discs goes in the direction of assimilation: the disc on the perceived-lighter square appears lighter than the disc on the perceived-darker square (see Figure 1.9). The effect was found to be weaker in a display with the same luminance relationships, but without the cues to depth and detail of the checkerboard display. This provides evidence to suggest that the perceptual interpretation of a display with three-dimensional geometry and variety of different surface reflectances, contributes to a stronger assimilation effect. As the physical features of the stimuli were held constant, this provides strong evidence to suggest that higher-level processes must be involved in producing these effects. In this example, the lightness of two identical patches appears different, despite them sharing the same luminance as each other *and* being placed on squares of equal luminance. This also suggests that the target surfaces are affected by the *lightness* (not luminance) of their immediate surround.

The types of processing involved in contrast and assimilation has largely been investigated in behavioural and psychophysical studies, i.e. those which investigate the effect of specific stimulus manipulations on the perception of the stimulus, which will be outlined in more detail in the next section. Investigation of the types of processing from a neurophysiological perspective has not been done as extensively, but relevant examples will also be reviewed in section 1.4.

1.3. Behavioural and Psychophysical Investigations of Contrast and Assimilation

The effects of manipulations such as colour, intensity, or luminance; size, spatial frequency or articulation; and separation of elements by distance or depth can be mapped onto key features of the anchoring theory (Gilchrist et al., 1999) such as the luminance rule, area rule, and frameworks, respectively. Each of these will be discussed in more detail in the following sections. Contrast has arguably been studied more systematically than assimilation, though some studies have begun to bring these two phenomena together to outline parallels and differences between them. The following sub-sections will review the existing literature investigating the ways in which luminance, size, and separation of surfaces influence contrast and assimilation effects.

1.3.1. The effects of the luminance of surfaces.

Highest-luminance rule.

According to the anchoring theory (Gilchrist, 2014; Gilchrist et al., 1999), the highest luminance in a framework is used as an 'anchor', in relation to which the other surfaces in the framework are assigned a relative lightness value. The concept of a highest-luminance rule predates the proposal of anchoring theory, having featured in the work of Wallach (1948) and Land and McCann (1971). The highest-luminance rule has outlived the 'Grey World' hypothesis (Helson, 1943; 1964), a similar concept which suggested that the average luminance in the scene is perceived as a middle-grey, and the lightness of other surfaces in the scene are 'anchored' relative to this. In Bressan's (2006) double anchoring theory, the lightness of a surface is derived from a weighted average of the lightness values assigned in each framework which it belongs to, relative to *two* anchors. The first of these anchors is the highest-luminance in the framework, which operates as delineated in the original anchoring theory. The second anchor is a

surround-luminance anchor. This refers to the region that perceptually groups with the target surface - this is not necessarily adjacent to the surface in the retinal image.

Arguably the best evidence for a highest-luminance anchor comes from Li and Gilchrist's (1999) 'dome' studies. In a dome-shaped visual field featuring nothing but one line separating a region painted black and a region painted mid-grey, Li and Gilchrist found that observers reported these regions to be middle-grey and white, respectively. Thus, the part of the surface with the highest physical luminance (i.e. the painted mid-grey) is perceived as white, and the other part of the surface is assigned a lightness value in relation to this anchor, as shown in Figure 1.10. The highest luminance rule is consistently favoured over the average-luminance rule (e.g. Bruno, 1992; Bruno, Bernardis, & Schirillo, 1997; Cataliotti & Gilchrist, 1995; Schirillo & Shevell, 1993), though Anderson, Whitbread, and de Silva (2014) argued that the highest luminance is not a fixed invariant anchor point, but is rather an approximate mapping of the highest luminance onto the lightness scale.

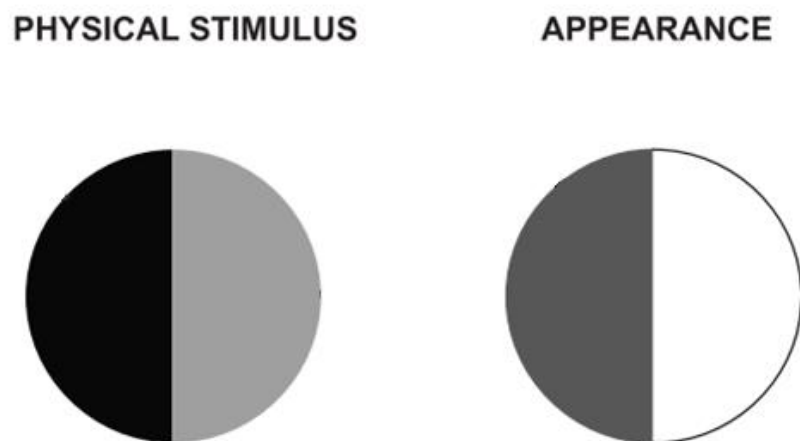


Figure 1.10. The physical stimulus of the painted dome used by Li and Gilchrist (1999; left) and a representation of how this stimulus is perceived (right).

Some evidence against the assignment of the highest lightness (white) to the highest-luminance surface in a display has also been presented. For example, Rudd and Zemach (2005) demonstrated that two identical surfaces in a display, both with the

highest physical luminance value, can be perceived to differ in lightness (see Figure 1.11). This finding is in conflict with a highest-luminance rule, which would predict that both of the equally-highest-luminance surfaces would be perceived as white. Thus, as Rudd and Zemach argued, it is plausible that the lightness of the highest-luminance surface can also be influenced by lower-luminance surfaces in the display, taking into account the spatial structure of the display (i.e. distances between the edges of the component surfaces).

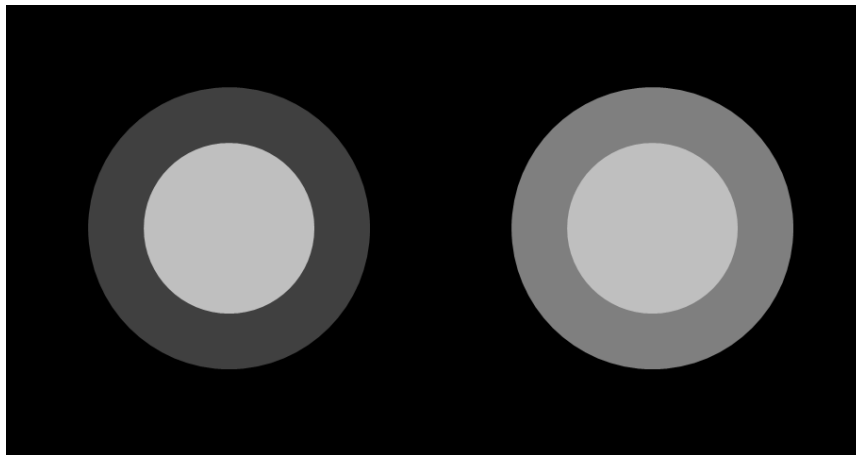


Figure 1.11. An example of the type of stimulus used by Rudd and Zemach (2005). The targets (inner circles) both have identical luminance, and their luminance is the highest luminance in the display. However, they can appear to differ in lightness.

A lot of research in this area considers only surfaces under uniform illumination. However, when part of the scene is under shadow, the surface with the *lowest* luminance in the shadowed region can serve as a reference or anchor for determining the lightness of other surfaces within the shadow (Soranzo & Agostini, 2006). Maertens et al. (2015) also suggested that the lightness, rather than luminance, of an inducing surface can affect a target surface, in a stimulus display where one inducer-target pair were shown to be in shadow.

Luminance of inducers in contrast and assimilation stimuli.

When two stimuli are presented simultaneously (as in the simultaneous contrast display), a ‘contrast’ or ‘assimilation’ effect is defined on the basis of the direction of

the perceived difference between two grey targets. In these cases, it is not possible to disentangle the effects of black inducers from the effects of white inducers. Therefore it is necessary to use a matching system external to the stimulus itself in order to examine the effects of inducer luminance independently.

Economou, Zdravković and Gilchrist (2007) showed that the ‘error’ in lightness matching (i.e. the difference between the actual luminance of the grey target and the luminance of the match selected by the participant) in the simultaneous lightness contrast display is greater for the grey target on the black background than it is for the grey target presented on the white background, in both CRT screen and paper conditions. This finding is consistent with the anchoring theory, which predicts that simultaneous contrast occurs due to ‘lightening’ of the grey on the black background, which is perceived as a ‘compromise’ between its local (white) and global (mid-grey) values. This suggests that contrast effects are stronger with black inducers than with white inducers. However, the reverse has also been shown, for example, Murgia, Prpic, Santoro, Sors, and Agostini (2016) demonstrated a stronger contrast effect with white inducers than with black inducers.

With regard to assimilation, Soranzo, Galmonte and Agostini (2010) reported that assimilation effects were stronger with black inducers than with white inducers. Assimilation appears to occur more reliably in a grey target with dark inducers than when the inducers are lighter than the grey target. In fact, Beck (1966) reported that *contrast* occurred when the reflectance of inducing-lines was higher (lighter) than that of the grey target/background, and that assimilation occurred only when the inducing-lines were darker than the grey target/background. De Weert and Spillman (1995) argued that the differences between grey targets when assimilation is taking place is a *relative* difference. That is, when compared to one another, a grey target with dark

inducers appears darker than a grey target with light inducers (i.e. an ‘assimilation’ effect) – however, when compared to an ‘external’ grey (i.e. a comparison square to match) both targets are assigned a luminance value which is lower (darker) than the actual value of the grey targets. Thus, de Weert and Spillman reported that the black inducers resulted in an assimilation effect but, in this case, a small *contrast* effect was observed with the white inducers. Further to this, there has also been a report of ‘assimilation’ displays producing a contrast effect with dark inducers, and *no* effect with light inducers (Agostini, Daris & Galmonte, 2001).

Luminance of surfaces and figure/ground segmentation.

De Weert and Spillman (1995) also proposed that the assimilation effect with dark inducers could be a result of the dark surfaces being perceived as ‘figure’ and the areas bordering the dark areas (i.e. the grey target) being perceived as ‘ground’. Following this logic, in a stimulus with black inducers, the grey target is seen as ‘ground’, because it is the lighter surface; whereas in a stimulus with white inducers, the grey target is seen as ‘figure’, because it is the darker surface.

With regards to the effect of figure-ground segmentation on lightness perception, Coren (1969) reported that whether a grey target is perceived as ‘figure’ or ‘ground’ affects the strength of a contrast effect. Coren’s results also appear to suggest that, for white and grey stimuli (compared to black and grey stimuli), there is a larger perceived difference between ‘grey-as-figure’ and ‘grey-as-ground’, though this is not explicitly tested. Festinger, Coren and Rivers (1970) extended this by reporting that contrast occurs when a grey target is seen as ‘figure’, but *assimilation* occurs when it is seen as ‘ground’. Festinger et al. proposed that this is mediated by allocation of attention to surfaces in a display, such that surfaces allocated a relatively high proportion of attention (such as ‘figures’) undergo lightness contrast, whereas surfaces

which are given less attention (such as backgrounds) undergo lightness assimilation. If de Weert and Spillman's suggestion that dark surfaces are more likely to be perceived as 'figures' is correct, then the allocation of attention to the inducers in the black-and-grey stimulus, and to the target in the white-and-grey stimulus would provide an explanation for the observation of assimilation in a black-and-grey stimulus but contrast in a white-and-grey stimulus.

When perceived as ground, a dark region appears lighter than a figure of the same luminance (Boyaci, Şimşek & Subaşı, 2014) even with equal surface area (see figure 1.12). This is consistent with other findings that 'figures' undergo a greater contrast effect than 'grounds'. Wolff (1934) reported that in displays constructed so that the luminance of figures and ground are reversed in a second display, the light 'figures' in the first display appear much lighter than the light 'ground' in the second display, and the dark 'figures' appear much darker than the dark 'ground'.

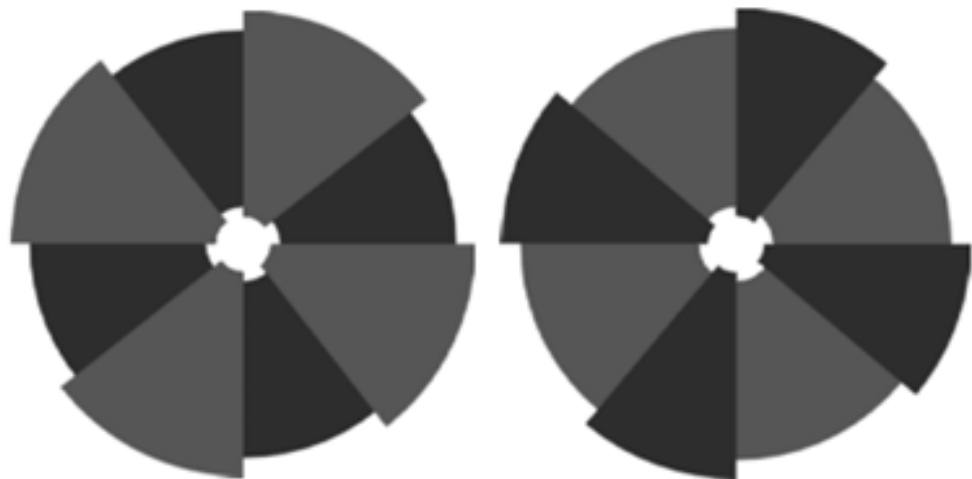


Figure 1.12. An example of figure-ground segmentation affecting lightness (Boyaci et al., 2014). In the left image, the lighter grey segments are perceived as 'figure', and are perceived to be darker than the same luminance segments in the right image, which are perceived as 'ground'.

Luminance of the target.

The anchoring theory predicts that the relationship between luminance of targets

and simultaneous contrast is such that darker achromatic targets should increase the strength of contrast. For a grey-on-black target, darkening the target would produce a larger discrepancy between the ‘local’ and ‘global’ lightness values, thus the grey-on-black target would appear even lighter. For grey-on-white targets, darkening the target would reduce the scale normalisation aspect of anchoring, because the luminance range would be larger than if the target was middle-grey. Conversely, others such as Kingdom, McCourt and Blakeslee (1997) suggest a negative U-shaped function, in which contrast is strongest when mid-grey targets are used, and weaker with both lighter and darker targets. Empirical evidence has supported the former theory's predictions over that of the latter, with the strength of contrast following the pattern predicted by anchoring theory (Economou, Zdravković & Gilchrist, 2007).

1.3.2. The effects of surface size.

The size or spatial frequency of surfaces has a large role in determining whether a target undergoes a contrast or an assimilation effect. Kanizsa (1979) described fragmentation of inducing elements as a necessary condition for assimilation to occur rather than contrast, and subsequent research has generally obtained contrast effects with low spatial frequency stimuli, and assimilation effects with high spatial frequency stimuli.

It has also been established that the size of surfaces in a display can modulate the strength of contrast effects. As described by Kanizsa (1979), a contrast effect is stronger when the inducing surface is larger than the target surface, than when the inducing surface is smaller. The effect of equivalent manipulations on assimilation-producing stimuli has received less attention, however, it can be assumed that the inverse is true, i.e. smaller inducing surfaces favour stronger assimilation effects.

Area rule.

The area rule proposed as a part of the anchoring theory (Gilchrist et al., 1999), states that increasing the area of the surface can result in a perceived lightening of that surface. In discussing this rule, Gilchrist (2006) refers to 'perceived area' (as opposed to 'physical'/'retinally visible' area) of surfaces, thus including the 'invisible' parts of occluded surfaces which are perceived by amodal completion, an idea consistent with previous findings that for lightness perception, perceived size has greater importance than retinal size (Cataliotti & Gilchrist, 1995; Bonato & Gilchrist, 1999).

Size of surfaces and figure-ground segmentation.

Koffka (1935, pp.178) described that the surface area of a surface seen as ground is perceived to be larger than the area of the surface that is actually visible. Boyaci, Şimşek and Subaşı (2014) suggested that amodal completion occurs for whichever region is perceived as ground, i.e. it 'completes' to form an occluded surface which goes behind the figure. Thus, the perceived surface area of a 'figure' is the same as the visible area of 'figure', but for 'ground', the perceived surface area may be the sum of the visible area of the 'ground' *plus* the surface area that is invisible/occluded by the 'figure' (i.e. perceived surface area of ground = visible area of 'ground' plus visible area of 'figure'). Thereby, as Bonato & Gilchrist (1999) suggest, figure-ground segmentation alters the perceived area of surfaces and has an indirect effect on lightness.

Thus, even in displays where the figure and ground surfaces are given apparently equal surface areas, the visual system may process the display in such a way that the representation of the ground is much larger than that of the figure. However, in displays which achieve opposite lightness effects (i.e. contrast and assimilation) having different configurations of inducers but the same overall surface area of inducer, then the perceived surface area of the figure and of the ground should be the same in the two types of display.

Manipulation of spatial frequency with equivalent area.

Of course, when investigating the effects of area on perceived lightness, care must be taken to avoid confounds which can be introduced by changing the size of a surface, such as differences in relative area, and in the average luminance of the stimulus as a whole. Using stimuli consisting of a circle with dark and light sectors, Boyaci, Şimşek and Subaşı (2014) investigated differences between 'contiguous' and 'non-contiguous' stimuli. 'Contiguous' stimuli consisted of only two sectors, one dark and one light. 'Non-contiguous' stimuli had sectors of the same luminance as those in the 'contiguous' stimuli, each with the same total surface area, but the sectors were split into smaller segments and interspersed with each other (see Figure 1.13). The results showed that the lower-luminance sectors appeared lighter as their total area increased. This suggests that the area rule applies for both 'contiguous' and 'non-contiguous' stimuli, taking account of total surface area rather than simply the area of one segment.



Figure 1.13. Boyaci et al. (2014)'s examples of 'contiguous' (left) and 'non-contiguous' (right) stimuli.

In addition to this, Boyaci et al. (2014) reported a difference in the functional form of the area rule between results obtained with the two sets of stimuli ('contiguous' vs 'non-contiguous'), and suggested that the judgment of lightness must occur prior to the higher-level perceptual combination of the same-luminance sectors. Although it was also acknowledged that a purely low-level mechanism would also be unable to account for the results, a role for lower-level spatial summation mechanisms was implicated for the 'non-contiguous' sectors, given the finding that, for 'non-contiguous' stimuli, the lightness effect was larger than predicted by individual area but smaller than predicted

by total combined area.

1.3.3. The effects of depth and distance.

The magnitude of an induced lightness effect such as contrast declines as lateral distance between the inducing and target surfaces increases (Cataliotti & Bonato, 2003; Blakeslee & McCourt, 2013). The anchoring theory (Gilchrist et al., 1999) would explain the effects of distance between inducers and target using the concept of frameworks. Increasing distance between frameworks weakens the 'strength' of the reciprocal effects of anchor(s) in either framework. It is not clear what effect an equivalent manipulation would have on a stimulus which tends to produce assimilation.

The use of depth separation as a method to separate surfaces within a stimulus is a way to investigate the effect of grouping and frameworks on contrast and assimilation effects. In addition, comparing coplanar and depth-separated conditions is relevant in determining the level(s) of processing involved in contrast and assimilation effects. For example, Shevell, Holliday, and Whittle (1992) described 'pre-cortical' mechanisms involving local contrast between neighbouring surfaces (see section 1.2.1), and 'cortical' mechanisms involving the influence of remote context (e.g. surfaces in different depth planes) which occurs at a higher-level of processing, after processes involved in depth perception such as binocular combination.

Coplanarity between two surfaces (i.e. two surfaces being in the same depth plane) can function as a perceptual grouping mechanism, in that two parts of a scene or image presented at the same apparent distance from the observer are perceived to belong more closely together than those presented in different depth planes (Koffka, 1935, pp.246). Although the Gestaltists did not explicitly specify coplanarity (i.e. shared depth planes) as a perceptual grouping mechanism, coplanarity can be conceptualised in terms of the Gestalt law of proximity, such that coplanar surfaces are likely to be

grouped together as a result of proximity based on depth, or perceived distance from the observer. Conversely, surfaces in different depth planes are perceived to have less proximity to one another, and therefore are not perceptually grouped together. It could be argued that differences between displays with 'figure' and 'ground' regions presented coplanar, and those with them separated by depth are due to the 'enhancement' of the perceived separation by depth of figure and ground.

The effects of depth separation on contrast and assimilation.

In stereoscopic displays, Soranzo, Galmonte and Agostini (2010) found that with small inducers, stimuli with the inducers and target presented on the same depth plane (coplanar) favour the perception of assimilation; whereas stimuli with the inducers presented at a depth plane in front of the target (non-coplanar) favour the perception of contrast. There is some evidence to suggest that the effect of depth separation differs depending on whether the target is in front of or behind the inducing surface. Relative to a coplanar condition, in stimuli where the target is perceived to lie in a depth plane in front of the inducer, the contrast effect is reduced, whereas when the target is perceived to lie behind the inducer, the strength of the contrast effect is increased (Morikawa & Papathomas, 2002). This could result from the way in which surfaces are processed as 'figures' or 'grounds', as a surface placed in front of another is likely to be perceived as the 'figure'.

Findings from stereoscopic studies appear to conflict somewhat with the findings of Wolff (1933). Wolff obtained a contrast effect for grey targets placed on darker/lighter backgrounds in the same depth plane, but observed that this effect is reduced when the targets were placed at a distance in front of the backgrounds. Instead, participants then reported that the two grey targets were equal, leading to the conclusion that contrast is strong with coplanar displays, and that contrast is eliminated in non-

coplanar displays. Thus the pattern of results is inconsistent with the trends suggested by stereoscopic studies, perhaps indicating differences in perception of real 3D stimuli compared to those presented stereoscopically.

Wolff's (1933) finding, as well as subsequent work with stimulus configurations presented in coplanar and distant conditions, has been instrumental in demonstrating that lightness contrast cannot be explained in terms of retinal processing alone. When the retinal/proximal stimulus configuration is kept identical in both conditions, but contrast is elicited in one condition and not the other, factors independent of the retinal image, namely, the spatial organisation and perceptual belongingness/relationships between the surfaces must be involved in producing the two different perceptual effects.

Regarding simple, flat, coplanar stimuli, Agostini and Bruno (1996) noted that the simultaneous contrast effect tends to be stronger when the stimulus is presented on a CRT screen than when presented using paper-based stimuli. However, when the paper stimulus is illuminated by a bright light, the strength of the contrast effects is similar with the CRT screen and the illuminated paper stimulus.

1.4. Neurophysiology of Lightness Perception

The preceding sections have covered the situations under which contrast and assimilation effects occur, and the effects of manipulating factors relating to the physical stimulus. However, an outline of the neurophysiological structures and processes involved in perceiving the lightness of a surface is also required to gain a more comprehensive understanding of how contrast and assimilation effects occur.

In order to perceive the lightness of a surface, the light reflected from the surface must be projected onto the back of the eye and reach the light-sensitive cells in the retina, known as photoreceptors (i.e. rods and cones). When light reaches the photoreceptors, these cells are hyperpolarised (membrane potential becomes more

negative), leading to the subsequent excitation of bipolar cells, and retinal ganglion cells, which ultimately transmit action potentials as the output from the retina. Bipolar cells have concentric centre-surround receptive fields, with either an OFF-centre with an inhibitory response to light; or an ON-centre with an excitatory response to light (Schiller, 1992). These can discriminate between light falling directly on its receptive field (resulting in hyperpolarization) and light falling to the side of its receptive field (resulting in depolarization). This pattern is continued in the retinal ganglion cells, which receive input from corresponding bipolar cells, providing two parallel pathways of processing luminance information. Retinal ganglion cells in particular are sensitive to differences in luminance within their receptive fields, suggesting that early visual processing is sensitive to local spatial variations in luminance, rather than absolute values. The firing rate of action potentials from a retinal ganglion cell represents the difference in the intensities of light falling upon the centre-part and surround-part of the cell's receptive field.

Interneurons mediate the path between 'sensory' photoreceptors and the 'response-transmitting' retinal ganglion cells, as shown in Figure 1.14. Bipolar cells are perhaps the simplest type of interneuron as they form the most direct ('vertical') path for signals to reach the ganglion cells. Signals can also reach the ganglion cells via more 'indirect' ('horizontal' or 'lateral') pathways, by means of horizontal cells and amacrine cells. These cells can modulate the input they receive from photoreceptors or bipolar cells, and influence the activity of surrounding cells.

The ability of cells to influence the activity of neighbouring cells provides a basis for lateral inhibition, which is often reported to underlie lightness contrast. Photoreceptor cells which are stimulated by a high-luminance (white) region will have an inhibitory effect on neighbouring cells stimulated by a mid-luminance (grey) region,

causing the grey surface to appear darker. Conversely, cells stimulated by a low-luminance (black) region will not have such an inhibitory effect on neighbouring cells. Jameson and Hurvich (1975) proposed that the receptive fields of retinal cells can account for both contrast and assimilation, however, as outlined in section 1.2.1., this explanation is not considered a sufficient explanation for all instances of these phenomena. However, the interactive effects between neighbouring cells are a good example to illustrate the point that the visual system is not dealing with simple luminance values akin to those which can be measured with a photometer, but rather operating on recognising the relative lightness of surfaces, which can be influenced by neighbouring areas.

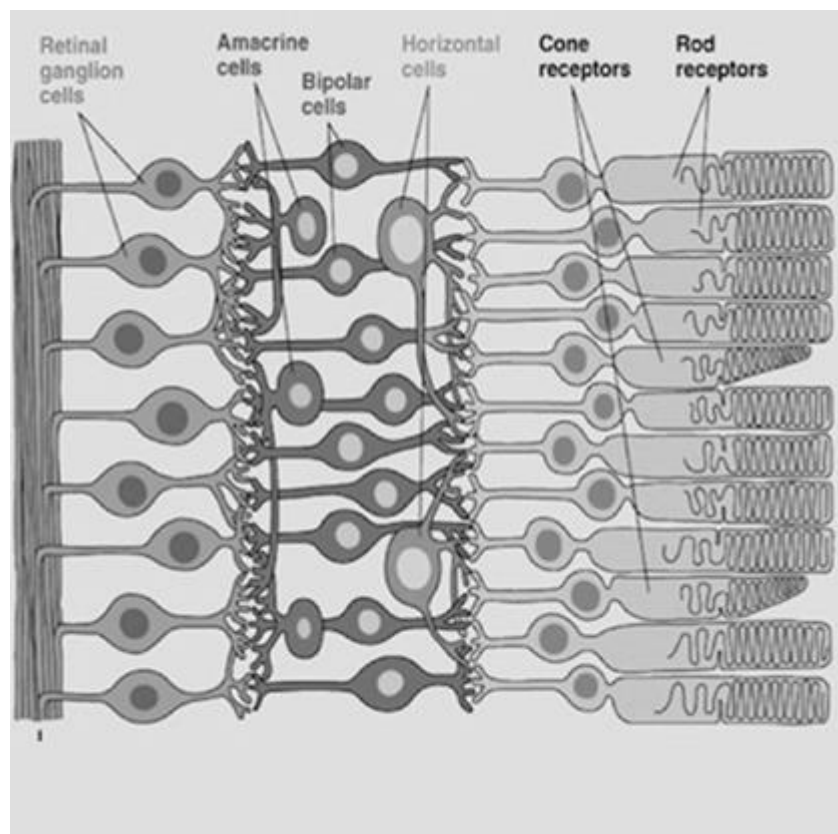


Figure 1.14. Retinal cells from rod/cone receptor cells, up to retinal ganglion cells

Visual perception of surfaces depends not only on the information extracted by the retina, but also on the way in which this information is interpreted in the higher-

level visual system. After being processed initially in the retina, incoming visual information is relayed via the optic nerve and lateral geniculate nucleus (LGN) before being processed in the visual cortex (see Figure 1.15). In the LGN, fibres from different cell types terminate in different layers, and the LGN is not thought to introduce significant functional changes to colour, brightness, or lightness perception (Valberg & Seim, 2008). In addition, surface perception relies on interactions between ON and OFF channels which appear to be segregated up to the cortical level (Schiller, 1992), which further supports the idea that lightness cannot be fully explained by low-level retinal mechanisms alone (Grossberg & Hong, 2006).

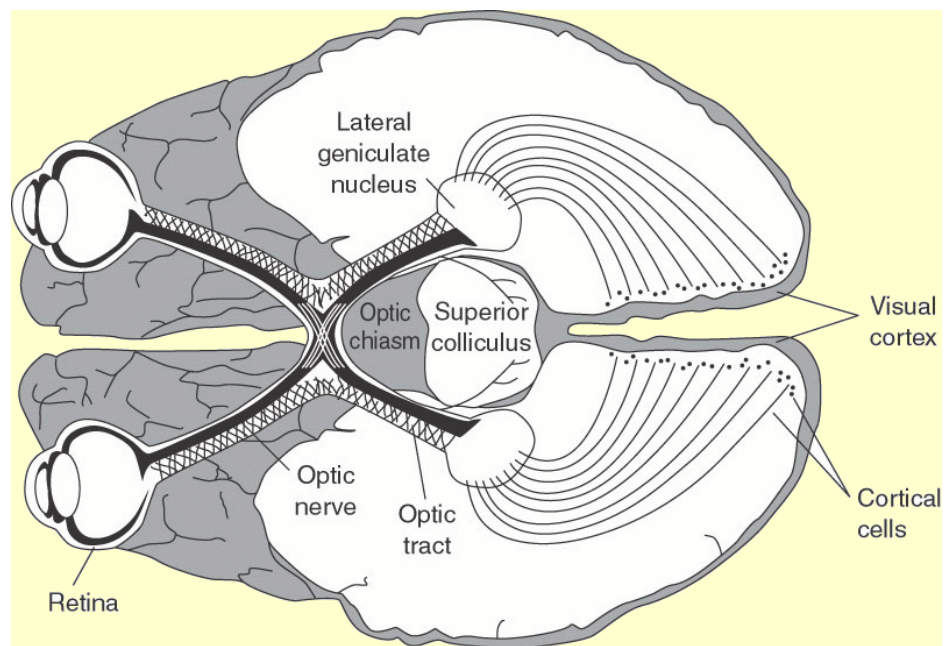


Figure 1.15. The visual pathway from the retina, via the optic nerve, to the LGN and then visual cortex (van der Helm, 2012).

The initial cortical processing takes place in primary visual cortex (area V1 in the occipital lobe). Information is also passed on to areas such as visual association cortex, including V2 and V3, which can also provide feedback information back to V1. Many of the cortical cells in areas V1 and V2 respond to edges (von der Heydt, Friedman, Zhou, & Pessoa, 2003). It has been suggested that V1 is the first point at

which information about surface lightness is represented (Kinoshita & Komatsu, 2001; MacEvoy & Paradiso, 2001; Rossi & Paradiso, 1999; Rossi, Rittenhouse, & Paradiso, 1996). Populations of neurons in V1 in monkeys have also been shown to respond selectively depending on both luminance and context, but that this activity does not directly correlate with perceived lightness (Ruff, Brainard, & Cohen, 2018).

Within ~40ms, edge detection occurs in V1, providing a sense of spatial organisation. Neurons here can respond to small changes in colour, spatial frequency, and orientation. At around 100ms and later, once feedback information is received from V2 and V3 (visual association areas), the global organisation of the stimulus is processed (Lamme & Roelfsema, 2000). The feedback connections (e.g. from areas such as V2 and V3) can modulate the V1 responses (Angelucci et al., 2003; Hupe et al., 2001) which are driven by the feedforward connections from the LGN. The later visual cortical areas have been associated with some of the 'higher-level' factors in visual perception. For example, V2 has been associated with determining figure-ground segregation (Qui & von der Heydt, 2005) and both V2 and V4 with border-ownership (Zhou, Friedman, & von der Heydt, 2000).

It is plausible that an understanding of the neurophysiological bases of lightness contrast and lightness assimilation would provide further helpful evidence in terms of delineating the types of underlying processing involved; whether the two phenomena can be conceptualised as part of the same (biological) process, or are attributable to different types of processing. However, the underlying neurophysiological mechanisms involved in perceiving context-dependent changes in lightness remain relatively unexplored. The neurophysiological section of this research will focus on cortical responses rather than earlier (e.g. retinal) processing, as lightness perception can be

of lightness in a modified version of the Craik-O'Brien stimulus (Boyaci, Fang, Murray & Kersten, 2010) and activation in V1 in response to illusory brightness in variants of White's illusion (Figure 1.16; Salmela & Vanni, 2013). Boyaci et al. also noted that the cortical activation associated with context-dependent changes in lightness is independent of attention to the stimulus.

On the basis of a finding that the perceptual interpretation of a surface strongly influences lightness assimilation, Maertens, Winchmann & Shapley (2015) made the suggestion that lightness perception, particularly with regards to assimilation, may involve higher-level cortical areas with sensitivity to perceptual organisation, such as V4 and lateral occipital areas, though as yet there is no neuroimaging evidence to support this idea.

When participants viewed changes in the brightness of a surface induced by variations in the luminance of the area surrounding the surface, fMRI signals had similar magnitude, but delayed response, in comparison to the fMRI signals observed when viewing actual changes in luminance (Boucard, van Es, Maguire & Cornelissen, 2005). Boucard et al. concluded that fMRI signals do not explicitly indicate the representation of brightness in the visual cortex, but that visual regions may be indirectly involved in surface brightness perception, and suggested further investigation of the temporal, as well as spatial, characteristics of brain activity associated with brightness perception. Pereverzeva and Murray (2008) also provided evidence to support a correlation between V1 fMRI activity and perceived lightness changes, in stimuli using modulation of the surrounding luminance to induce perceptual changes in the lightness of a target.

Findings from fMRI research provide evidence to suggest that context-related changes in lightness perception are associated with activity in brain regions associated

with early visual processing, particularly V1, which is highlighted in several of the previously-described studies. However, these findings do not give any information about potential differences or similarities between contrast and assimilation (as two types of lightness perception), nor do they indicate anything about the timing of neural activity associated with lightness perception.

1.4.2. Findings from electrophysiological studies.

Electroencephalography (EEG) is a suitable tool to investigate the temporal characteristics of the neural processing underlying the perception of contrast and assimilation. EEG uses electrodes placed on the scalp to record fluctuations in the synchronous electrical activity from large populations of neurons, specifically, pyramidal cells which are oriented perpendicular to the surface (Jackson & Bolger, 2014; Nunez & Srinivasan, 2006). These can record continuously over a period of time, with sensitivity to millisecond by millisecond changes in neural activity – thus, a high degree of temporal resolution.

The event-related potential (ERP) can be thought of as a 'snapshot' of this recorded activity, related to processing of a particular stimulus. An ERP is derived from the recorded EEG data by averaging together all of the sections of the recorded data associated with each stimulus/condition. This process of averaging removes 'noise' (i.e. activity resulting from ongoing neural processes unrelated to the stimulus, which is assumed to be random) whilst retaining the activity which is relevant to the stimulus ('signal').

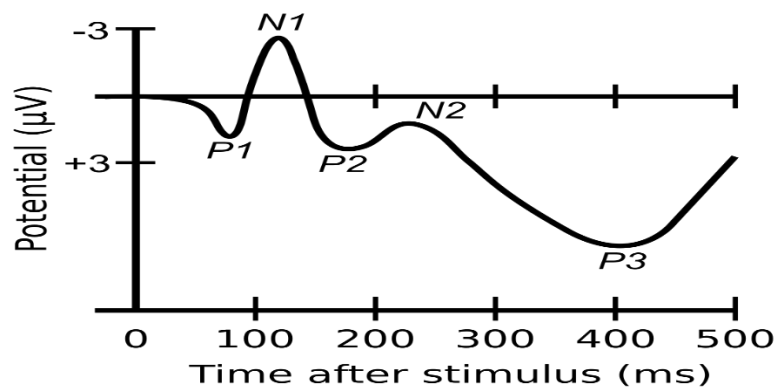


Figure 1.17. Example ERP waveform. Positive and negative deflections are numbered according to their position in the waveform.

ERP measurements are typically made by classifying sections of the waveform into 'components' or 'peaks', typically described in terms of their polarity (positive-P or negative-N) and sequence in the waveform, as shown in Figure 1.17. The first of these is 'P1', which usually represents the first positive deflection between 100-130ms post-stimulus. Many areas of the cortex are activated and contribute to the P1 time range (Foxe & Simpson, 2002), and the component has been shown to reflect stimulus features such as spatial frequency (Luck, 2014), selective attention (Hillyard, Vogel, & Luck, 1998), and arousal (Vogel & Luck, 2000), rather than higher-level or top-down processing. The amplitude of P1 can be affected by the luminance of a stimulus, with higher luminance resulting in a larger amplitude for the occipital P1 (Johannes, Münte, Heinze, & Mangun, 1995) and increased mean amplitude of the visual evoked potential (up to and including P1) as luminance increases (Fimreite, Ciuffreda, & Yadav, 2015). ERP components relating to sensory differences among stimuli are typically elicited before 200ms and are predominant in the occipital cortex (Heslenfeld, Kenemans, Kok, & Molenaar, 1997).

The P1 is followed by the N1 (approximately 150-200ms post-stimulus), which is generated in extrastriate, rather than striate, cortex (Gomez-Gonzales, Clark, Fan, Luck, & Hillyard, 1994), with occipital and parietal sources (Yamazaki et al., 2000). In

the lateral occipital area, N1 is typically larger when selective attention is enhanced (Hillyard, Hink, Schwent, & Picton, 1973), and is larger in discrimination tasks than in detection tasks (Mangun, 1995), suggesting that it reflects discriminative processing (Hopf, Vogel, Woodman, Heinze, & Luck, 2002). N1 is present in both hemispheres when stimuli are presented to the centre of the visual field (Wascher, Hoffmann, Sanger, & Grosjean, 2009) and is usually largest in the occipital electrode sites (Hopf et al., 2002). N1 amplitude can be increased when there is enhanced processing of a stimulus (Coull, 1998). The amplitude of parietal N1 and latency of occipital N1 can be affected by the luminance of a stimulus, with higher luminance resulting in a larger amplitude and shorter peak latency (Johannes, Munte, Heinze, & Mangun, 1995). N1 latency can also increase as a function of processing effort (Callaway & Halliday, 1982).

Whilst earlier components such as P1 and N1 have been associated with attention and processing, the later components such as N2 and P3 have been associated with perceptual organisation and stimulus interpretation (Sokhadze et al., 2017). Components associated with processes such as perceptual grouping and closure have a latency of 230-300ms (e.g. Doniger et al., 2000). The P2 has frequently been described in relation to visual search tasks (e.g. Philips & Takeda, 2009). The N2 has also been implicated in tasks involving shifting attention (Patel & Azzam, 2005), perceptual closure and the formation of a perceptual representation (Potts, Patel, & Azzam, 2004).

1.4.3. ERP investigations of lightness effects

Thus far, there has been little investigation of the time course, magnitude, and localisation of electrical brain activity associated with the perceptual coding of brightness and lightness, although some relevant findings have been reported. McCourt and Foxe (2004) investigated electrophysiological responses to a variant of White's illusion (see White, 1979) in which grey targets of identical luminance appear to differ

in brightness when placed on black bars versus when placed on white bars. This study focused on the C1 component, which is the initial component of the visual evoked response potential (ERP); is localised in the parieto-occipital region; is known to reflect the early activation of striate cortex (Foxe & Simpson, 2002); and has been shown to receive substantial contributions from area V1 (e.g. Clark & Hillyard, 1996; Jeffreys & Axford, 1972; Mangun et al., 1993). McCourt and Foxe showed that differences in perception of the target surface were associated with differences in the amplitude of the C1 component at parieto-occipital electrode sites, with grey-on-white targets eliciting larger amplitude than grey-on-black targets. These findings demonstrate a brightness effect in the C1 component (around 70ms post-stimulus-onset).

With the White's illusion style stimulus used by McCourt and Foxe (2004), it appears that contrast is occurring in a major proportion of trials, as it is reported that grey patches presented on white were more likely to be judged as darker, and grey patches presented on black were more likely to be judged as lighter. Therefore, this evidence cannot be used to make a comparison between contrast and assimilation. In addition, although McCourt and Foxe focused on early ERP components, it remains of interest to examine later components with regard to contrast and assimilation. This is particularly relevant where further manipulations of the stimulus conditions, such as size of inducers and perceptual organisation of the stimulus come into play, as these factors may be processed by different, perhaps higher-level mechanisms than the colour (black vs white) of inducers. The early effect reported by McCourt and Foxe is arguably an index of the perceptual changes, but the research does not show whether this effect may be modified by further stimulus manipulations.

Another illusory-lightness effect which has been used in ERP research more recently is the 'Craik-O'Brien-Cornsweet' illusion which, as outlined above, involves

two grey areas of equal luminance which are perceived as differing in lightness. Like the lightness contrast and lightness assimilation effects, there is uncertainty as to the underlying mechanisms of the perceived lightness difference between two physically-identical grey patches in a Craik-O'Brien-Cornsweet stimulus. Sulykos and Czigler (2014) conducted an ERP study in which the Craik-O'Brien-Cornsweet stimulus was used as a tool to examine the relationship between changes at the level of perceptual experience and changes in visual mismatch negativity (vMMN). The study incorporated a variant of the stimulus, as well as control stimuli featuring identical contrast gradients (termed 'Cornsweet edges'), and 'real luminance difference' stimuli featuring the same lightness as the illusory stimulus - caused by real luminance differences rather than illusory or induced differences (see Figure 1.18).



Figure 1.18. The variant of the Craik-O'Brien-Cornsweet stimulus used by Sulykos and Czigler (left); and the identical control (centre) and real luminance difference stimulus (right).

Sulykos and Czigler (2014) reported several ERP differences between the illusory 'Craik-O'Brien-Cornsweet' condition, and the control conditions. Firstly, in the illusory condition, the P1 component had both enhanced amplitude and shorter latency in the anterior right lateral region compared to control conditions. Secondly, the N1 component had a wider distribution and a shorter latency in the illusory condition in comparison to the control/real conditions. No significant differences in the P2 component between the illusory and control/real conditions were found. These findings suggest that the perception of illusory changes in lightness differs from the perception

of 'real', physically-defined differences in luminance, and that these differences can be shown particularly in early (P1 and N1) ERP components.

Research into the ERP responses associated with contrast-inducing and assimilation-inducing stimuli will build upon this evidence, by investigating the differences between the processing of two types of lightness effect: contrast and assimilation. McCourt and Foxe (2004) and Sulykos and Czigler (2014) have investigated specific illusory lightness effects, the latter by comparing an illusory condition (an induced/illusory difference in lightness) with an equivalent control condition (a real difference in luminance), providing evidence that differences in perceived lightness of a surface can influence relatively early ERP components. However, lightness contrast and lightness assimilation have not been directly compared and studied together from an ERP perspective, in the way that they have been in the purely behavioural and psychophysical literature.

1.5. Aims and Scope of the Project

Having reviewed literature pertaining to lightness contrast and lightness assimilation specifically, as well as more general research and theories of lightness processing, from both behavioural/psychophysical perspectives and neurophysiological perspectives, the subsequent chapters will report the experimental work. The general aims of this project are to investigate lightness contrast and lightness assimilation alongside one another, using both behavioural and electrophysiological methods to examine the responses associated with these two phenomena. Previous literature has often focused on either contrast or assimilation, however, studying both in parallel will provide a more detailed account of context-dependent changes in the perception of lightness, and allow direct comparisons to indicate points at which the responses to contrast-eliciting stimuli versus assimilation-eliciting stimuli are similar or diverge.

The first study, which will be reported in chapter 2, aimed to assess the effect of depth separation, beginning with stimuli previously shown to elicit either contrast or assimilation, and introducing depth separation between the target and inducing surfaces. As outlined in section 1.3.3., determining the effect of depth separation can give insight into the level of processing involved in contrast/assimilation effects, and previous research has typically investigated the effect of depth separation on either a contrast-eliciting coplanar stimulus, or an assimilation-eliciting coplanar stimulus, without making a direct comparison between the effect of depth separation on a contrast effect and the effect of depth separation on an assimilation effect. When making comparisons between studies, there are often confounds between presentation methods (e.g. stereoscopic vs 3D displays) and stimulus features. In this study, stimuli designed to elicit contrast and assimilation in coplanar conditions were constructed from identical materials in order to test and compare the effect of depth separation between the target and inducing surfaces.

The second and largest part of the project aimed to investigate the electrophysiological (ERP) responses associated with stimuli known to elicit contrast and assimilation, thus investigating the time course of the associated neural processing. This comprises two sections: the methodological considerations and the ERP work. There is relatively little neurophysiological research pertaining to lightness contrast and lightness assimilation specifically, hence the electrophysiological aspect of the project is more exploratory, though guided by neurophysiological research in areas relevant to lightness perception. The ERP work aims to give insight into the time course of the underlying neural activity, investigating whether contrast and assimilation result from different underlying processing, thereby contributing to existing knowledge regarding

whether ‘low’ or ‘high’ –level factors (see section 1.2.) are important in the perception of contrast and assimilation effects.

Chapter 3 details the methodological studies used to establish which stimuli would most consistently produce contrast/assimilation effects when using a forced-choice paradigm rather than the more commonly-used matching or adjustment tasks, as well as other considerations necessary to apply ERP measurement to the task, such as timing and repeated presentation of stimuli. Subsequently, the analysis of the ERP study itself will be detailed in chapter 4, including analysis of response time (RT), ERP amplitude and latency, and brain-behaviour correlations, which have not previously been analysed with regards to contrast and assimilation. Finally, chapter 5 will present a general discussion of the findings, bringing together findings from the behavioural measures and the electrophysiological measures where appropriate.

Chapter 2: The Effects of Depth Separation on Lightness Contrast and Lightness

Assimilation

Determining the effect that depth separation of surfaces has upon surface lightness perception is important for an assessment of the types of processing underlying phenomena such as lightness contrast and lightness assimilation. Previously, it has been suggested that if there is no difference between the lightness of a target in a coplanar display, and a corresponding target when placed in a non-coplanar display, then lightness computations must occur at a lower level of processing, prior to the processing of depth (e.g. Gibbs and Lawson, 1974; Julesz, 1971). Conversely then, an effect of depth separation on lightness perception would imply the involvement of higher-level processing (Gilchrist, 1977; Gogel & Mershon, 1969; Mershon, 1972; Soranzo, Galmonte, & Agostini, 2010).

Coplanarity between surfaces (i.e. surfaces lying in a single depth plane) can function as a proximity-based perceptual grouping mechanism (e.g. Gilchrist, 2014; Koffka, 1935). Thus, manipulation of depth can be considered as a manipulation of the strength of perceptual grouping between surfaces. Perceptual grouping itself has a role in the Anchoring Theory (Gilchrist et al., 1999), in terms of the formation and strength of ‘frameworks’ within which a surface’s lightness value is computed. The disruption of grouping between surfaces by separating the surfaces into different depth planes may affect the strength of perceptual grouping; alter the relationship between surfaces such that they change from being in a single framework to being in separate frameworks; or change the perception of ‘figure’ and ‘ground’ within the stimulus. This forms a basis for a non-directional hypothesis that depth separation will affect lightness perception.

Previous studies have investigated the effects of depth separation with stimuli which, in their ‘original’ coplanar conditions produced either contrast (Fujimoto &

Ashida, 2015; Gibbs & Lawson, 1973; Menshikova, 2013; Wolff, 1933) or assimilation (Soranzo, Galmonte & Agostini, 2010). Typically, in coplanar displays, low spatial frequency stimuli elicit contrast, while high spatial frequency stimuli elicit assimilation (e.g. Helson & Joy, 1962; Helson, 1963; Kanizsa, 1979). In non-coplanar displays, the effects observed appear to differ from the effects observed in the corresponding coplanar displays: some findings show contrast effects occurring in both conditions (e.g. Gibbs and Lawson, 1971) others report a 'shift' between assimilation and contrast (Soranzo et al., 2010). These studies were discussed in more detail in Chapter 1.

Given that apparent inconsistencies between some of the previous findings may result from differences in spatial frequency or stimulus configuration, the study discussed in the following sections included two stimulus configurations: 'large' (can be thought of as low spatial frequency), and 'small' (can be thought of as high spatial frequency) – referring to the stimuli in terms of the size of the inducing surface). The study also included two levels of inducer luminance: 'white' (high-luminance) and 'black' (low luminance). In addition, previous studies' spatial frequency/stimulus configuration may be confounded with methods of producing depth separation; therefore in the current study all stimuli were constructed from paper to produce physical 3D depth separation.

Considering the evidence discussed so far, the hypotheses for the current study are as follows:

- 1) In coplanar conditions, a contrast effect will arise with large inducers, and an assimilation effect with small inducers. Thus, a two-way interaction between stimulus configuration and inducer colour is hypothesised within the coplanar conditions.

- 2) It is expected that stimuli with large inducers, when placed into a non-coplanar configuration, will continue to produce a contrast effect, albeit an effect with a smaller magnitude than the corresponding effect in coplanar conditions.
- 3) For stimuli with small inducers, a ‘shift’ from an assimilation effect in the coplanar condition to a contrast effect in the non-coplanar condition is expected, as reported by Soranzo, Galmonte, and Agostini (2010) with stereoscopic depth separation. Thus, because both stimulus configurations are expected to produce contrast effects in the non-coplanar conditions, there should be no two-way interaction (stimulus configuration x inducer colour) within the non-coplanar conditions, but there should be a main effect of inducer colour.

2.1. Method

2.1.1. Participants.

Twenty participants (15 females and 5 males; mean age = 26.6), with no prior knowledge of the experiment, were recruited from Sheffield Hallam University. The sole pre-requisite for participation was that participants had normal (or corrected-to-normal) visual acuity. The sample size was indicated by an a priori power analysis with $\alpha=0.05$, power=0.90, and effect size $f=0.25$.

2.1.2. Design and stimuli.

The experimental design consisted of three independent variables: intensity of inducers (‘white’ and ‘black’); stimulus configuration (‘large’ and ‘small’ – referring to the stimuli in terms of the size of the inducing surface); and depth separation (‘coplanar’ and ‘non-coplanar’). The stimuli chosen reflect displays which traditionally elicit contrast responses (large inducer; e.g. the simultaneous contrast display); and those

which have previously been shown to elicit assimilation responses (small inducers; e.g. see Soranzo, Galmonte, & Agostini, 2010). The eight conditions were presented in a 2x2x2 within-participants design (see Figure 2.1). The dependent variable was the lightness of the grey target, measured in terms of the luminance of a patch chosen by participants as matching the grey target.

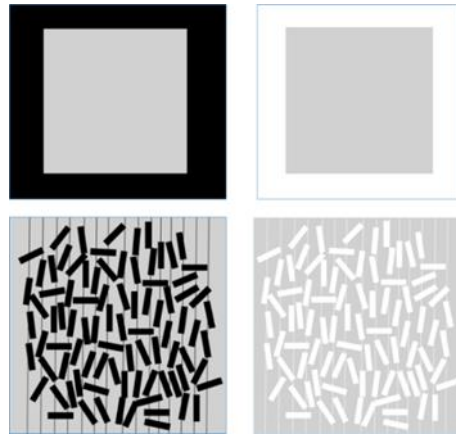


Figure 2.1. Conditions used in study 1 (not to scale). This figure illustrates two of the three independent variables – ‘Colour’: Black; and White; and ‘Stimulus configuration: Large (top row); and Small inducers (bottom row). To include the third variable (‘Distance’), each of these four configurations was presented in Coplanar (‘flat’; as shown; all parts of the display at the same distance from the observer); and Non-coplanar (the black/white inducing elements placed at a distance in front of the grey target).

The stimuli were constructed from paper, as follows. A grey paper (31.9 cd/m^2) served as the target surface. This was placed on a larger blue background surface which shared approximately the same luminance as the target, in order to minimize any potential inducing effect of the background. Luminance values were measured with the stimuli ‘in situ’, using a photometer positioned at the same distance as participants viewed the stimuli.

For the four coplanar conditions, the inducers were printed onto the target. For the four non-coplanar conditions, inducers were cut (using a laser-cut printer which allowed for precise cuts) from white (54.2 cd/m^2) or black (3.4 cd/m^2) paper, and suspended from a wooden frame, placed at a distance of 28cm in front of the target, so that the grey target was visible at a distance behind the inducers. The stimuli were

presented behind a blue paper with a square viewing window (10.3cm x 10.3cm) cut out (see Figure 2.2). Participants were seated approximately 120cm from the target. All stimuli were presented under normal illumination, and the light sources were above the display, therefore avoiding any shadows cast on the stimuli.

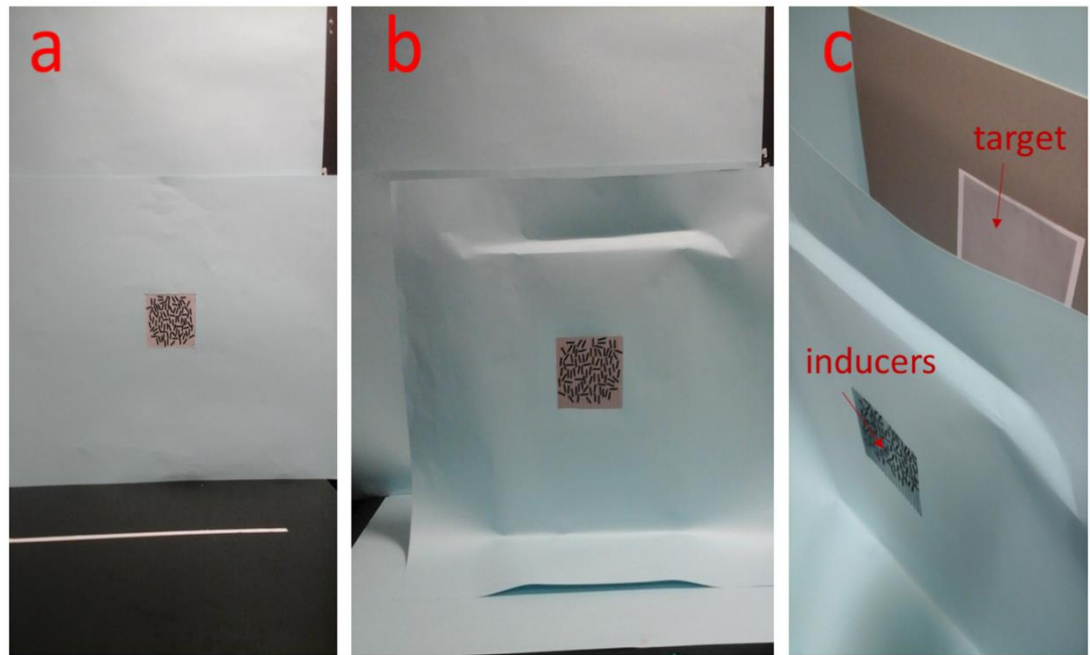


Figure 2.2. Photographs of the experimental set-up a) from the participant's viewpoint of the stimulus for the Black, Small inducer Coplanar condition. b) from the participant's viewpoint of the stimulus for the Black, Small inducer, Non-coplanar condition. c) from the researcher's perspective, to illustrate the inducers suspended from the frame at a distance in front of the target grey against the wall. d) Schematic representation of the experimental display.

Inducers were formed in the following dimensions. For the ‘large’ inducer conditions, the visible grey area (8cm x 8cm) was surrounded by a frame-shaped inducer which extended from the outside edge of the visible grey area to the inside edge of the viewing window. The ‘small’ inducers consisted of 88 small rectangles (1.2cm x 0.3cm) distributed across 15 thin lines (in order to suspend the rectangles from the wooden frame in the non-coplanar conditions). In each condition, the total visible surface area of the grey target was approximately equal.

Alongside each of these stimuli, one of twelve matching charts was presented. For each trial, a chart was selected at random, so that the participant saw the patches in a different order each time. These charts contained twelve achromatic patches, ranging in equal logarithmic steps from 14 cd/m² to 47 cd/m², arranged in random order from left to right. Matching patches were presented on a black and white checkerboard background rather than, for example, a plain white background, in order to minimise potential effects of the background on the matching patches themselves. Figure 2.3 shows one example of a matching chart.

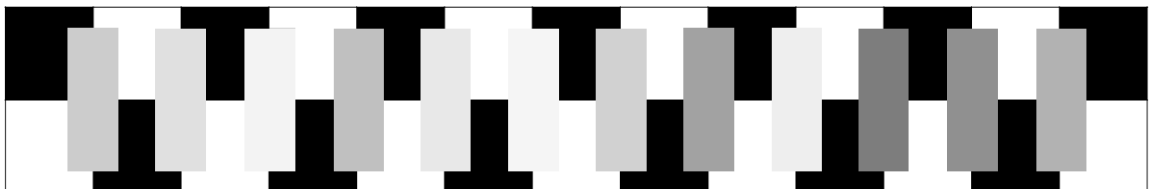


Figure 2.3. Example matching chart.

2.1.3. Procedure.

Participants were required to read through an information sheet and sign a consent form before commencing the study (see Appendix 1). They were instructed that the researcher would be changing elements of the display, and that their task was to choose the patch on the matching chart which “looks as though it is the same shade of grey paper as the target was cut from”.

Between trials, participants were asked to turn away from the display to allow the researcher to change the inducers, frame position, and matching chart, according to a randomised list. Participants then turned back to face the display and verbally gave the number corresponding to the grey they wished to choose from the matching chart. There was no time limit for participants to decide on a response. Participants each responded to two repetitions of each stimulus.

2.2. Results

Each matching chart response was converted into the logarithm of the luminance value corresponding to the chosen patch. This is consistent with the Weber-Fechner Law which states that subjective perception of a stimulus property (lightness) is proportional to the logarithm of the stimulus intensity (luminance) (Fechner, 1860/1912). For each of the responses, the difference between the actual target luminance and the participants' selected luminance was calculated using the following formula:

$$\text{Difference} = \log(\text{luminance of chosen matching patch} / \text{luminance of target})$$

Two outliers, being more than three standard deviations from their respective condition means, were transformed to the next-most extreme response within the same condition (Tabachnick & Fidell, 2014). Each participant responded to two stimuli per condition, so for each of the eight conditions, a mean difference per participant was calculated.

The mean difference between selected- and actual- luminance values for each condition are shown in Figure 2.4, with zero representing the actual luminance value of the target (baseline). Positive values represent a perception of the target that is lighter

than the baseline, whereas negative values represent a perception of the target that is darker than the baseline.

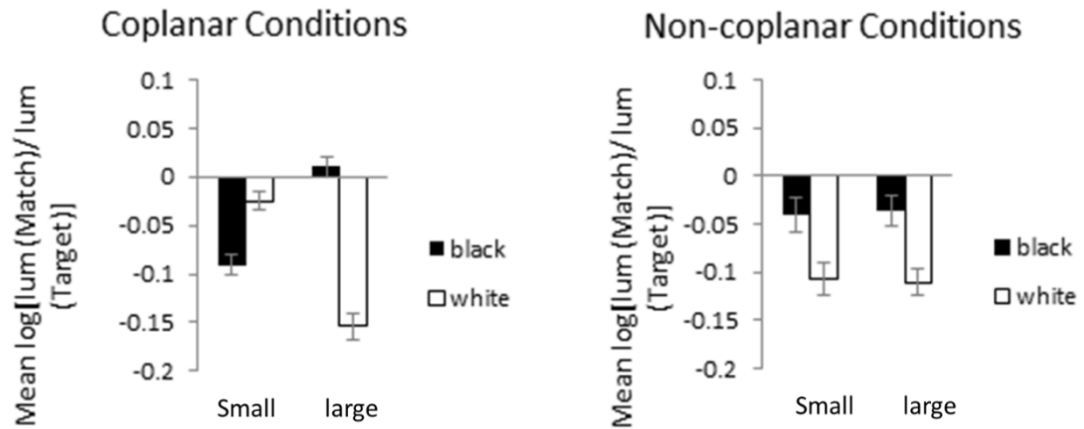


Figure 2.4. Mean difference between baseline and perceived luminance of the target (log luminance) for each condition. Zero represents the baseline value (measured luminance of the target). Positive values indicate that the match was perceived to be lighter than the target and negative values indicate that the match was perceived to be darker than the target. Error bars represent standard error.

The transformed data were analysed using a 2x2x2 repeated-measures analysis of variance (ANOVA), showing a significant three-way interaction between stimulus configuration, inducer colour, and depth separation ($F(1,19) = 39.15$, $p < .001$, $\eta_p^2 = .67$). This interaction was then further explored by analysing the data separately for coplanar conditions and non-coplanar conditions, using two 2x2 ANOVAs.

In the coplanar conditions, the two-way interaction between stimulus configuration and inducer colour was significant ($F(1,19) = 97.10$, $p < .001$, $\eta_p^2 = .84$). Post-hoc t-tests with Bonferroni correction showed that, for small inducer conditions, targets were judged darker with black inducers than with white inducers ($t(19) = 6.434$, $p < .001$), representing an assimilation effect.¹ For large inducer conditions, targets were

¹ Whilst assimilation is described as an effect whereby the target appears to ‘shift’ towards the luminance of the inducer, there is some evidence to suggest that assimilation can be a relative, rather than an absolute difference. De Weert & Spillmann (1995) reported that, as shown in the present results, both targets are judged to be darker than the baseline (darker than the physical luminance of the target). Technically, this would make the effect with white inducers a small contrast effect (as the target lightness is judged further away from the inducer lightness). However, given that, relative to the target with black

judged *lighter* with black inducers than with white inducers ($t(19) = 8.498, p < .001$), representing a contrast effect.

In the non-coplanar conditions, there was no significant two-way interaction between stimulus configuration and inducer colour ($F(1,19) = .172, p = .68, \eta_p^2 = .01$). There was no significant main effect of stimulus configuration in the non-coplanar conditions ($F(1,19) = .007, p = .935, \eta_p^2 < .001$), but a significant main effect of inducer colour was found ($F(1,19) = .098, p = .003, \eta_p^2 = .371$). Post-hoc t-tests with Bonferroni correction showed that targets were judged lighter with black inducers than with white inducers for both small inducers ($t(19)=2.881, p=.010$) and large inducers ($t(19)=3.266, p=.004$), thus representing contrast effects for both types of inducers.

2.3. Summary and Discussion

The analysis shows that the pattern of results obtained in the coplanar conditions did not hold once the inducers and target underwent depth separation, into the non-coplanar conditions. In coplanar conditions, the luminance of inducers had a different effect on lightness perception of the target depending on the configuration of the inducers: with large inducers, targets were judged to be darker with white inducers than with black inducers; with small inducers, targets were judged to be lighter with white inducers than with black inducers. However, in non-coplanar conditions, the stimulus configuration did not appear to have an effect. In the non-coplanar conditions, targets were perceived as lighter with black inducers than with white inducers.

In the subsequent discussion, a result is categorised as a ‘contrast’ effect if the target was judged as taking on the opposite quality of the inducers (i.e. lighter with black inducers/darker with white inducers); and an ‘assimilation’ effect if the target was

inducers with the same configuration, the target with white inducers is judged *lighter*, this effect can be described as (‘relative’) assimilation.

judged as taking on the same quality of the inducers (i.e. darker with black inducers/lighter with white inducers). When applying this definition to the results of this experiment, it makes sense to consider each level of the inducer colour variable at a time. Given that targets with white inducers always appeared darker than the baseline reflectance value in this experiment, all of these are categorised as contrast responses, albeit of varying magnitudes. For small inducer conditions, a small contrast effect is observed in the coplanar condition, which becomes a larger contrast effect in the non-coplanar condition. For large inducer conditions, an opposite pattern: a larger contrast effect in the coplanar condition becomes a smaller contrast effect in the non-coplanar condition. The magnitude of the two contrast effects with white inducers in the non-coplanar conditions is similar.

Targets with black, large, coplanar inducers also undergo a small contrast effect. The remaining black inducer conditions, however, would be categorised as assimilation effects because those targets are perceived to be darker than the baseline reflectance value of the target. A larger assimilation effect in the small inducer, coplanar condition becomes smaller in the corresponding non-coplanar condition. As with the contrast effects for white inducers in the non-coplanar conditions, the magnitude of the two assimilation effects for black inducers in the non-coplanar conditions is similar. In the non-coplanar conditions, the magnitude of the contrast effects (with white inducers) is larger than the magnitude of the assimilation effects (with black inducers). Table 2.1 provides a summary of the classification of contrast and assimilation for each condition.

Table 2.1. Categorisation of Contrast and Assimilation responses for each condition.

Distance	Stimulus	Inducer colour	Effect
Coplanar	Small inducer	Black	Assimilation
		White	Contrast
	Large inducer	Black	Contrast
		White	Contrast

Non-coplanar	Small inducer	Black	Assimilation
	Large inducer	White	Contrast
	Small inducer	Black	Assimilation
	Large inducer	White	Contrast

2.3.1. The effects of depth separation.

Depth separation appears to have a different effect depending upon whether the stimulus features small or large inducers. The effect whereby the target appears darker with black inducers than with white inducers in the small inducer coplanar conditions is reversed by depth separation; and the contrast effect observed in large inducer conditions is reduced by depth separation. The current results are to a certain extent consistent with the findings in which, with stimuli with small inducers, assimilation is observed in coplanar conditions and contrast in non-coplanar conditions (Soranzo, Galmonte & Agostini, 2010), showing a reversal of the effect; and with findings in which, with stimuli with large inducers, contrast is observed in both coplanar and non-coplanar conditions (Gibbs & Lawson, 1974; Julesz, 1971; Menshikova, 2013).

The current findings do however show inconsistencies with the findings of some studies in which depth has been manipulated using crossed/uncrossed disparity as opposed to physical 3D depth (Fujimoto & Ashida, 2015; Morikawa & Papathomas, 2002). In these studies, a contrast effect observed in ‘coplanar’ conditions appeared to be enhanced/increased with uncrossed disparity (i.e. the target surface being perceived as lying in a depth plane behind the inducing surface, as in the current study). This discrepancy could be a result of the differing methods of manipulating depth separation.

It can be assumed that the retinal image when viewing stimuli in the non-coplanar condition is approximately equal to the retinal image when viewing the equivalent coplanar stimulus. Despite this, corresponding stimuli appear to result in a

different perception of the target lightness depending on whether the target and inducing surfaces are coplanar. Thus, the current findings provide further evidence to suggest that central/cortical processing mechanisms play a role in assimilation as well as in contrast. This is contradictory to the Anchoring Theory's claim that assimilation is attributable to low-level processing (Gilchrist et al., 1999).

Spatial frequency or stimulus configuration is an important factor in reconciling some of the apparent inconsistencies between the results of previous studies of the effects of depth separation on lightness perception. If depth separation is viewed as a manipulation which 'disrupts' the initial (coplanar) contrast and assimilation effects, an observation can be made that the effect of depth separation depends on the 'starting point', i.e. the type of effect produced in the coplanar condition, which may depend on the configuration of the inducers. Given that the effects observed in non-coplanar conditions gave rise to a contrast effect, rather than assimilation, it can also be argued that assimilation (in the coplanar conditions) is disrupted by depth separation to a greater extent than is contrast. This suggests that perhaps assimilation is the less robust of the two phenomena, as contrast continues to occur in non-coplanar conditions.

2.3.2. Asymmetries associated with colour of inducers.

The results demonstrate that the effects of inducer colour are not 'symmetrical' when comparing equivalent conditions which differ only in this variable. For the coplanar, large inducer conditions, the contrast effect observed with white inducers is larger in magnitude than the contrast effect observed with black inducers. This is inconsistent with previous findings indicating that, in a simultaneous lightness contrast (SLC) display, the magnitude of the difference between the luminance value of a target and its perceived lightness value is greater for a target-on-black than for a target-on-white (Economou, Zdravković & Gilchrist, 2007). The background of the matching

chart has previously been reported to contribute to the relative magnitude of contrast effects with black versus white inducers, with a larger contrast effect with black inducers when the matching chart has a white background; a larger contrast effect with white inducers when the matching chart has a black background; but approximately equal when the matching chart has a checkered background (Zavagno, Daneyko, & Agostini, 2011).

In each of the other pairs of stimuli, the results show different types of effects depending on the inducer colour. In coplanar, small inducer conditions, an assimilation effect for black inducers is observed, which is larger in magnitude than the contrast effect for white inducers – an effect consistent with de Weert and Spillman's (1995) account of asymmetrical lightness effects in high spatial frequency stimuli. In the non-coplanar conditions, an assimilation effect for black inducers is observed, which is smaller in magnitude than the contrast effect for white inducers. The effect of inducer colour on the strength of contrast and assimilation effects will be discussed further in section 5.2.

2.3.3. Perceptual grouping and figure-ground segmentation

The modulation of the contrast and assimilation effects from the coplanar to the non-coplanar conditions suggests a potential role for perceptual grouping, mediated by the proximity of surfaces, which is stronger in the coplanar conditions and weakened by depth separation. Perceptual grouping has previously been linked with lightness contrast (e.g. Agostini & Galmonte, 2003; Agostini & Proffitt, 1993). It could be that contrast is favoured when elements of the display are clearly separated, whereas assimilation is more likely to occur when the target and inducers are perceptually grouped in one unified depth plane. This idea was suggested by King (1988), who noted that a transition from assimilation to contrast could occur as a function of decreasing

‘positional similarity’ or closeness of the centres of target/inducing bars in a display (as in Helson & Joy, 1962); or as a function of decreasing similarity in the colour of target/inducing regions (as in Beck, 1966). It was suggested that when a stimulus is manipulated such that its component regions become less similar on some dimension, the regions are more likely to be perceived as separate entities, rather than part of one single surface.

Interestingly, assimilation is observed also in non-coplanar conditions with black inducers (regardless of spatial frequency/stimulus configuration). Conversely, assimilation did not occur with white inducers. The luminance of a surface can influence whether it is perceived as ‘figure’ or as ‘ground’ such that darker surfaces in a scene are more likely to be perceived as ‘figures’ whereas the lighter surface is more likely to be perceived as ‘ground’. Thus, with black inducers, the target may be seen as ground; and with white inducers, the target may be seen as figure.

When a grey target is perceived as ‘figure’, it undergoes a stronger contrast effect than when it is seen as ground (Coren, 1969; Koffka, 1935). Festinger, Coren & Rivers (1970) attributed this to an attentional ‘overweighting’ of figure relative to ground, showing that when attention is directed towards a grey target/figure, it undergoes a contrast effect, whereas when attention is directed away from a grey target (i.e. when the grey is ‘ground’), it undergoes an assimilation effect.

The finding in the current study that assimilation is stronger or more likely to occur with black inducers, whereas contrast occurs with white inducers can be accounted for to an extent by a combination of these concepts. Under the reasoning of de Weert and Spillmann (1995), in stimuli with black inducers, the inducers are likely to be perceived as figures and the target as ground. Thus, as Festinger et al. (1970) suggest, attention is directed away from the target (towards the inducer ‘figures’)

resulting in an assimilation effect. Conversely, in stimuli with white inducers, the target is the lowest-luminance and is therefore likely to be perceived as figure, and the inducers as ground. Thus, attention is directed towards the target, resulting in a contrast effect.

2.4. Conclusion

The findings of this study demonstrate that depth separation has an effect on lightness, whereby the different patterns of contrast and assimilation effects in coplanar stimuli of differing configurations are transformed into similar effects for both stimulus configurations in the non-coplanar conditions. Given that equivalent stimulus configurations produce different effects when presented in a coplanar versus a non-coplanar arrangement, this supports the idea that low-level retinal factors alone are unable to account for the observed effects. It can therefore be inferred that higher-level processing plays an important role in the occurrence of both contrast and assimilation. This prompts further, neurophysiological, investigation of the differences in processing underlying contrast and assimilation.

Chapter 3: Considerations for the ERP Task and Methodological Studies

Following an initial behavioural study, an exploratory ERP study was designed to begin to form a bridge from the extensive behavioural/psychophysical literature on the topic of lightness contrast and lightness assimilation into an understanding of the associated neural processing. ERPs are commonly employed to study cognitive processes even when there is little prior research directly linking the features of the waveforms to the specific phenomena under study (Otten & Rugg, 2005). The ERP work reported in subsequent chapters requires certain adjustments and considerations in the selection of participants, the type of task completed, and collection and analysis of data. This chapter aims to detail the rationale for elements of the methodology for the ERP work, beginning with a brief overview of ERPs in order to outline some of the design considerations to be made.

3.1. Brief Overview of ERPs

Event-related Potentials (ERPs) are ‘snapshot’ waveforms extracted from continuous EEG data, which are related to a specific stimulus presentation and/or response; and are derived from the continuous EEG recording. Multiple instances of small windows of measurement (e.g. 1000ms from a stimulus onset) are cut from the continuous recording and averaged together in a process that reduces extraneous noise (i.e. recorded activity unrelated to the task) and results in an ERP waveform. Relatively high numbers of trials are required to achieve a good signal-to-noise ratio in the ERP waveform due to the small amplitude of electrophysiological activity and the potential of recording extraneous noise (Luck, 2014). A good signal-to-noise ratio is important in trying to ensure that the ERP waveforms reflect the process(es) of interest.

The ERP approach is time-locked in nature and has high temporal resolution (Dien, 2009) and is therefore ideally placed for the investigations of the temporal

characteristics underlying the processing associated with visual stimuli. The ERP approach is more limited in spatial resolution, as such, localisation of the specific neuroanatomical origins of the activity recorded is beyond the scope of this research. Combining the ERP approach with behavioural measures of task performance (such as response time and classification/type of response) provides an objective indication of the task performance (i.e. perception of stimuli) and allows separation of ERPs to different types of responses (i.e. constructing separate ERP waveforms associated with different behavioural responses). The behavioural response is important in providing a link between the processing in the brain and the manifestation of this processing in the perceptual task, and the ERP data is important in expanding the available information beyond what can be gleaned from behavioural data alone, i.e. providing an indication of the brain activity associated with the processes under investigation.

3.2. Participants

Several participant characteristics can be controlled for in order to minimise variability unrelated to the investigation. Participants for the methodological studies (section 3.4) and the EEG experiment (chapter 4) were required to have normal (or corrected-to-normal) visual acuity, to ensure that differences in visual ability did not affect responses. As is typical in electrophysiological studies, participants for the EEG task were also required to have no history of neurological problems/disorders which could result in atypical EEG rhythms (e.g. epilepsy) and be right-handed (confirmed using a revised version of the Edinburgh Handedness Inventory; Oldfield, 1971; Veale, 2014) in order to avoid potential difficulties in EEG/ERP analysis and interpretation arising as a result of differences in hemispheric lateralisation between right- and left-handed individuals (Galín, Ornstein, Herron, & Johnstone, 1982). Gender and age were not specifically balanced due to the constraints of recruitment (i.e. recruiting from a

student population biased towards young adults and females), however Galin et al. (1982) showed no differences between genders on any EEG measure in right-handed participants.

Participants were reimbursed for their time with either participation credits ("PsyCredits" for undergraduate psychology students) or "Love2Shop" High Street vouchers (www.highstreetvouchers.com). In accordance with ethical approval procedures (see appendix 1.1), each participant received an information sheet outlining the study requirements, completed a consent form and handedness questionnaire before commencing the study, and received a debrief sheet at the end of the study (shown in appendices 1.2-1.5).

3.3. Task Design

When considering the task to be completed by participants, it is important to acknowledge that whereas psychophysical/behavioural studies often collect only a few responses per condition, averaging ERPs from the EEG recording requires a large number of trials per condition in order to obtain a good signal-to-noise ratio; and that the ERPs must be time-locked to the onset of the stimulus. It is also necessary that participants' responses can be coded categorically so that ERPs associated with different types of responses (i.e. 'contrast responses' or 'assimilation responses') can be distinguished and compared. In order to better suit these requirements, a 2-alternative forced-choice (2AFC) task paradigm was used. In this task, a stimulus is presented alongside a comparison square (of equal luminance to the target), and participants must indicate whether the target appears darker or lighter than the comparison square.

A 2AFC task brings with it a required definition of contrast and assimilation operating at either side of a physical baseline representing the 'true' measured luminance value of the target. Daneyko & Zavagno (2008) outlined a distinction

between a “within approach” in which the method demonstrates the perceptual difference between two targets in two conditions; and a “between approach” in which the method is concerned with establishing the difference between the perceived quality of a target, and the physical property of that target. The 2AFC method is closest to the “between approach”, as a response is categorised as contrast or assimilation on the basis of a response given relative to a comparison square. Of course, the 2AFC method is not able to estimate the *magnitude* of the difference between the perceived lightness of the target and the physical measured luminance value, but it is able to give a categorisation of the type of response given, as shown in Table 3.1.

Table 3.1. Categorisation of responses for the 2AFC task.

Inducers	Response (judging the target relative to the comparison square with no inducers)	Categorisation of response
Black	Target is Lighter than Comparison	Contrast
	Target is Darker than Comparison	Assimilation
White	Target is Lighter than Comparison	Assimilation
	Target is Darker than Comparison	Contrast

3.4. Stimulus Design – Methodological Studies

Two types of stimuli were selected, with the aim of using a 'contrast-inducing' stimulus, and an 'assimilation-inducing' stimulus. The 'contrast-inducing' stimuli were adapted from traditionally-presented simultaneous contrast displays (consisting of grey squares presented on black and white backgrounds), with each half of the traditional display being used as a separate stimulus. The 'assimilation-inducing' stimuli were adapted from Soranzo, Galmonte & Agostini (2010), consisting of a grey square with smaller black or white fragments scattered over the grey. The luminance of the stimuli were measured with a photometer at 95.78 cd/m² for the white inducers; 0.55 cd/m² for the black inducers; and 29.89 cd/m² for the grey targets. Methodological studies with each of these types were conducted as described below to try to maximise the rate of

contrast responses (to contrast-inducing stimuli) and assimilation responses (to assimilation-inducing stimuli) for the purposes of investigating the ERP responses associated with contrast- and assimilation- responses.

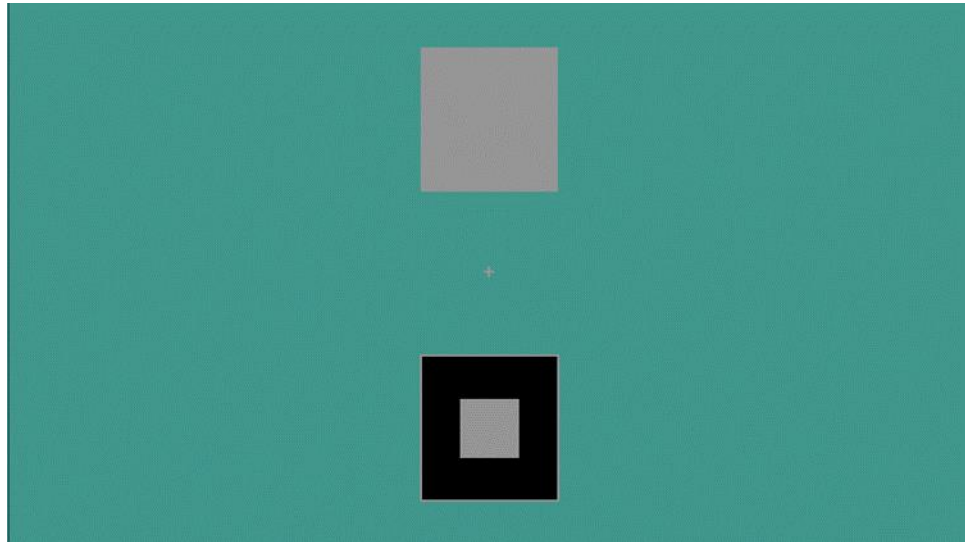


Figure 3.1. The stimulus (bottom, in this case a ‘contrast’ stimulus in the form of half of the traditional simultaneous contrast display) and the comparison square (top), as presented in the tasks.

In line with a 2AFC paradigm, the stimulus and the comparison square were presented above and below the centre point of the screen, as shown in Figure 3.1. The remainder of the screen was set to the same measured luminance as the greys in the stimulus (but a blue-green hue rather than grey) to try to minimise the likelihood that responses were influenced by the luminance of the background. In any case, both the stimulus and the comparison square were presented on the same background colour, so in the event of a contrast- or assimilation- effect arising from the background, both greys would undergo the same effect, in theory cancelling out a potential confound.

The stimulus could either be in the top position or bottom position on each trial. This was randomised, ensuring that an equal number of each possibility occurred within each testing session. Another counterbalancing concern arises from the wording of the task question: ‘Which is darker/lighter?’. This was addressed by splitting the overall

number of trials for a task in half, and presenting a block of trials for which the question to be answered is 'Which is darker?', a short break, and then a second block of trials for which the question to be answered is 'Which is lighter?', or vice versa. The order of the questions would be counterbalanced, with each participant randomly starting with either the 'Which is darker?' or the 'Which is lighter?' task.

3.4.1. 'Contrast' stimuli – large inducer.

Stimuli designed to elicit contrast responses were created as a 5cm x 5cm square, containing a smaller, 2cm x 2cm square in the centre. Two versions of the stimuli were created: in one case the grey target square was surrounded by the black/white inducer; in the other, the smaller square was black/white, surrounded by the target grey (shown in Figure 3.2). The purposes of this comparison were twofold: firstly, to investigate whether changing the arrangement of target and inducer has an effect on the proportion of contrast responses given; secondly, to investigate which of these stimuli would elicit the greater proportion of contrast responses and hence be more useful in the ERP work, in which a larger number of contrast responses would mean a better signal to noise ratio in the ERP waveforms.

These stimuli were tested with a sample of 10 participants meeting the criteria stipulated in section 3.2. Stimuli were presented 8 times each, in a 2AFC task (see section 3.3) with the task ('which is lighter' or 'which is darker') and the stimulus position (above comparison square or below) counterbalanced across trials. The results showed that contrast responses occurred more consistently when the target was surrounded by the inducer ($M = 89.79\%$ 'contrast' responses; $SD = 6.60$) than when the inducer was surrounded by the target ($M = 73.17\%$ 'contrast' responses; $SD = 18.73$) across trials with black inducers and trials with white inducers ($t(9) = 2.917, p = .017$).

On the basis of this observation, it was decided that the stimuli in which the target is surrounded by the inducer would be used in the ERP study to elicit ‘contrast’ responses.





Inducer in the centre		Target in the centre	
			
66.0%	80.3%	83.1%	93.8%

Figure 3.2. Inducer-surrounded-by-target and target-surrounded-by-inducer stimuli. Percentages show the proportion of responses indicating contrast for each stimulus.

This finding can also be extended beyond the purposes of testing to feed into the ERP study methodology. Consistently for both colours of inducers, the rate of contrast responses was higher when the grey target was surrounded by the inducer, suggesting an additional contextual influence upon the strength/likelihood of a contrast response. Arguably, the targets surrounded by inducers are more likely to be regarded as ‘figures’ than as ‘ground’ which, as suggested by Coren (1969), can make the target more likely to undergo a contrast effect (see section 1.2.3).

3.4.2. ‘Assimilation’ stimuli – small inducers.

As with the paper-based stimuli used in the depth separation study (chapter 2), the stimuli designed to elicit ‘assimilation’ responses were prepared such that the total surface area of ‘target’ and ‘inducer’ was equivalent between the ‘large inducer’ and ‘small inducers’ conditions. The small inducer stimuli consisted of a 5x5 cm square scattered with 88 small rectangles (0.75 x 0.3cm) accumulating to a total surface area matching the inducer surface area in the large inducer (‘contrast’) stimuli. As with the ‘contrast’ stimuli, these stimuli were tested with a sample of 10 participants meeting the criteria stipulated in section 3.2. Stimuli were presented 8 times each, in a 2AFC task (see section 3.3) with the task (‘which is lighter’ or ‘which is darker’) and the stimulus

position (above comparison square or below) counterbalanced across trials. The results showed that the rate of assimilation when thin vertical lines (as featured in the paper-based stimuli in the study) was lower for stimuli without the lines added (see Figure 3.3).





With vertical lines		With no vertical lines	
			
58.8%	50.6%	70.5%	57.5%

Figure 3.3. Stimuli with and without lines added. Percentages show the proportion of responses indicating assimilation for each stimulus.

3.4.3. Fixation.

A fixation cross is typically used in ERP studies to prepare participants for the onset of a stimulus, and along with instructions, to encourage participants to avoid making large eye movements which could lead to artifacts in the recording. However, there is little research regarding the effect of fixation on contrast and assimilation effects. To investigate this, two variants of the task were created in order to compare the responses to stimuli presented with or without a fixation cross. In the non-fixation variant, a cross appeared for 500ms to signal that a stimulus was about to be presented, but disappeared when the stimulus was presented. In the fixation variant, the cross remained in place for the duration of the whole task.

Table 3.2. Mean percentage of ‘correct’ responses in the ‘non-fixation’ and ‘fixation’ variants

	Non-fixation variant	Fixation variant
‘Contrast’ responses to large inducer stimuli	87.5	86.9
‘Assimilation’ responses to small inducer stimuli	53.7	47.9

As Table 3.2 shows, the rate of contrast responses to the large-inducer stimuli appears to be unaffected by whether or not the fixation cross is present ($t = 0.08$, $p = .941$). On the other hand, the rate of assimilation responses to the small-inducer stimuli is lower with the inclusion of a fixation cross, though this did not reach significance ($t = 0.43$, $p = .677$), although Burnham (1953) suggested that assimilation is facilitated by observing stimuli without rigid fixation. Fixation crosses did not significantly reduce the rate of contrast responses, and were kept for the EEG task to remind participants to avoid making excessive eye movements.

3.4.4. Control stimuli and practice trials.

Participants were given a brief 2AFC task (identical to the task for data collection) in order to familiarise themselves with elements of the task (i.e. instructions, buttons on the control pad) and an opportunity to ask questions or clarify any misunderstandings about the task. The task consisted of each stimulus presented twice, and 4 ‘catch’ trials (see below), giving a total of 12 trials. The practice task was repeated at a halfway point during the testing session, between blocks of trials, i.e. when the question changed from ‘Which is darker?’ to ‘Which is lighter?’ or vice-versa.

In order to check that participants were maintaining attention and responding appropriately during the testing blocks, ‘catch’ trials were included. Eight of these stimuli were constructed, in the same configuration as the experimental stimuli, except that there was an obvious difference between the grey of the target and the grey of the comparison square. There was one “target obviously lighter than comparison” stimulus and one “target obviously darker than comparison” stimulus corresponding to each of the four experimental conditions. Catch trials were included at random intervals amongst the experimental stimuli, at a frequency of 3 catch trials for every 10 stimuli.

3.5. Task Procedure and Inter-Stimulus Interval

For each trial, a fixation cross was presented for 500ms, followed by the stimulus (i.e. the stimulus and the comparison square) for 3000ms, followed by a brief blank screen before the next trial begins. When a participant gave a response, the trial ended and progressed on to the blank screen (i.e. the trial ended as soon as a response was given, but participants had a maximum of 3000ms to respond, after which the trial would automatically end). The methodological tests showed that participants felt that they could comfortably respond within 3000ms of stimulus onset. The blank screen inter-stimulus interval was set to randomly select a duration between 500ms and 1500ms on each trial. This is appropriate in an ERP study, to ensure that the stimulus onsets occur at random (rather than regular) intervals therefore are less likely to repeatedly coincide with oscillations unrelated to the ERP activity under investigation. This is often used in ERP studies to minimise the effect of a potential source of artifactual activity from anticipatory activity which can occur during a cycle of identical timings between stimuli.

As briefly mentioned earlier, ERP tasks require a higher number of trials per condition than behavioural tasks. Participants therefore responded to 80 trials per condition. Randomisation of presentation order also helps to avoid the possibility of any residual effect from one stimulus condition having any impact on the response to the following stimulus condition.

In order to minimise the effect of ocular artifacts on sections of the EEG recording, participants were instructed to try to time their blinks between trials. The practice tasks (see previous section) allowed an opportunity to practice this – the EEG recording monitor was observed by the researcher during the practice trial in order to

feed back to participants regarding the timing of their blinks. Participants were also asked stay still during the tasks to reduce any movement-based artifacts.

3.6. Stimulus Presentation and EEG Recording Equipment

The task was presented on a CRT screen monitor (NEC MultiSync FP2141sb) using E-prime (version 2.0.10.353; Psychology Software Tools Inc.). The CRT screen was chosen (rather than an LCD monitor) as it offers a more uniform display, for example in terms of the luminance and colour appearing constant regardless of viewing angle. Time-locked event markers (numerical codes) for stimulus onset (labelled according to condition) and response input were transmitted from E-Prime to ASAlab via amplifiers using a parallel port connection. Participants used a game-style control pad (Logitech Precision) chosen for ease and comfort of use as well as being familiar to many participants.

The EEG recording system consisted of 128 Ag/AgCl electrodes mounted in a Waveguard EEG cap, arranged according to the five percent electrode system (Oostenveld & Praamstra, 2001) – an extension of the traditional 10/20 system (Jasper, 1958; American Encephalographic Society, 1994) in which electrodes are placed at 5% points along lines of latitude and longitude. A 128 electrode system allows an improved signal-to-noise ratio for electrode clusters compared to a 64 electrode system (Dien, 1998). This type of cap allows standard spacing of electrodes across all participants and minimal bridging between electrodes. An external ground electrode was also placed on the forehead.

The 128 electrodes recorded data via a cascaded set-up using two linked 64-channel amplifiers, through a SynFi fibre-to-USB converter. The recording software used was ASAlab 4.7.12 (Advanced Source Analysis laboratory; www.ant-neuro.com). Electrode impedances were adjusted to below 50k Ω using electrode gel. The sampling

rate was set at 512 Hz, meaning that 512 data points were recorded for each electrode per second.

3.7. ERP Analysis Methodology

EEG data were processed for each participant prior to further analysis. Firstly, the recorded data was re-referenced to an average reference (AVG'). A large array of electrodes, as present in the 128-electrode configuration, can provide a good approximation of the true average (Dien, 1998). Any 'rogue' (i.e. particularly noisy) channels were disabled and then interpolated using the ASA channel interpolation feature.

High-pass and low-pass filters were applied separately rather than as a band-pass filter. The high-pass filter cut-off was 0.01Hz, 12dB/octave. The low cut-off value was chosen because higher cut-offs are thought to distort data and reduce the amplitude of lower-frequency components (Duncan-Johnson & Donchin, 1979), but filtering out frequencies lower than 0.01 Hz can remove slow voltage shift artifacts caused by drifts in electrode impedance or sweating with minimal distortion (Luck, 2014; Tanner et al., 2016). The low-pass filter cut-off was 40 Hz, 24 dB/octave, to filter out muscle movement and line frequency noise such as that from AC electrical devices. Artifact detection was carried out first by visual inspection and marking of obvious ocular artifacts (i.e. eye blinks), then by automated artifact detection to find recorded activity greater than 70 μ V. The ASA artifact correction procedure uses a PCA method to separate signal and artifact (Ille, Berg, & Sherg, 2002).

Sections of the EEG data to be averaged into ERP waveforms were derived by pairing the time-locked event markers for stimulus onset (coded according to condition) with the event markers for response inputs and segmenting data from 100ms pre-stimulus to 1000ms post-stimulus. Any segments coinciding with artifacts which could

not be corrected were rejected (i.e. not used for subsequent averaging). The ERPs were computed by averaging all the remaining trials (after artifact rejection) according to their condition and response codes, resulting in two possible ERPs per condition (one for responses coded as contrast; one for responses coded as assimilation). Baseline correction, which subtracts the average pre-stimulus voltage from the waveforms, was conducted to ensure that the waveforms for different conditions all began as close as possible to the “zero, zero” point and therefore can be compared.

There is little electrophysiological evidence directly pertaining to lightness contrast and lightness assimilation, so an exploratory approach, motivated by relevant literature, must be taken to selecting regions of interest for analysis. The occipital and parietal regions were selected for initial analysis, due to these areas being involved in visual processing (Colombo, Colombo, & Gross, 2002), with primary visual cortex being located in the occipital lobe. Previous research relevant to lightness effects (e.g. McCourt & Foxe, 2004) has also highlighted occipital and parietal electrode sites.

Electrodes were grouped into clusters for statistical analysis, according to proximity (i.e. electrodes neighbouring one another) and similarity of the overall grand average waveforms. Groups were also intended to be symmetrical, to enable comparisons between corresponding clusters in each hemisphere. Grouping electrodes into clusters is an often-used method in ERP analysis (Picton et al., 2000) which can improve signal to noise ratio and increase statistical power (Dien, 2017; Oken & Chiappa, 1986).

Collapsed grand average waveforms, that is, ERP waveforms which are averaged from all data, regardless of condition/response type, were also constructed (see Luck & Gaspelin, 2017; Handy, 2005) These were used to define measurement windows for the peaks/components to be analysed, by inspecting the overall shape of

the waveforms, and focusing upon components which are consistently present and prominent in visual paradigms, such as P1 and N1. Using an overall collapsed waveform to define measurement windows allows windows to be selected prior to analysis whilst ensuring that they are appropriate for the data collected (i.e. components fall within the specified measurement window). Measurement windows ideally should be >50ms when using mean amplitude (Luck, 2014). The clusters and time windows will be specified in more detail in the EEG study results chapter.

3.8. Quantification of ERP Measurements

ERPs are commonly described in terms of components with specified measurement windows (e.g. P1 80-120ms, N1 120-190ms) which can sometimes differ between studies. Several methods are available for quantifying the properties of an ERP waveform in order to make statistical comparisons between conditions. For each measurement window, a measure of amplitude and a measure of latency was used.

3.8.1. Amplitude.

Traditional ERP analysis has often used the peak amplitude, which is the highest amplitude value within a measurement window, making use of only a single point in the ERP waveform. Mean amplitude makes use of more of the continuous data in a waveform – treating the ERP component as something which extends over time, rather than using a single point as is the case in peak amplitude measures, which are also easily distorted by factors such as high-frequency noise; overlapping ERP components; and differences in signal-to-noise ratio or latency variability across conditions. Mean amplitude also ensures that the comparison between two (or more) conditions makes use of all of the waveform data points within the specified measurement window, allowing examination of the ‘component’ more broadly (Woodman, 2010). This therefore ensures that amplitude is measured across the same latency range in each

condition (whereas peak amplitude can easily become a comparison of the amplitude at different latencies in different conditions). Luck (2016) provides a fuller review of the advantages and disadvantages of peak measures compared to mean- and area- based measures, although mean measurements have outperformed peak measurements in simulations (Clayson, Baldwin, & Larson, 2013) in terms of reduced bias.

Mean amplitude is also a more legitimate measurement to use in cases where waveforms with differing noise levels, or those based on different numbers of trials are being compared. This is particularly relevant to some of the comparisons in this work, for example when comparing waveforms of sub-groups of participants based on their behavioural responses (which leads to unequal n in the two groups, ergo a difference in the number of trials included in the two waveforms).

3.8.2. Latency.

Latency measures based on the ‘peaks’ of a waveform share some of the problems of peak amplitude measures. Specifically, peak latency does not take into account the shape or distribution of the waveform, can easily be distorted, and is particularly sensitive to noise. Fractional area latency is less sensitive to noise, and is a more rigorous way of using the area contained by a section of the waveform to estimate the ‘midpoint’ latency, thereby taking into account more of the information provided by the waveform than a single peak point (Woodman, 2010). This finds the latency point at which the area contained under a section of the waveform can be split into two equal-area parts.

3.9. Statistical Considerations and the Jackknife Approach

Statistical analysis of ERP data will require three-way ANOVAs, with factors condition, hemisphere (left and right), and electrode cluster (occipital, occipital-parietal, parietal). The Greenhouse-Geisser correction has been used in

reporting ANOVAs when there are more than two levels of a factor (Luck, 2014, p.320). This is relevant when comparing more than two conditions or more than two clusters of electrodes in an analysis, because there is likely to be heterogeneity of variance with three or more electrode areas, due to the tendency for covariance to be lower for a pair of electrode areas situated a distance apart, than for a pair of electrode areas situated near to one another.

Traditional ERP analysis constructs a grand average (composed of all participants' data) waveform to describe the data, but uses the amplitude and latency values of components calculated from the ERPs of each individual participant. In doing so, the improved signal-to-noise ratio of the grand average waveforms is not used in the analysis. An approach which uses grand averages in statistical analysis is the 'jackknife' method (e.g. Abdi & Williams, 2012; Kiesel et al., 2008; Miller, Patterson & Ulrich, 1998), which involves the computation of 'leave-one-out' grand averages, whereby each participant is replaced by a 'subaverage' of the other $n-1$ participants within the same group/condition. The resulting 'subaverage' waveforms will have a substantially larger signal-to-noise ratio compared to an individual participant's waveform (Miller et al., 1998), thereby reducing within-participant variance (Abdi & Williams, 2012) and potentially minimising irrelevant between-participant effects such as those arising as a result of differences in mood or arousal (Kornmeier, Wörner, & Bach, 2016). This is particularly useful in cases where some conditions may be more affected by poor signal-to-noise ratio due to a smaller number of trials/participants.

The jackknife approach has been demonstrated as a method which can increase statistical power whilst retaining Type 1 error rates (Kiesel et al., 2008), but since the jackknife technique is based on averaged data, the variance of the set of subaverage scores is smaller than the variance of the original scores would be (Ulrich & Miller,

2001). Therefore, adjustments to the computations of standard statistical tests have been developed: Miller et al. (1998) provided an adjusted equation for the standard error, and Ulrich and Miller (2001) derived an adjustment of F values in ANOVA for factorial designs

The t and F values resulting from statistical tests performed using ‘jackknifed’ data will be artificially inflated (because the error variance has been artificially reduced). This must be addressed by adjusting the test statistics. For t -tests, by dividing the t value by $(N-1)$; for F -tests, dividing the F ratio by $(N-1)^2$ (Luck, 2014). An adjustment was also made to the effect sizes, calculating the adjusted $\eta^2 = 1/(1+1/F_{adj} * df_{error}/df)$ for ANOVAs with adjusted F -values (R. Ulrich, personal communication, November 15, 2017).

3.10. Methodology Summary

This chapter has outlined the rationale for several aspects of the methodology required for the ERP work. These include the use of a 2AFC task/paradigm, variable inter-stimulus interval, and processing of the EEG/ERP data prior to statistical analysis. The following chapter will build on this, outlining more specific details in the procedure and analysis, and presenting the results of the ERP study.

Chapter 4: ERP Study

Lightness contrast and lightness assimilation have not previously been directly compared from an electrophysiological viewpoint, although other lightness effects have been investigated (see section 1.4). With regard to ERP differences associated with lightness perception, previous research has reported differences in amplitude at ~70ms post stimulus onset associated with differences in perception of grey-on-white versus grey-on-black targets (McCourt & Foxe, 2004). In addition, Sulykos and Czigler reported differences in amplitude and latency of P1 and N1 between an ‘illusory lightness difference’ condition and a ‘real luminance difference’ condition. These findings suggest that differences in lightness can be reflected in early ERP measurements.

It is expected that contrast and assimilation will share some elements of processing, given that they are both lightness effects, arising from the same task/stimulus presentation method. However, ERPs provide a suitable method to detect subtle differences in processing, and have shown differences with other lightness effects in previous research. This may contribute to an understanding of the point(s) at which contrast and assimilation diverge in their underlying processing, and help to further explanations of why contrast may occur in one instance but assimilation in another. The electrophysiological processing associated with contrast and assimilation may also provide evidence to determine whether higher-level (i.e. cortical rather than retinal) processing can be implicated in assimilation as well as contrast.

This chapter reports the exploratory ERP study investigating the electrophysiological activity associated with lightness perception. Within this chapter, the Method section is intended to provide a brief overview to give context for the subsequent results sections. More detailed methodological information can be found in

the previous chapter. The Results section covers behavioural data first, before moving on to ERP comparisons between conditions.

4.1. Method

4.1.1. Participants.

Thirty participants volunteered in exchange for either undergraduate research participation credits or a high street shopping voucher. The age of participants ranged from 18 to 48 years (mean = 23.57, SD = 8.41) and there were 23 females and 7 males. All participants were right-handed and had normal or corrected-to-normal vision and reported no history of neurological problems/disorders. One participant was excluded from analysis for not completing the whole task, another was excluded for giving too many incorrect responses to ‘catch’ trials (i.e. those with a physical luminance difference between target and inducer, designed to check participants' attention to the task).

4.1.2. Design and stimuli.

The stimulus conditions followed a 2 (colour: black, white) x 2 (stimulus configuration: large, small inducers) within-subjects design. For analysis purposes, however, two additional variables relating to the electrode positions were included, so each analysis was 2 (condition) x 2 (hemisphere: left, right) x 3 (electrode cluster: occipital, occipital-parietal, parietal). The dependent variables were the response type (i.e. whether a participant indicated a contrast or assimilation response), the speed of response (RT), and the ERP amplitude and latency measures.

The stimuli were designed in two configurations (‘large’, and ‘small’ inducer sizes) and colour of inducers (white, black). The 'large' stimuli consisted of 5cm x 5cm square, containing a smaller, 2cm x 2cm square in the centre, whereas the 'small' stimuli

consisted of a 5x5 cm square target scattered with 88 small rectangles (0.75 x 0.3 cm) accumulating to a total surface area matching the inducer surface area in the large inducer ('contrast') stimuli. Figure 4.1 shows the stimuli used. The luminance values of surfaces measured with a photometer were 95.78 cd/m² for the white inducers; 0.55 cd/m² for the black inducers; and 29.89 cd/m² for the grey. Participants were presented with each condition 80 times (320 in total: 80 x 4 stimulus conditions) along with 96 'catch' trials (see section 3.4.4) distributed randomly amongst the experimental stimuli. Participants were seated at a 57cm distance from the screen, thus, the visual angle of the stimuli was approximately the same as the stimulus dimensions, given that 1cm viewed at a distance of 57cm is equal to 1 degree of visual angle.

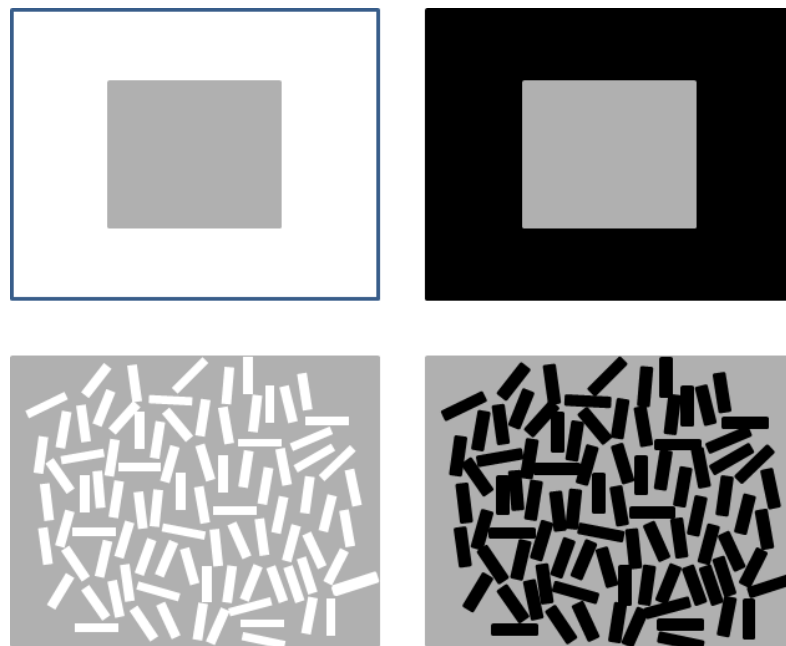


Figure 4.1. The four stimulus conditions: White Large and Black Large inducers (top), and White Small and Black Small inducers (bottom).

Each stimulus was presented along with a blank grey 'comparison' square of identical physical luminance to the 'target' grey, as depicted in Figure 4.2. The distance between the central position of the fixation cross and the nearest edge of the stimulus or comparison square was 3cm. In half of the trials, participants were asked to indicate

which grey square was the darkest grey; and in the other half of trials, they were required to indicate which grey square was the lightest grey. All participants completed tasks with both instructions, and the order of the task instructions was counterbalanced between-participants.

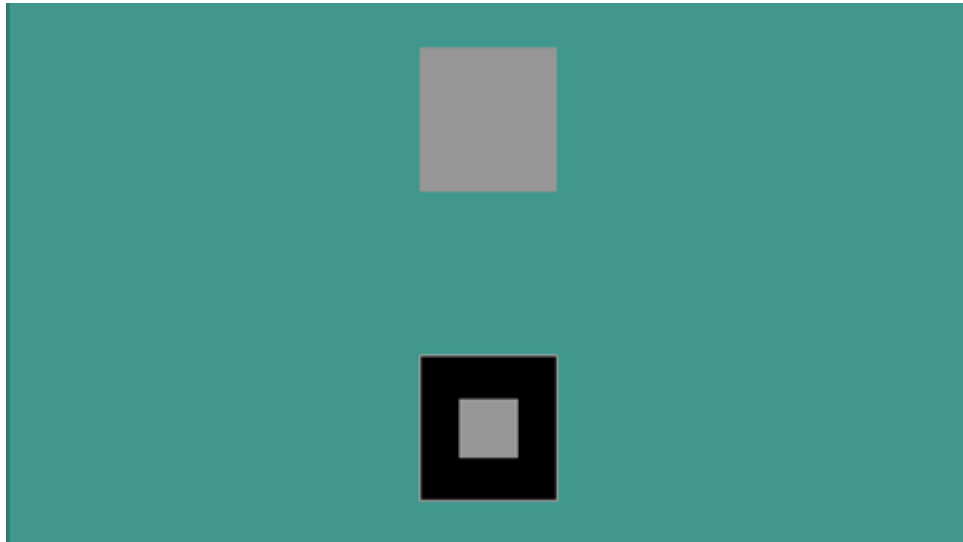


Figure 4.2. The stimulus and comparison square presented above and below the centre of the screen.

4.1.3. Procedure.

After completing the consent form and handedness questionnaire, participants were then set up with EEG recording equipment (i.e. the electrode cap). The instructions for their task were given verbally, as well as being presented on the screen. Participants were provided with a gamepad to indicate their answers. They were requested to indicate which one between the top or bottom of the screen was the lighter or darker grey, according to the experimental condition. The upper button on the front of the gamepad was pressed with the right index finger and indicated the grey presented at the top of the screen. To indicate the grey presented at the bottom participants were requested to press the lower button of the gamepad with right middle finger.

In each trial, a fixation cross (500 ms) was presented, followed by presentation of the stimulus (3000 ms), which in turn was followed by a variable inter-stimulus

interval (blank screen), of between 500ms and 1500ms. Participants completed a short series of practice trials in order to familiarise themselves with the task. The main task was divided equally into four blocks of approximately 5 minutes each, with three short breaks. Each block therefore contained 80 experimental stimuli (20 x 4 conditions) and 24 ‘catch’ trials.

4.1.4. Electrophysiological methods.

This section gives an overview of the electrophysiological recording and processing relevant to the analysis carried out for the ERP study; further details and rationale were reported in chapter 3. The EEG was recorded from 128 Ag/AgCl electrodes mounted in a Waveguard EEG cap, plus an external ground electrode, placed on the forehead. Electrode impedances were adjusted to be below 50k Ω . Task-specific information, namely a code for each stimulus image presented and a code for each response button pressed by the participant, was recorded onto the EEG data file.

Processing of data.

Behavioural data, i.e. the type of response given (‘contrast’ vs ‘assimilation’) and response time (RT), were used in conjunction with the EEG data.

For the EEG data, offline processing was conducted per individual participant, prior to further analysis, in accordance with the processing steps outlined in the methodological chapter. Epochs of the EEG data were derived by pairing the condition markers with the response markers and segmenting data from 100ms pre-stimulus to 1000ms post-stimulus. The ERPs were computed by averaging together trials according to their condition and response codes.

Electrode sites from the areas associated with visual processing (occipital and parietal cortex) were selected for analysis as these areas are associated with visual

processing and have been highlighted in previous lightness-related ERP research (e.g. McCourt & Foxe, 2004), as well as showing clear ERP peaks in the current data. These were separated into three clusters per hemisphere according to observation of similarity between ERPs at neighbouring electrode sites. Figure 4.3 shows the electrode sites included in each ‘cluster’ for analysis.

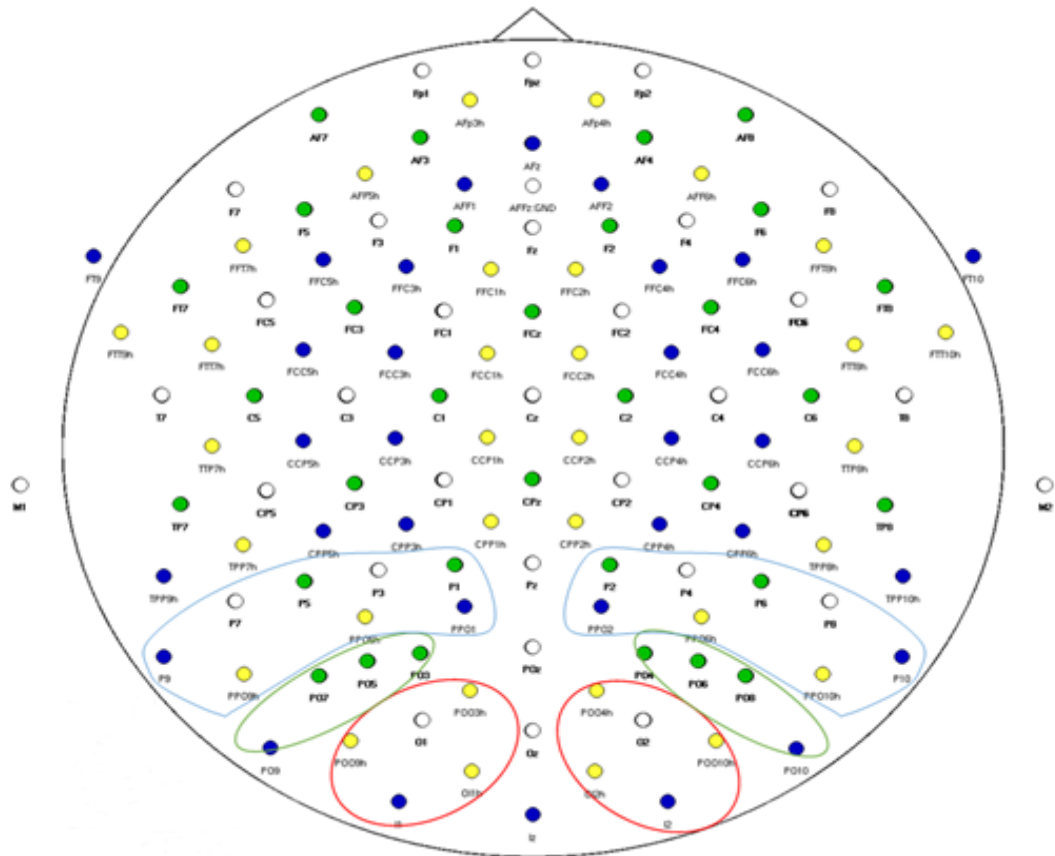


Figure 4.3. Electrode clusters in their relative positions. The electrodes included in the ‘occipital’ cluster are circled in red; ‘occipital-parietal’ in green; and ‘parietal’ in blue.

Measurement windows for P1 (70-120ms), N1 (130-180ms), and N2 (190-230ms) were selected based upon visual inspection of the individual waveforms, as well as a ‘collapsed average’ localiser, in which all participants and conditions were averaged together in order to gain an approximation of the general shape and timing of the waveform peaks. The mean amplitude during the measurement window was

measured, as was the 50% fractional area latency (i.e. the latency which lies at the mid-point of the total area under the waveform within the measurement window).

4.2. Results: Behavioural Data

4.2.1. Response Type

Each response was categorised as either a ‘contrast’ or ‘assimilation’ response. In conditions with black inducers, a ‘contrast’ response is when the participant indicated that the target appeared lighter than the comparison square; an ‘assimilation’ response is when the participant indicated that the target appeared darker than the comparison square. Conversely, in conditions with white inducers, a ‘contrast’ response is when the participant indicated that the target appeared darker than the comparison square; an ‘assimilation’ response is when the participant indicated that the target appeared lighter than the comparison square. If a participant did not respond on a particular trial, this was counted as a ‘miss’ and therefore not taken as either type of response. For each condition, a total (out of a possible 80 trials per participant) was calculated for each type of response. None of these total values fell outside of 3 standard deviations from their respective condition mean, so were not considered to be outliers.

Figure 4.4 shows the mean number of each response type within each condition. Assimilation responses appear to be more frequent than contrast responses in the condition with black, small inducers (Black Small); the reverse is true for the condition with white, large inducers (White Large) condition. For the remaining two conditions, however, there does not seem to be such a consistent pattern.

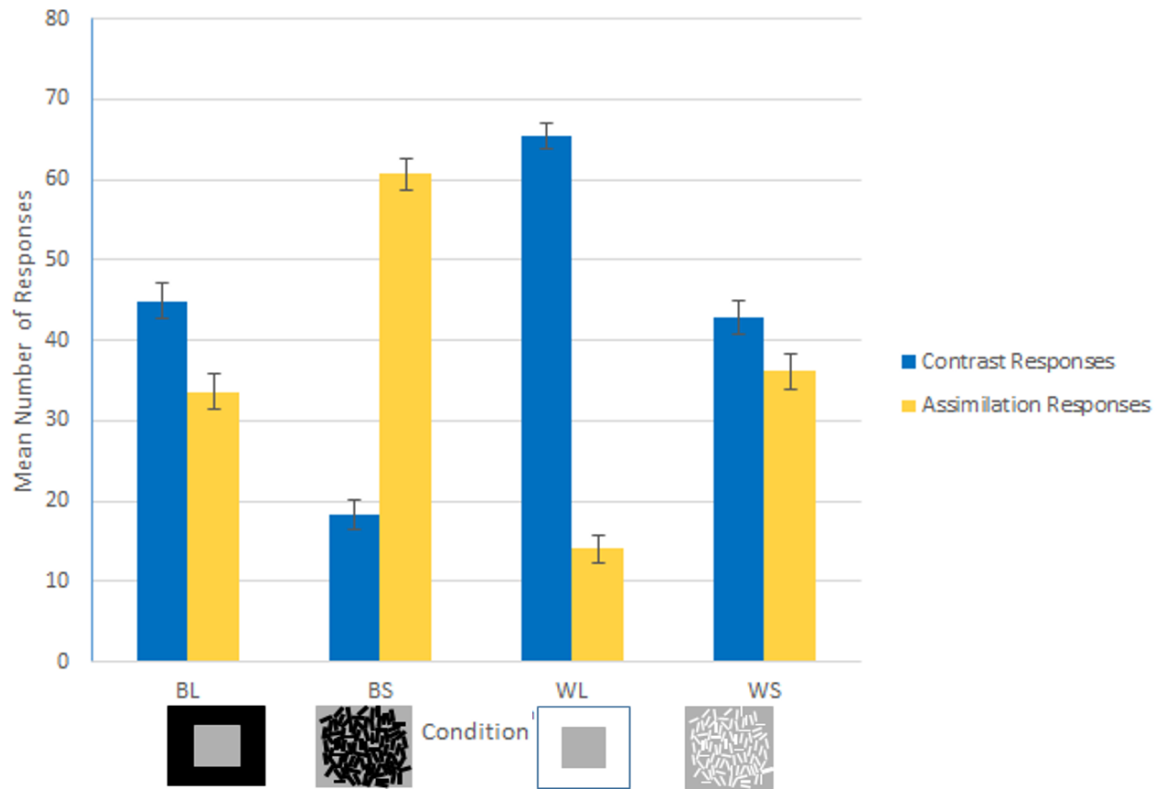


Figure 4.4. Mean number of each type of response in each condition. Error bars show standard error.

A 2x2 repeated measures ANOVA was carried out, examining the effect of colour (black, white) and size (large, small) of inducers on the proportion of contrast responses and assimilation responses. For the purposes of this analysis, the proportion of contrast responses per participant forms the dependent variable. The conditions will be referred to in terms of the properties of inducers: as 'Black Large', 'Black Small', 'White Large', and 'White Small'.

There was a significant main effect of inducer colour upon the proportion of contrast responses, $F(1,27) = 21.44$, $p < .001$, $\eta_p^2 = .44$, whereby there was a lower proportion of contrast responses in conditions with black inducers than in conditions with white inducers. There was also a significant effect of the configuration of inducers, $F(1,27) = 80.86$, $p < .001$, $\eta_p^2 = .75$, whereby there was a higher number of contrast

responses in conditions with large inducers than in conditions with small inducers.² The interaction between inducer colour and stimulus configuration was not significant, $F(1,27) = .712$, $p = .406$, $\eta_p^2 = .03$. The White Large condition elicited the most contrast responses, whereas the Black Small condition elicited the most assimilation responses.

Further to this, dependent t-tests were carried out within each condition, comparing the number of contrast responses with the number of assimilation responses. There was no significant difference between number of contrast and assimilation responses in the Black Large condition, $t(27) = 1.30$, $p = .207$, nor the White Small condition, $t(27) = 0.79$, $p = .438$. In the Black Small condition, there were significantly more contrast responses than assimilation responses, $t(27) = 5.67$, $p < .001$. In the White Large condition, there were significantly more assimilation responses than contrast responses, $t(27) = 7.54$, $p < .001$. This is consistent with the perception of assimilation being more reliable with black inducers than with white inducers (e.g. Soranzo et al., 2010) and the perception of contrast being more reliable with white inducers than with black inducers (e.g. Beck, 1966) but not consistent with Economou, Zdravković & Gilchrist (2007) finding that contrast effects are stronger with black inducers.

4.2.2. Categorical representation of response type data.

The results show that some participants appear to give consistent responses (i.e. either mostly contrast or mostly assimilation responses) within a condition, whereas others give more mixed responses (see Appendix 2). A criterion is needed in order to determine whether a participant's distribution of responses is not simply chance-level performance. This criterion was set at 53 (out of 80) responses - this was deduced by comparing a hypothetical dataset with a set of evenly-split responses. The hypothetical

² Naturally, the direction of these main effects is reversed for the number of assimilation responses: a higher proportion of assimilation responses in conditions with black inducers than in conditions with white inducers, $F(1,27) = 20.21$, $p < .001$, $\eta_p^2 = .43$, and a lower proportion of assimilation responses in conditions with large inducers than in conditions with small inducers, $F(1,27) = 76.40$, $p < .001$, $\eta_p^2 = .74$.

dataset differed significantly from the evenly-split (40-40) responses when its distribution was 53-27 ($\chi^2(1) = 4.39, p = 0.037$). Thus, it was taken that the performance of a participant giving ≥ 53 responses of a particular type (contrast/assimilation) was significantly different from a chance-level performance.

On this basis, where ≥ 53 responses out of 80 trials were contrast responses, the participant was taken to have given consistent contrast responses for that condition (likewise for assimilation). It could be assumed that a higher proportion of contrast (or assimilation) responses is indicative of a stronger contrast (or assimilation) effect. In a condition where a participant experiences the effect strongly, they would be more likely to give a high number of responses than in a condition where they perceive the effect less strongly. This can also be linked to the ‘difficulty’ of a condition – in cases where a participant perceives a weaker contrast/assimilation effect, the participant may find that it is more difficult to decide upon their response in the forced-choice task.

Where responses were more mixed (i.e. between 28 and 52 responses of each type within the same condition) this was deemed not to differ significantly from a ‘chance-level’ performance and therefore the participant was categorised as having given ‘inconsistent’ responses in that condition. In a case where a participant has given ‘inconsistent’ responses, it is not possible to tell from the data whether this is due to the participant genuinely perceiving the stimulus differently in different trials; or giving mixed responses due to being unsure/guessing or not perceiving a very strong contrast/assimilation effect.

Table 4.1. The number of participants categorised as each type of response within each of the conditions.

Condition	‘Consistently contrast’	‘Consistently assimilation’	‘Inconsistent’
‘Black Large’	13	7	8
‘Black Small’	1	20	7
‘White Large’	22	2	4
‘White Small’	12	7	9

Table 4.1 shows the number of participants who could be categorised as giving consistent contrast or assimilation responses, or inconsistent responses to each of the four stimulus types. A chi-square analysis of this data showed a significant result ($\chi^2(6) = 40.28, p < .001$), showing that the distribution of frequencies within the table deviate from what would be expected by chance. This shows a similar pattern to the overall analysis of response type in the previous section: Black Small and White Large have a clear majority of assimilation and contrast responses, respectively, whereas the response types are less consistent for the other conditions. The categorisation of participants in each condition according to the consistency of their responses will be important for ERP analysis later.

4.2.3. Response time (RT) data.

The mean RT for each type of response (i.e. contrast responses and assimilation responses) within each condition was calculated per-participant. Then, the mean across-participants was calculated according to the categorisation of their general response type within the condition (as distributed in table 4.1). For those participants giving inconsistent responses within a condition, the mean of their ‘contrast’ responses and ‘assimilation’ responses within that condition were calculated separately rather than collapsing both response types into a single mean.

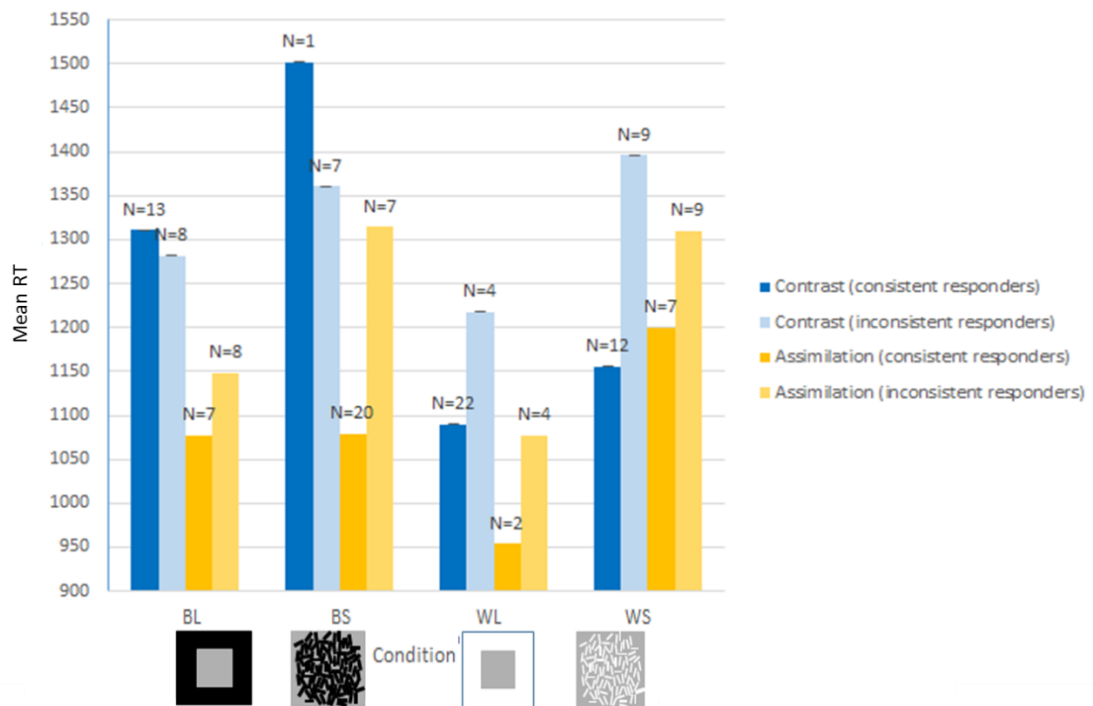


Figure 4.5. Mean RT for each type of response within each condition, separated according to whether a participant's response was consistent or inconsistent. For participants giving consistently either contrast or assimilation responses, mean RTs are presented only for their majority type of response are averaged as 'consistent responders'. For participants giving inconsistent responses, RTs for both contrast and assimilation, men RTs for both types of response are taken.

Within each condition, between-group comparisons were conducted to compare the RT for each type of response between those who had inconsistently given the response, and those who had consistently given the response. For example, the RT for 'contrast' responses for those who consistently gave 'contrast' responses was compared to the RT for those who gave less consistent 'contrast' responses. No significant differences were found (see table 4.2 for comparisons and p-values).

Table 4.2. Significance values for comparisons of Response Time between those giving consistent responses and those giving inconsistent responses.

Condition	Type of response	P-value
‘Black Large’	Contrast responses	1.000
	Assimilation responses	1.000
‘Black Small’	Contrast responses	*
	Assimilation responses	.117
‘White Large’	Contrast responses	1.000
	Assimilation responses	1.000
‘White Small’	Contrast responses	.573
	Assimilation responses	1.000

*No test of difference conducted in this case as only one participant consistently gave ‘contrast’ responses in this condition

Given that the RT for participants with ‘inconsistent’ responses did not differ significantly from those with ‘consistent’ responses, these participants will not be excluded for the purposes of initial RT analysis across the conditions – thereby permitting a within-participants approach, parallel to that of the Response type analysis in the previous section. The overall mean RT per condition and response type, for all participants, are shown in Figure 4.6.

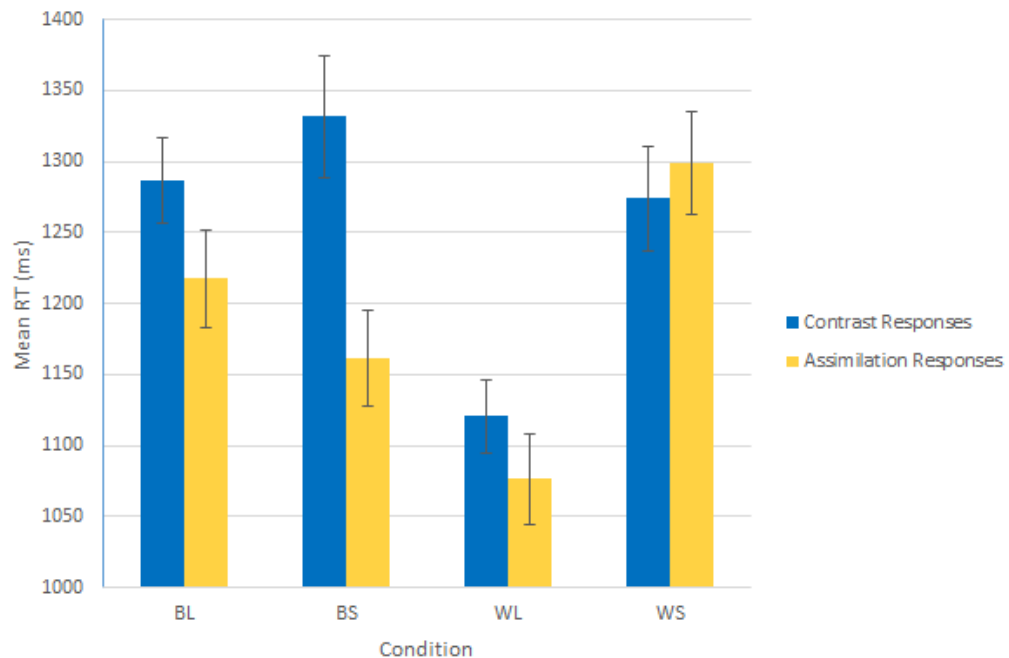


Figure 4.6. Overall mean RT for contrast and assimilation responses in each condition. Error bars represent standard error.

RTs were subsequently analysed using a 2 (response type) x 4 (condition) repeated measures ANOVA. There was a significant main effect of response type, $F(1, 27) = 8.46, p = .007, \eta_p^2 = .239$, with contrast responses ($M = 1251.38\text{ms}$) being slower on average than assimilation responses ($M = 1188.74\text{ms}$), when collapsed across all conditions. However, in post-hoc comparisons within each condition, RT did not significantly differ between contrast and assimilation response types in Black Large ($t(27) = 2.03, p = .052$); in White Large ($t(27) = 1.02, p = .317$); or in White Small ($t(27) = .50, p = .618$). However, in the Black Small condition, assimilation responses were significantly faster than contrast responses ($t(27) = 2.75, p = .01$). The 2x4 ANOVA also showed a significant effect of condition, $F(1, 81) = 9.37, p < .001, \eta_p^2 = .258$. The interaction between condition and response type was close to significance, $F(3, 81) = 2.63, p = .056, \eta_p^2 = .089$.

Pairwise comparisons revealed no significant difference between Black Large and Black Small ($p > 0.999$) or between Black Small and White Small ($p = .999$), although when considering only the assimilation responses, these were significantly faster in Black Small than in White Small ($p = .009$). RTs were significantly slower in Black Large than in White Large ($p < .001$). RTs were also significantly slower in White Small than in White Large ($p = .002$).

The conditions in which RT is generally slower (i.e. Black Large and White Small) correspond to the conditions in which the response type is more inconsistent. This may reflect the contrast/assimilation effect being less obvious or clear in these conditions than in the other conditions, as participants seem to have taken longer to decide upon their response.

4.3. ERP Data

The EEG data was processed as outlined in section 3.7. ERPs were averaged for three clusters of electrodes per hemisphere (see section 4.1.4), resulting in ‘Left Occipital’ (LO), ‘Left Occipital-Parietal’ (LOP), ‘Left Parietal’ (LP), ‘Right Occipital’ (RO), ‘Right Occipital-Parietal’ (ROP), and ‘Right Parietal’ (RP).

4.3.1. Making comparisons between pairs of conditions.

The consistency of a participant’s responses (see section 4.2.2.) within a condition is relevant to the ERP analysis for several reasons. Firstly, there is uncertainty as to whether those with ‘inconsistent’ responses perceived the stimuli in the same way (i.e. is a contrast response from an ‘inconsistent’ responder the same as a contrast response from a ‘consistent’ responder? Are ‘inconsistent’ responders more likely to be giving guesses or unsure of their response?). Secondly, ‘consistent’ responders in a condition will have a better signal-to-noise ratio in the individual ERP waveform compared to the ‘inconsistent’ responders, due to a larger number of trials being included for ‘consistent’ responders. This also complicates potential comparisons between ‘consistent’ and ‘inconsistent’ responders within a condition – particularly given that in many conditions there are large differences in the number of participants categorised as ‘consistent’ or ‘inconsistent’ responders.

In order to address the problems outlined above, the initial ERP analysis will focus on cases where a participant has given consistent responses. Taking forward the cases where response type is classified as being consistent presents a difficulty in analysing across all four conditions. The reason for this is that a participant giving consistent responses in a particular condition may give inconsistent responses in other conditions.

In tasks where the dependent variable is, for example, the chosen luminance value, responses can be analysed together regardless of whether the response type is a contrast or an assimilation response. For example, in the depth separation study, the chosen luminance values in each condition were analysed, and only later categorised as 'contrast' or 'assimilation' on the basis of the average chosen luminance in the condition. The 2AFC task in this study however, means that by default, each response is categorised as either a contrast or an assimilation response. Of course, contrast and assimilation responses must be considered separately if the aim is to examine the ERP activity associated with each of the two phenomena. This therefore introduces an additional variable in to the analysis: the response type. Therefore, there are three sets of comparisons, based on the variables of response type; inducer colour; and stimulus configuration.

Between-subjects/within-condition comparisons

In two conditions, there were several participants consistently giving contrast responses, and several consistently giving assimilation responses. The first two comparisons will investigate this division in the data, by comparing ERPs to the two types of response whilst holding constant the condition.

1. Comparison of ERPs for contrast versus assimilation within the 'Black Large' condition
2. Comparison of ERPs for contrast versus assimilation within the 'White Small' condition

Given that the condition is held constant, Comparisons 1 and 2 will be useful in localising potential differences in the ERPs associated with differences between processing/perceiving contrast and processing/perceiving assimilation. Initially, the split

between contrast and assimilation responses in these two conditions was a somewhat unexpected result, as stimuli were intended to elicit either contrast or assimilation responses, not both. However, the emergence of the different responses allows the comparison of ERPs to two different perceptions of exactly the same physical stimulus. These comparisons will be the most interesting with regard to the aim of identifying differences (or similarities) between the ERP activity associated with contrast, and that associated with assimilation, as any differences found here can only be attributed to the difference in perception.

Within-subjects/between-condition comparisons

The following comparisons will make use of participants who have given consistent responses across more than one condition. The first two hold constant the type of response and the stimulus configuration, with the comparison being between the inducer colour.

3. Comparison of ERPs for contrast responses between the 'Black Large' condition and the 'White Large' condition.

4. Comparison of ERPs for assimilation responses between the 'Black Small' condition and the 'White Small' condition.

Given that the type of response will be held constant, any differences in the ERPs will be due to the colour of the inducer (black vs white) which appears to contribute to the strength of the effect. The behavioural data show that contrast is more consistent with white inducers and assimilation is more consistent with black inducers. Therefore, Comparisons 3 and 4 may show differences relating to the strength of the contrast and assimilation responses, respectively.

The next comparisons will then hold constant the type of response and the inducer colour, with the comparison being between the stimulus configuration:

5. Comparison of ERPs for assimilation responses between the 'Black Large' condition and the 'Black Small' condition.

6. Comparison of ERPs for contrast responses between the 'White Large' condition and the 'White Small' condition.

Comparisons 5 and 6 are made possible by the division of responses in the 'Black Large' and 'White Small' conditions. These will be useful in highlighting any effects of the different stimulus configurations which are not necessarily associated with a shift between contrast and assimilation. The within-participants comparisons will therefore provide useful knowledge given that comparing between contrast and assimilation often involves a confounding comparison between the configurations of the stimuli (i.e. contrast and assimilation are often studied with different stimuli).

For each of the six comparisons outlined above, 2 (condition) x 2 (hemisphere: left, right) x3 (electrode cluster: occipital, occipital-parietal, parietal) ANOVAs were conducted for the mean amplitude and 50% fractional area latency of P1, N1, and N2. In addition, an RT comparison for the subset of participants included in each ERP comparison is included. There are small sample sizes in these cases, unequal samples in the between-participants comparisons, and the data show non-normal distributions and outliers. Therefore, the RT comparisons were made using non-parametric tests: Wilcoxon Signed Ranks Test for the four within-participants comparisons; and Mann-Whitney U Test for the two between-participants comparisons.

4.3.2. Contrast versus assimilation responses within the ‘Black Large’ condition

In the Black Large condition, there were several participants consistently giving contrast responses, and several consistently giving assimilation responses (as well as some giving very mixed responses). This analysis will compare the ERPs of the “contrast responders” with those of the “assimilation responders”. Given that the condition is held constant, the analysis of the different responses allows the comparison of ERPs to two different perceptions of exactly the same physical stimulus, as any differences found here can only be attributed to the difference in perception between contrast responses and assimilation responses.

In this condition, the difference in RT between those consistently giving contrast responses ($N = 11$) and those consistently giving assimilation responses was not statistically significant ($N = 6$), $U = 16$, $z = -1.71$, $p = .088$. This is consistent with the overall RT analysis with all participants, which showed no significant difference between contrast RTs and assimilation RTs in this condition.

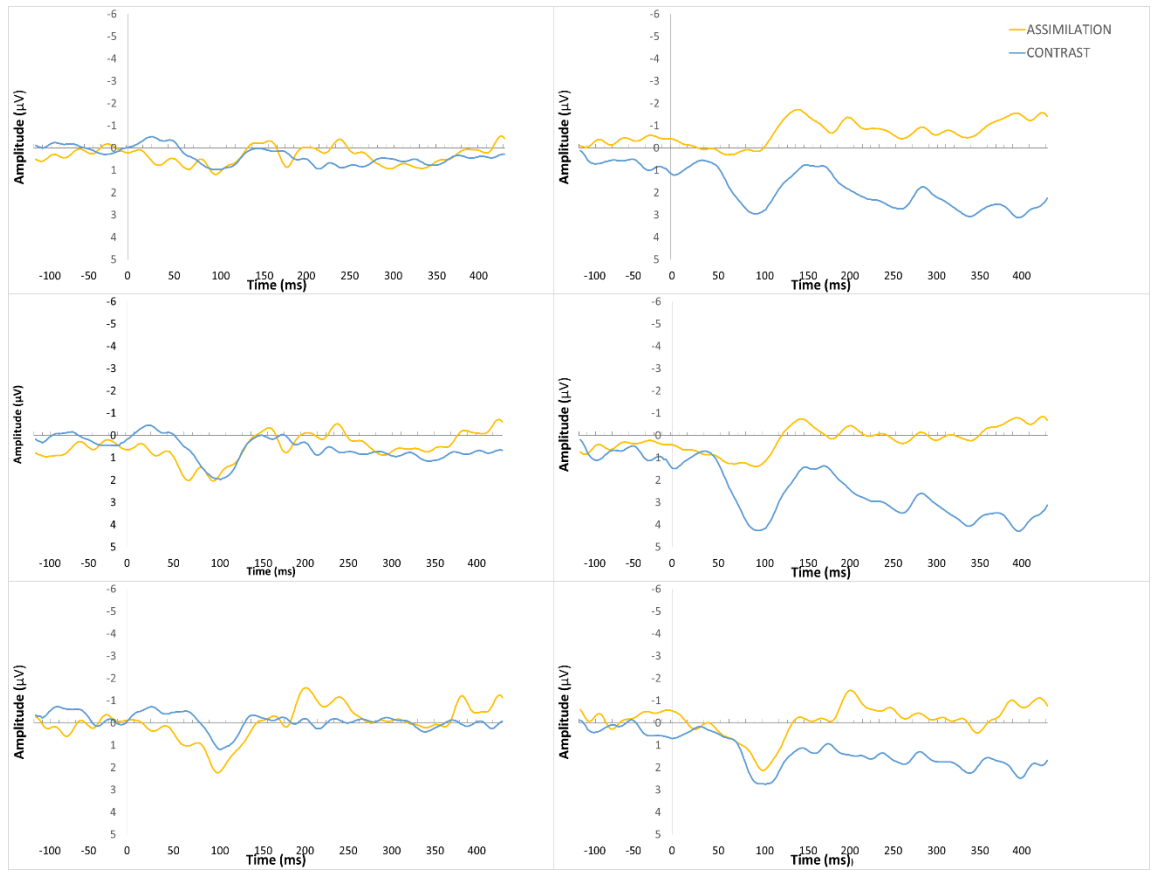


Figure 4.7. ERP waveforms as averaged into clusters for analysis at left and right parietal (P; top), occipital-parietal (OP; middle) and occipital (O; bottom) sites for contrast responses (shown in blue) and assimilation responses (shown in yellow).

ERP Amplitude.

For the mean amplitude of P1, the three-way interaction between response type (contrast vs assimilation), hemisphere (left vs right), and electrode cluster was not significant ($F(1.95, 27) = 1.02, p = .372, \eta_p^2 = .068$). All two-way interactions were non-significant (all p values $> .08$). There was a significant main effect of electrode cluster ($F(1.48, 20.74) = 35.78, p < .001, \eta_p^2 = .720$), but no other significant main effects, although Figure 4.7 shows that the difference between contrast and assimilation appears to be more pronounced in the right hemisphere than in the left. Post-hoc comparisons for the effect of electrode cluster showed no significant difference in P1 amplitude between the occipital and occipital-parietal clusters ($p > .999$), but that the P1 amplitude

in the parietal cluster was greater than that in the occipital clusters ($p < .001$) and occipital-parietal clusters ($p < .001$), as is shown in the top panel of Figure 4.8.

For the mean amplitude of N1, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.67, 23.37) = 1.95, p = .170, \eta_p^2 = .122$). All two-way interactions were non-significant (all p values $> .06$). There was a significant main effect of electrode cluster ($F(1.59, 22.27) = 4.24, p < .001, \eta_p^2 = .770$), but no other significant main effects. Post-hoc comparisons for the effect of electrode cluster showed no significant difference in N1 amplitude between the occipital and occipital-parietal clusters ($p = .564$), but that the N1 amplitude in the parietal cluster was greater than that in the occipital clusters ($p < .001$) and occipital-parietal clusters ($p < .001$), as is shown in the middle panel of Figure 4.8.

For the mean amplitude of N2, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.74, 24.38) = 0.20, p = .788, \eta_p^2 = .014$). There were significant main effects of hemisphere ($F(1, 14) = 19.92, p = .001, \eta_p^2 = .059$) and cluster ($F(1.56, 21.82) = 49.48, p < .001, \eta_p^2 = .78$), but no significant effect relating to response type. There was a significant hemisphere x electrode cluster interaction ($F(1.74, 24.38) = 8.36, p = .002, \eta_p^2 = .374$). Post-hoc tests showed that the amplitude was greater in the parietal clusters than in the occipital and occipital-parietal clusters, for both hemispheres (all p -values $< .001$), as is shown in the bottom panel of Figure 4.8. Across hemispheres, the amplitude was greater in the right occipital cluster than in the left occipital cluster ($p < .001$) but there was no significant difference between hemispheres for the occipital-parietal ($p = .757$) or parietal ($p = .184$) clusters.



Figure 4.8. Mean amplitude and latency per condition, hemisphere, and cluster for the time periods of P1, N1, and N2. The amplitudes are greatest in the parietal cluster at all three time periods. Error bars represent standard deviation.

ERP Latency.

For the P1 latency, there were no significant effects relating to response type or hemisphere. There was a significant main effect of electrode cluster ($F(1.40, 19.64) = 32.14, p < .001, \eta_p^2 = .70$), with the parietal cluster showing longer P1 latency than the occipital ($p = .002$) and the occipital-parietal ($p < .001$) clusters, and no significant difference between the occipital and occipital-parietal clusters ($p = .140$).

For the N1 latency, there were significant main effects of hemisphere ($F(1, 14) = 8.98, p = .010, \eta_p^2 = .39$) and cluster ($F(1.17, 16.41) = 7.29, p = .013, \eta_p^2 = .34$), but no significant effect relating to response type. There was a significant hemisphere x electrode cluster interaction ($F(1.32, 18.42) = 6.25, p = .016, \eta_p^2 = .31$), with the left hemisphere showing longer N1 latency than the right in the occipital cluster ($p = .008$), but no significant differences between hemisphere for the occipital-parietal ($p = .315$) or parietal ($p = .338$) clusters.

For the N2 latency, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.07, 15) = 0.23, p = .653, \eta_p^2 = .016$). All two-way interactions were non-significant (all p values $> .33$). There was a significant main effect of electrode cluster ($F(1.37, 19.15) = 19.03, p < .001, \eta_p^2 = .576$), with the parietal cluster showing longer N2 latency than the occipital ($p = .034$) and the occipital-parietal ($p < .001$) clusters, and no significant difference between the occipital and occipital-parietal clusters ($p = .088$).

Summary.

Within this comparison, there were no significant main effects of response type, nor any significant interactions involving the response type. Significant main effects of electrode cluster, or an interaction between hemisphere and cluster, were apparent in the amplitude and latency measures of each of the components, whereby the parietal cluster showed greater amplitudes than the occipital and occipital-parietal clusters.

4.3.3. Contrast versus assimilation within the ‘White Small’ condition

In the White Small condition, there were also several participants who consistently gave contrast responses, and several who consistently gave assimilation responses (as well as some with very mixed responses). This analysis will compare the

ERPs of the “contrast responders” with those of the “assimilation responders”. Given that the condition is held constant, the analysis of the different responses allows the comparison of ERPs to two different perceptions of exactly the same physical stimulus, as any differences found here can only be attributed to the difference in perception.

In this condition, there was no significant difference in RT between those consistently giving contrast responses ($N = 11$) and those consistently giving assimilation responses ($N = 7$), there was no significant difference in response times, $U = 34$, $z = -0.41$, $p = .684$. This is consistent with the overall RT analysis with all participants, which showed no significant difference between contrast RTs and assimilation RTs in this condition.

ERP Amplitude.

For the mean amplitude of P1, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.63, 21.19) = 1.97$, $p = .169$, $\eta_p^2 = .132$). There were significant main effects of hemisphere ($F(1, 13) = 17.13$, $p = .001$, $\eta_p^2 = .57$) and cluster ($F(1.65, 21.38) = 37.25$, $p < .001$, $\eta_p^2 = .74$), but no significant effects relating to response type. There was a significant hemisphere x electrode cluster interaction ($F(1.63, 21.19) = 6.82$, $p = .008$, $\eta_p^2 = .34$), with the right hemisphere showing greater P1 amplitude than the left in occipital ($p < .001$), occipital-parietal ($p = .008$), and parietal ($p = .006$) clusters. This can be seen in the top panel of Figure 4.10.

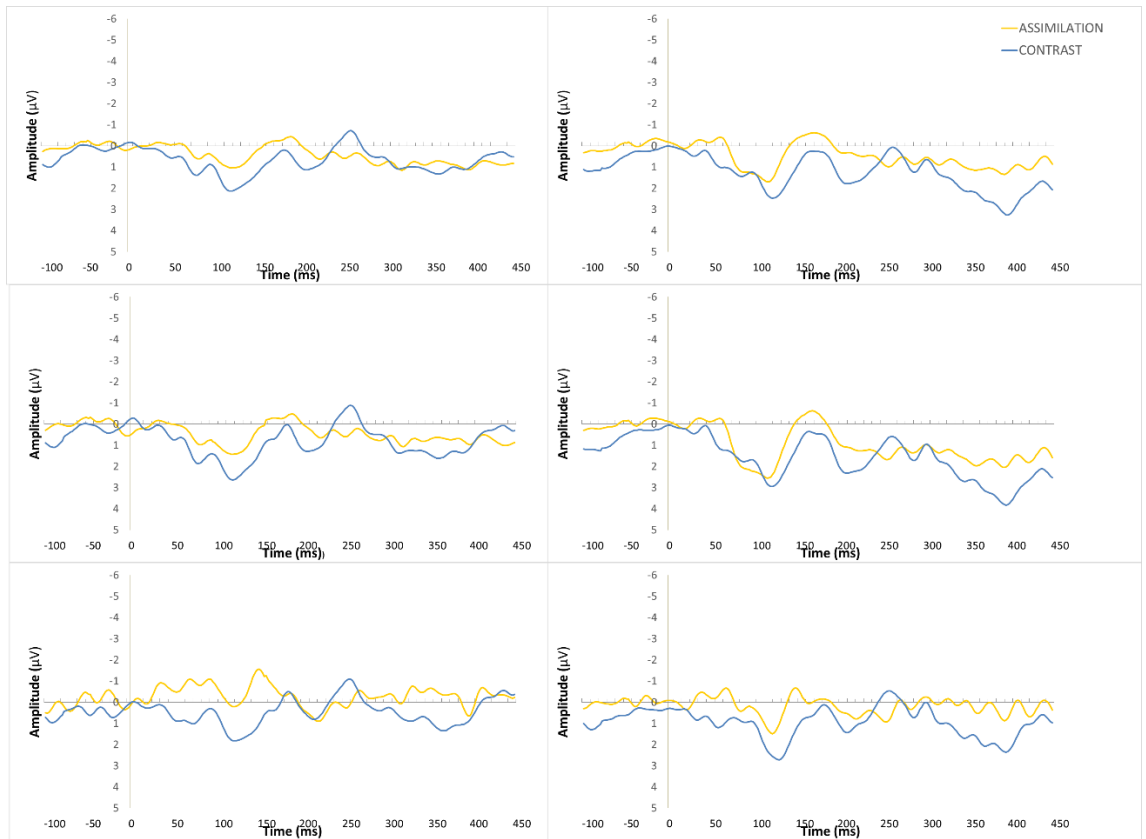


Figure 4.9. ERP waveforms as averaged into clusters for analysis at left and right parietal (P; top), occipital-parietal (OP; middle) and occipital (O; bottom) sites for contrast responses (shown in blue) and assimilation responses (shown in yellow).

For the mean amplitude of N1, the three-way interaction between response type, hemisphere, and electrode cluster was significant ($F(1.85, 24.03) = 4.57, p = .020, \eta_p^2 = .260$). Post-hoc two-way ANOVAs showed that the response type x electrode cluster interaction was not significant in the right hemisphere ($F(1.97, 29.12) = 1.00, p = .379$) but was significant in the left hemisphere ($F(1.74, 22.67) = 4.00, p = .031$), whereby the N1 amplitude was greater for assimilation responses than for contrast responses in the left occipital area ($t(13) = 2.26, p = .042$), but no significant differences in N1 amplitude within the left occipital-parietal or parietal areas. This difference is shown in the middle panel of Figure 4.10, where the difference between contrast and assimilation is clearest in the left occipital cluster. There was also a significant main effect of electrode cluster ($F(1.48, 19.26) = 51.60, p < .001$), with post-hoc comparisons showing no significant difference in N1 amplitude between the occipital and occipital-parietal

clusters ($p = .644$), but that the N1 amplitude in the parietal cluster was greater than that in the occipital clusters ($p < .001$) and occipital-parietal clusters ($p < .001$).



Figure 4.10. Mean amplitude and latency per condition, hemisphere, and cluster for the time periods of P1, N1, and N2. Error bars represent standard deviation.

For the mean amplitude of N2, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.62, 21.02) = 0.65$, $p = .500$, $\eta_p^2 = .048$). There was a significant main effect of electrode cluster ($F(1.40, 18.12) = 34.75$, $p < .001$, $\eta_p^2 = .489$), but no significant effects relating to response type. Post-hoc comparisons for the effect of electrode cluster showed no significant difference in N2 amplitude between the occipital and occipital-parietal clusters ($p > .999$), but that the N2 amplitude in the parietal cluster was greater than that in the occipital clusters ($p <$

.001) and occipital-parietal clusters ($p < .001$), as shown in the bottom panel of Figure 4.10.

ERP Latency.

For the P1 latency, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.07, 13.96) = 0.10, p = .770, \eta_p^2 < .01$). There was a significant main effect of electrode cluster ($F(1.11, 14.44) = 4.65, p = .045, \eta_p^2 = .26$), but no other significant main effects or interactions. Post-hoc comparisons for the effect of electrode cluster showed no significant difference in P1 latency between the occipital and parietal clusters ($p > .999$), nor between the occipital and occipital-parietal clusters ($p = .127$) but that the P1 latency in the occipital-parietal cluster was shorter than that in the parietal clusters ($p < .001$).

For the N1 latency, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.19, 15.40) = 0.63, p = .466$). There was a significant main effect of electrode cluster ($F(1.08, 14.01) = 5.66, p = .030$), but no other significant main effects or interactions. Post-hoc comparisons of electrode cluster showed no significant difference in N1 latency between the occipital and parietal clusters ($p = .678$), nor between the occipital and occipital-parietal clusters ($p = .471$) but that the N1 latency in the occipital-parietal cluster was shorter than that in the parietal clusters ($p < .001$).

For the N2 latency, the three-way interaction between response type, hemisphere, and electrode cluster was not significant ($F(1.10, 14.25) = 1.22, p = .313, \eta_p^2 = .086$). There was a significant main effect of electrode cluster ($F(1.14, 14.76) = 9.63, p = .006, \eta_p^2 = .426$), but no other significant main effects or interactions. Post-hoc comparisons between electrode clusters showed no significant difference in N2 latency

between the occipital and parietal clusters ($p > .999$), nor between the occipital and occipital-parietal clusters ($p = .076$) but that the N2 latency in the occipital-parietal cluster was shorter than that in the parietal clusters ($p < .001$).

Summary.

Within this comparison, the only effect involving response type was that the N1 amplitude was greater for assimilation responses than for contrast responses in the left occipital area only. There were no response type related effects for latency or other components. As with the previous response type comparison, there were also significant main effects of electrode cluster, or an interaction between hemisphere and cluster, in the amplitude and latency measures of each of the components, whereby the parietal cluster showed the greatest amplitudes.

4.3.4. Contrast responses in the ‘Black Large’ condition and the ‘White Large’ condition.

It was also possible to analyse within a response-type (i.e. using either only contrast responses or only assimilation responses) to examine the effect of inducer colour and stimulus configuration. Based on behavioural data (number and speed of responses), the inducer colour is thought to modulate the strength of the contrast or assimilation effect, for example, the contrast effect was stronger with white inducers than with black inducers. This comparison will make use of participants who have given consistent contrast responses in both ‘Black Large’ and ‘White Large’ conditions, thereby holding constant the type of response and the stimulus configuration, with the comparison being between the inducer colour. Any between-condition effects here would reflect either sensory differences arising from the difference in colour, or differences relating to the strength of the contrast effect itself, given that the contrast effect is thought to be stronger with the white inducer than with the black inducer.

In participants who consistently gave contrast responses in both the Black Large and White Large conditions ($N = 9$), the contrast responses to White Large (median = 1207.79ms) were significantly faster than Black Large (median = 1441.65ms), $z = -2.67$, $p = .008$. This is consistent with the overall RT analysis with all participants, which showed a significant difference in RTs between these two conditions.

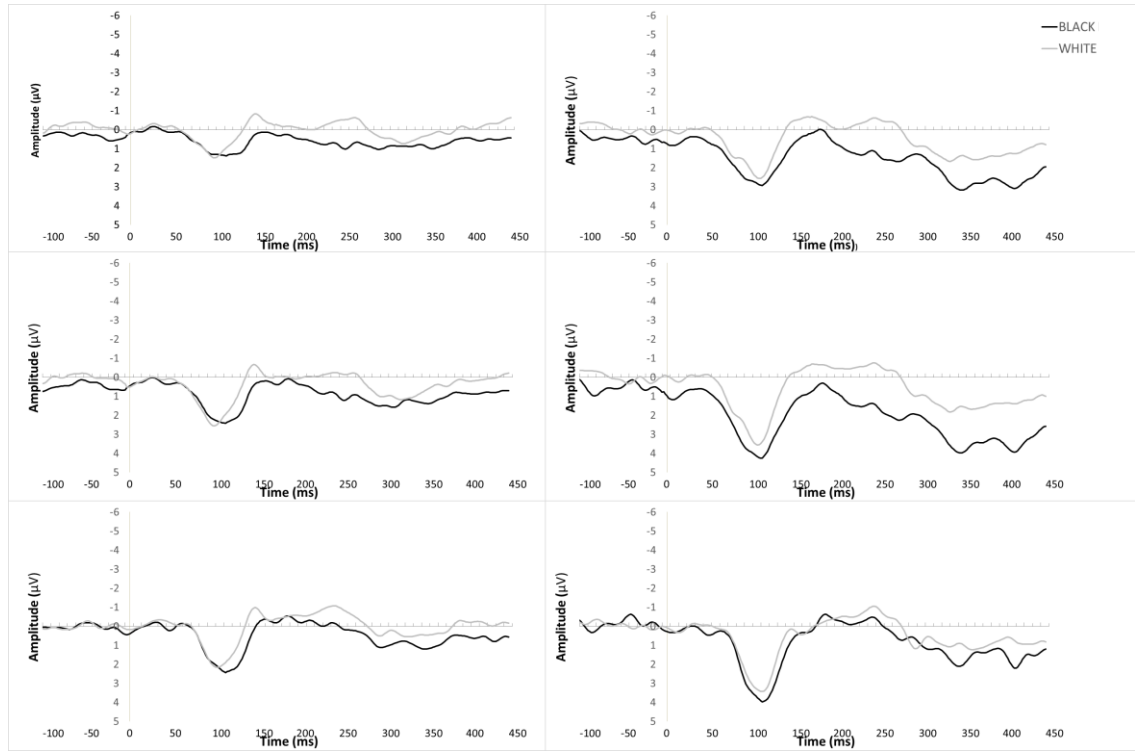


Figure 4.11. ERP waveforms as averaged into clusters for analysis at left and right parietal (P; top), occipital-parietal (OP; middle) and occipital (O; bottom) sites for contrast responses to Black Large (shown in black) and White Large (shown in grey) conditions.

ERP Amplitude.

For the mean amplitude of P1, there was a significant three-way interaction between condition, hemisphere, and cluster ($F_{adj}(1.72, 13.75) = 5.98$, $p = .029$, $\eta^2 = 0.43$). This was followed-up by two post hoc 2 (condition) x 3 (cluster) ANOVAs, for each hemisphere separately. In the left hemisphere, there were no significant main effects nor interaction ($p > .05$). In the right hemisphere, however, there was a

significant main effect of condition, whereby the Black Large condition was associated with a larger P1 mean amplitude than the White Large condition ($F_{adj}(1, 8) = 9.81, p = .001, \eta^2 = 0.55$). Post hoc t-tests showed that the significant difference between conditions was only significant in the right occipital-parietal cluster ($t_{adj} = 3.07, p = .015$). This can be seen in the right, middle panel of Figure 4.11, and top panel of Figure 4.12.

For the mean amplitude of N1, there was a significant three-way interaction between condition, hemisphere, and cluster ($F_{adj}(1.33, 10.62) = 13.91, p = .004, \eta^2 = 0.64$). However, there were no significant two-way interactions (all p -values $> .1$) nor any significant main effects (all p -values $> .2$). When separated by hemisphere, the post-hoc tests did not show any significant effects, although the condition x cluster interaction was close to significance in the right hemisphere only, ($F_{adj}(1.17, 9.39) = 4.90, p = .054, \eta^2 = 0.38$).

For the mean amplitude of N2, there was a significant three-way interaction between condition, hemisphere, and cluster ($F_{adj}(1.10, 8.83) = 7.16, p = .028, \eta^2 = 0.47$). However, there were no significant two-way interactions (all p -values $> .1$) nor any significant main effects (all p -values $> .1$). Although the amplitude in the Black Large condition was generally more positive than the White Large, as can be seen in Figures 4.11 and 4.12, post-hoc tests did not show any significant effects (all p -values $> .1$).

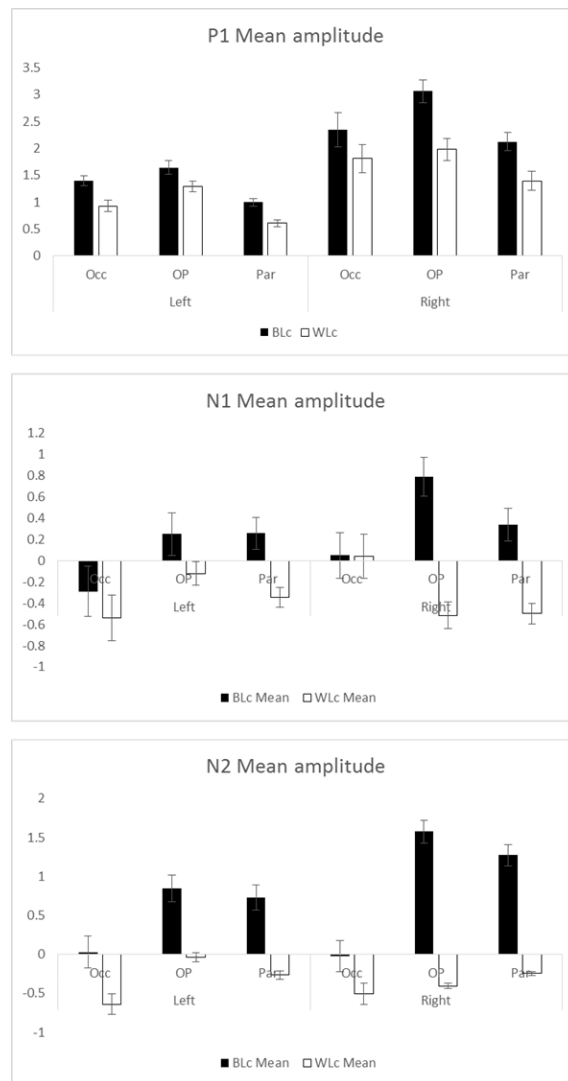


Figure 4.12. Mean amplitude per condition (Black Large, BL; White Large, WL), hemisphere, and cluster for the time periods of P1, N1, and N2. Error bars represent standard deviation.

ERP Latency.

For the fractional latency of P1, N1, and N2, there were no significant three-way interactions (p -values $> .8$) nor any significant two-way interactions (all p -values $> .6$) or main effects (all p -values $> .1$).

Summary.

Within this comparison, the only significant effect in the ERP analysis concerned the amplitude of P1, in which there was a significant difference between conditions (Black Large being greater than White Large) in the right occipital-parietal

electrode cluster. This links to the difference in RT, in which contrast responses were faster in the White Large condition than in the Black Large condition. Thus, contrast responses in the White Large condition are faster, and associated with smaller P1 amplitude, which is consistent with the idea that the contrast effect is stronger / more easily recognised with the white inducer.

4.3.5. Assimilation responses in the ‘Black Small’ condition and the ‘White Small’ condition

This comparison will make use of participants who have given consistent assimilation responses in both ‘Black Small’ and ‘White Small’ conditions, thereby holding constant the type of response and the stimulus configuration, with the comparison being between the inducer colours, as in the previous section with contrast responses. Any between-condition effects here would reflect either sensory differences arising from the difference in colour, or differences relating to the strength of the assimilation effect itself, given that the assimilation effect is thought to be stronger with the black inducers than with the white inducers.

In participants who consistently gave assimilation responses in both the Black Small and the White Small conditions ($N = 5$), there was no significant difference in response time, $z = -1.21$, $p = .225$. This is consistent with the overall RT analysis with all participants, which showed no significant difference in RT between these two conditions.

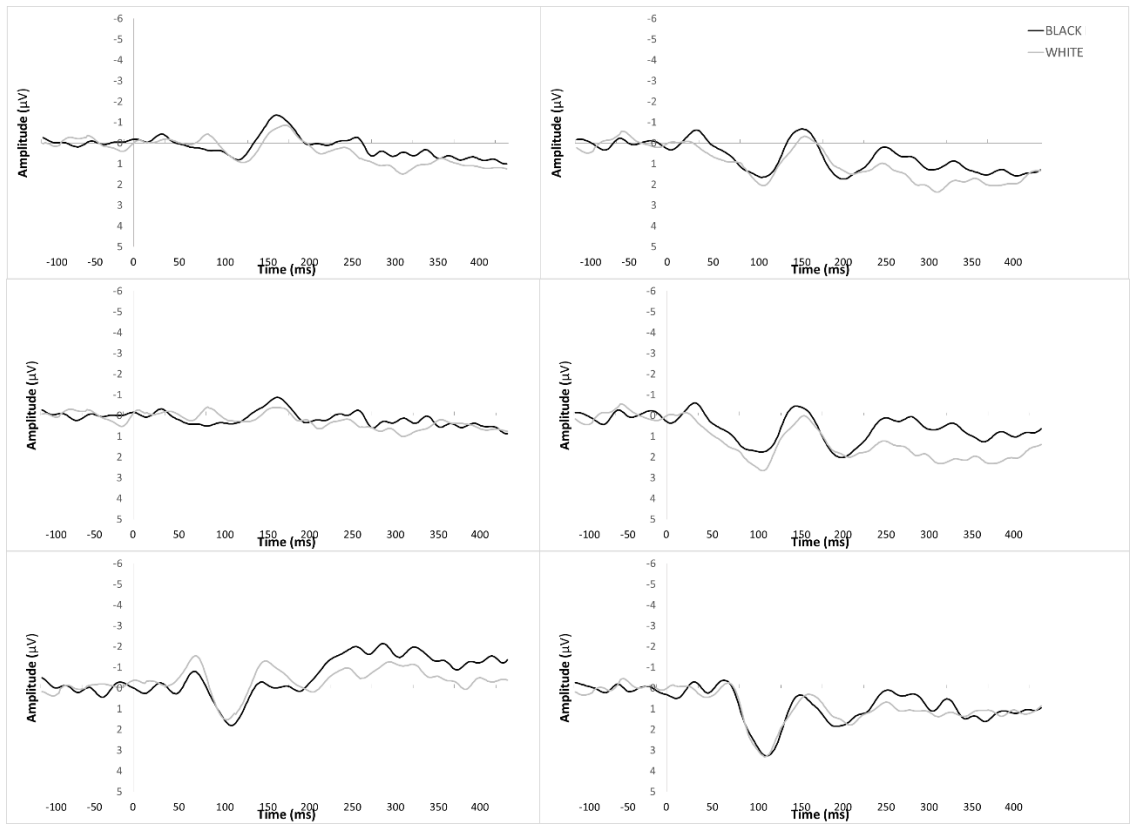


Figure 4.13. ERP waveforms as averaged into clusters for analysis at left and right parietal (P; top), occipital-parietal (OP; middle) and occipital (O; bottom) sites, for assimilation responses to Black Small (shown in black) and White Small (shown in grey) conditions.

ERP Amplitude.

For the mean amplitude of P1, there was no significant three-way interaction ($F_{adj}(1.12, 4.49) = 1.25, p = .327, \eta^2 = 0.23$), nor any significant two-way interactions or main effects (all p -values $> .1$), although Figures 4.13 and 4.14 suggest greater amplitude in the right hemisphere than in the left.

For the mean amplitude of N1, there was no significant three-way interaction ($F_{adj}(1.06, 4.22) = 1.37, p = .307, \eta^2 = 0.26$), nor any significant two-way interactions or main effects (all p -values $> .1$), although, as with P1, Figure 4.14 suggests a difference between hemispheres.

For the mean amplitude of N2, there was a significant three-way interaction between condition, hemisphere, and cluster ($F_{adj}(1.53, 6.12) = 7.00; p = .038, \eta^2 = 0.64$).

This was followed-up by three post hoc 2 (condition) x 2 (hemisphere) ANOVAs. There were no significant interaction or main effects in the occipital-parietal and the parietal clusters (all p -values $> .05$). In the occipital cluster, however, there was a significant two-way interaction between condition and hemisphere ($F_{adj}(1, 4) = 12.45$; $p = .002$, 0.76).

Post-hoc two-tailed paired t -tests were carried out to examine the condition x hemisphere interaction in the occipital cluster. However, there were no significant differences between the left and right hemisphere in the Black Small condition ($t_{adj}(4) = 1.56$, $p = .193$) nor the White Small condition ($t_{adj}(4) = 1.13$, $p = .323$). Nor were there any significant differences between Black Small and White Small in the left ($t_{adj}(4) = 1.47$, $p = .216$) or right ($t_{adj}(4) = 0.50$, $p = .645$) hemispheres. The lack of significant post-hoc effects in spite of a significant interaction may be a result of small sample size in this case. The descriptive statistics (see Figure 4.14) do however suggest that the N2 mean amplitude differs in these clusters, with the mean amplitude being more negative in the left occipital area than in the right; and the mean amplitude being greater for White Small than for Black Small in both hemispheres.

ERP Latency.

For the fractional latency of P1, N1, and N2, there were no significant three-way interactions (p -values $> .4$) nor any significant two-way interactions (all p -values $> .2$) or main effects (all p -values $> .1$).

Summary.

Within this comparison, the only significant effect concerned the amplitude of N2, specifically an interaction between condition and hemisphere within the occipital

electrode cluster, with more positive amplitude in the right hemisphere and in the White Small condition, although post-hoc tests did not show significant differences.

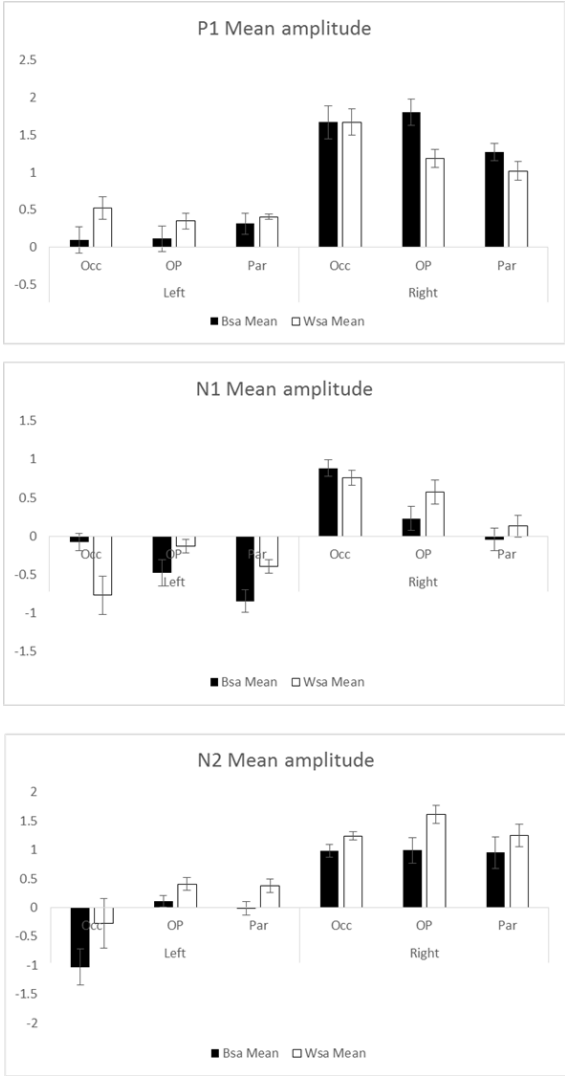


Figure 4.14. Mean amplitude per condition (Black Small, BS; White Small, WS), hemisphere, and cluster for the time periods of P1, N1, and N2. Error bars represent standard deviation.

4.3.6. Assimilation responses in the ‘Black Large’ condition and the ‘Black Small’ condition

This comparison will make use of participants who have given consistent assimilation responses in both ‘Black Large’ and ‘Black Small’ conditions, thereby

holding constant the type of response and the inducer colour, with the comparison being between the stimulus configurations. Any between-condition effects here would reflect either sensory differences arising from the difference in stimulus configuration/complexity, or differences relating to the strength of the assimilation effect itself. As stimulus configuration is typically cited as a determining factor in whether a contrast or assimilation effect is observed, this will be useful in highlighting any effects of the different stimulus configurations which are not necessarily associated with a shift between contrast and assimilation.

In participants who consistently gave assimilation responses in both the Black Large and the Black Small conditions ($N = 6$), the contrast responses to Black Small (median = 885.98ms) were significantly faster than Black Large (median = 964.09), $z = -1.99, p = .046$.

ERP Amplitude.

For the mean amplitude of P1, there was no significant three-way interaction ($F_{adj}(1.09, 5.46) = 2.21, p = .197, \eta^2 = 0.31$), nor any significant two-way interactions or main effects (all p -values $> .1$). Figure 4.15 shows that the two conditions do not differ greatly in most clusters at P1.

For the mean amplitude of N1, there was no significant three-way interaction ($F_{adj}(1.04, 5.18) = 2.76, p = .158, \eta^2 = 0.36$), nor any significant two-way interactions or main effects (all p -values $> .1$).

For the mean amplitude of N2, there was no significant three-way interaction ($F_{adj}(1.53, 6.12) = 4.48, p = .079, \eta^2 = 0.53$), nor any significant two-way interactions or main effects (all p -values $> .3$).

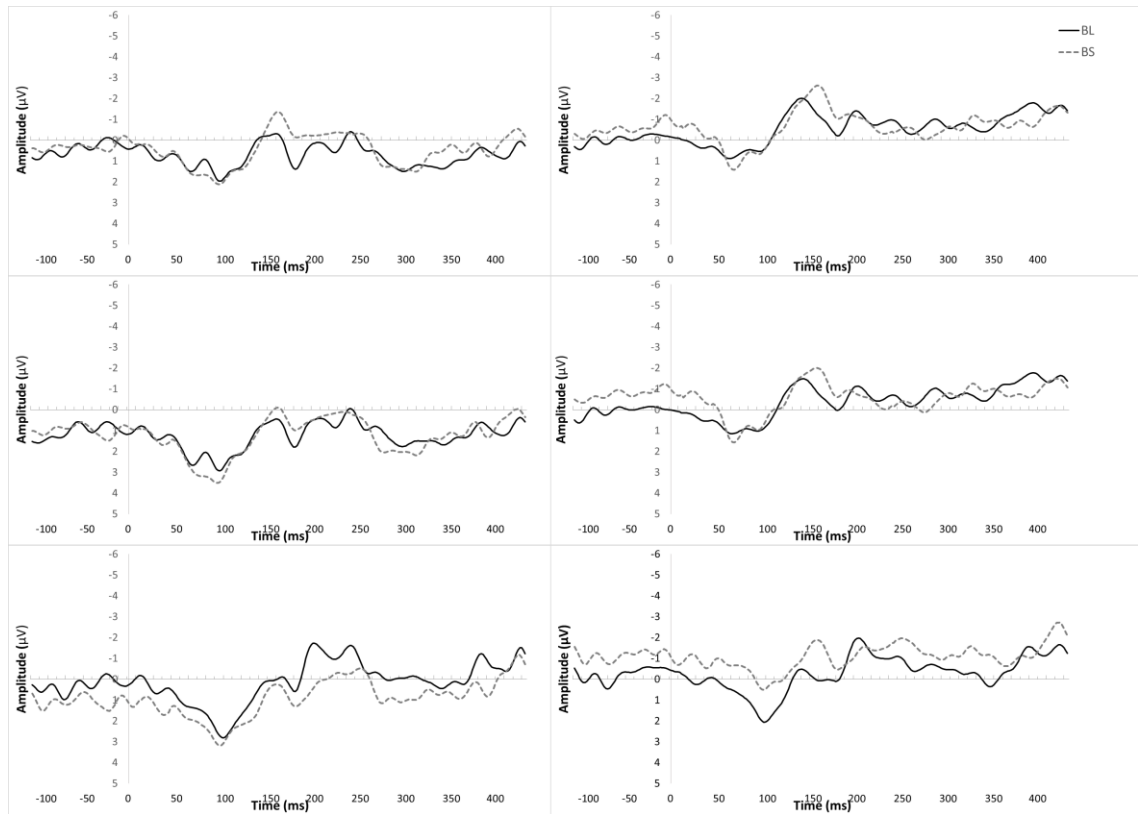


Figure 4.15. ERP waveforms as averaged into clusters for analysis at left and right parietal (P; top), occipital-parietal (OP; middle) and occipital (O; bottom) sites, for assimilation responses to Black Large (solid line) and Black Small (dashed line) conditions.

ERP Latency.

For the fractional latency of P1, N1, and N2, there were no significant three-way interactions (p -values $> .5$) nor any significant two-way interactions (all p -values $> .4$) or main effects (all p -values $> .2$).

Summary.

There were no significant effects or interactions for amplitude or latency of any component within this comparison.

4.3.7. Contrast responses in the ‘White Large’ condition and the ‘White Small’ condition.

This comparison will make use of participants who have given consistent contrast responses in both ‘White Large’ and ‘White Small’ conditions, thereby holding constant the type of response and the inducer colour, with the comparison being between the stimulus configurations. Any between-condition effects here would reflect either sensory differences arising from the difference in stimulus configuration/complexity, or differences relating to the strength of the contrast effect itself.

In participants who consistently gave contrast responses in both the White Large and the White Small conditions ($N = 11$), there was no significant difference in response time, $z = -1.69$, $p = .091$.

ERP Amplitude.

For the mean amplitude of P1, there was no significant three-way interaction ($F_{adj}(1.57, 15.74) = 0.30$, $p = .592$, $\eta^2 = 0.03$). However, the two-way interaction between condition and cluster was significant ($F_{adj}(1.84, 18.36) = 4.61$, $p = .046$, $\eta^2 = 0.32$), but there were no other significant two-way interactions (p -values $> .9$) or main effects (p -values $> .1$).

When examining the significant condition x cluster interaction, post-hoc tests showed no significant differences between conditions in the occipital ($p = .141$), occipital-parietal ($p = .865$), or parietal ($p = .839$), although there appears to be a larger difference between conditions in the occipital clusters than in the other clusters in Figure 4.16.

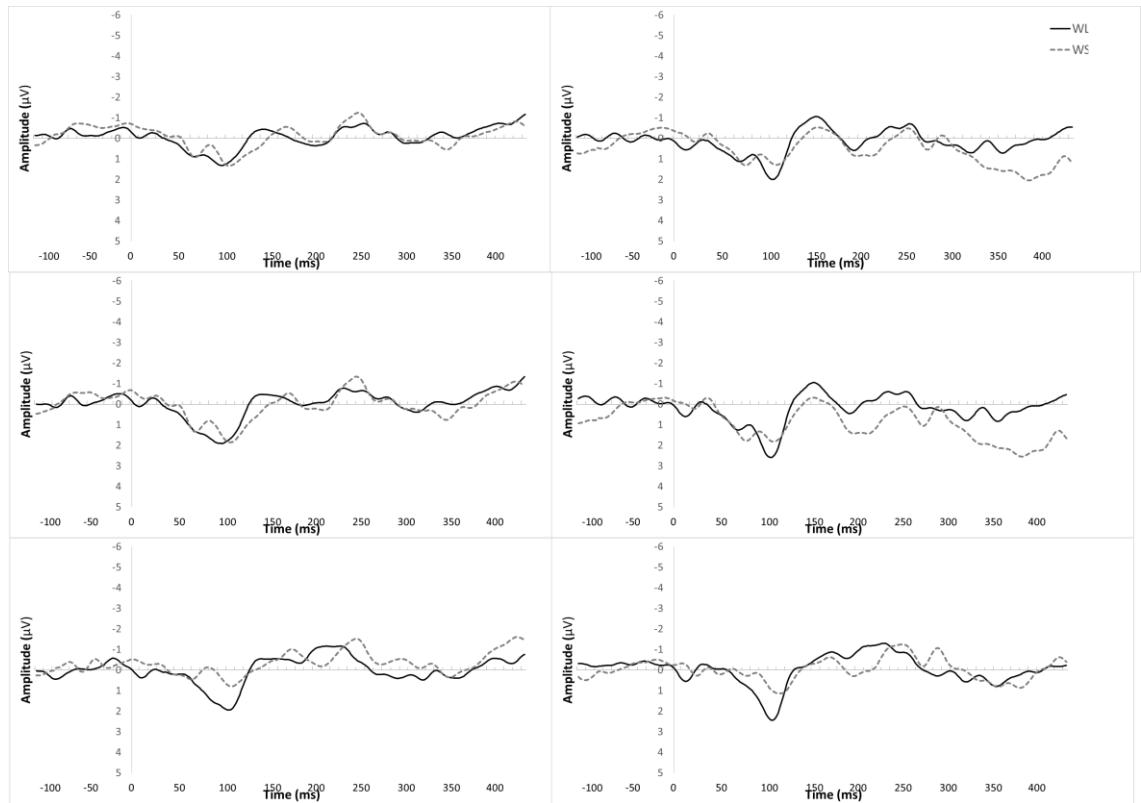


Figure 4.16. ERP waveforms as averaged into clusters for analysis at left and right parietal (P; top), occipital-parietal (OP; middle) and occipital (O; bottom) sites, for contrast responses to White Large (solid line) and White Small (dashed line) conditions.

For the mean amplitude of N1, there was no significant three-way interaction ($F_{adj}(1.48, 14.75) = 0.02, p = .887, \eta^2 < 0.01$), nor any significant two-way interactions or main effects (all p -values $> .3$).

For the mean amplitude of N2, there was no significant three-way interaction ($F_{adj}(1.41, 14.07) = 0.72, p = .412, \eta^2 = 0.07$), nor any significant two-way interactions or main effects (all p -values $> .1$).

ERP Latency.

For the fractional latency of P1, N1, and N2, there were no significant three-way interactions (p -values $> .5$) nor any significant two-way interactions (all p -values $> .4$) or main effects (all p -values $> .4$).

Summary.

Within this comparison, the only statistically significant effect concerned the amplitude of P1, specifically, an interaction between condition and electrode cluster in the left hemisphere, which showed non-significant post-hoc results but suggests greater P1 amplitude for White Large than for White Small in the occipital clusters.

4.3.8. Overall comparison of contrast versus assimilation responses

An overall analysis, including all participants, was also carried out to compare the ERPs associated with contrast responses versus those associated with assimilation responses, regardless of condition. Thus, for this analysis, conditions were not entered as a variable, and the independent variables were simply response type (i.e. contrast and assimilation), and hemisphere and cluster.

For the amplitude of P1, N1, and N2, there were no significant three-way interactions (p -values $> .7$), nor any significant two-way interactions (all p -values $> .4$) or main effects (all p -values $> .7$). Similarly, for the fractional latency of P1, N1, and N2, there were no significant three-way interactions (p -values $> .6$), nor any significant two-way interactions (all p -values $> .6$) or main effects (all p -values $> .4$).

4.4. Correlations between Behavioural and ERP Measures

The number of (contrast or assimilation) responses in a condition has been taken to represent the strength of the effect in the conditions. In the ‘Black Small’ (assimilation) and ‘White Large’ (contrast) responses, there were no significant correlations between the strength of effect and the ERP measures. Those conditions showed a clear dominance of one response type over the other, so there was less variation in how strongly the effect was perceived in these cases.

In the ‘Black Large’ condition, there were several significant correlations in the right occipital area for both contrast and assimilation responses. There were significant

positive correlations between number of assimilation responses and P1 amplitude ($r(20) = .49, p = .022$) and P1 latency ($r(20) = .48, p = .023$), whereas there were significant negative correlations between number of contrast responses and P1 amplitude ($r(23) = -.50, p = .010$) and P1 latency ($r(20) = -.48, p = .014$). There were also significant positive correlations between number of assimilation responses and N2 amplitude ($r(20) = .60, p = .003$) and N2 latency ($r(20) = .59, p = .004$), but no corresponding correlations for contrast responses and N2. Thus, the P1 amplitude and latency increase as the number of assimilation responses increases, but decrease as the number of contrast responses increases. Similarly, the N2 amplitude and latency increase as the number of assimilation responses increases.

The correlations for the ‘White Small’ condition formed a less consistent pattern. For P1 amplitude, there was a positive correlation in the right occipital-parietal area for assimilation responses ($r(23) = .42, p = .036$) and a negative correlation in the left occipital area for contrast responses ($r(19) = -.48, p = .029$). Thus, in the ‘White Small’ condition, the P1 amplitude in the right hemisphere increase as the number of assimilation responses increases, as in the ‘Black Large’ condition.

There was a negative correlation for N2 amplitude in the right occipital-parietal area for assimilation responses ($r(23) = -.46, p = .019$), but no N2 amplitude correlation for contrast responses. For N2 latency, there was a negative correlation in the right occipital-parietal area for assimilation responses ($r(23) = -.53, p = .007$) and a positive correlation in the left occipital area for contrast responses ($r(19) = .45, p = .041$). These correlations are the opposite in direction to the N2 correlations observed in the ‘Black Large’ condition.

4.5. Summary

The results of this study show that the proportion of contrast and assimilation responses is affected by both the colour and the configuration of inducers: black inducers produced more assimilation responses, whereas white inducers produced more contrast responses; small inducers produced more assimilation responses, whereas large inducers produced more contrast responses. The ‘White Large’ and ‘Black Small’ conditions elicited predominantly contrast and assimilation responses, respectively. The ‘Black Large’ and ‘White Small’ conditions elicited more mixed responses, with some participants favouring either response, or providing mixed responses. The RT data was consistent with this finding, as the conditions with clear/dominant effects (i.e. ‘White Large’ and ‘Black Small’) had generally faster responses than the conditions with more mixed responses (i.e. ‘Black Large’ and ‘White Small’), suggesting that the perceptual effects are weaker or less obvious in the latter conditions.

In general, there were no significant differences in ERP amplitude or latency when comparing between contrast and assimilation, with the exception of a greater N1 amplitude for assimilation responses than for contrast responses in the left occipital area – this effect was apparent in the ‘White Small’ condition only. For both contrast and assimilation responses, ERP amplitudes were generally greater in the parietal clusters than in the occipital and occipital-parietal clusters.

A stronger contrast effect in the ‘White Large’ condition (compared to the ‘Black Large’ condition) was associated with faster RTs, and smaller P1 amplitude in the right occipital-parietal cluster, suggesting that participants find the contrast effect more obvious or easy to detect with the white inducer. Consistent with this, the P1 amplitude correlates negatively with the strength of the contrast response, and positively with the strength of the assimilation response, in the right occipital-parietal cluster.

However, a stronger contrast effect in the ‘White Large’ condition (compared to the ‘White Small’ condition) was associated with *greater* P1 amplitude in the occipital clusters, though this was non-significant in post-hoc tests. The findings from this study will be discussed in more detail along with those from earlier sections, in the following chapter.

Chapter 5: General Discussion

The experiments described in previous chapters were designed to investigate lightness perception and some of its underlying mechanisms, by means of studying lightness contrast and lightness assimilation alongside one another, investigating the conditions under which these effects occur and are strengthened/weakened, as well as the associated electrophysiological activity occurring in the brain when contrast and assimilation effects occur. Specifically, the depth separation study (chapter 2) sought to examine how contrast and assimilation were affected by placing surfaces in different depth planes. The methodological work (see chapter 3) aimed to examine some factors which can increase the proportion of contrast/assimilation responses elicited, and provide evidence to support the choice of stimuli for the ERP work (chapter 4), which in turn aimed to begin to identify the time course of processing associated with lightness perception, and the patterns of neural activity associated with the perception of stimuli eliciting contrast and assimilation responses, as well as any similarities or differences in the neural activity associated with these lightness effects. In this chapter, key findings will first be summarised and then discussed in more detail.

5.1. Overview of Key Findings

Behavioural data across both the depth separation study (coplanar conditions) and the ERP study showed contrast effects with large inducers and assimilation effects with small inducers, as expected. The magnitude of effects (depth separation study) and number of responses and response time (ERP study and methodological studies) showed that contrast responses were faster and stronger with white than with black inducers, whereas assimilation responses were faster and stronger with black than with white inducers. The results relating to the direction and magnitude of contrast and assimilation

effects will be discussed further in section 5.2, and those relating to the speed of responses in section 5.3.

The ERP results showed no differences in amplitude or latency between contrast and assimilation responses when collapsed across conditions, or when examined within conditions, with the exception of a greater N1 amplitude in the left occipital area for assimilation responses than for contrast responses, in the ‘White Small’ condition. Across both contrast and assimilation responses, the parietal area showed greater amplitude and longer latencies than the occipital and occipital-parietal areas. This result will be discussed in section 5.4.

When considering only contrast responses, the P1 amplitude was larger with ‘Black Large’ inducers than with ‘White Large’ inducers. Along with the behavioural data, this presented a larger amplitude for the condition in which responses were slower and the contrast effect was weaker. In the ‘Black Large’ condition, P1 amplitude decreased as the proportion of contrast responses given increased. In addition, the P1 amplitude was also larger with ‘White Large’ inducers than with ‘White Small’ inducers. In this case however, this presented a *smaller* amplitude for the condition in which responses were slower and the contrast effect was weaker, though in this case the result was not statistically significant. These results will be discussed in sections 5.5 and 5.6.

When considering only assimilation responses, there were no ERP differences between conditions aside from an interaction in the occipital cluster between condition and hemisphere (comparing assimilation responses in the ‘White Small’ and ‘Black Small’ conditions). This interaction suggested that the ‘White Small’ condition elicited larger N2 amplitude than the ‘Black Small’ condition, and this difference was greater in

the left occipital area than in the right occipital area. This will also be discussed in sections 5.5 and 5.6.

5.2. Direction and Magnitude of Contrast and Assimilation Effects

(Behavioural/Psychophysical Data)

The depth separation study showed that in coplanar conditions, the targets with the large inducer were judged to be darker with the white inducer than with the black inducer (contrast effect); and targets with the small inducers were judged to be darker with black inducers than with white inducers (assimilation effect). This pattern of results did not hold when the inducers and target underwent depth separation. In non-coplanar conditions, the configuration of inducers did not seem to affect the direction of the perceived difference in lightness between the targets: in both cases, targets were judged to be darker with white inducers than with black inducers (i.e. contrast effects). The effect of depth separation/coplanarity was discussed in more detail in section 2.3, but coplanar contrast and assimilation effects are disrupted (i.e. weakened/reversed) by depth separation, implying that both effects require higher-level (cortical) processing (see de Weert & van Kruysbergen, 1997; Soranzo, Galmonte, & Agostini, 2010). This is because the retinal image is assumed to be equal between the corresponding coplanar and non-coplanar conditions, therefore retinal processing is unlikely to account for differences in the strength or direction of the effect occurring as a result of depth separation (see also section 2.3.1.).

Further to the direction of the effects, the relative magnitude can also be considered. In the depth separation study the magnitude is inferred by the size of the difference between the measured luminance value of the target and the mean lightness judgment. In coplanar conditions with large inducers, the contrast effect was larger with white inducers than with black inducers. This pattern also holds for the contrast effects

observed in the non-coplanar conditions with both types of inducers. In coplanar conditions with small inducers, the assimilation effect was larger with black inducers; in fact, for white inducers, the effect was actually a contrast effect.

In the ERP study and methodological work, all stimuli can be considered 'coplanar' as they were presented on-screen. The behavioural responses showed that large inducers produced more contrast responses overall, and small inducers produced more assimilation responses overall, which is consistent with the results for the coplanar conditions in the depth separation study. The magnitude of the contrast/assimilation effect cannot be inferred in the same way as in the depth separation study due to the nature of the 2AFC task, so the consistency (proportion) of each type of response in each condition is taken as an indicator of the strength of the effect.

Specifically, there were significantly more assimilation responses than contrast responses with 'Black Small' inducers, and significantly more contrast responses than assimilation responses with 'White Large' inducers, suggesting a stronger assimilation effect with black inducers and a stronger contrast effect with white inducers. In the other two conditions ('Black Large' and 'White Small') the responses were a mixture of contrast and assimilation responses. This was somewhat unexpected as it is generally reported that these stimuli produce more consistent contrast and assimilation responses, respectively (e.g. Beck, 1966; Helson, 1963; Soranzo, Galmonete, & Agostini, 2010; Wade, 1996). However, it is consistent with the idea that contrast is stronger in the 'White Large' condition (compared to the 'Black Large') and assimilation is stronger in the 'Black Small' condition (compared to the 'White Small'), because in the conditions where the effect is thought to be weaker, participants may have given mixed responses due to uncertainty around a less obvious perceived difference between the target and comparison square. This was also supported by data from the methodological studies,

where assimilation responses were always more prevalent with black inducers than with white inducers of equivalent configuration; and contrast responses were always more prevalent with white inducers than with black inducers of equivalent configuration.

Table 5.1 summarises the main results relating to the type of response/effect for each stimulus type. The coplanar stimuli from the depth separation study produced the same effects as the on-screen stimuli, in that overall the large inducer stimuli predominantly elicited contrast responses and the small inducer stimuli predominantly elicited assimilation responses. The finding that contrast is stronger with white inducers and assimilation with black inducers is also consistent across the studies.

Table 5.1. Categorisation of lightness effects for 2D stimuli across studies.

Study	Stimulus	Finding
Depth separation study (coplanar conditions)	Large inducer	Contrast effect; greater effect for white inducers
	Small inducers	Assimilation effect for black inducers; small contrast effect for white inducers
Methodological studies	Large inducer	Contrast effect; higher proportion of contrast responses for white inducers
	Small inducers	Assimilation effect; higher proportions of assimilation responses for black inducers
ERP study	Large inducer	More contrast responses overall; more consistent effect for white inducers
	Small inducers	More assimilation responses overall; more consistent effect for black inducers

The finding that the contrast effects were stronger with white inducers than black inducers is inconsistent with the predictions of Anchoring Theory (Gilchrist et al., 1999) and with some previous reports, for example stating that the simultaneous contrast illusion arises primarily as a result of a contrast effect on the target surrounded

by black (Economou, Gilchrist, & Zdravković, 2007). This difference could result from a difference in stimulus design: Economou et al. (2007) presented a ‘traditional’ simultaneous lightness contrast display (two grey targets, one surrounded by white and one surrounded by black) whereas the current work presented only ‘half’ of this display at a time (i.e. either black or white inducer, not both), thereby changing/removing the ‘global framework’. However, others have reported a stronger contrast effect when a grey disc was grouped with white inducers than when it was grouped with black inducers (Murgia et al., 2016) which suggests that the Anchoring Theory does not predict the strength of contrast effects in all cases.

The finding that the assimilation effects were stronger with black inducers than with white inducers is consistent with the findings of Soranzo, Galmonte, & Agostini (2010). It is also consistent with Murgia et al.’s (2016) finding of a stronger assimilation effect when a grey target was intentionally grouped with black inducers than when grouped with white inducers. Beck (1966) and de Weert and Spillman (1995) also reported that assimilation occurred with black inducers whilst contrast occurred with white inducers, which is consistent with the results of the depth separation study (small inducer conditions) in particular, and with the forced-choice task, where some participants giving contrast responses in the ‘White Small’ condition and others giving assimilation responses whereas responses in the ‘Black Small’ condition were more consistently assimilation responses.

Although there are some inconsistencies between the current research and previous literature with regard to the contrast effect being stronger with the white inducer, these would be explained if contrast and assimilation are to be conceptualised as opposing processes: one effect is strengthened in conditions with white inducers whereas the other is strengthened in conditions with black inducers. It should be noted

that the inducer colour alone is not being regarded as a determining factor for whether a stimulus elicits a contrast response or an assimilation response, but that it is important *in conjunction* with the configuration of the inducers.

It could be argued that the configuration and colour of inducers are both contributing factors when making judgements about the salience of each surface within an image. De Weert and Spillman (1995) suggested that assimilation effects with inducers that were darker than the target could be a result of the dark surfaces being perceived as ‘figure’ and the areas bordering the dark areas (i.e. the grey target) being perceived as ‘ground’. This suggestion hints at the possibility that the colour and configuration of a stimulus can affect mediating processes, such as figure/ground segregation, which could subsequently alter the likelihood of a contrast versus assimilation effect for the stimulus concerned. In the context of the current results, the combination between large inducer and white inducer may be the most likely pairing to result in a figure-ground interpretation which favours contrast, whereas the combination between small inducers and black inducers may be the most likely pairing to result in a figure-ground interpretation which favours assimilation.

5.3. Speed of Contrast and Assimilation Responses

Unlike the strength of effects (discussed in the previous section) response time (RT) has not generally been reported and discussed in previous literature relating to contrast and assimilation. This is likely due to the constraints of task type/paradigm. For example, participants are usually given an unlimited amount of time to make a lightness judgement (as in the depth separation study), and the speed of response is not recorded, whereas the forced choice task used in the ERP study allows easy measurement of the speed of responses. RT analysis showed that in general, assimilation responses were faster than contrast responses. When comparing between the four experimental

conditions, the 'White Large' condition showed the fastest responses overall. The conditions with faster RTs are the same conditions which showed stronger contrast and assimilation responses as determined by the consistency of responses, i.e. the 'White Large' and 'Black Small' conditions, respectively. The conditions with slower overall RTs, namely the 'Black Large' and 'White Small' conditions, are also the conditions which showed a mixture of contrast and assimilation responses rather than a clear majority of either response type.

The finding that contrast responses were faster in the 'White Large' condition than in the 'Black Large' condition suggests that the contrast effect is more obvious in the 'White Large' condition; likewise, the finding that assimilation responses were faster in the 'Black Small' condition than the 'White Small' condition suggests that the assimilation effect is more obvious in the 'Black Small' condition. Participants take longer to decide upon a response in conditions where the effect may not be as easily apparent. This is supported also by the number of responses of each type per condition, which has been taken to represent the strength of the contrast or assimilation effect. The coherence between the RT data and the number of responses reinforces the assumption that these measures can be used to indicate the strength of the contrast or assimilation effects in the ERP study, as the difference between participants' chosen luminance match and the measured luminance of the target is used to indicate the strength of the contrast or assimilation effects in the depth separation study. The speed of contrast and assimilation responses is clearly related to the strength of the effects (as measured by proportion of responses and/or the size of the difference between measured and perceived target lightness).

5.4. ERP Responses when specifically comparing Contrast and Assimilation

A primary task addressed by the ERP analysis was to examine and compare the ERP waveforms associated with contrast responses and the ERP waveforms associated with assimilation responses, and to identify differences in the associated neural processing. Given that contrast and assimilation are both lightness-related effects, some level of similarity in the underlying processing is to be expected, however, it was of interest to attempt to discover potential sources of difference between the two effects, particularly as they can be thought of as operating in opposite directions (i.e. contrast makes targets appear more different to their inducers whereas assimilation makes targets appear more similar to their inducers).

The overall comparison of contrast responses versus assimilation responses (collapsed across all conditions with the aim of identifying any contrast versus assimilation differences irrespective of stimulus condition), showed no significant differences in amplitude or latency of P1, N1, or N2. The nature of the response types in the ‘Black Large’ and ‘White Small’ conditions (i.e. some participants having given mostly contrast responses and others having given mostly assimilation responses) allowed comparisons to be made between contrast and assimilation within the same stimulus condition – this is an ideal ERP comparison as only the perceptual interpretation is different and the visual stimulus remains constant. However, the analysis of the contrast versus assimilation responses within the ‘Black Large’ condition showed no effect of response type on ERP measures.

The analysis of the contrast versus assimilation responses within the ‘White Small’ condition showed an interaction between response type and electrode cluster within the left hemisphere (but not the right) for N1 amplitude, whereby there was a greater negative deflection for contrast responses than for assimilation responses in the

left occipital area, but no difference between assimilation and contrast in the left occipital-parietal or parietal areas. In previous research, an increase in N1 amplitude has been associated with enhanced processing and attention (e.g. Hillyard, Hink, Schwent, & Picton, 1973; Sokhadze et al., 2017), suggesting a potential role for a higher level of attention resulting in a contrast response rather than an assimilation response, which would be in agreement with the suggestion that attended-to stimuli undergo contrast effects whereas less-attended stimuli undergo assimilation effects (Festinger, Coren, & Rivers, 1970; see section 1.2.3.). However, this difference in N1 amplitude was not apparent for all comparisons between contrast and assimilation, and it is not possible to conclude whether the target or inducer is receiving more attention in either case.

When considering the levels of processing involved in contrast and assimilation, a difference at the time period of N1 suggests that there is a difference in processing at a higher cortical level, as N1 is thought to have extrastriate origins (Gomez-Gonzales, Clark, Fan, Luck, & Hillyard, 1994). This difference could also result from a difference between contrast and assimilation in terms of the influence of higher-level processing such as the global perceptual organisation of the stimulus (e.g. the ‘frameworks’ or figure-ground segmentation implied by the stimulus), as this information can be fed back to V1 from ~100ms (Lamme & Roelfsema, 2000).

There were no other effects concerning response type (contrast vs assimilation) on ERP measures. The general lack of significant differences in ERP measures between contrast responses and assimilation responses when all else is held constant suggests that contrast versus assimilation responses are largely not associated with different electrophysiological processing in the occipital and parietal regions in the time windows up to 300ms following stimulus onset. It could be intuitively assumed that a null result suggests that the same processing is involved with both contrast and assimilation,

however, Otten and Rugg (2005) outline several reasons why this conclusion would not necessarily be correct. The most important of these is that ERPs reflect only the brain activity which is detectable by scalp electrodes; typically synchronous activity from populations of pyramidal neurons oriented perpendicular to the electrode positions (Jackson & Bolger, 2014), and the neural activity which differentiates two response types may not have the properties necessary for detection by electrodes on the scalp. Therefore it is not possible to conclude that a non-significant difference implies completely equivalent neural processing.

5.4.1. Effects of electrode cluster, independent of response type.

Effects of electrode cluster in each measurement window were found in the analyses seeking to examine differences between contrast and assimilation responses to the same stimulus. Regardless of response type, the ERPs in the ‘Black Large’ and the ‘White Small’ conditions showed greater activation in the parietal area when compared with the occipital and occipital-parietal areas. This suggests that the level of neural activity and processing is greatest in the parietal areas for both contrast and assimilation effects. This can be regarded as a similarity in processing between the two effects: contrast and assimilation effects in this paradigm arise with maximal activity in the parietal cortex, and recognition/experience of the two effects may be similarly ‘complex’ in that they are associated with this cortical activity.

Activation in the parietal cortex has been associated with a wider variety of cognitive tasks, including attention and spatial representations (Culham & Kanwisher, 2001). Neuroimaging has also shown greater fMRI responses in the parietal lobe for ‘ungrouped’ objects than for ‘grouped’ objects (Xu & Chun, 2007), suggesting that activity in the parietal cortex can also be involved in representations of perceptual grouping. The activity in the parietal cortex implies that contrast and assimilation occur

with processing beyond an initial ‘recognition’ in early visual occipital areas. In addition to the evidence from the depth separation study (see sections 2.3 and 5.2), this supports the idea that the processing underlying contrast and assimilation extends to the higher cortical (parietal) level, though this finding does not indicate any difference between contrast and assimilation.

5.5. ERP Responses concerning the Inducer Colour

Further ERP analysis compared ERPs associated with the same type of response between different coloured inducers, specifically: contrast responses with ‘Black Large’ inducers versus contrast responses with ‘White Large’ inducers; and assimilation responses with ‘Black Small’ inducers versus assimilation responses with ‘White Small’ inducers. Any effects here could reflect the difference in the strength of the effect between black and white inducers, however, it is important to consider that stimuli differing in luminance will likely result in differential responses throughout the visual system (Ellemberg, Hammarrenger, Lepore, Roy, & Guillemot, 2001), which is known as a physical stimulus confound (Hillyard & Picton, 1987).

For the contrast responses, there was greater early activity (P1 amplitude) in the ‘Black Large’ condition than in the ‘White Large’ condition in the right occipital-parietal area. For the assimilation responses, there was no such effect. Given that the same effect of inducer colour was not present for both the contrast and assimilation responses (i.e. the effect was not common to all comparisons where black versus white inducers was a factor), it can be assumed that the P1 difference between the ‘Black Large’ and ‘White Large’ conditions is associated with the strength of the perception rather than simply the physical stimulus confound of inducer colour. The larger amplitude in the lower-luminance condition is also inconsistent with previous research suggesting that lower luminance would be associated with a smaller P1 amplitude

(Fimreite, Ciuffreda, & Yadav, 2015; Johannes, Münte, Heinze, & Mangun, 1995), and is not consistent with the finding that grey-on-white targets elicited larger amplitudes than grey-on-black targets (McCourt & Foxe, 2004; although this was reported ~70ms, which is earlier than P1).

This finding shows that a point at which a distinction in processing of the ‘Black Large’ and ‘White Large’ stimuli occurs within the P1 time window and in the right occipital-parietal area, although processing of both stimuli continues past this time and on to the parietal area, as discussed in section 5.4.1. The difference in P1 amplitude could therefore reflect a difference in the amount of processing given to the stimulus, rather than simply luminance-based processing which occurs at a retinal level. The increased activity for contrast responses in the ‘Black Large’ condition compared to contrast responses in the ‘White Large’ condition corresponds to the ‘Black Large’ condition showing a weaker contrast effect (i.e. less consistent contrast responses), as well as slower responses than in the ‘White Large’ condition. Together these findings indicate that ‘Black Large’ has the less obvious contrast effect and can be regarded as the more ‘difficult’ of these two conditions, requiring more processing in the right occipital area. Given that white inducers favour a stronger contrast effect (see section 5.2.), a lower level of neural activity may indicate that the ‘decision’ about the target lightness has been made more quickly and with less processing resources than with black inducers.

5.6. ERP Responses concerning the Stimulus Configuration

ERPs were also compared between different stimulus configurations, specifically: assimilation responses with ‘Black Large’ inducers versus assimilation responses with ‘Black Small’ inducers; and contrast responses with ‘White Large’ versus contrast responses with ‘White Small’ inducers. Again, any effects here could

reflect the difference in the strength of the effect between large and small inducers, however, it is important to consider that stimuli differing in configuration will inherently modulate ERP components – particularly the earlier components and those related to sensory and perceptual processing such as P1 and N1 (Woodman, 2010).

When considering the assimilation responses in ‘Black Large’ and ‘Black Small’ conditions, there were no effects for either amplitude or latency of P1, N1, or N2. Therefore, the ERP measurements were not influenced by either the difference in stimulus configuration, or the difference in the strength of the assimilation effect (the assimilation effect was stronger in the ‘Black Small’ than in the ‘Black Large’ condition) in this case. When considering the contrast responses in ‘White Large’ and ‘White Small’ conditions, the P1 amplitude in occipital areas was greater in the ‘White Large’ than in ‘White Small’ condition, though this was not statistically significant. Consistent across both comparisons (Large versus Small in both black inducers and white inducers), the stimulus configuration did not significantly influence the ERP measures.

5.7. Brain-Behaviour Correlations

In addition to examining the neural activity associated with contrast versus assimilation responses, the activity associated with a change in the strength of either effect has also been examined. The number of responses in a condition was assumed to represent the strength of that effect in that condition. The ‘Black Small’ (assimilation) and ‘White Large’ (contrast) conditions did not show any significant correlations between the strength of the contrast/assimilation effect and any ERP measures. Given that these conditions elicited generally consistent responses, this could result from low variability in terms of the strength of the effects, i.e. the contrast/assimilation effect is fairly strong in general.

In the ‘Black Large’ condition, however, the P1 amplitude and latency in the right occipital area both correlated with the number of responses. For assimilation responses, the correlation was positive (more assimilation responses/stronger perception of an assimilation effect being associated with larger amplitude and longer latency); whereas for contrast responses, the correlation was negative (more contrast responses/stronger perception of a contrast effect being associated with smaller amplitude and shorter latency). The latter is consistent with the earlier finding of a smaller P1 amplitude in the right occipital-parietal area for ‘White Large’ than for ‘Black Large’, i.e. the stronger contrast effect was associated with smaller amplitude than the weaker contrast effect (see section 5.5.). Thus, stronger contrast effects have been associated with smaller P1 amplitudes across two aspects of analysis: both between two conditions, and within the ‘Black Large’ condition.

Given that the P1 amplitude is smaller in a condition generating a stronger contrast effect *and* P1 amplitude correlates negatively with the strength of the perception of a contrast effect, this is evidence to suggest that P1 amplitude can be regarded as an indicator of the strength of a contrast effect. If these correlations can be found consistently for contrast and assimilation effects, this would add neurophysiological evidence to the argument that contrast and assimilation form part of a continuum of lightness effects (e.g. Helson, 1963; Kingdom, 2011).

In the ‘White Small’ condition, however, the pattern of correlations between strength of effect and ERP measures was not as coherent. As with the ‘Black Large’ condition, the P1 amplitude positively correlated with the strength of assimilation (right occipital-parietal area) and negatively correlated with the strength of contrast (left occipital area). These correlations did not present in consistent hemispheres/clusters, but

the increased P1 amplitude associated with more assimilation responses/stronger perception of an assimilation effect is consistent with the findings discussed above.

5.8. Theoretical Implications and Future Directions

Following from the current research, a sufficient theory of lightness contrast and assimilation would need to take account of several findings. Firstly, theories should acknowledge the potential for processing at the cortical level (i.e. higher parietal area as well as occipital and retinal processing) in both contrast and assimilation. Both effects were disrupted when the target and inducer were separated by depth, also suggesting that the effects occur at a higher level than only retinal, as a change in depth (while keeping the same retinal image) resulted in different effects. In most cases, contrast and assimilation did not differ significantly in the ERP analyses, suggesting ongoing cortical processing is a part of both phenomena. There was however a difference in parietal activity between contrast and assimilation with white small inducers, suggesting a difference in processing at a later stage.

Secondly, theories should account for the ‘asymmetry’ associated with inducer colour, i.e. explain why white inducers favour a stronger contrast effect whilst black inducers favour a stronger assimilation effect. This could be linked to the role of figure-ground, or attentional salience or weighting of different surfaces or ‘frameworks’. Further research is also needed to identify explanations for cases when this result is not observed, as although it is a consistent finding in the current work, there are some examples where this has not been the case (see section 5.2.).

Finally, theories need to give scope for explaining contrast and assimilation as part of a continuum of effects or explaining the shift between contrast and assimilation in a way which is not only reliant on spatial frequency. This would take into account the finding that sometimes, particularly in a forced-choice task, an identical stimulus can

result in either a contrast or an assimilation response from different individuals, or indeed on different occasions for the same individual. The finding that activity in the right occipital-parietal area (P1 time window) increased with stronger assimilation effects and decreased with stronger contrast effects also implies a possible neural marker for a continuous variation in the strength or type of perceived effect.

5.8.1. P1 amplitude as a possible marker of the strength of the contrast/assimilation effect.

The current electrophysiological work was exploratory in nature. However, it has provided evidence when comparing both between and within conditions to suggest that the P1 amplitude is relevant to the strength of the contrast effect as measured by the consistency/proportion of contrast responses given, in terms of smaller amplitude being associated with a stronger contrast effect. Thus, future research can make use of this to form specific hypotheses regarding whether manipulating stimuli to alter the strength of a contrast effect would also result in altered P1 amplitude.

The correlational analysis also showed the inverse: that for assimilation, a larger amplitude is associated with a stronger effect. It would be interesting to investigate whether a parametric variation in stimuli (so as to create stimuli which varied along a continuum in perceived strength of the contrast/assimilation effect) would result in the same correlational result.

5.8.2. Different patterns of responses in the ‘Black Large’ and ‘White Small’ conditions.

It has been noted that contrast appears stronger with white inducers than with black inducers, which may account for the observation of predominantly contrast responses in the ‘White Large’ condition, but more mixed responses in ‘Black Large’ in the 2AFC task. The same has been applied to assimilation, which appears stronger with

black than with white inducers, and results in largely assimilation responses in the ‘Black Small’ condition, but more mixed responses in ‘White Small’. However, when examining the responses of individual participants, it is clear that in both the ‘Black Large’ and ‘White Small’ conditions, some participants gave a majority of contrast responses, some gave a majority of assimilation responses, and some gave a more even mixture of contrast and assimilation responses. From the current data, it is not clear why this should be the case.

5.9. Limitations of the Current Work

The stimulus configurations were chosen as examples which produce good rates of contrast/assimilation responses, in order to examine the effects of manipulating depth, and to examine the ERPs associated with contrast/assimilation responses. However, the stimulus configurations do present a potential confound in terms of the possible figure-ground arrangement. In the stimuli designed for contrast responses, the grey target is surrounded by the black/white inducer, whereas in the stimuli designed for assimilation responses, the black/white inducers are surrounded by the grey. In the methodological tests, targets surrounded by inducers resulted in more contrast responses than inducers surrounded by targets, hence they were chosen to elicit contrast responses and examine the associated ERP activity.

The fact that contrast and assimilation effects generally result from different physical stimuli presents a challenge in dissociating changes due to the direction or strength of the contrast/assimilation effect perceptually experienced, from changes due to the colour or configuration of the stimulus. This was partially addressed in the ERP study by making comparisons between responses of the same type, with the same colour inducer, but with different configurations. This did not show a consistent ERP effect relating to stimulus configuration.

This divergence of response types (i.e. some participants consistently giving contrast responses and some consistently giving assimilation responses) within the ‘Black Large’ and ‘White Small’ conditions provided an opportunity to compare contrast versus assimilation responses to the same visual stimulus. However, those analyses were limited to smaller sample sizes due to making use of subsets (based on behavioural data) of the larger sample initially intended to undergo only within-subjects analyses. This means that the results of the between-subjects analyses may suffer from low statistical power (for example, the post-hoc power calculations for the three-way interactions showed power values ranging from 0.05 to 0.55).

A potential limitation is that the same stimuli were presented many times (80 times each), which could reduce the strength of the contrast/assimilation effect over time due to repeated exposure to the stimulus. In previous (non-ERP) research, stimuli have typically been presented a very small number of times. The possible effect of such repeated exposure is not well documented, though Gilchrist (2005, pp.167-8) described a “hysteresis effect” whereby presenting the same observer with multiple stimuli reduces the perceived difference in lightness. Despite this, the derivation of ERPs from the recorded EEG data does require a large number of trials per condition in order to gain a sufficient signal-to-noise ratio. It could be argued that this could be addressed by using several different stimulus configurations within each condition, to reduce the number of repetitions of the same stimulus. However, doing so would introduce stimulus configuration as a confounding variable within conditions: the configuration itself may result in differences in ERP waveforms, and it would not be appropriate to average these together to form a single ‘condition’ waveform.

5.10. Concluding Comments

The behavioural results throughout this work show a stronger contrast effect with white inducers, and a stronger assimilation effect with black inducers. This is supported not only by the magnitude of the effects observed using the matching-chart method, but also by the distribution of response types and speed of responses (RT, which has not typically been measured previously in relation to contrast and assimilation) in the forced-choice task, showing that both paradigms are effective in assessing the direction and strength of lightness effects.

From the ERP data, the most consistent finding concerns early activity (P1 amplitude), particularly in the right occipital and occipital-parietal area. This activity increased as the strength of assimilation increased, and decreased as the strength of contrast increased. This was further supported by greater activity in a condition where the contrast effect was perceived less strongly ('Black Large') than where the contrast effect was perceived more strongly ('White Large'). It remains of interest to discover whether a similar effect can be shown with other stimuli; or indeed stimuli which generate a 'continuum' of contrast/assimilation effects varying in strength.

Concerning the level(s) of processing involved in contrast and assimilation, the current work provides further evidence to support cortical involvement rather than retinal processing alone. Both contrast and assimilation showed ongoing electrophysiological activity in the occipital and parietal cortex, implying processing at visual cortical areas such as V1, and beyond. Although contrast and assimilation did not show ERP differences in most conditions, there was a difference at the N1 measurement window ('White Small'), which shows a point of divergence between the two phenomena at a cortical level. The effect of depth separation/coplanarity also adds weight to the argument that cortical processing is required for both contrast and

assimilation effects, as both effects were changed (i.e. reduced or reversed) by depth separation, despite the 2D stimulus arrangement and retinal image remaining unchanged, thus retinal mechanisms alone cannot fully account for the effects.

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Word count: 35, 215

Appendix 1 – Ethical Approval and Associated Documents

1.1 – Confirmation of ethical approval



Our Ref AM/SW/42-ACA

Ms S Acaster
Flat 1
68 Bannerdale Road
Sheffield
S7 2DP

Dear Steph

Request for Ethical Approval of Research Project

Your research project entitled "Behavioural and electrophysiological indices of the perceptual phenomena of contrast and assimilation" has been submitted for ethical review to the Faculty's rapporteurs and I am pleased to confirm that they have approved your project.

I wish you every success with your research project.

Yours sincerely

A handwritten signature in black ink that reads "Anna Macaskill".

Professor A Macaskill
Chair
Faculty Research Ethics Committee

Office address :
Business Support Team
Faculty of Development & Society
Sheffield Hallam University
Unit 4, Sheffield Science Park
Howard Street, Sheffield, S1 1WB
Tel: 0114-225 3308
E-mail: DS-ResearchEthics@shu.ac.uk

1.2 – Participant Information sheets

Information sheet - Visual Perception study: “Match the grey”

What is the study about?

The aim of the study is to investigate how different manipulations of visual scenes affect the way in which people perceive colours. As the participant, you will be required to perform a simple task in which you will respond to stimuli consisting of different coloured shapes placed in varying configurations in front of you. Your task is to indicate, on the chart provided, which shade of grey is most like the grey target indicated by the researcher.

Are there any restrictions on who can participate?

Participants in this research must have normal or corrected-to-normal vision – this means that if you need to wear glasses or contact lenses, you would need to wear them for the tasks.

What if I change my mind about participating in the study?

Your participation in the research is entirely voluntary.

You have the right to withdraw from the study at any point, without having to give a reason and with no negative consequences. If you feel uncomfortable at any point or do not wish to continue participating, please let the researcher know, and they will stop the study, remove the equipment, and allow you to leave.

If after completing the study you wish to withdraw your data, you may contact the researcher (see below) within 14 days of participation, to ask that data from your session be removed.

What will happen to the information from the study?

The responses given will be kept anonymous and confidential, and will be analysed to investigate the differences in responses between the different types of stimuli you will see during the study.

The data from all participants will be analysed together – your individual data will not be presented alone, and you will not be identifiable from any analysed data. You will be given a code so that your data can be kept anonymously. Only the researcher and research supervisors associated with this specific project will have access to data prior to analysis. The results of this study will be written up as part of a PhD thesis. The results may also be published in the visual perception research literature at a later stage.

What if I have further questions?

You are welcome to ask any questions you may have at the beginning of the session, before consenting to take part. You may also ask questions during the session (e.g. if you are confused about the task) and after the session is complete, either at the end of the session, or subsequently via email. Please do not hesitate to contact the following people regarding this research:

Researcher: Steph Acaster (s.acaster@shu.ac.uk)

Information sheet: EEG study of visual perception of colours**What is the study about?**

The aim of the study is to investigate how different manipulations of visual scenes affect the way in which people perceive colours. While EEG is being recorded you, the participant, will be required to perform a simple task in which you will respond (by

pressing a button) to stimuli consisting of different coloured shapes, thereby answering a question such as ‘Which square is darkest?’.

Are there any restrictions on who can participate?

Participants in this research must have normal or corrected-to-normal vision – this means that if you need to wear glasses or contact lenses, you would need to wear them for the tasks.

Participants must also be right-handed (you would be required to complete a handedness inventory before the task) and must not have a history of neurological problems.

What will the EEG recording involve?

EEG (electroencephalograph) involves measuring the natural electrical activity of the brain. This is measured through the scalp using small electrodes that are integrated into a cap which is worn just like a hat (see Figure 1). A special hair gel that improves the conductance of the signal from the brain will be used on each of the electrodes in the cap.

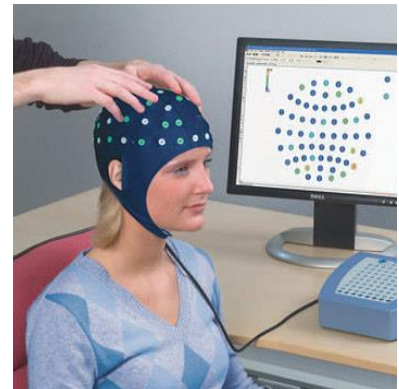


Figure 0.1: EEG cap by Advanced Neuro Technologies (ANT)

The whole procedure is non-invasive – it does not hurt and is not likely to cause great discomfort. However, you may want to wash your hair after the study to remove the gel (facilities are provided for this).

The EEG signal will be recorded while you sit looking at and responding to images on the computer screen. Meanwhile the researcher will monitor the task progress on a

different computer in the adjacent room. You will always be able to communicate with the researcher if you need to.

What will I have to do during EEG recording?

Different images (stimuli) will be presented on the computer screen. You will be asked to fixate on a little cross and pay attention to these images that follow the fixation cross. Each time, a set of two grey squares will appear, and your task is to make a decision about them, e.g. decide which one is the darkest grey. You will need to press a button to indicate your decision (the buttons will be specified in on-screen instructions for each task).

Full instructions will be given before the start of the recording and each task and you will be presented with a trial set of practice stimuli to familiarise yourself with the task requirements.

It is important that you try to refrain from blinking your eyes and movements of the head and body (especially when the images are being displayed) as much as possible to prevent interference in the recording.

How long will the EEG session last?

The whole experiment including the appliance of the net and practice session is expected to last up to 90 minutes, but the actual experiment task (where you will be responding to stimuli) is expected to take 30 minutes or less.

What if I change my mind about participating in the study?

Your participation in the research is entirely voluntary.

You have the right to withdraw from the study at any point, without having to give a reason and with no negative consequences. If you feel uncomfortable at any point or do

not wish to continue participating, please let the researcher know, and they will stop the study, remove the equipment, and allow you to leave.

If after completing the study you wish to withdraw your data, you may contact the researcher (see below) within 14 days of participation, to ask that data from your session be removed.

What will happen to the information from the study?

The EEG recorded data and information for all the participants will be analysed to investigate the differences in responses between the different types of stimuli you will see during the study. The data from all participants will be analysed together – your individual data will not be presented alone, and you will not be identifiable from any analysed data. You will be given a code so that your data can be kept anonymously. Only the researcher and research supervisors associated with this specific project will have access to data prior to analysis. The results of this study will be written up as part of a PhD thesis. The results may also be published in the visual perception research literature at a later stage.

What if I have further questions?

You are welcome to ask any questions you may have at the beginning of the session, before consenting to take part. You may also ask questions during the session (e.g. if you are confused about the task) and after the session is complete, either at the end of the session, or subsequently via email.

Please do not hesitate to contact the following people regarding this research:

Researcher: Steph Acaster (s.acaster@shu.ac.uk)

Director of Studies: Dr Naira Taroyan (n.a.taroyan@shu.ac.uk)

1.3 – Consent Form

Visual Perception and EEG Study Consent Form

TITLE OF STUDY: Behavioural and electrophysiological indices of contrast and assimilation

Please answer the following questions by circling your response

- | | | |
|---|--------------|-------------|
| Do you have normal (or corrected-to-normal) eyesight? | YES | NO |
| Do you have any history of neurological problems? | YES | NO |
| Are you right-handed or left-handed? | RIGHT | LEFT |
| | | |
| Have you read and understood the information sheet about this study? | YES | NO |
| Have you been given the opportunity to ask questions about this study? | YES | NO |
| Have you received enough information about this study? | YES | NO |
| Do you understand that you are free to withdraw your data from this study without giving a reason up to 14 days after the study session? | YES | NO |
| Do you give permission for your anonymised responses to be used as part of the data set for the researcher's PhD thesis and any future research/publications? | YES | NO |
| Do you agree to take part in this study? | YES | NO |

In signing this consent form, you are confirming that you have voluntarily decided to take part in this study, having read and understood all of the information in the sheet for participants. You are also confirming that you have had adequate opportunity to discuss the study with the researcher and that all questions have been answered to your satisfaction.

Unique ID (please create a memorable code consisting of 2 letters and 3 numbers, e.g. AB123):

Signature of participant: Date:.....

Name (block capitals):

Signature of researcher:

Date:

Steph Acaster, HC 1.05, Heart of Campus Building, Collegiate Crescent Campus, Sheffield Hallam
University, Sheffield S10 2BP E-mail: s.acaster@shu.ac.uk

1.4 – Handedness Questionnaire

Edinburgh Handedness Inventory (revised)					
Please mark the box that best describes which hand you use for each item					
	Always Left	Usually Left	No Preference	Usually Right	Always Right
Writing					
Drawing					
Throwing					
Scissors					
Toothbrush					
Knife (without fork)					
Spoon					
Match (striking)					
Computer mouse					

Please write down your Age: _____ and Gender: _____

Participant debriefing sheet: EEG study of visual perception of colour

In this study, you were asked to decide whether the grey part of a stimulus looked darker or lighter than a grey comparison square. The responses given by the button-press demonstrate whether you experienced contrast or assimilation for each stimulus. When the grey looks more different to the other colour (black or white) in the stimulus, contrast has occurred. On the other hand, when the grey looks more similar to the black or white, then assimilation has occurred.

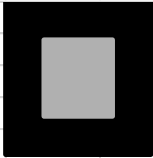

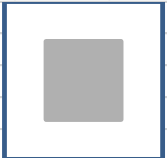

The stimuli in the study were varied as follows:

- Colour – black vs white parts of the stimulus
- Size – large vs small parts of the stimulus
- Depth – all parts of the stimulus at the same perceived depth (2D) vs one part perceived as being in front of the other part (3D)

These variations are thought to affect whether contrast or assimilation occurs when viewing the stimuli. The aim of this particular study was to investigate this further, by exploring how electrical brain activity correlates with these variations, and investigating the potential differences in brain activity between contrast-producing and assimilation-producing stimuli. The data collected by the EEG recording can give more precise information about the timing and sequence of processing than the button-press task alone. The results of this study will therefore contribute to a more detailed account of the processing that underlies the way in which surfaces can appear different as a result of their context.

Appendix 2 – Distribution of Responses per Condition in the ERP Study

This table shows the number of contrast responses, assimilation responses, and misses (i.e. trials with no response given) for each participant in each condition. Each row represents one participant. Cells shaded in green indicate that the participant has given a consistent response type.

											
BlackLarge			BlackSmall			WhiteLarge			WhiteSmall		
Contrast	Assim.	Miss	Contrast	Assim.	Miss	Contrast	Assim.	Miss	Contrast	Assim.	Miss
40	40	0	7	73	0	64	16	0	37	43	0
59	21	0	24	55	1	72	8	0	61	19	0
60	12	8	2	77	1	75	4	1	32	41	7
73	6	1	0	79	1	77	3	0	77	1	2
76	3	1	4	75	1	78	2	0	50	29	1
12	68	0	2	78	0	78	2	0	70	10	0
3	76	1	2	78	0	67	13	0	63	17	0
42	38	0	4	75	1	80	0	0	80	0	0
61	11	8	5	71	4	73	5	2	35	43	2
56	22	2	44	32	4	79	1	0	65	10	5
39	41	0	11	69	0	26	54	0	12	68	0
39	38	3	32	43	5	71	8	1	61	16	3
46	32	2	49	31	0	66	14	0	44	35	1
27	45	8	2	77	1	72	6	2	3	75	2
77	2	1	48	28	4	78	1	1	37	39	4
13	66	1	9	71	0	51	27	2	28	51	1
24	56	0	1	78	1	78	1	1	54	24	2
69	11	0	37	41	2	47	33	0	21	59	0
57	23	0	25	55	0	77	3	0	59	21	0
46	33	1	5	75	0	12	68	0	3	77	0
56	22	2	15	65	0	78	2	0	49	31	0
78	2	0	74	4	2	79	1	0	27	53	0
67	13	0	38	41	1	58	22	0	21	59	0
18	62	0	8	72	0	76	4	0	59	21	0
45	35	0	38	42	0	70	10	0	64	16	0
10	68	2	6	74	0	27	52	1	24	55	1
56	24	0	18	62	0	52	28	0	8	72	0
8	72	0	2	78	0	71	9	0	54	26	0