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I Expect, Therefore I See:

Individual Differences in Visual

Awareness

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Thesis submitted for the degree of Doctor of Philosophy

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STATEMENT

This thesis is written in an article format; the middle chapters consist of discrete articles written in a style that is appropriate for publication in peer-reviewed journals in the field. The first chapter comprises an introduction to the theoretical framework that informed this research and an overview of the relevant background research literature, as well an introduction of the research undertaken. The final chapter consists of a discussion of the findings of the present research, their critical evaluation within the context of the field, outstanding questions and future research directions.

Chapter Two is written in the style of an article appropriate for the peer-reviewed journal Neuroscience of Consciousness. The author contributions are as follows: NA was responsible for study design, data collection, analysis, and write-up of the manuscript; JW, JMB, and AKS provided feedback on the study design, analyses, and made corrections to the writing of the manuscript. This paper has been published as:

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Chapters Three to Five have been written according to American Psychological Association style guidelines and have not been published or submitted for publication. The author contributions for Chapters Three to Five are as follows: NA was responsible for the study design, data collection, and write-up of the manuscripts; JW, JMB, and AKS provided feedback on the study design, analyses, and suggested corrections to the writing of the manuscript.

I hereby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

Nora Andermane

14th August 2019

Signature: …………………………………………………

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LIST OF ABBREVIATIONS

ADHD – Attention Deficit Hyperactivity Disorder

AQ – Autism-Spectrum Quotient

ASD – Autism-Spectrum Disorder

BOLD – Blood oxygen-level dependent

CAPS – Cardiff Anomalous Perceptions Scale

CB – Change blindness

CE – Continuity error

CFQ – Cognitive Failures Questionnaire

CS – Contrast sensitivity

EEG – Electroencephalography

ERPs – Event-related potentials

FDR – False discovery rate

FEP – Free energy principle

fMRI – functional magnetic resonance imaging

FWE – Family wise error

GM – Grey matter

IB – Inattentional blindness

IPS – Intraparietal sulcus

KMO – Kaiser-Meyer-Olkin

MEG – Magnetoencephalography

MRI – Magnetic resonance imaging

ms – milliseconds

MT – Middle temporal

MTL – Medial temporal lobe

MVPA – Multi-voxel pattern analysis

PPC – Posterior parietal cortex

ROI – Region of interest

RT – Response time

rTMS – Repetitive transcranial magnetic stimulation

SBB – Structural brain behaviour

SCSQ – Sussex Cognitive Styles Questionnaire

SD – Standard deviation

SEM – Standard error of the mean

SPL – Superior parietal lobe

TIV – Total intracranial volume

TMS – Transcranial magnetic stimulation

TOJ – Temporal order judgement

qCSF – Quick contrast sensitivity function

V1 – Primary visual cortex

V2 – Secondary visual cortex

VSTM – Visual short-term memory

VVIQ – Vividness of Visual Imagery Questionnaire

VWM – Visual working memory

WBA – Whole brain analysis

WM – Working Memory

THESIS SUMMARY

Predictive processing theories posit that awareness of the visual world emerges as the brain engages in predictive inference about the causes of its sensory input. At each level of the processing hierarchy top-down predictions are corrected by bottom-up sensory prediction error to form behaviourally optimal inferences about the state of the visual world. Research suggests there may be individual differences in predictive processing mechanisms such that some individuals are more reliant on prior knowledge, whereas others assign more weight to sensory evidence. Predictive processing biases are thought to manifest in a range of typical and atypical perceptual experiences including proneness to perceptual illusions, sensory sensitivity in autism, and hallucinations in psychosis. The overarching aim of this thesis was to investigate whether in the general population predictive processing biases predict individual differences in visual awareness. Change blindness was selected as the central paradigm of investigation, as it can be conceptualised as a failure to incorporate a novel change into the current prediction about the state of the visual world.

The empirical work in *Chapter 2* aimed to characterise individual differences in visual change detection using naturalistic scenes and to identify the perceptual and cognitive measures that predict noticing ability. There were reliable individual differences in change detection that generalised to ecologically valid displays. The ability to notice visual changes was predicted by the strength and stability of perceptual predictions, as measured by the accuracy of visual short-term memory and attentional control in the face of distractors.

In *Chapter 3* I used voxel-based-morphometry to investigate whether inter-individual variability in brain structure predicts individual differences in visual

awareness. The latter was assessed by the change blindness task as well as its strongest predictor measures (visual short-term memory, attentional capture, and perceptual rivalry). Regions of interest (ROIs) were selected in the parietal and visual cortices based on previous evidence that these areas are causally involved in the awareness of visual stimuli. This study aimed to discover whether the average grey matter density in the ROIs predict susceptibility to CB. The ROI-based analyses revealed the average grey matter density in left posterior parietal cortex predicted visual short-term memory accuracy but none of the other hypothesised relationships were significant.

Chapter 4 aimed to measure individual differences in the reliance on prior knowledge by employing the Mooney face detection task. In this task participants disambiguated faces in two-tone degraded images before and after the presentation of the original versions of the images. Better change detection was predicted by Mooney face detection without any prior knowledge of the images, a measure of 'perceptual closure' or an ability to generate a gestalt of a scene. The attention to detail subscale of the autism spectrum also predicted superior change detection. Reliance on prior knowledge in visual perception (assessed by improvement in Mooney face detection *after* seeing original images) did not consistently predict atypical perceptual experiences associated with the autism spectrum or schizotypy.

Chapter 5 was an investigation into, firstly, whether there is a general predictive processing bias, which manifests across different methods of inducing prior knowledge, or whether such a bias is paradigm-specific and, secondly, whether reliance on priors predicts perceptual experiences and traits. All prior manipulations in this study lead to an increased tendency to see the expected stimulus in a binocular rivalry display, except adaptation, which lead to a suppression of visual awareness. Attentional control, perceptual priming, expectancy, and imagery loaded onto a common factor, suggesting

that the strength of selective attention is closely linked with the facilitatory effect of expectation. The strength of adaptation predicted superior change detection and perceptual priming predicted the propensity to experience perceptual illusions.

Taken together, these findings suggest that there are reliable individual differences in visual change detection, and these are predicted by the strength of visual short-term memory representations, attentional control, perceptual closure ability, as well as the strength of low-level adaptation. Possessing expectations facilitates the entry of the corresponding percept into awareness, irrespective of the method of prior induction. The facilitatory effect that priors exert on visual awareness across different methods is closely linked with the ability to exert attentional control. This suggests that the effects of expectations on awareness may be attentional. However, predictive processing biases were method-specific in that a facilitatory effect using one prior induction method will not necessarily predict the magnitude of the effect using a different method. Some prior effects (e.g., perceptual priming, imagery, and adaptation) yielded correlations with perceptual experiences and traits in the general population. As the research in this thesis is correlational, future studies will need to delineate the effects of expectation, attention, and adaptation on visual awareness and explore the neural representations of these mechanisms.

CHAPTER 1 INTRODUCTION AND THESIS OVERVIEW

1.1 Noticing the visual world

Our awareness of the visual world seems effortless. Whenever we open our eyes, we have access to a rich, colourful image of our environment that we can freely explore according to our goals. Importantly, we tend to have a belief that we have all the visual information we currently need and will become aware of it if something happens to suddenly change. It may come as a surprise then when we miss large and important changes in our visual environment. This may be a particular issue for some people over others; some of us may be more observant of the environment and notice little details in another person's appearance, whereas others may be more distractible and get lost in mind-wandering. What may visual change detection reveal about the mechanisms generating the subjective awareness of the visual world? Importantly, can the differences between individuals in their ability to notice tell us something about the processes involved? The evolving theoretical thought regarding the mechanisms of perception points to the idea that visual awareness may not so much depend upon what sensory signal we receive from the environment, but rather the internal explanatory models that we have built about the world. There is growing evidence that our prior knowledge and expectations powerfully shape what we attend to and become aware of. The Bayesian predictive processing framework suggests that what draws our attention likely depends not only on the characteristics of the visual environment but also on our beliefs. In this thesis I aim to investigate if individuals differ in the extent that they rely on expectations when perceiving visual stimuli and how this relates to their ability to notice visual changes. I will start this chapter by introducing predictive processing theories and summarising their central tenets. I will then go on to describe how the interactions between expectation, sensory evidence, and attention are thought to give

rise to visual perception. Following this I will introduce the distinction between unconscious and conscious processing and consider what may be the mechanism that determines which contents enter visual awareness at any given moment. I will then discuss the possibility that individuals may reliably differ in their ability to become aware of visual changes and how such a trait may be underpinned by a tendency to be influenced by expectations. Finally, I will provide the rationale for each of the four studies comprising this thesis.

1.2. Visual perception in the predictive brain

Predictive processing is an influential theoretical framework, which has been gaining recognition in recent years due to the parsimony of its purported mechanisms and its promise to provide a unified theory of the human brain. Its roots can be traced back to Hermann von Helmholtz (Helmholtz, 1860; Westheimer, 2008) who suggested that perception can be understood as a process of unconscious inference. This idea was further developed by Richard Gregory who used the example of visual illusions to argue that the perceptual process has many parallels with the scientific process – perception is a hypothesis that the brain generates in response to sensory stimulation (Gregory, 1968; 1980). Gregory pointed out that no object is purely concrete or sensed directly, as any sensation necessarily involves the prior assumptions and understanding built into the system that perceives it. In its current form the theoretical framework is grounded in Bayesian statistics and comprises several branches, including the free energy principle (FEP) as outlined by Karl Friston (Friston, 2010; Feldman & Friston, 2010) and predictive coding further elaborated by authors such as Jakob Hohwy (Hohwy, 2013) and Andy Clark (Clark, 2013; 2015).

According to predictive coding frameworks such as the FEP (Friston, 2010) the mechanism that underpins visual perception is the same one at the core of the central organisational principle of any living organism and has evolved due to the pressure to resist entropy and maintain homeostasis (Seth, 2014; Seth & Tsakiris, 2018). This mechanism is thought to be free energy minimisation (Friston, 2010; Feldman & Friston, 2010) and can be defined as the attempt of the organism to generate a model of the world (including that of itself) in order to infer the causes of its sensory signal, generate evolutionarily adaptive behaviour, and remain in physiological equilibrium. The model is probabilistic and is extrapolated to new sensory data based on prior knowledge (both in terms of the knowledge generated during an organism's lifetime and that encoded through its evolutionary history). When a model is generated but it is not optimal for the current environmental context (i.e., the organism finds itself in an unpredicted state), this results in surprise and creates an error signal. This kind of scenario is energetically costly and thus threatens homeostasis. Due to the outside world being ever-changing and the sensory data being variable and ambiguous the organism has only two strategies to minimise free energy and maintain homeostasis; one is to retain its model by selectively sampling the environment through action and the other is to adjust the model via perception. This is a general principle thought to operate across different perceptual modalities and cognitive domains, although it will be considered in more detail in relation to predictive processing frameworks of visual perception.

1.2.1 Prediction, prediction error, and attention

To generate an optimal visual inference, the brain has developed a strategy of extracting statistical regularities in the sensory signal and predicting its hidden causes based on experience. Predictive processing proposes that there are two opposing

processes at play in the human brain for the purpose of generating and maintaining a model of the visual world. On the one hand, the brain generates top-down predictions, which are the most likely interpretation of the sensory signal. However, the system needs to continuously update these to dynamically represent the visual world. Therefore, the brain registers any mismatches between the prediction and the sensory signal received and propagates an error signal in the cortical hierarchy in a bottom-up direction. Ultimately, the function of this signal is to reorganise and update any predictions that do not optimally represent the state of the visual world. Note that an optimal visual representation is not necessarily veridical; it is defined as optimal based on whether it is useful to the organism for action, given that perception serves the larger goal of survival and reproduction (Seth & Tsakiris, 2018)

A key aspect of predictive coding frameworks is that the process of perceptual inference is hierarchical (Rao & Ballard, 1999). This means that the same mechanism of prediction and prediction error minimisation operates at each level of the cortical hierarchy. For example, the neurons at the higher levels in the cortical hierarchy predict the activity of neurons at the lower levels. These representations are then compared and any discrepancy between the two is converted into a prediction error signal, which is sent to the higher-level neurons to adjust their prediction. At each level the prediction error is iteratively minimised, which results in a multi-level prediction that is continuously dynamically constrained by sensory evidence. In the domain of visual perception, this hierarchical prediction is equivalent to a perception of the current state of the visual world. In other words, what we perceive at any moment is the visual system's best estimate, given its prior knowledge and the sensory evidence it receives from the environment (see Figure 1.1 for an illustration of the terms prior and prediction error according to Bayesian statistics).
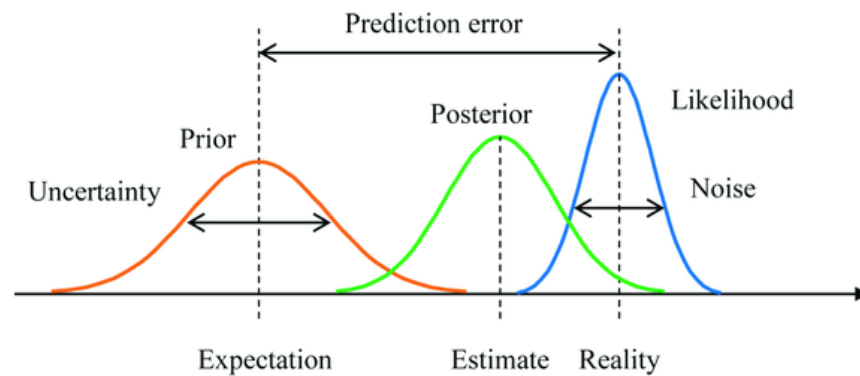
Figure 1.1 An illustration of Bayesian inference

The prior distribution corresponds to the expectation and its variance with the uncertainty associated with it. The likelihood function corresponds to the sensory evidence and its variance is the associated noise. The prediction error is the difference between the prior and the sensory evidence. The posterior distribution is the estimate corresponding to the current percept and is created by combining the prior with the likelihood, each weighted by their precision (inverse of variance). The posterior is shifted towards the likelihood if the prior is flatter (more uncertain) or the likelihood is sharper (less noisy). The image is taken from Yanagisawa, Kawamata, and Ueda (2019).

Generally, the role of prior knowledge is to prepare the organism to act optimally, given the evidence collected from the environment so far. That is, to anticipate the causes of sensory input based on previous experience. However, this is not only to be taken in the sense that the expectation is a future projection. Within the field of visual perception, whatever we currently perceive is our brain's best estimate of what the sensory input it receives represents (i.e., the hidden cause), given prior knowledge. This is continuously adjusted at every level of the hierarchy to minimise the error, as previously described. Our perception of visual stimuli is influenced by priors that have been generated throughout the evolutionary history, for example the probability of the source of light originating from above and the probability of shadows being cast (Kleffner & Ramachandran, 1992). Our visual system has adjusted to the natural environments we have historically encountered, such that we have a finer

discrimination of cardinal orientations (vertical and horizontal), which are the most commonly seen orientations in natural scenes (Girshick, Landy, & Simoncelli, 2011). However, priors that have been generated by learning in our recent experience can also influence perception. For example, the visual system dynamically adjusts to the statistics of the colour space of the environment (e.g., Webster, 2011; Bosten, Beer, & MacLeod, 2015). There is evidence that even reliable priors that capture predictable structure of the environment, such as the light-from-above prior, can be re-trained in a short space of time. Adams, Graf, and Ernst (2004) showed that by pairing stimuli that are typically perceived as convex with conflicting haptic feedback indicating a felt concave shape (and vice versa) the inferred position of the light that falls on the stimulus can be shifted post-training. This training also affected responses to a novel set of stimuli showing that training influences the perceived position of the light source, rather than object-based associations. Furthermore, new priors can be induced such that the typical phenomenology of the visual world can be altered in an entirely novel way. Bor and colleagues (2014) demonstrated that previously non-synaesthetic individuals can begin to experience grapheme-colour synaesthesia after a 9-week colour association training period, such that the trained colour is consistently experienced in the mind's eye when viewing letters in the outside world (e.g., on signposts). The training also significantly altered responses in behaviour tasks such as the Stroop task, mirroring the behavioural performance of synaesthetes (i.e., improved congruency effects). In sum, visual perception is dependent on prior knowledge and learnt associations and, most importantly, these are plastic so can be dynamically adjusted to affect the corresponding phenomenology.

Within the framework of predictive processing the role of prediction error is to prevent expectations that no longer accurately represent the state of the visual world to

determine perception and influence behaviour. The error signal updates inferences at all levels of the cortical hierarchy, such that deviations from the evidence that are behaviourally important are registered and work to reorganise the priors. In visual perception, sometimes the errors that are propagated up the visual hierarchy evidently do not succeed in updating the current visual percept. This describes situations where human observers fail to perceive visual information, even though it may be processed to some extent in the brain; the phenomena that illustrate this scenario will be discussed in more detail in the next chapters. The general aim of the error within this framework is to convey information about perceptual change in the visual world for the organism to be able to strike a balance between retaining stable models regarding reliable aspects of reality, whilst dynamically incorporating new information into their moment-to-moment models of the changing visual world.

In addition to coding what is probable (i.e., the hidden causes of sensory input), the visual system also needs to estimate the noise and uncertainty associated with the environment, the context, and the stimuli it perceives. Furthermore, encoding the probability and precision of visual information subserves the larger behavioural goals of the organism. Some visual stimuli may be very probable but not particularly behaviourally relevant or informationally rich; others may be improbable but have a strong signal or motivational relevance. In order to support adaptive behaviour, the visual system needs to dynamically estimate the precision of visual stimuli given the context. Under predictive processing frameworks, coding the precision of predictions and prediction errors is the function of attention (Feldman & Friston, 2010; Hohwy, 2012). That is, attention is thought to be a distinct type of inference; not one inferring what probable (as perception does) but one inferring what is precise (Hohwy, 2012). More specifically, attention is thought to be the optimisation of expectations about

precision (i.e., the inverse of variance or uncertainty) of a prior and is encoded as dynamic modulation of post-synaptic gain of prediction error units (Feldman & Friston, 2010). Depending on how much uncertainty is associated with particular stimuli, attention is allocated on a moment-to-moment basis by assigning greater weight to the prediction errors that are expected to have highest signal-to-noise ratio. This dynamic precision adjustment of sensory evidence in turn is thought to depend upon high-level priors, such as motivational states or goals, and expectations (Hohwy, 2012; Kanai, Komura, Shipp, & Friston, 2015). In this way, attention is intimately linked with expectation, in that it dynamically weights up the precision of the most motivationally relevant visual stimuli. Note that both exogenous (i.e., stimulus-driven) and endogenous (i.e., voluntary) attention can be characterised this way, as stimulus-driven attention is still supported by an underlying prior that stimuli with high signal-to-noise ratio have a high relevance for the organism.

1.2.2 The role of expectation in visual perception

There is extensive evidence for the profound influence of priors or expectations on perception (for a recent review see de Lange, Heilbron, & Kok, 2018). Expectations are demonstrated to make the visual system more sensitive to the expected stimulus such that it becomes more likely to be perceived (Chalk, Seitz, & Seriès, 2010; Lupyan & Ward, 2013; Denison, Piazza, & Silver, 2011). For example, under conditions where a manipulation is introduced to suppress awareness (e.g., inter-ocular suppression in continuous flash paradigms) images cued by words are more likely to be detected (Lupyan & Ward, 2013). Expected percepts also enter awareness faster (Chang, Kanai, & Seth, 2015; Denison et al., 2011) and based on weaker sensory evidence (Melloni, Schwiedrzik, Müller, Rodriguez, & Singer, 2011). Discrimination ability is enhanced by

expectation; for example, finer differences between the orientation angles of two gratings can be detected if the first grating is of an expected relative to unexpected orientation (Kok, Jehee, & de Lange, 2012). In terms of signal detection theory, possessing expectations of the upcoming stimulus created by valid cues may indeed boost performance and reaction time, relative to invalid cues; however, it may be that expectations actually slightly reduce sensitivity to the signal and instead shift the criterion towards the expected percept (Rahnev, Lau, & de Lange, 2011). Expectation may be particularly important in scenarios where the visual input is weak, unreliable or ambiguous – these are the cases when perception is biased more towards the direction of prior knowledge (Stocker, & Simoncelli, 2006; Sterzer, Frith, & Petrovic, 2008; Girshick et al., 2011). For example, Girshick and colleagues (2011) found that when making orientation judgements under conditions of perceptual uncertainty, people are biased towards cardinal (horizontal and vertical) orientations. Additionally, there are demonstrations that after training the expected stimuli can be 'hallucinated' even when no physical stimulus is present. For example, individuals perceive motion in expected directions when no stimulus is present (Chalk et al., 2010). These results highlight that expectations boost perception and discriminability of visual stimuli that are physically present, as well as bias perception towards the expected when the stimuli are ambiguous or even entirely absent.

In terms of the neural basis of the effect of expectations, there is a debate in the research literature as to how exactly this process operates. It is generally accepted that expectations of visual stimuli reduce, suppress or attenuate the neuronal activity of visual cortex (Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008; Summerfield & Egner, 2009). This is usually taken as an indication that the prediction errors associated with the expectation are suppressed (Friston, 2005). However, this same

sensory attenuation response could be accomplished through two distinct strategies – sharpening or dampening. A process of sharpening would reduce the activity of neurons coding irrelevant information and retain or even boost the activity of cells coding the expected stimulus. In contrast, dampening would reduce the activity of the neurons involved in the expected representation, which would be consistent with the suppressing or 'explaining' away prediction errors (Hohwy, 2013; Friston, 2005). Imaging studies using multi-voxel pattern analysis (MVPA) techniques show evidence for the sharpening hypothesis, as when a cue validly predicts the orientation of a grating, the overall blood oxygen-level dependent (BOLD) signal in primary visual cortex (V1) is reduced but the pattern of activation associated with that orientation can be decoded with greater accuracy, relative to unexpected orientations (Kok et al., 2012). Furthermore, activity in voxels preferring the unexpected orientation is lower than in voxels coding the expected stimuli, consistent with the sharpening account. This suggests that expectations suppress the irrelevant features of the signal, whereas the units coding the expected stimulus remain active, thus enhancing sensitivity to it. Possessing expectations regarding an upcoming visual stimulus (e.g., the direction of moving dots) has been shown to activate dorsolateral prefrontal cortex, as well as intraparietal sulcus (IPS), and result in a heightened effective connectivity between these regions and the corresponding sensory areas (in this case, the middle temporal (MT) area) (Rahnev et al., 2011). This suggests that the processing of prior expectations involves recurrent activity (both feed-forward and feedback) between higher order areas and areas coding the sensory representations of the stimulus.

1.2.3 The role of attention in visual perception

Attention is thought to be a limited capacity process that biases the competitive interactions between representations of stimuli such that attended stimuli are prioritised for processing (Desimone & Duncan, 1995; Kastner & Ungerleider, 2000). Attention is defined as a process that represents the salience of information. Broadly, there are two ways information can be salient – motivationally or perceptually. This corresponds to the division of attention into endogenous or voluntary and exogenous or stimulus-driven. A stimulus can be salient in terms of the organism's motivational state defined by the current task goals and thus attention can be allocated endogenously, that is, at will. Alternatively, a stimulus can be salient by the virtue of being novel or distinct from its surrounding area in terms of perceptual characteristics (e.g., colour, contrast, temporal contrast) and therefore capture attention exogenously. An example of a perceptually salient stimulus is one with a high temporal contrast – abrupt visual onsets are demonstrated to capture attention involuntarily and may have special status among salient stimuli (Yantis, & Jonides, 1984; Jonides, & Yantis, 1988). The effects of exogenous attention are studied in the attentional capture paradigm developed by Theeuwes (1992). Here, a salient visual stimulus (e.g., a stimulus that stands out in terms of its colour) is prioritised against the volitional goals of individuals, causing interference in the form of delayed response time to a less salient target. Endogenous and exogenous attentional cues have been used to probe the behavioural effects of attention. In the classic Posner paradigm (Posner, 1980) endogenous attention is manipulated by showing a central cue (e.g., an arrow), which informs the individual where the stimulus is likely to occur and therefore where attention should be voluntarily allocated. Exogenous cues are peripheral abrupt onsets leading to attentional capture. Both endogenous and stimulus-driven attentional cues facilitate the processing of visual

stimuli at the location of the cue, as shown by reduced response times (Posner, 1980). Therefore, from a behavioural standpoint the function of attention seems to be to increase the sensitivity to visual signal.

It is important to note here that the distinction between exogenous and endogenous attention is not entirely straightforward. Salience can be assigned based on other properties besides the relative novelty of perceptual characteristics, for example, emotional relevance – emotion in faces (of both positive and negative valence) also captures attention even when task irrelevant (Hodsoll, Viding, & Lavie, 2011). What captures attention oftentimes is motivationally salient in terms of its evolutionary benefit (i.e., it is behaviourally relevant due to having been so in the past). An example besides emotional cues would be the perceptual salience of the colour red: it may not be currently motivationally salient; however, it has been so in our evolutionary past when foraging for ripe fruit (Snowden, Snowden, Thompson, & Troscianko, 2012). Recent perceptual experiences can also guide attention implicitly. For example, learnt associations between distractors and targets can guide attention and make visual search more efficient upon repeated presentation of the stimuli, even if the patterns of associations are not explicitly recognised (Chun, & Jiang, 1999). Similarly, intertrial priming increases attentional capture when the distractors were previously encountered as targets (Pinto, Olivers & Theeuwes, 2005). Visual stimuli held in working memory (WM) can also attract attention and improve performance when they are targets as well as hinder it when they are presented as distractors (Soto, Hodsoll, Rotshtein, & Humphreys, 2008; Soto, Rotshtein, & Kanai, 2014). These results point to the conclusion that a variety of visual stimuli can drive attention in a bottom-up (involuntary) way. In all of these cases attention is attracted because there are some prior expectations regarding what is informative given the context (in the terminology

of predictive processing, precision expectations), even if these do not translate into explicit top-down goals. The theoretical distinction between exogenous and endogenous attention is not clear-cut in the sense that attentional capture and implicit attentional guidance frequently depends upon memory and expectations based on recent perceptual experience, as well as long-term priors determined by our evolutionary past. What may define voluntary attention then is the ability to disengage from previously attended stimuli.

In terms of the temporal dynamics of stimulus-driven and voluntary attention in visual perception, it is argued that the initial feed-forward sweep of attention through the visual field is entirely stimulus-driven – the visual system may automatically determine saliency of objects at different spatial locations of the visual field (Theeuwes, 2010). The location with the highest salience is thought to produce pre-reflexive attentional capture. This process may only be amenable to volitional control after 100 – 150ms (Theeuwes, Atchley, & Kramer, 2000), at which point the identity of the stimulus can be ascertained and endogenous attention/executive control can take over in order to disengage from salient locations based on explicit task-related goals. Pre-empting attentional capture may, however, be possible by narrowing the attentional window and focusing attention relative to a more diffuse attentional state (e.g., fixating on the location of the target prior to onset, Yantis, & Jonides, 1990; Belopolsky, Zwaan, Theeuwes, & Kramer, 2007). This may because focusing attention on a particular spatial location prevents salience computations across the rest of the visual field. Developing an attentional set based on particular stimuli features may also mitigate the effects of attentional capture, such that it may not be completely prevented but a stronger attentional set can help to disengage from salient but irrelevant stimuli faster (Belopolsky, Schreij, & Theeuwes, 2010). Note that the attentional set in these

paradigms is typically induced by an expectancy cue regarding the identity or feature of the target (e.g., 'diamond'), which highlights the close correspondence between expectation and feature-based attention.

The work by Nilli Lavie (1995; 2010) additionally has demonstrated that attentional capture is dependent on perceptual load. When the complexity of visual information in the environment is high, the perceptual load exhausts attentional resources and salient distractors are not selected for attentional processing. Perceptual load can be defined as the number of items that are relevant for identifying the target or more generally perceptual processing demands (e.g., requiring discrimination instead of simple detection). Free attentional resources are available when perceptual load is low and thus attentional capture by salient distractors can take place. Note that increasing the load of internally maintained visual short-term memory (VSTM) representations also has a similar effect on reducing stimulus-driven attention to irrelevant peripheral distractors (Konstantinou & Lavie, 2013), perhaps due to creating an attentional set based on these representations (Belopolsky et al., 2010). Neuroimaging studies suggest that high perceptual (and VSTM) load results in less attentional capture because the sensory representations of the distractor in visual cortex are activated to a lesser degree (or in some cases not at all) under high relative to low perceptual load (Lavie, 2005; 2010). In contrast, increasing cognitive load by maintaining digits in WM increases attentional capture by irrelevant visual distractors (Lavie, Hirst, De Fockert, & Viding, 2004; Lavie, 2010). This is thought to be because in order to avoid task-irrelevant distraction one needs to exert cognitive control and maintain current task goals. The Load Theory therefore suggests that there are two mechanisms at play for selecting relevant over irrelevant visual stimuli – one is passively using perceptual characteristics of the environment to select salient information and the other is active attentional

control (i.e., through WM) to select task-relevant stimuli and avoid distraction (Lavie et al., 2004). Both processes are complementary and their usefulness for filtering out distractors depends on the nature of the distractors and the environment (high versus low perceptual load).

In sum, during the feed-forward sweep stimulus-driven attention may operate reflexively based on salience estimates, given the properties of the visual stimuli and the surrounding context. The physical characteristics of the stimuli such as their novelty, the complexity of the scene, the emotional relevance of stimuli, and recent exposure and memory-based representations all influence 'salience maps' of frontoparietal regions and the allocation of stimulus-driven attention (Corbetta & Shulman, 2002). Endogenous attention may be defined as a process that enables individuals to develop an attentional set based on expected stimuli features, to voluntarily allocate attention in space, to control the window of attention (e.g., focused versus diffuse), and to disengage from attentional capture once the identity of the stimulus is known and does not accord with the current explicit task goals. Exogenous and endogenous attention are complementary in that endogenous attention cannot be maintained indefinitely (attentional capture cannot be prevented) but capture cannot last either (Corbetta & Schulman, 2002; Hohwy, 2012).

In terms of the neural correlates of visual attention, the consensus from research using imaging techniques is that attention (exogenous and endogenous) increases the neural activity of visual areas that code the attended features or spatial locations thus increasing sensory gain and perceptibility. For example, transient peripheral attentional cues boost retinotopically specific activity in extrastriate visual areas and increase discrimination of visual stimuli at the cued locations (Liu, Pestilli, & Carrasco, 2005). The baseline activity of location-specific extrastriate visual areas prior to stimulus

presentation is likewise increased after endogenous attentional cueing (Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999). In addition to evidence regarding spatial attention boosting neural activity, feature-based (e.g., shape-specific) endogenous attention too increases baseline activation of feature-specific neural populations in the occipital cortex, as shown using MVPA (Stokes, Thompson, Nobre, & Duncan, 2009). There is in fact evidence that the baseline activity of sensory areas could be the correlate of expected precision, as increased activity in extrastriate areas before the onset of visual stimulus predicts detection sensitivity (i.e., more hits and correct rejections) and baseline activity in fusiform area predicts detection of faces in Rubin's vase (Hesselmann, Sadaghiani, Friston, & Kleinschmidt, 2010; Hesselmann, Kell, Eger, & Kleinschmidt, 2008).

In terms of the cortical regions differentially involved in attentional processing, exogenous capture is associated with activity in parietal regions of the cortex, whereas voluntary disengagement from capture may be related to processing in frontal regions (Lavie, 2005). De Fockert, Rees, Frith, and Lavie (2004) investigated the neural basis of the attentional capture task and found that the presence of a singleton distractor was associated with bilateral activation of the superior parietal cortex. This area is known to be involved in spatial shifts of attention (Corbetta & Schulman, 2002), suggesting that it may initiate attentional shifts to salient distractors. Indeed, studies applying repetitive transcranial magnetic stimulation (rTMS) over posterior parietal cortex (PPC) during the attentional capture task show that the magnitude of the singleton interference effect (with and without inter-trial priming) is reduced by the disruption of right PPC (Hodsoll, Mevorach & Humphreys, 2008). This supports the idea that parietal cortex may encode salience maps that guide attention. Activation of left lateral precentral gyrus was also observed in attentional capture, the magnitude of which was negatively

correlated with the response time delay due to capture (De Fockert et al., 2004). This suggests that activation of frontal cortex may enable to resolution of attentional capture, i.e., disengaging from the irrelevant distractor. A lack of correlation between PPC activity and interference magnitude may reveal that the extent of attentional capture is determined primarily by how easily one can disengage attention rather than salience-based attentional shifts per se.

1.2.4 Summary

To summarise, predictive processing theories propose that the brain dynamically generates a probabilistic model of its sensory input, as well estimates its precision (i.e., inverse of variance or uncertainty), and actively samples the world for evidence of this model. All three of these functions respectively, perception, attention, and action, interact within the visual system to minimise prediction error or free energy in order to avoid surprise (entropy/uncertainty). Under predictive processing, the repertoire of visual inference is: (1) dynamically adjusting the visual representation based on evidence, (2) estimating which sensory evidence is more informative given the high-level goals and low-level salience of sensory evidence, and (3) actively directing attention, eye and body movements to gain more evidence for a particular visual representation.

Predictive processing is a promising framework because it can potentially explain an abundance of disparate perceptual, cognitive, and behavioural phenomena in terms of a common mechanism. The explanatory power of this theory may reveal that it accurately describes a process that is central to human cognition. However, there is a need to explore the experimental evidence for and against this theoretical framework further, because it tends to be amenable to post-hoc explanations for unexpected results

by accommodating different and even contrasting findings (Bowers & Davis, 2012). For example, there are reasons to hypothesise that unexpected information will be particularly salient and draw attention, as it violates an existing belief therefore is surprising (and energetically costly). However, it can also be proposed that expected information will be salient and draw attention, as it confirms an existing belief, so less evidence is required to notice it. In fact, there is empirical evidence for both hypotheses (Itti & Baldi, 2009; de Lange et al., 2018), which complicates interpretation as to what leads to detection – novelty or predictability? It would be necessary to clarify several aspects that are currently under debate or entirely unknown. First, what may distinguish between unconscious and conscious processing within the predictive processing framework? If all cognitive operations work through the mechanism of prediction and prediction error correction; then what specifically about these processes determine which cognitive operation will enter awareness at any given moment?

1.3. Attention and visual awareness

Although consciousness is thought to be a natural consequence of the prediction error minimisation process, predictive processing does not explicitly differentiate between conscious and unconscious cognitive operations. That is, the same iterative process of prediction and prediction error signalling is thought to be at work throughout the cortical hierarchy (Friston, 2010). Of course, the question arises, what is different about the mechanism that generates an unconscious process as opposed to a percept that reaches conscious awareness? What might be the functional role of conscious awareness of the visual world if statistical regularities in the visual domain can be extracted implicitly (Turk-Browne, Scholl, Chun, & Johnson, 2009)? Richard Gregory wrote that the existence of consciousness within this process of hypothesis generating and revision

is mysterious; however, he alluded to the idea that consciousness may be particularly

necessary when mismatches between inferences and sensory evidence occur (Gregory,

1980). A central process of cognition that may provide an insight with regards to which

predictions enter visual awareness and which prediction errors are used to update them

is the phenomenon of attention.

1.3.1 Attention: a predictive processing mechanism gating conscious perception

Attention is conceptualised as a process that dynamically prioritises the

processing of certain internal models relative to others, based on expectations relating to

precision of the model given its current context (Hohwy, 2012; Schröger, Kotz, &

SanMiguel, 2015). This suggests attention may be the process influencing which

perceptual models enter awareness at any given moment. With this in mind, the current

contents of visual awareness can be defined as the prediction that is (1) accurate, that is,

most probable given the previous experience and current input, and (2) currently

estimated to be most precise, namely, perceptually or motivationally salient, and

therefore attended to. There may be exceptions to this, as it has been suggested that

conscious perception may still be possible for states that are inaccurate but relatively

precise or accurate but not very precise, a possible candidate of latter being gist

perception (see Figure 1.2 for an illustration) (Hohwy, 2012). Apart from these

exception states, predictive processing mechanisms suggest that a conscious percept

will be the internal model that is currently most accurate (i.e., best minimises prediction

error) whilst also being most precise. Although various perceptual models may be

currently possible, through adjusting the gain of certain prediction error units over

others, attention may be the process that determines which models gain sensory evidence faster and thus are consciously represented.
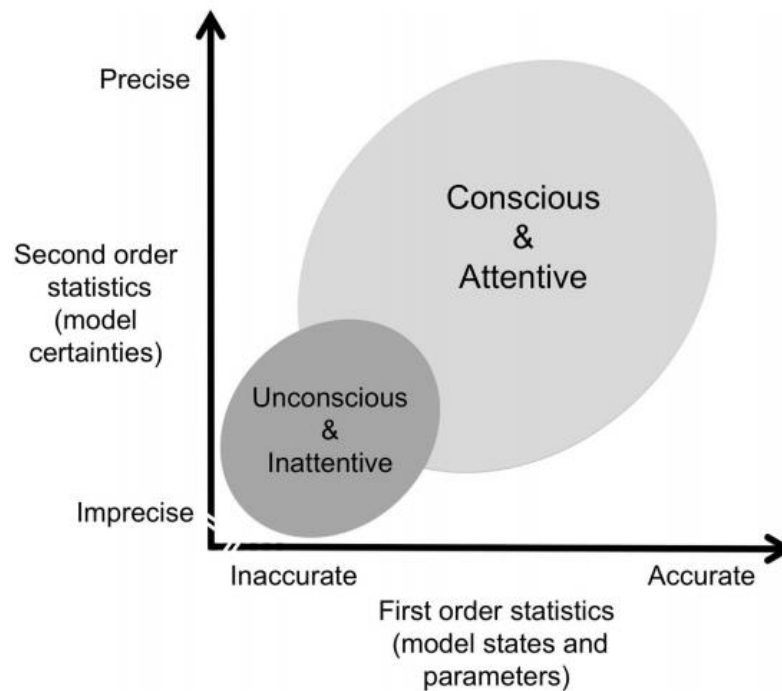
Figure 1.2 The properties of perceptual models that enter visual awareness.

The first order statistics reflect the inverse amplitude of prediction errors, whereas the second order statistics reflect the inverse amplitude of uncertainty about predictions. The perceptual model that populates visual awareness is the one that has high accuracy (represents the visual world well) but also has high precision (is attended). This does not preclude the possibility that some conscious perceptual states may have relatively less precision but more accuracy or more precision but less accuracy. It does suggest the majority of conscious perceptual states will be both probable and attended. Image taken from Hohwy (2012).

1.3.2. Dissociation between attention and awareness

Given the proposal that attention may gate the access of perceptual models to awareness, it may be worthwhile to consider counter-evidence, as some researchers have suggested that attention and awareness can be dissociated using lab-based manipulations, and that attention may not be sufficient or even necessary for awareness (Koch & Tsuchiya, 2007). Stimuli that are attended, whether exogenously or

endogenously, are not always consciously registered. For example, spatial attention can lead to enhanced processing of masked primes, as evidenced by the influence of cued masked primes on reaction times in a subsequent target discrimination task with congruent targets (Kentridge, Nijboer, & Heywood, 2008), despite the primes never becoming consciously visible. Additionally, spatial attention is captured by salient stimuli such as nude images that have been rendered consciously invisible by interocular suppression with high contrast noise patches, as evidenced by facilitated subsequent discrimination of visible targets presented in the same location (Jiang, Costello, Fang, Huang, & He, 2006). These examples of attentional selection and processing without awareness demonstrate that attention can be allocated to stimuli that are salient or relevant outside of awareness, and these can lead to improved processing at the associated spatial locations or unconscious priming by the relevant features. Thus, attentional allocation alone may not be sufficient for conscious perception when masking or other highly disruptive stimuli are introduced.

Furthermore, it has been argued that top-down attention may not be necessary for the initial fast feed-forward sweep of visual processing, which results in the conscious perception of the gist of the scene, as this process occurs very quickly. In predictive processing terms this would correspond to the accurate (probable) but imprecise (not fully attended) state (Hohwy, 2012). For example, Kirchner and Thorpe (2006) found that only about 120ms are required for highly accurate semantic categorisation of scenes. In this study two natural scenes were flashed side by side for 20ms and subjects had to report the presence of an animal by initiating a saccade to the correct side. This result suggests that the visual processing leading up to conscious detection and categorisation of objects is extremely fast, faster than the speed at which top-down attention can be initiated (i.e., about 100 – 150ms, Theeuwes et al., 2000;

Theeuwes, 2010). Selective attention may be engaged later on to prioritise the processing of particularly relevant locations or features of the extracted gist (Koch & Tsuchiya, 2007).

The necessity of attention for awareness is also called into question by demonstrations of conscious processing and discrimination of stimuli with near absence of top-down attention in dual task paradigms. Here, discrimination between categories of briefly peripherally presented scenes (e.g., animal present or absent, vehicle present or absent) is still possible when engaging top-down attention in a demanding central task (Li, VanRullen, Koch, & Perona, 2002). Crucially, the accuracy of categorisation is unchanged relative to single task conditions and performance in the central task does not decrease due to the peripheral categorisation. This effect is also present when discriminating between peripherally presented male and female faces in a dual task paradigm, although performance is impaired when categorising computationally easier but ecologically less important stimuli such as green-red or red-green discs (Reddy, Wilken, & Koch, 2004). Together these results seem to indicate that attention may not be required for the initial steps of building a conscious representation of the natural visual scene and extracting its semantic meaning.

However, after a closer consideration of this evidence, it is questionable whether awareness and attention truly dissociate under natural continuous conscious perception of the visual world. It must be noted that in lab-based studies where attended stimuli do not become consciously visible, some manipulation is typically present to prevent the stimuli from entering awareness, such as masking (Kentridge et al., 2008) or interocular suppression (Jiang et al., 2006). Under these conditions, although precision may be initially allocated to the subliminal stimulus, it is then disrupted or masked by a salient distractor. Thus, what these paradigms show is that subsequent performance can benefit

from spatial or feature-based allocation attention even if attentional processing is disrupted by masking and therefore does not lead to awareness. Similarly, it is arguable whether a central task that requires focal attention in dual-task paradigms completely exhausts attentional resources (e.g., covert attention) (Li et al., 2002; Reddy et al., 2004), especially if it is not perceptually complex (Lavie, 1995). The task instruction to detect faces may, for example, serve as an attentional set that increases precision or baseline activity of face representations giving them competitive advantage even when focal attention is engaged in the central task.

It would also be helpful to ascertain whether pre-attentive visual processing, as in the case of fast peripheral presentations under dual task conditions, can lead to a rich conscious experience of the scene to be able to claim visual processing with minimal or absent attentional resources still leads to conscious perception. The initial fast feed-forward sweep of visual processing terminates at high-level cortical areas that have large receptive fields and code abstract, position and viewpoint invariant object representations (Campana & Tallon-Baudry, 2013). This leaves us with a vivid representation in the sense that semantic content of the scene is extracted but the representation is coarse in that consciously it only provides us with the experience of gist. Detailed perception follows from cortical re-current feedback to low-level areas and attentional selection of particular representations for amplification of signal and thus more focused processing (Lamme, 2003). It is questionable whether the gist perception that it sufficient for simple semantic categorisation could sustain conscious awareness if it was not followed-up by cortical feedback mechanisms and selective attentional processing. In fact, disruption of re-current processing typically impairs awareness (Lamme, 2003). Therefore, although attention and awareness can be

dissociated in the lab, the argument that attention is not necessary for conscious detection of visual stimuli is not convincing.

1.3.3 Summary

The debate sketched out here largely corresponds to the division of awareness into phenomenal and access consciousness, whereby the former is described as the phenomenal experience of perceptual content but the latter is defined as the part of this experience accessible for memory, planning, reasoning, and decision-making systems, as well as voluntary action and introspective report (Block, 2005; 2011). The key distinction here is that what is available for phenomenal awareness may not always be possible to access and report, as phenomenal representations are thought to compete for access to the planning and output systems. Although phenomenal awareness or a percept of a gist may be generated very quickly and possibly in the near absence of attention (Kirchner & Thorpe, 2006; Li et al., 2002; Campana & Tallon-Baudry, 2013), it is unclear if such representations could support conscious detection of visual change. The representations available for phenomenal awareness may be subserved by a temporally fragile but rich stage of visual STM, which then contributes to the more accessible and robust but limited capacity VSTM (Lamme, 2003; Sligte, Scholte, & Lamme, 2008; Sligte, Scholte, & Lamme, 2009). Attention may be the cognitive process that determines which contents of phenomenal awareness become accessible for report. This thesis aims to investigate visual change detection and therefore this type of process likely requires access consciousness. Although phenomenal awareness can be supported in the near absence of attention, attention may be necessary in order to become aware of visual stimuli and be able to report them.

1.4. Predictive processing biases and individual differences in visual awareness

Overall, predictive processing theories (Friston, 2010; Feldman & Friston, 2010, Hohwy, 2013; Clark, 2013) propose that the relative impact on expectations versus sensory evidence on visual perception may depend on their estimated reliability or precision, which is dynamically adjusted by attention. For example, when the sensory signal is weak or ambiguous, more weight will be assigned to prior knowledge (Stocker, & Simoncelli, 2006; Sterzer et al., 2008; Chalk et al., 2010; Girshick et al., 2011). In contrast, when signal is strong or reliable, expectations may contribute to the perceptual estimate less. What is particularly interesting from an individual differences perspective is whether individuals have a bias to rely on internal representations versus weight sensory evidence more, as different strategies for exploring the visual world specifically or cross-modal sensorium more generally.

If reliable inter-individual predictive processing biases do exist, it may be worthwhile to consider how they manifest in visual experience. One possibility is that they may operate in a domain-general way, affecting the perception and cognition across modalities. There are some reasons to think this may be the case, one potential phenomenon representing a predictive processing bias being sensory sensitivity, which increases in the general population across multiple modalities with the increase of scores on autistic traits (Robertson & Simmons, 2013; Horder, Wilson, Mendez, & Murphy, 2014). On the other hand, it is possible that there will be modality-specific biases. Within this thesis, I take on the task of investigating how a predictive processing bias may manifest by narrowing down the domain to visual perception. To understand the connection between predictive processing bias and individual differences in visual

awareness, it is necessary to, firstly, consider how prediction and prediction updating

mechanisms relate to the conscious experience of visual stimuli in the general

neurotypical population, and, secondly, whether these biases could be revealed in

atypical perception.

Under ecologically valid conscious visual perception, that is, when awareness

and attention are not purposefully dissociated, the contents that are consciously

perceived are equivalent to internal representations that the system has estimated to be

most probable and precise. In other words, the model that enters awareness is one that,

given prior knowledge, currently best minimises prediction error. Based on this

premise, individual differences in the tendency to rely on prior knowledge versus assign

greater weight to prediction error, given the same visual context, may result in

awareness that is populated by distinct perceptual experiences. However, how may

these experiences manifest subjectively? Attention as assignment of precision may

inform the characteristics of predictive processing biases. For example, if individuals

reliably assign greater precision to priors over sensory evidence, this essentially means

that they will tend to on the whole consider sensory information as less reliable

(associated with greater uncertainty) than their inner visual models. Alternatively,

individuals may tend towards assigning high precision to sensory evidence. This

difference in how sensory input (prediction error within this framework, Feldman &

Friston, 2010) is treated will ultimately affect the stability of internal models. If

prediction error is prioritised, then perceptual models may be unstable and subject to

frequent change. On the other hand, if sensory evidence is treated as unreliable (i.e., the

signal-to-noise ratio needs to be especially high to reach a threshold for updating of a

prediction), then perceptual models may be stable but perhaps not accurately reflect

changes in the visual environment.

1.4.1 Change blindness

One potential window to predictive processing biases, in terms of individual differences in visual experiences, may be the phenomenon of change blindness (CB) (Rensink, O'Regan, & Clark, 1997; Simons & Levin, 1997). Here, people look at a visual scene and fail to notice an object that keeps appearing and disappearing within the scene (see Figure 1.3 for an example). This object can even be fixated, attended to (Ryan, Althoff, Whitlow, & Cohen, 2000), and processed to some extent, as revealed by above chance recognition of missed objects (Hollingworth & Henderson, 2002) but still fails to enter awareness. Change blindness displays commonly work because an interfering visual transient (e.g., a flicker or 'mudsplash') is introduced, which masks the appearance and disappearance of the target object. There are several interpretations as to why the CB effect occurs. The dominant explanation is that the interference caused by the transient interrupts exogenous orienting to the stimulus which otherwise would be deemed salient, interrupting the encoding of the scene in VSTM; therefore, making the system rely on endogenous active search to find the object (Beck, Muggleton, Walsh, & Lavie, 2005). What is interesting is that this paradigm of failure of visual awareness could reveal whether people differ in their ability to become aware of visual change despite the interference, and if so, this could reveal an underlying predictive processing bias.

Figure 1.3 An example of a change blindness display with natural scenes

The pre-change scene is displayed on the left; the post-change scene is displayed on the right. In the post-change scene, there is some extra greenery behind the statue. The scenes alternate and are typically separated by brief presentation of a blank screen, which creates a flicker that masks the onset of the change during continuous presentation. Images obtained from a webpage created by Rensink (2017).

In terms of predictive processing mechanisms, successful change detection can be understood as an incorporation of a model of the changing object into the current prediction regarding the state of the visual world. The incorporation of the change would normally be achieved through exogenous attention via high expected precision of a sudden onset, as attention would be drawn to the sudden appearance or disappearance of an object due to its perceptual salience, thus amplifying its signal and allowing it to reorganise contents of awareness. This is not possible or easy due to the flicker, which may change precision expectations, given its strong signal – strong signals are expected to be precise and abrupt onsets are always prioritised (Yantis, & Jonides, 1984; Jonides, & Yantis, 1988). So, the task of finding the changing object must be carried out via endogenous serial search (assigning precision voluntarily) for the changing elements within the scene, which requires a good enough representation of the scene as well as ability to disengage from capture by the flicker. When a change is finally noticed, this may be due to different reasons – it could be because the internal scene representation

was strong enough to guide endogenous search effectively and register a mismatch
between the model and sensory evidence. Alternatively, it may be because the
interference of the flicker could be overcome and the onset and offset of the changing
object finally captured attention exogenously. Either way, individual differences in
change detection could reveal a bias in the predictive processing mechanisms – reliance
on internal models versus reliance on sensory evidence.

1.4.2 Bistable perception

Another type of visual experience that is argued to reflect predictive processing
mechanisms is the phenomenon of binocular and perceptual rivalry (Blake &
Logothetis, 2002; Hohwy, Roepstorff, & Friston, 2008). In binocular rivalry the field of
vision is separated through a mirror stereoscope and each eye is shown a different image
(see Figure 1.4). Instead of permanently composing the two images into a joint one, the
visual system periodically shifts between conscious registration of one image versus the
other, with occasional merging of the two. There are large and stable individual
differences in binocular rivalry alternation rate, and these have a substantial genetic
contribution (Miller et al., 2010). Perceptual rivalry is a similar phenomenon, although
achieved when naturally viewing stimuli that are inherently bistable in their
interpretation. An example of this is the Necker cube or the rabbit-duck illusion (see
Figure 1.5); whereby, as in binocular rivalry, the visual system stabilises on one
interpretation, which is then disrupted in favour of the alternative, never combining the
two. The rate of alternation between the two interpretations in perceptual rivalry is
predicted by brain structure, specifically, grey matter density in the parietal cortex
(Kanai, Bahrami, & Rees, 2010; Kanai, Carmel, Bahrami, & Rees, 2011). The
mechanisms of binocular and perceptual rivalries are multi-faceted, as these are argued

to include contributions from low-level processing at the level of the retina, subcortical areas and visual cortex such as inter-ocular suppression, adaptation and inhibition of visual representations, as well as high-level attentional selection processes (Blake & Logothetis, 2002). It has been proposed that individual differences in rivalry rate may be reflective of a deeper underlying bias for either perceptual stability (i.e., reliance on priors) or instability (i.e., weighting up prediction error) (Kanai et al., 2011). That is, a faster alternation rate when confronted with a bistable stimulus may reveal an individual is prone to updating their perceptual predictions more readily due to assigning a greater weight to the prediction error signal.
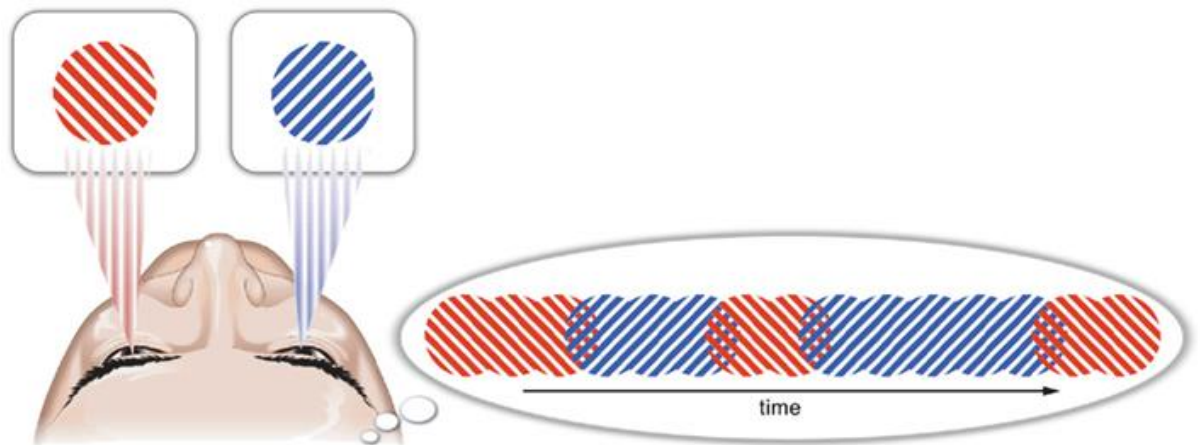
Figure 1.4 An illustration of the phenomenon of binocular rivalry

A mirror stereoscope is used to present a different grating to each eye – one grating is left-slanted and the other is right-slanted. Instead of continuously seeing a blend of the two gratings the observer perceives one grating (e.g., the left slanted) and after a while the percept changes into the competing grating (e.g., the right slanted). The subjective experience continuously alternates between the two percepts. Image taken from Dieter & Tadin (2011).
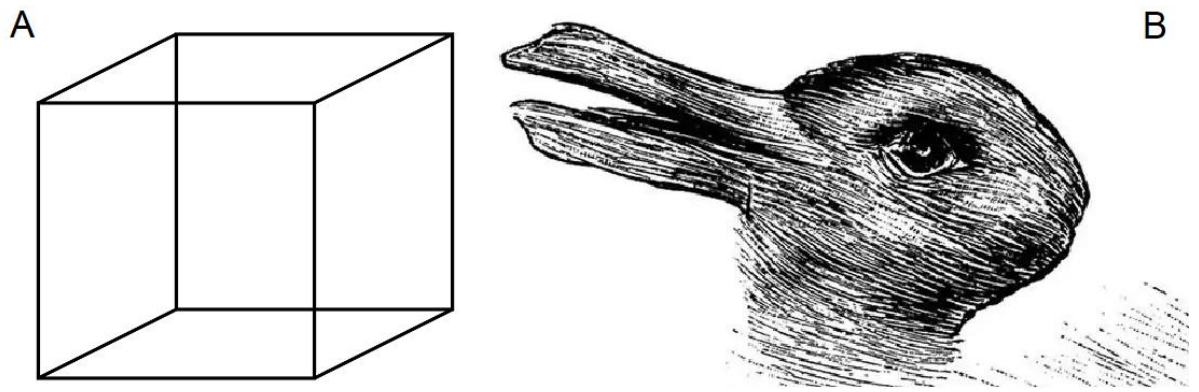
Figure 1.5 Two bistable stimuli illustrating the phenomenon of perceptual rivalry

The Necker cube (A) and the rabbit-duck illusion (B). In both images two perceptual interpretations are possible and only one at a time can be subjectively experienced.

1.4.3 Atypical perceptual profiles: psychosis

Psychopathology or unusual perceptual profiles may also serve to reveal imbalances in predictive processing. The two non-neurotypical conditions that are consistently linked to predictive processing bias in the research literature are schizophrenia and autism. In the case or schizophrenia, within the domain of visual awareness, individuals experiencing psychosis are thought to either be overly reliant on perceptual priors or in fact overweight perceptual prediction errors (Adams, Stephan, Brown, Frith, & Friston, 2013; Sterzer et al., 2018). More generally, people with schizophrenia relative to controls tend to 'jump to conclusions' of form predictions and beliefs quickly based on weak evidence (Garety, Hemsley, & Wessely, 1991; Dudley & Over, 2003) and also find it more difficult to change strong beliefs when confronted with disconfirmatory evidence (Woodward, Moritz, Menon, & Klinge, 2008). People with early symptoms of psychosis or high in schizotypy measures are more likely than controls to use prior knowledge to form inferences when presented with ambiguous input, such as degraded two-tone images of faces (Teufel et al., 2015). Individuals who

tend to hear voices are also more susceptible to experience perceptual hallucinations after conditioning (Powers, Mathys, & Corlett, 2017). Predictive processing imbalances may explain the most profoundly uncanny symptom of psychosis, which is the experience of hallucinations. Researchers have termed this as the experience of overly strong top-down priors (Powers, Kelley, & Corlett, 2016) which are not sufficiently constrained by sensory evidence to replicate reality well-enough for it to agree with the model of reality that neurotypicals generate.

1.4.4 Atypical perceptual profiles: autism

Another atypical perceptual profile that may reveal predictive processing biases presents itself in the experiences of autism. People high on the autism spectrum according to the Autism-Spectrum Quotient (AQ) scale (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), or with the medical diagnosis, tend to have specific types of perceptual and cognitive difficulties as well as enhancements. In addition to the central difficulties associated with Autism Spectrum Disorder (ASD), such as impairments to reasoning about the social domain, especially the mental states of others (Baron-Cohen, Leslie, & Frith, 1985), there is a collection of consistent perceptual traits. For example, individuals with ASD tend to have fine visual discrimination abilities and propensity for attention to detail (Mottron, Dawson, Soulieres, Hubert, & Burack, 2006), as well as improved visual search (Keehn et al., 2009; O'Riordan, Plaisted, Driver, & Baron-Cohen, 2001). However, these enhancements tend to co-occur with an increased tendency for sensory sensitivity and affective dysregulation due to being overwhelmed by the processed sensory information (Samson et al., 2014; Ward, 2018). Some researchers have argued that the pattern of perceptual experiences in autism is indicative of weak priors, which would lead to enhanced processing of, and

attention to, sensory signals, heightening their influence on perceptual experience
(Pellicano & Burr, 2012). The account of hypo-priors (i.e., attenuated influence of
perceptual predictions) would be consistent with various observations, for example the
weaker susceptibility to visual illusions in children with ASD (Happé, 1996). An
alternative view is that people with ASD do not have weaker priors, at least not
perceptual ones, as this would be incompatible with superior performance (Teufel,
Subramaniam, & Fletcher, 2013). Instead, individuals on the spectrum may assign
greater weight to prediction errors, irrespective of whether they are reliable, perhaps due
to an inability to contextually downregulate the precision (Van de Cruys et al., 2014). In
other words, violations of expectations are assigned great precision inflexibly, even in
contexts where noise is responsible for the error and it is best disregarded. This is
thought to result in a fine-grain perception of visual detail but a limited ability to form
abstract representations such as those governing the social world (which require
tolerating uncertainty or noise), as well as a lower ability to adapt to or disregard
irrelevant perceptual detail (a feature of sensory sensitivity) (Ward, 2018).

Psychosis and autism may not be distinct disorders but rather a collection of
experiences at the extreme ends of a spectrum (Crespi & Badcock, 2008). Individuals in
the general population may also experience anomalous perceptual experiences such as
hearing voices and seeing visual illusions and can be induced to experience these in
experimental settings. For example, when no stimulus is presented individuals report
seeing apparent motion in the most commonly occurring direction of the movement
after forming expectations of motion (Chalk et al., 2010). This highlights the idea that
there may be a propensity to assign weight to internal models (or perhaps limited ability
to constrain them with sensory evidence) that may not only manifest in atypical
conditions but also can be measured in the general population.

1.4.5 Summary

Taken together, this evidence suggests that there may be some credence to the suggestion that predictive processing biases manifest in perceptual experience. However, it is yet unclear whether this can be inferred only from exploring atypical visual experiences, which are affected by other influences, such as presence and absence of medication in psychosis (an issue with studies inferring predictive processing differences, given medication is used to counter-act the symptoms), as well as potential influence of compensatory mechanisms. Or, whether the balance between reliance on prior knowledge versus sensory evidence is a strategy of perceptual inference that can manifest individual differences in visual awareness in the general population. If so, these would be expected to be reflected in visual tasks where the detection of novel change is necessary, as this requires an incorporation of new information into a perceptual model.

1.5. Thesis overview and aims

This thesis applies individual differences as a research methodology to explore the underlying mechanisms that support visual awareness. The overarching aim of this thesis is to investigate individual differences in CB and to explore whether the ability to notice changes reveals an underlying predictive processing bias to either weight prior knowledge or sensory evidence more in visual perception. The investigation focuses on individual differences within the general population of healthy adults, although it also aims to infer connections between predictive processing biases and sub-clinical atypical perceptual profiles within this population, such as the experience of perceptual anomalies and autism spectrum traits.

Chapter 2 aimed to characterise individual differences in change detection using naturalistic scenes in order to establish whether there are reliable, generalisable differences in noticing ability. It also aimed to identify the perceptual and cognitive measures that are the strongest predictors of change detection ability. To this end, a battery of tasks was selected, assessing high-level abilities such as VSTM and attentional control, as well as low-level sensitivity to signal. By selecting both tasks pertaining to encoding and maintenance of visual information, as well as detection sensitivity, I aimed to get at the distinction between forming stable and strong perceptual predictions versus sensitivity to error signal. In *Chapter 3,* the aim was to investigate the neural basis of change detection ability and that of its strongest predictors using voxel-based morphometry. The study asked whether grey matter density in parietal and visual cortex regions could predict susceptibility to CB. The regions of interest (ROIs) were selected based on literature review, which indicated that these areas are causally involved in initiating changes in visual awareness, as well as being related to the quality and capacity of VSTM representations. The aim of *Chapter 4* was to look more closely at individual differences in the tendency to assign weight to perceptual priors by selecting a paradigm that could measure the strength of the bias prior knowledge exerts on perception. To this end, a Mooney face detection task was selected, which requires detecting faces in transformed, ambiguous two-tone images. The Mooney face detection sensitivity before and after acquiring knowledge of the original images was assessed and correlated with change detection, as well as atypical perceptual traits pertaining to schizotypy and the autism spectrum. *Chapter 5* was an investigation into whether there is a general predictive processing bias, which manifests using different methods of manipulating prior knowledge. Different methods previously shown to inducing perceptual expectations and to alter the experience of binocular

rivalry were selected. The aim was to discover if individuals vary a long a trait-like tendency to 'see the expected' in the rivalry display, that manifests across different methods of inducing perceptual priors. The expectation-based biases on visual awareness of binocular rivalry were then correlated with change detection, as well as perceptual traits that are considered typical (visual imagery, distractibility) and atypical (perceptual anomalies, attention to detail in the autism spectrum).

CHAPTER 2

Individual Differences in Change Blindness are Predicted by the Strength and Stability of Visual Representations

2.1. Abstract

The phenomenon of change blindness reveals that people are surprisingly poor at detecting unexpected visual changes; however, research on individual differences in detection ability is scarce. Predictive processing accounts of visual perception suggest that better change detection may be linked to assigning greater weight to prediction error signals, as indexed by an increased alternation rate in perceptual rivalry or greater sensitivity to low-level visual signals. Alternatively, superior detection ability may be associated with robust visual predictions against which sensory changes can be more effectively registered, suggesting an association with high-level mechanisms of VSTM and attention. We administered a battery of 10 measures to explore these predictions and to determine, for the first time, the test-retest reliability of commonly used change detection measures. Change detection performance was stable over time and generalised from displays of static scenes to video clips. An exploratory factor analysis revealed two factors explaining performance across the battery, that we identify as *visual stability* (loading on change detection, attention measures, VSTM, and perceptual rivalry) and *visual ability* (loading on iconic memory, temporal order judgments, and contrast sensitivity). These results highlight the importance of strong, stable representations, and the ability to resist distraction, in order to successfully incorporate unexpected changes into the contents of visual awareness.

2.2. Introduction

Change blindness (CB) is a striking phenomenon that contradicts our intuitions about possessing rich and detailed representations of our visual world and highlights the limitations of the top-down and bottom-up neurocognitive mechanisms underlying subjective visual awareness. Long-standing behavioural research on CB has established that people tend to be surprisingly poor at noticing sudden, unexpected changes in the visual environment, whether the changes occur in static displays of visual scenes (Rensink et al., 1997; Simons & Rensink, 2005), dynamic motion pictures (Levin & Simons, 2000) or in real world settings (Simons & Levin, 1998). A common technique for inducing CB is to introduce a visual transient between the pre-change and post-change scenes, such as a flicker or 'mudsplash' in static displays (Rensink, 2000; O'Regan, Rensink, & Clark, 1999), camera pans or cuts in dynamic video clips (Levin & Simons, 1997; Smith & Milne, 2009), or presenting the change across saccades (Grimes, 1996). It is argued that when a visual transient is introduced, the bottom-up signal of the change is masked by the interference, which disrupts exogenous orienting to the change (Rensink et al., 1997; Beck et al., 2005). This in turn is thought to impair encoding of the change into VSTM and to bias the visual system towards an endogenous, effortful visual search for the change. Change detection is improved with cueing, expectations of change, relevance to current task goals, and for contextually central and socially relevant stimuli (Simons, 2000; Simons & Rensink, 2005; Ro, Russell, & Lavie, 2001). Despite decades of research, little is known about individual differences in the ability to detect visual changes. In this study we explored, for the first time, whether people reliably differ in their ability to notice changes in naturalistic scenes. Furthermore, we examined using a predictive processing framework whether

change detection is predicted by inter-individual variability in the selection and maintenance of visual information (attention and visual memory) or perceptual sensitivity (detection and discrimination of simple stimuli).

The theoretical framework of predictive processing (Rao & Ballard, 1999; Friston, 2010; Hohwy, 2013; Clark, 2013; 2015) considers the human brain as a hierarchically-organised hypothesis-testing system that engages in predictive inference about the environmental causes of sensory input. Visual perception emerges from recurrent, bottom-up and top-down interactions in visual pathways (Hohwy et al., 2008). Discrepancies between the prediction (i.e., the most likely interpretation of the visual input) and afferent sensory data generate prediction error signals that flow in the bottom-up direction in the visual hierarchy to update the current prediction. Crucially, the system perpetually strives to minimise prediction error to accomplish behaviourally optimal visual inferences. In this theoretical framework, CB could arise from a failure to update the current prediction of the state of the visual world. This in turn could occur due to a variety of reasons within this framework; the prediction error generated by the change may be too weak or imprecise to create a shift in awareness, the representation of the pre-change scene could be too weak or imprecise to consciously register a deviation from it, or it could be a combination of both processes. For example, a weaker representation could engender a less precise prediction error. There is some evidence that missed changes are still processed at some level in the visual system, given above chance recognition performance on forced-choice memory tests with undetected items (Hollingworth & Henderson, 2002). This suggests the prediction error signal generated by the change is transmitted but does not reorganise the contents of awareness due to some limitation in the interactions of predictive and corrective mechanisms of visual inference. By adopting an individual differences approach to the phenomenon of CB,

our aim is to reveal the predictive processing mechanisms that support superior change detection.

We adjudicate between two broad, albeit not mutually exclusive, theoretical possibilities as to why some individuals may be better than others at noticing change. On the one hand, superior change detection may be reliant on forming robust, stable, and accurate predictions about the visual world. This is in line with existing research demonstrating that CB arises in some part due to impaired encoding and maintenance of scene representations in VSTM. For example, disruption of a VSTM-associated region in parietal cortex with transcranial magnetic stimulation (TMS) during the presentation of pre-change scene leads to greater CB than post-change (Tseng et al., 2010), suggesting having a good representation of the scene prior to the change is crucial. Furthermore, being able to resist distraction by visual transients and successfully allocate top-down attention in accordance with VSTM representations is likely to support faster detection: exogenous orienting to changes in the CB task is disrupted by visual transients and is overcome by engaging in endogenous visual search (Beck et al., 2005). Consequently, it can be hypothesised that higher VSTM accuracy, lower susceptibility to attentional capture, and lower distractibility will predict superior change detection.

An alternative hypothesis is that visual change detection is enhanced by a tendency to assign a greater weight to low-level sensory signal. This would boost the strength of prediction error that is transmitted up the visual hierarchy to correct perceptual inferences. Greater perceptual sensitivity, quantified by such psychophysical measures as temporal order judgement and contrast sensitivity, have been shown to predict performance on a range of different visual tasks, including visual search (Ward, Rothen, Chang, & Kanai, 2017), so could potentially also support change detection.

Similarly, the alternation rate in perceptual rivalry paradigms, where individuals are faced with a constant but ambiguous stimulus (e.g., a Necker cube) and subjectively perceive two alternating visual interpretations, has been argued to reflect this kind of bias towards assigning more weight to sensory evidence. Specifically, Kanai and colleagues (2011) posit that individuals who subjectively experience a faster alternation rate when viewing bistable stimuli assign greater weight to sensory prediction error, and thus update their visual inferences faster. Inter-individual differences in various types of perceptual rivalry are large and have high test-retest reliabilities (Miller et al., 2010), which suggests an intriguing possibility that they index a general predictive processing bias which could manifest in other visual abilities including change detection. If this low-level sensitivity hypothesis is correct, we expect a high alternation rate in perceptual rivalry, high contrast sensitivity, and a low threshold for temporal order judgements to predict superior change detection. This interpretation is intuitively appealing, as we expect sensitivity to minute differences in signal to be associated with having a more detailed representation of the visual world.

In summary, the main focus of present research was to determine whether it is the strength of high-level cognitive capacities or low-level perceptual sensitivity (or both) that supports the formation of accurate and behaviourally optimal moment-to-moment representations of the visual world. All tasks involve some low-level element (given that they all involve visual stimuli) and a high-level element (minimally the task instructions), but the theoretically interesting question is where in this hierarchy lies the bottleneck that determines individual differences in performance (and there may be multiple bottlenecks). The assumption made here is that the bottleneck in tasks such as VSTM and avoiding distraction is at the level of later 'high level' visual processes (involved in selection and maintenance of visual information) but that the bottleneck in

tasks involving discrimination of weak visual signals lies in early 'low level' visual processes (involved in simple detection of visual information). In addition, we consider that the two alternative hypotheses may be related; possessing robust representations may enable the individual to generate more precise prediction errors, which may boost conscious detection of visual change. In this case, we would expect both attentional and memory measures, and perceptual sensitivity measures to predict detection performance.

To explore these hypotheses, we administered a battery of 10 different tasks, some of which we presented over two sessions to determine their test-retest reliabilities. We employed two measures of change detection; the commonly used 'flicker' CB paradigm with naturalistic scenes and short video clips containing continuity errors. To measure the strength of high-level representations we included a VSTM task assessing three sub-components of VSTM (iconic, fragile, and robust) that reflect early versus later memory processes and differ in their capacity and proneness to be over-written (Sligte et al., 2008; 2009). To assess the ability to exert top-down control in the presence of distractors, we administered an attentional capture task and the Cognitive Failures Questionnaire (CFQ) (Broadbent, Cooper, FitzGerald, & Parkes, 1982), which assesses self-report distractibility. We used two psychophysical measures of sensitivity to low-level visual signal; temporal order judgment threshold and contrast sensitivity. Additionally, we included a perceptual rivalry task involving an ambiguous structure-from-motion sphere in order to measure the tendency to update visual predictions in light of conflicting input (Kanai et al., 2011); high alternation rate may indicate assigning greater weight to prediction error (a low-level bottleneck) whereas a low alternation rate may reflect greater stability of perceptual predictions (a high-level bottleneck).

Collectively, these eight tests were motivated by the theoretical framework outlined above. In addition, we included two tests that are more exploratory in nature; the Vividness of Visual Imagery Questionnaire (VVIQ) (Marks, 1973; 1995), and a test measuring a visual pattern recognition aspect of general intelligence (Condon & Revelle, 2014). Our approach was to (a) focus on the small number of correlations that were hypothesised *a priori* and that clearly address the two proposed hypotheses (b) regard other correlations as exploratory, in which the effect size and direction of correlation is noted in order to make predictions for confirmatory research (McBee & Field, 2017), and (c) conduct a factor analysis of all the measures. The latter is important because it enabled us to take a holistic view of the dataset in a single analysis and identify which perceptual and cognitive abilities are associated with the tendency to notice visual changes.

2.3. Method

2.3.1 Participants

Sixty-three adult participants (Aged 18 – 38, Mean = 20.46, SD = 4.16; 54 female) with normal or corrected-to-normal vision and no reported colour vision deficiencies took part in this study. The participants were undergraduate students at the University of Sussex who received course credit and adults from the Brighton community who were reimbursed in cash. The study consisted of a battery of 10 perceptual and cognitive measures and comprised two separate sessions. All 63 participants completed the initial testing session (2h), and 60 participants returned to the lab 1-4 weeks later to complete the final re-test session (1h). Due to time constraints and technical issues a few participants did not complete all of the tasks in Session 1;

appropriate N values are provided in Table 2.1. The study was approved by the Science and Technology Cross-Schools Research Ethics Committee (C-REC), at the University of Sussex.

2.3.2 Materials and Design

The test battery consisted of 10 different tasks; two different change detection tasks (CB and continuity error (CE) detection task), a VSTM task, an attentional capture task, a perceptual rivalry task, two basic psychophysical measures (temporal order judgment (TOJ) and contrast sensitivity (CS) tasks), a questionnaire to assess self-reported distractibility (Cognitive Failures Questionnaire (CFQ), Broadbent et al., 1982), a questionnaire assessing the vividness of mental imagery (Vividness of Visual Imagery Questionnaire (VVIQ), Marks, 1973), and a test of general intelligence (matrix reasoning task, Condon & Revelle, 2014). All of the tasks were presented in Session 1 but only the CB, CE, attentional capture, VSTM, and perceptual rivalry tasks were presented in Session 2 to determine their test-retest reliabilities. Figure 2.1 provides an illustration of the trial structure of each task. More information regarding stimulus viewing parameters is provided in Table 7.1 in the Appendix A.
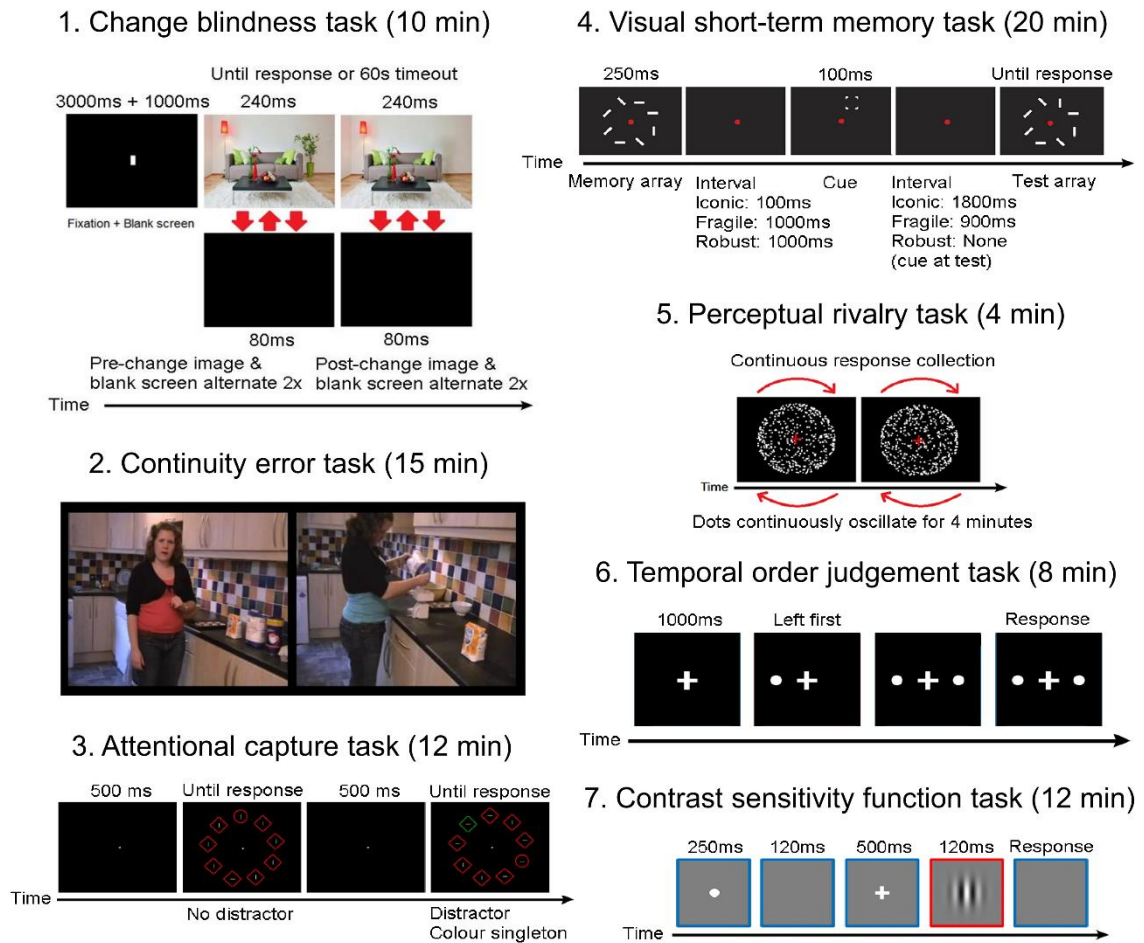
Figure 2.1 The stimuli and trial structure of the tasks

The tasks are numbered according to the order of presentation. In the change blindness task, (1) the flickering cycle of pre-change scene, post-change scene and blank screen alternated for 60s (if no response was given): the task was to click on the change. In the continuity error task, (2) the task was to describe any unexpected changes in video clips (e.g., the actor's shirt changes colour). In the attentional capture task, (3) participants reported the orientation of the line inside the circle whilst ignoring the diamonds. In the visual short-term memory task, (4) participants reported if the cued rectangle in the test array was the same or different as in the memory array; the time interval before and after the cue varied depending on condition. In the perceptual rivalry task, (5) participants clicked the mouse any time they subjectively perceived the ambiguous structure-from-motion sphere to change the direction of rotation. In the temporal order judgement task, (6) the objective was to determine which of the dots appeared first. In the contrast sensitivity task, (7) participants had to report if they saw a Gabor patch before or after the fixation cross.

1. Change blindness task

The CB task was adapted from the landmark study by Rensink and colleagues (1997) and required participants to find changing objects within flickering natural indoor scenes. Sixty image pairs were obtained from a CB database (Sareen, Ehinger, & Wolfe, 2016); one image was an original indoor scene and in the other image one of the objects (e.g., a vase) was removed. Half of the object changes occurred on the left side of the image and half occurred on the right. The task was presented using Inquisit Millisecond software and consisted of one practice trial and 30 randomly intermixed experimental trials. On each trial the pre-change and post-change scenes alternated with a blank screen in between the two, creating a flickering cycle of image presentations lasting 60 seconds. Participants were instructed to use a mouse to click on the object that keeps appearing and disappearing. The next trial began after the mouse click or, in the case of no response, when the image cycle finished (after 60s). There was an inter-trial interval of 1000ms and a black screen with white fixation square was presented for 3000ms before each trial. Different image pairs were presented in Sessions 1 and 2. To separate correct from incorrect responses, ROIs within each image were defined around the centre coordinates of the changed object (Mean radius = 1°), and mouse clicks with coordinates outside ROIs (Mean radius = 2°) were labelled as misses.

2. Continuity error detection task

In this task participants viewed short video clips, originally used by Smith and Milne (2009), containing continuity errors. The clips were spliced from a 20-minute film on the topic of baking; during this film an actor goes through each step of the recipe and gives instructions, whilst occasionally unexpected changes are introduced across cuts or pans in the camera angle. This task was presented using Inquisit

Millisecond software, and participants viewed 10 clips that lasted on average 51 seconds; eight clips contained one continuity error and two contained none. The continuity errors involved sudden changes to central-actor, central-object, marginal-actor, or marginal-object related aspects of the scene, with equal numbers of each change type. After watching each clip participants were presented with two general questions about the baking instructions to gauge their level of attentiveness and were asked to describe any continuity errors in the text box provided. Different video clips were presented in Sessions 1 and 2.

3. *Attentional capture task*

The attentional capture task was similar to that described by Kanai, Dong, Bahrami, and Rees (2011b). This task was presented using E-prime software and measures the extent to which participants are distracted by salient task-irrelevant stimuli. The task consisted of 12 practice trials and 300 experimental trials (4 blocks). A colour singleton distractor was present on 140 of the trials and absent on 148 trials. On each trial participants were presented with 9 shapes: 8 diamonds and 1 circle. Each shape contained either a horizontal or a vertical line – this was assigned randomly. The colour of the shapes varied; when no colour singleton was present all shapes were either green or red, whereas when a colour singleton was present all shapes were either green or red, but one diamond was the opposite colour. Participants were instructed to report the orientation of the line inside the circle (e.g., horizontal or vertical) by keyboard responses as quickly and accurately as possible, whilst trying to ignore the diamonds. Attentional capture was estimated by subtracting the average correct response times (RTs) in the condition with no distractor from the condition with the distracting colour singleton.

4. Visual short-term memory task

The VSTM task measured three different VSTM processes; iconic, fragile, and robust VSTM. In this task, adapted from Sligte and colleagues (2008; 2009), participants detected changes in the orientation of cued rectangles. The VSTM task was presented using MATLAB (Mathworks Inc) and Psychtoolbox (Brainard, 1997) and consisted of 288 trials (48 trials x 6 blocks); the initial block was treated as practice. There were three types of trials with different cue onset times and after-cue intervals. In the iconic VSTM condition a cue was presented 100ms after the off-set of the memory array followed by an 1800ms blank interval, targeting iconic VSTM store which has an unlimited capacity and largely relies on after-image. In the fragile VSTM condition a cue was presented 1000ms after the offset of the memory array followed by 900ms blank interval; this was designed to target fragile VSTM store thought to be relatively high capacity but prone to over-writing. In the robust VSTM condition a cue was presented 1000ms after the offset of memory array simultaneously with the test array appearing on the screen; this was designed to target robust VSTM store thought to store about four items. Each of these trial types was presented 96 times randomly intermixed. The test array included the words 'same' and 'different' in the top right and left corners of the screen, respectively. This prompted participants to click the right mouse button if the orientation of the cued rectangle in the test array matched its orientation in the memory array and the left mouse button if it did not. During the inter-trial interval (1600ms) participants saw a green fixation point after a correct response and a red 'Error!' feedback after an incorrect response. Participants were instructed to respond as accurately as possible without prioritising speed. The measure of interest was accuracy in each of the three cue conditions.

5. *Perceptual rivalry task*

The stimulus used in this task was the ambiguous structure-from-motion rotating sphere described by Kanai and colleagues (2010). It was presented using MATLAB and Psychtoolbox (Brainard, 1997), and is typically experienced as an ambiguous sphere that appears to rotate either to the left or right, with the perceived direction of rotation alternating. The sphere consisted of 200 white dots moving sinusoidally with a red fixation cross in the middle and was presented against a black background. The sphere was continuously presented on the screen for two blocks of 2 minutes and participants had to respond by clicking the mouse whenever the sphere appeared to switch its direction of rotation. The measure derived was the total count of the reported perceptual alternations over the 4-minute presentation of the sphere.

6. *Temporal order judgement (TOJ) task*

In this task taken from Ward and colleagues (2017), participants were presented with two adjacent stimuli in rapid succession using MATLAB and Psychtoolbox (Brainard, 1997) and were asked to indicate which stimulus was presented first. The stimuli consisted of two white discs presented side-by-side against a black background. Participants were required to make keyboard responses to indicate whether the left or the right stimulus appeared first. The discs remained on the screen until the participant made a response. The inter-trial interval was 500ms. A staircase procedure was used, where the initial difference between the onsets of the two discs was 35.29ms, and this value was then adjusted in steps of 11.76ms determined by the monitor's refresh rate. The onset difference was reduced after three successively correct trials and increased after every incorrect trial. Each change in onset difference represented a reversal, and ten reversals were required before the termination of the task. The measure of interest

was the TOJ threshold time, which was calculated as the mean of the last ten onset differences (in milliseconds).

7. *Quick contrast sensitivity function (qCSF) task*

The qCSF is a test of sensitivity to contrast as a function of spatial frequency (Hou et al., 2010; Lesmes, Lu, Baek, & Albright, 2010), taken from Ward and colleagues (2016). Participants had to detect Gabor patches using a two-interval forced choice paradigm. Participants were asked to press one of two keys to indicate whether a Gabor patch appeared before or after a fixation cross; they had 2 seconds after the offset of the stimulus to respond. The task was presented using MATLAB and Psychtoolbox (Brainard, 1997) and consisted of 100 test trials. The estimated measures were four parameters of contrast sensitivity as a function of spatial frequency; these consisted of peak sensitivity (γmax), peak spatial frequency (fmax), bandwidth (β) or the contrast sensitivity function's full width at half-maximum, and truncation level or reduced gain at low spatial frequencies (δ).

8. *Vividness of Visual Imagery Questionnaire*

This questionnaire by Marks (1973) assesses the extent to which people can vividly imagine visual scenes. Participants were presented with a description of a visual scene and then prompted to imagine the scene with their eyes closed. The vividness of the imagined scene was then assessed on 5-point scales ranging from "No image at all" to "Perfectly clear & vivid as if I was actually seeing it". The questionnaire took 10 minutes to complete, consisted of 32 separate questions in two blocks of 16, and was presented using Inquisit Millisecond software. The obtained value was the total vividness score.

9. Self-reported distractibility

Self-reported distractibility was assessed with the CFQ designed by Broadbent and colleagues (1982), which involves various questions regarding everyday blunders and failures of attention and memory. The questionnaire took about 5 minutes to complete. Several lines of research have shown that CFQ consists of separate, albeit related, underlying factors; these often differentiate between questions pertaining to distractibility versus forgetfulness (Wallace, Kass, & Stanny, 2002; Rast, Zimprich, Van Boxtel, & Jolles, 2009). Therefore, only the total scores of questions that are a part of the distractibility factor identified by Wallace and colleagues (2002) were analysed.

10. Matrix reasoning task

An estimate of general intelligence (*g*) was obtained by assessing performance in a visual shape matrix reasoning task. This task consisted of 11 progressive matrices obtained via the Cambridge ICAR database (Condon & Revelle, 2014) and these were presented as a paper and pen questionnaire in order of difficulty, with a time-limit of 15 minutes. It has been established that much shorter versions of progressive matrices with as few as 12 questions can have acceptable psychometric properties and predictive power (Bors & Stokes, 1998, Hamel & Schmittmann, 2006). Therefore, a short version of matrix reasoning task was justified for the purposes of this study. The percentage of correct responses was calculated.

2.3.3 Procedure

All participants signed informed consent. The initial session lasted two hours, consisted of 10 different tasks, and participants could take breaks in between the tasks.

The task order in Session 1 was fixed for every participant: CB task, CE task, attentional capture task, VSTM task, perceptual rivalry task, TOJ task, CS task, VVIQ, CFQ, and matrix reasoning task. Session 2 lasted one hour, and again the task order was fixed: CB task, CE task, attentional capture task, VSTM task, and perceptual rivalry task. A fixed order of tasks was used for all participants to maximise the differences between individual performances when all other variables are held constant (as recommended by Mollon, Bosten, Peterzell, & Webster, 2017). The initial two change detection tasks in both sessions, as well as the last three questionnaires from Session 1 were completed seated comfortably 57 cm from the computer screen (screen resolution = 1920 x 1080) with the light on in the room, whereas the remaining tasks in both sessions were completed seated 100 cm from a CRT monitor (screen resolution = 1280 x 1024) in a dark room with participants' heads resting on a chinrest.

2.4. Results

2.4.1 Data preparation

For the CB task the coordinates of the reported change locations were analysed and responses with coordinates outside the ROI were considered a failure to detect the change and added to misses. The cumulative percentage of correctly identified changes was calculated at each time point (e.g., percentage correct with RTs of below 1s, 2s, 3s ... 60s; see Figure 2.2 for an illustration). An inverse exponential function ($Y = \alpha e^{\beta / X}$) was then fit to this data, where Y is the cumulative percentage correct, X is the time in seconds, α is the asymptote, and β relates to steepness/curvature. Given that all participants should be able to detect the change, given infinite time, the asymptote should be about 1.0. A greater parameter β indicates that participants are more likely to

reach asymptote quickly: i.e., detect changes faster. The test-retest reliability (N = 59) of α was relatively low but significant, $r = .26$, $p = .044$, whereas the test-retest reliability of parameter β was moderate and significant, $r = .45$, $p < .001$. We used β to represent CB performance, as it most reliably reflects change detection over time both in terms of accuracy and RT. See Appendix A for a more detailed description of data preparation (e.g., Figure 7.1 for the test-retest reliabilities of percent correct at different time points).
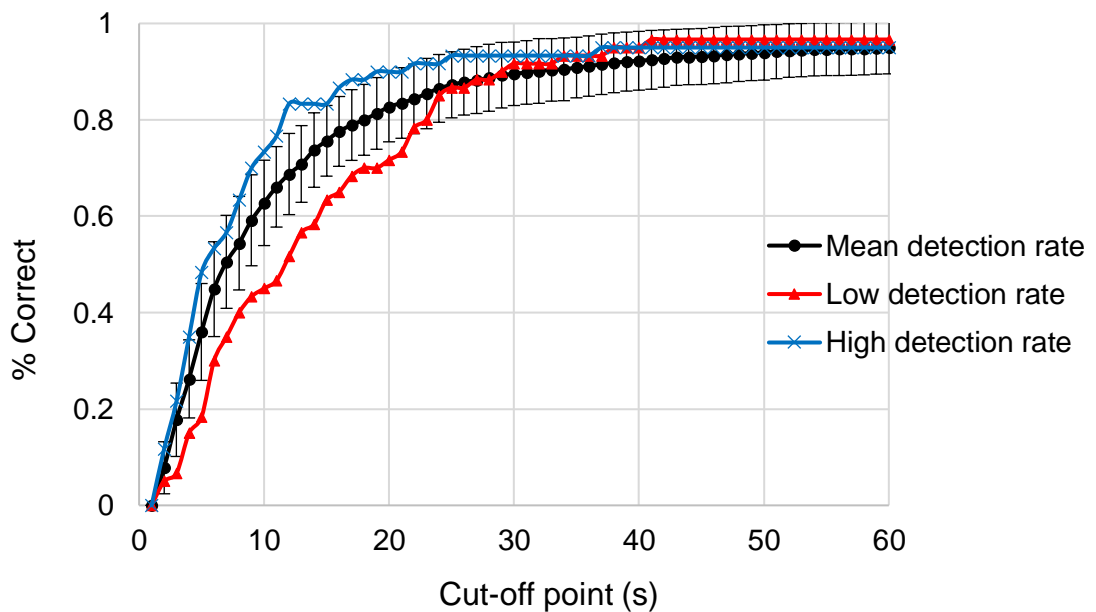
Figure 2.2 The mean cumulative percent correct in the CB task at different time points along with standard deviation error bars and the cumulative percent correct for the highest and lowest performing participants in terms of the β value.

2.4.2 Analyses

For tasks presented over two sessions (CB, CE, attentional capture, VSTM, perceptual rivalry tasks) measures were derived as the average from both sessions but for those who did not complete Session 2, only Session 1 data was used. The summary statistics, as well as the test-retest reliabilities of the measures are presented in Table

2.1. In terms of practice effects, paired t-tests between Session 1 and Session 2 data revealed that performance on most tasks significantly or marginally significantly improved on Session 2, although the effect sizes were small ($r < .3$); CE % correct, t (59) = -2.65, $p = .010$, $r = -0.23$; attentional capture, t (59) = 3.06, $p = .003$, $r = 0.21$; iconic VSTM, t (59) = -4.00, $p < .001$, $r = -0.18$, fragile VSTM, t (59) = -3.73, $p < .001$, $r = -0.18$; robust VSTM, t (59) = -1.95, $p = .057$, $r = -0.12$. The only exceptions were CB parameter β, t (58) = 3.57, $p = .001$, $r = 0.24$, with significantly poorer performance on Session 2, suggesting a more difficult stimulus set. For perceptual rivalry the number of perceptual alternations was significantly greater in Session 2 than in Session 1, t (57) = -3.55, $p = .001$, $r = -0.22$. We correlated performance across each task; a Pearson correlation matrix of CB task and other measures is available in Table 2.2 (for the full correlation matrix see Figure 7.2 in Appendix A). We applied the false discovery rate (FDR) Benjamini-Hochberg procedure (Benjamini & Hochberg, 1995) to correct for multiple comparisons. Out of the 14 correlations between CB task performance and other perceptual and cognitive measures, five significant correlations survived the correction. Two significant correlations did not survive; these are the correlations between CB task performance and perceptual rivalry, and robust VSTM accuracy. Scatterplots of the significant correlations between CB task performance and other measures can be seen in Figure 2.3.

Table 2.1 The summary statistics of the measures

The listed measures are as follows: CB parameter β, the percentage of correctly identified changes in continuity error videos, attentional capture in milliseconds, iconic, fragile, and robust VSTM percent accuracy, the number of alternations in perceptual rivalry, TOJ threshold in milliseconds, CS parameters γmax, fmax, β, and δ, CFQ distractibility score, VVIQ score, and the matrix reasoning task percent accuracy. The final three columns indicate the Pearson test-retest correlation between the Session 1 and Session 2 scores of each test, together with the associated N, lower and upper 95% bootstrapped confidence intervals, and significance values (2-tailed), respectively.

Measure	N	Mean	SD	r (N)	95% CI	p-value
CB β	62	-5.27	1.15	.45 (59)	.20, .65	< .001
CE % correct	63	48.51	12.07	.02 (60)	-.21, .29	.865
Att. Capture	63	59.89	36.98	.50 (60)	.29, .66	< .001
VSTM Iconic	63	85.01	9.35	.76 (60)	.64, .86	< .001
VSTM Fragile	63	74.69	10.25	.72 (60)	.58, .82	< .001
VSTM Robust	63	62.86	8.55	.54 (60)	.31, .70	< .001
Perceptual rivalry	62	37.77	16.18	.58 (58)	.28, .85	< .001
TOJ	63	51.50	21.61			
CS γmax	54	1.46	.28			
CS fmax	54	.37	.15			
CS β	54	.45	.10			
CS δ	54	-.45	.21			
CFQ	63	21.86	4.44			
VVIQ	63	120.37	18.60			
Matrix	61	63.04	20.25			

Is change detection performance stable over time?

The test-retest reliabilities of all measures except the CE percentage correct were moderate to high (r ranged from 0.45 to 0.76). It must be noted that the change detection tasks were the only two tasks where different stimuli (i.e., different images of indoor scenes in the CB task and different video clips in the CE task) were presented in each of the two sessions. Therefore, it was anticipated that the test-retest reliabilities would be lower for the change detection tasks than for the other measures such as the VSTM task, where the stimuli were identical in both sessions. The CE task did not yield

a significant test-retest reliability, presumably because of the very few trials (8 videos with continuity errors per session) and variability inherent in the format of the task.

What is the relationship between different change detection paradigms?

The CB parameter β was significantly positively related to CE percentage correct, $r = .42$, $p = .001$. The faster the detection rate in the CB task, the more continuity errors participants noticed in the video clips. This result suggests that the ability to notice visual changes is relatively stable over different stimulus sets (e.g., static naturalistic scenes, dynamic video clips). This finding indicates that change detection performance in the standard 'flicker' CB task can be generalised to more ecologically valid displays.

Do measures of visual short-term memory and attentional control predict change detection performance?

The CB parameter β task was significantly positively associated with accuracy of the later sub-divisions of VSTM, fragile VSTM, $r = .33$, $p = .009$, and robust VSTM, $r = .26$, $p = .041$, such that increased accuracy of these components of VSTM was associated with superior performance in the CB task (although the latter did not survive the FDR correction).

The CB parameter β was significantly negatively correlated with attentional capture, $r = -.41$, $p = .001$. This suggests people with decreased tendency for attentional capture or superior ability to disengage from distracting stimuli were faster to detect visual changes in the CB task. CB parameter β was also significantly negatively associated with the distractibility component of the CFQ questionnaire, $r = -.30$, $p =$

.017, indicating that highly distractible people tend to notice visual changes more slowly.

Do measures of TOJ, CS, and perceptual rivalry predict change detection?

The CB task performance correlated significantly with TOJ threshold, $r = -.33$, $p = .008$, such that the participants who could differentiate the temporal order of the onset of two stimuli closer in time were able to detect changes in the flickering scenes faster. This association was also found with the continuity error video task performance, $r = -.26$, $p = .041$. However, none of the contrast sensitivity parameters were significantly associated with CB task performance.

The number of perceptual alternations in perceptual rivalry was significantly but negatively associated with CB parameter β, $r = -.28$, $p = .030$. Faster alternation rate when viewing the ambiguous rotating sphere was associated with poorer change detection. This relationship suggests that the ability to form relatively stable visual predictions in light of conflicting incoming signals is associated with a superior change detection. However, it must be noted that this correlation did not survive correction for multiple comparisons.
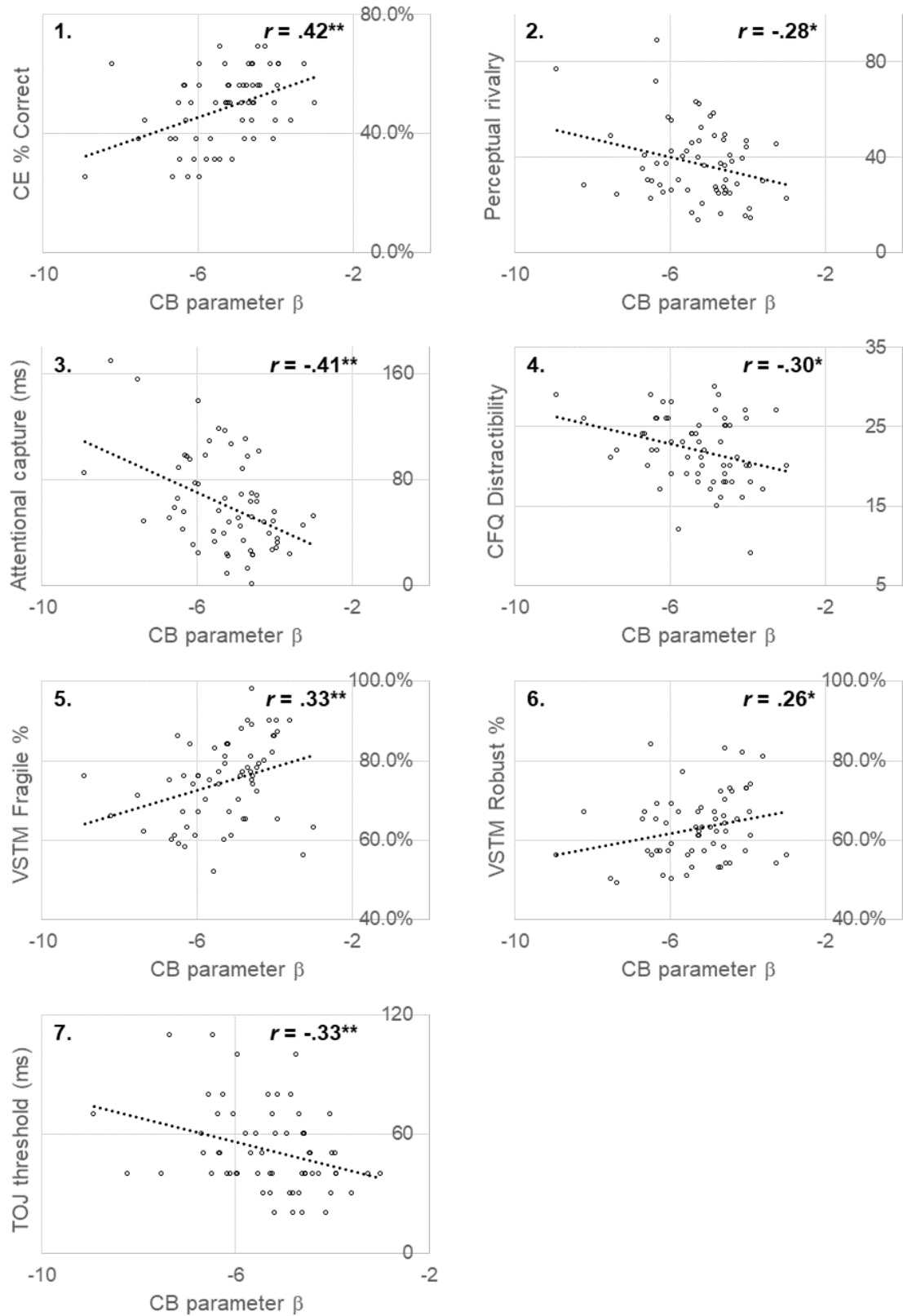
Figure 2.3 Scatterplots illustrating the significant correlations between CB parameter β and the other perceptual and cognitive measures

The percentage of correctly identified changes in continuity error videos (1), number of alternations in perceptual rivalry (2), attentional capture (3), CFQ distractibility score (4)

fragile VSTM accuracy (5), robust VSTM accuracy (6), TOJ threshold (7). The associated Pearson's r coefficient along with its two-tailed significance level (* $p < .05$, ** $p < .01$, *** $p < .001$) is provided on each panel.

Table 2.2 Pearson correlations between CB parameter β and selected measures

The correlated measures are as follows: the percentage of correctly identified changes in continuity error videos, attentional capture, iconic, fragile, and robust VSTM percent accuracy, the number of alternations in perceptual rivalry, TOJ threshold, CS parameters γmax, fmax, β, and δ, CFQ distractibility score, VVIQ score, and the matrix reasoning task percent accuracy, together with the associated significance values (2-tailed), lower and upper 95% bootstrapped confidence intervals, and N, respectively. For the measures tested on two sessions values were averaged across both sessions. The significant correlations that survived the Benjamini-Hochberg correction are bolded.

	CE % correct	Att. Capture	VSTM Iconic	VSTM Fragile	VSTM Robust	Perceptual rivalry	TOJ	CS γmax	CS fmax	CS β	CS δ	CFQ	VVIQ	Matrix
β														
r	**.42**	**-.41**	.10	**.33**	.26	-.28	**-.33**	.22	.14	-.15	.03	**-.30**	.17	-.05
p	**.001**	**.001**	.420	**.009**	.041	.030	**.008**	.116	.319	.292	.809	**.017**	.184	.726
lCI	**.16**	**-.61**	-.18	**.08**	-.02	-.52	**-.53**	-.03	-.17	-.48	-.21	**-.51**	-.12	-.29
uCI	**.63**	**-.16**	.42	**.55**	.51	.01	**-.13**	.45	.40	.17	.26	**-.03**	.45	.19
N	**62**	**62**	62	**62**	62	61	**62**	53	53	53	53	**62**	62	60

Factor Analysis

A principal axis factor analysis with a sample size of 52 participants was conducted on the 15 measures listed in Table 2.2 with orthogonal rotation (varimax). The Kaiser-Meyer-Olkin measure revealed that the sample was adequate (KMO = .55, higher than the acceptable standard of 0.5 (Hutcheson & Sofroniou, 1999)). Bartlett's test of sphericity was significant ($p < .001$), thus the hypothesis that the correlation matrix is an identity matrix was rejected. An initial factor analysis was run to identify the eigenvalues for each factor in the data and to analyse the Scree plot. Six factors had

eigenvalues over Kaiser's criterion (Kaiser, 1958) of 1 and in combination explained 68% of variance. However, the Scree plot showed an inflection point at the third factor (see Figure 7.3 in Appendix A); therefore, only two factors were retained, and the analyses were re-run. The two retained factors explained 36% of the variance. Table 2.3 shows the factor loadings after rotation.

We term the first factor as 'visual stability' and interpret it as reflecting a high-level ability to form strong, robust visual representations and resist distraction. This is evidenced by the finding that accuracy of the later, more abstract sub-components of VSTM - fragile and robust - load highly and positively onto this factor, whereas iconic VSTM does not. In addition, this factor is associated with experiencing fewer alternations (i.e., greater perceptual stability) when viewing an ambiguous rivalry stimulus. The negative loading of attentional capture and self-reported distractibility further supports the interpretation that this factor represents stability of visual representations in face of distractors. Crucially, the factor loadings indicate that having strong, stable, and accurate visual representations is associated with superior change detection ability, as both change detection tasks loaded highly and positively onto this factor. It must be noted that general intelligence loaded negatively onto this factor, indicating that visual stability and superior change detection cannot be explained simply by having a better executive function associated with intelligence.

We interpret the second factor, 'visual ability', as reflecting low-level perceptual sensitivity. This is suggested by the high loading of the iconic VSTM sub-component, which relies on lingering activity in the early visual system (Sligte et al., 2008; 2009). This factor also loaded on TOJ and on two parameters of contrast sensitivity (CS γmax and CS β). These CS parameters describe, respectively, the overall height (i.e., ability to detect over wide range of contrasts) and width (i.e., ability to detect over wide range of

spatial frequencies) of the contrast sensitivity function. The negative loading of TOJ on this factor indicates that being able to identify the onset order of two stimuli when they occur close in time is associated with a higher latent capacity for visual sensitivity. However (and contrary to our initial predictions), the TOJ task cannot be construed as a 'pure' measure of visual sensitivity given that it also loads on the first factor and correlates significantly with CB. The TOJ task, like VSTM and CB, requires a comparison of visual signals over time and space. Similarly, the fragile VSTM loading on both factors suggests that performance on this STM sub-component is influenced by both sensitivity to signal and stability of representation. The high loading of general intelligence, as measured by matrix reasoning, on this visual ability factor is consistent with earlier research linking sensory discrimination and general intelligence (Deary, 1986; Lindenberger & Baltes, 1994; Anstey, Dain, Andrews, & Drobny, 2002). Crucially, our measure of CB had a relatively low loading on this factor, which indicates that the mechanisms underlying change detection may not be directly related to perceptual sensitivity.

Table 2.3 Exploratory factor analysis with varimax rotation

Factor loadings with the absolute value equal to or greater than .30 are bolded (N = 52).

	Visual stability	Visual ability
CB β	**.75**	.26
CE % correct	**.43**	.23
Attentional capture	**-.40**	-.09
VSTM Iconic	.19	**.57**
VSTM Fragile	**.46**	**.65**
VSTM Robust	**.48**	.28
Perceptual rivalry	**-.39**	.01
TOJ	**-.30**	**-.52**
CS γmax	-.04	**.61**
CS fmax	.08	.19
CS β	-.25	**.39**
CS δ	.12	-.01
CFQ	**-.30**	-.18
VVIQ	.28	-.02
Matrix	**-.42**	**.43**

2.5. Discussion

We employed an individual differences approach to the study of CB in order to explore its neurocognitive basis in the visual hierarchy. After characterising the variation, reliability, and generalisability of change detection performance, we examined its predictors from a battery of perceptual and cognitive tests. We interpret our findings within the framework of predictive processing, in which change detection depends on successful updating of visual predictions in light of new sensory evidence.

More specifically, we examined whether CB performance is associated more strongly with the strength of perceptual predictions, or with sensitivity to sensory prediction errors. Our battery comprised ten different perceptual and cognitive measures that were selected to target both high- and low-level mechanisms thought to be involved in change detection. Finally, we carried out an exploratory factor analysis in order to reveal the underlying structure of the performance on our battery of tests.

Our results revealed reliable individual differences in the ability to notice visual changes. Performance in both tasks of change detection, the CB task and the CE task, was significantly correlated, suggesting that detection in the CB paradigm using naturalistic scenes generalises to more ecologically valid displays resembling everyday visual environments. There were several significant relationships between the variables that, for the most part, were in accordance with an association between strong visual representations and CB performance: higher fragile and robust VSTM accuracy, lower attentional capture, lower self-reported distractibility all predicted superior change detection. Perceptual rivalry alternation rate was negatively associated with CB performance, which suggests that perceptual stability may support the ability to detect changes. In addition, better TOJ performance also predicted superior change detection, which suggests sensitivity to temporal regularities may be important in change detection. No correlations were established between contrast sensitivity, general intelligence, and change detection; likewise, the vividness of mental imagery was not significantly correlated with CB.

The exploratory factor analysis revealed a two-factor solution. We identified the first factor as 'visual stability', which loaded strongly on both change detection tasks, fragile and robust VSTM accuracy, perceptual rivalry, attentional capture, and self-reported distractibility. These factor loadings indicate that detection ability is associated

with accuracy of the later sub-components of VSTM, with the ability to form relatively stable perceptual inferences in light of conflicting incoming signals (i.e., when viewing an ambiguous bistable stimulus), and with being able to resist attentional capture by task-irrelevant distractors both in a lab-based task and according to a self-reported distractibility measure. The psychophysical measures of iconic VSTM, TOJ threshold, and contrast sensitivity loaded on a separate factor that we termed 'visual ability'. However, it is to be noted that these measures are not process-pure and individual differences on some tasks (e.g., TOJ and fragile VSTM) contributed to both factors. Nonetheless, the two-factor structure that emerged suggests change detection is better predicted by the strength and stability of visual predictions rather than by sensitivity to visual signal.

Among the correlations summarised above, the negative correlation between perceptual rivalry alternation rate and change detection ability is of particular interest. Some authors have proposed that a faster perceptual alternation rate is indicative of a visual system that assigns more weight to prediction error, and consequently incorporates novel visual information into the predictions more readily (Hohwy et al., 2008; Kanai et al., 2011). Others have argued that it is unclear whether slow alternation rate in rivalry reflects strong, robust predictions or weak, noisy prediction errors (Sandberg et al., 2016); or conversely, whether a fast alternation rate reflects weak, unstable predictions or strong, precise error signals (Megumi, Bahrami, Kanai, & Rees, 2015). Our results suggest that persistence of perceptual predictions may actually bestow a benefit for detecting unexpected visual changes, perhaps because it is easier to detect an inconsistency between a strong representation and sensory evidence that contradicts it. In contrast, if an individual generates vague, fleeting representations of a scene during the CB task, the appearance or disappearance of an object within the scene

may not be consciously registered. This explanation is consistent with the finding that successful encoding of pre-change scene seems to be crucial for detecting a change (Tseng et al., 2010).

The loading of perceptual rivalry onto the 'visual stability' factor is also compatible with the well-established links between attentional control and percept dominance durations in bistable perception (Meng & Tong, 2004; Van Ee, Van Dam, & Brouwer, 2005). In perceptual rivalry, selective attention has been shown to increase the dominance duration of the attended percept and delay the competing percept from entering awareness (Van Ee et al., 2005). Eye-tracking studies reveal that when instructed to increase the dominance of particular percepts, participants fixate different regions of ambiguous stimuli (Van Dam & van Ee, 2006ab). This, arguably, may prioritise certain information, which could be used to sustain a stable visual prediction. In our perceptual rivalry task, participants were instructed to fixate on a cross at the centre of the sphere and were not asked to influence its rotation voluntarily. However, individual differences in the ability to sustain endogenous attention could have affected the rate of perceptual alternation, as attention can be decoupled from fixation (Toppino, 2003). It is conceivable that the factor structure of 'visual stability' reflects individual variation in how selective attention is allocated, given the high loadings on lab-based and self-report measures of the ability to resist distraction. For example, an increased ability to sustain selective attention could aid the stability of perceptual interpretation when viewing bistable stimuli.

We found that both lower attentional capture and self-reported distractibility were associated with superior change detection ability. This finding may reflect that people who are prone to attentional capture by task-irrelevant distractors have a high sensitivity to or poorer ability to disengage attention from visual transients such as the

flicker in CB task, leading to relatively greater disruption in the ability to detect changes

via exogenous shifts in attention. This interpretation is consistent with previous

suggestions that CB results from impaired ability to detect changes via exogenous

orienting due to the flicker (Beck et al., 2005) and that CB is overcome via engaging

endogenous attention. In order to assess whether increased attentional capture correlates

with reduced change detection ability even in contexts with no extremely salient

masking visual transients, future research could investigate the relationship between

attentional capture and gradual change detection (i.e., when one feature of an image

changes very slowly and is not detected). Furthermore, there are types of change

detection task where a tendency for greater attentional capture may confer a benefit.

One example is the inattentional blindness (IB) task in which participants engage in a

primary task rather than actively search for a change, so that attentional capture by a

salient unexpected stimulus is necessary to detect a change. There is some

circumstantial evidence for this hypothesis, as adults with attentional deficit disorder

tend to perform better than controls in IB paradigms (Grossman, Hoffman, Berger, &

Zivotofsky, 2015)

The association between the strength of VSTM and change detection was found

in both types of change detection paradigm (CB and CE tasks). Our study revealed that

only certain sub-components of VSTM relate to change detection performance; these

are the fragile and robust VSTM. In contrast, the iconic VSTM component was related

to perceptual sensitivity. Fragile VSTM loaded onto both factors, which may

demonstrate that it represents an intermediate stage of VSTM, which relies on both

perceptual sensitivity and memory-based processes. The finding that the later

components of VSTM loaded onto the 'visual stability' factor comprising attentional

capture and CFQ distractibility also supports the notion that WM and attention are not

distinct cognitive systems, but are intimately linked constructs which operate together in visual perception (Machizawa & Driver, 2011). For example, attention is required in order to retrieve particular aspects of visual representations from WM (Awh & Jonides, 2001). Furthermore, attention can be involuntarily captured by memory-matching distractor stimuli maintained in WM while engaging in visual search (Soto, Heinke, Humphreys, & Blanco, 2005; Soto et al., 2008) and yet this influence can also be strategically overcome when the WM-maintained item is entirely task-irrelevant (Woodman & Luck, 2007). In the CB task poorer ability to disengage from irrelevant distractors (e.g., flicker) may limit the ability to access and integrate recently stored visual representations, which may slow down change detection. Alternatively, having weaker VSTM representations may limit the ability to suppress visual transients and to focus attention on task-relevant representations of the scene that are necessary for the integration of a change into the current percept.

Our findings motivate further research on the relationship between change detection and reliance on perceptual predictions versus sensory prediction errors. Perceptual rivalry has been discussed as one paradigm potentially revealing bias in predictive processing; however, the rivalry rate is also heavily influenced by eye movements and attentional control, which complicates interpretation. Therefore, other paradigms measuring the reliance on prior knowledge versus sensory evidence may be necessary. For example, Melloni and colleagues (2011) showed that the threshold for subjective visibility of degraded stimuli is lower for previously seen items than for novel items. In a similar vein, valid predictions have been found to accelerate the entry of visual stimuli into awareness in such paradigms as motion-induced blindness (Chang et al., 2015) and continuous flash suppression (Pinto, van Gaal, de Lange, Lamme, & Seth, 2015, as well as to enhance perceptual metacognition (Sherman, Seth, Barrett, &

Kanai, 2015). A measure of individual differences in the visibility threshold of previously seen images, or the extent to which conscious access is accelerated by prediction, could provide an index of individual variability in the reliance on prior expectations in visual awareness, which could be correlated with change detection.

To conclude, we have shown that the ability to notice visual changes in naturalistic scenes is a relatively stable capacity that is generalisable to more ecologically valid CB paradigms. Our exploratory factor analysis suggests that individual differences in change detection are associated with the stability and strength of perceptual predictions to a greater degree than with visual sensitivity. The stability of perceptual rivalry, accuracy of late sub-components of VSTM, and proneness to attentional capture and distractibility all formed a common factor that predicted detection ability, whereas the factor of 'visual ability,' formed mostly of measures reflecting sensitivity to contrast and timing of stimuli, did not load as strongly onto change detection. Robust visual predictions may enable the visual system to detect mismatches between the existing representation and the incoming signal more readily, perhaps via a more efficient top-down allocation of sustained endogenous attention in accordance with current task goals, and/or a reduced tendency for exogenous attentional capture by task-irrelevant stimuli such as visual transients. A limitation of our study is that by being correlational in design it cannot assume any causality, only association. Therefore, our results motivate further research to probe the neurocognitive mechanisms that underlie prioritization of predictions versus sensory evidence and how individual differences in predictive processing biases may relate to change detection, attention, and visual awareness.

CHAPTER 3
The Neural Basis of Individual Differences in Visual Awareness

3.1. Abstract

Imaging and TMS research have demonstrated that fronto-parietal regions of the brain are functionally and causally involved in the selection, maintenance, and awareness of visual stimuli. For example, administering TMS to the right PPC impairs visual change detection. However, different regions of parietal cortex may have opposing roles in stabilising versus initiating shifts in visual awareness. For instance, the disruption of anterior versus posterior parietal regions results in an increase or decrease in alternation rate when viewing bistable stimuli, respectively. In the present study we ask whether structural brain differences measured by regional grey matter (GM) density predict individual differences in visual awareness. We previously found that better visual change detection is predicted by a greater VSTM accuracy, lower proneness to attentional capture, and a lower alternation rate in perceptual rivalry. Therefore, we hypothesised that the GM density in PPC regions implicated in visual awareness, specifically change detection and perceptual rivalry, will predict performance on these tasks. Although the opposing associations between GM density in focal parietal regions and perceptual rivalry were not replicated in the present research, we found that average GM density in left PPC predicted robust VSTM accuracy. Our finding is consistent with the role of left PPC in the encoding and maintenance of short-term visual representations and suggests increased GM in this region may afford more accurate representations.

3.2. Introduction

Change blindness (CB) is a well-established phenomenon demonstrating that the awareness of salient, unexpected changes in visual scenes, dynamic videos, and in real life settings becomes very difficult when a visual transient (e.g., flicker, 'mudsplash', cuts or pans of the camera) is presented between the pre-change and post-change state (Rensink et al., 1997; Simons & Rensink, 2005). It is known that people are generally poor at detecting visual changes in these tasks (e.g., depending on the exact paradigm approximately 50% of people fail to see a salient visual change; Jensen, Yao, Street, & Simons, 2011). Visual working memory (VWM) capacity has been identified as a positive predictor of successful change detection (Pringle, Kramer, & Irwin, 2004) and VWM also predicts the ability to resist attentional capture (Fukuda & Vogel, 2009; 2011). We recently discovered that change detection is predicted by the strength and stability of visual representations (Andermane, Bosten, Seth, & Ward, 2019). In our study greater VSTM accuracy, lower proneness to attentional capture in a lab-based task, and lower distractibility by self-report measure, as well as greater stability when viewing a perceptual rivalry display all predicted superior change detection. As we found stable individual differences in change detection, in the present study we aimed to link these to structural brain differences between individuals. Previous research using structural magnetic resonance imaging (MRI) analysis techniques such as voxel-based morphometry (VBM) has identified structural brain behaviour (SBB) associations with a range of perceptual and attentional measures (Kanai & Rees, 2011; Kanai et al., 2010; 2011; 2011b; Bergmann, Genç, Kohler, Singer, & Pearson, 2014). We aimed to extend this research and explore whether individual differences in awareness, assessed by change detection and its predictors, are related to the regional GM density of the brain.

Functional imaging studies demonstrate that awareness of visual changes is consistently associated with increased activation in the extrastriate visual cortex, bilateral parietal cortex, and right dorsolateral prefrontal cortex (Beck, Rees, Frith, & Lavie, 2001), as well as the inferior temporal gyrus, cerebellum, and pulvinar (Pessoa & Ungerleider, 2004). The right posterior PPC specifically seems to be causally involved in change detection, as disruption of this region with rTMS results in a slower and poorer change detection in a one-trial CB task with images of faces (Beck et al., 2005). The disruption of PPC may result in poorer visual awareness due to affecting one or more of the processes associated with this region; spatial orienting and attentional selection, sustained attention, or encoding and maintenance of the scene in VSTM. Tseng and colleagues (2010) showed that disruption to right PPC lead to significantly poorer performance specifically during the encoding of the pre-change scene relative to post-change scene, so this region may be particularly important for encoding scene representations.

Parietal cortex activity contributions to visual awareness may be distinct, however, depending on the region, as even parietal areas within the same hemisphere show opposite effects of updating versus stabilising awareness in perceptual rivalry. Functionally, the experience of the conscious percept in rivalry is associated with activity in ventral extrastriate cortex, as well as inferior and superior parietal lobules (Lumer, Friston, & Rees, 1998). In terms of structural relationships, Kanai and colleagues (2011) found that GM density of parietal cortex regions predicts the perceptual rivalry alternation rate when viewing an ambiguous rotating sphere. Crucially, greater GM density in right anterior superior parietal lobe (SPL) predicted longer percept durations (i.e., more stable perception), whereas GM density in bilateral posterior SPLs predicted increased alternation (e.g., perceptual instability) (Kanai et al.,

2010). Furthermore, applying TMS to these regions led to marked changes in rivalry alternation rate (Kanai et al., 2011); TMS to right anterior SPL increased alternation, whereas disruption of bilateral posterior SPLs stabilised perception (Kanai et al., 2010). The GM density of a close region to left posterior SPL predicts the distractibility component on self-report Cognitive Failures Questionnaire (Kanai et al., 2011b), consistent with the idea that processing in this region is related to perceptual/attentional instability. Kanai and colleague (2011) proposed that the structure of parietal regions may determine predictive processing biases, i.e., an individual's proneness to update perceptual predictions (see panel C in Figure 3.1 for an illustration of this hypothesis). Specifically, the right anterior SPL region may be causally involved in generating prediction about the contents of the visual awareness and stabilising perception. In contrast, the bilateral posterior SPL regions may register discrepancies between the prediction and the input and update the awareness in light of a mismatch. We hypothesise that the opposing effects of these regions on contents of visual awareness will be important in other visual experiences besides perceptual rivalry. If the purported role of anterior and posterior SPL is perceptual prediction generation and maintenance versus updating of predictions leading to shifts in awareness, individual differences in their GM density should also predict change detection in naturalistic scenes.
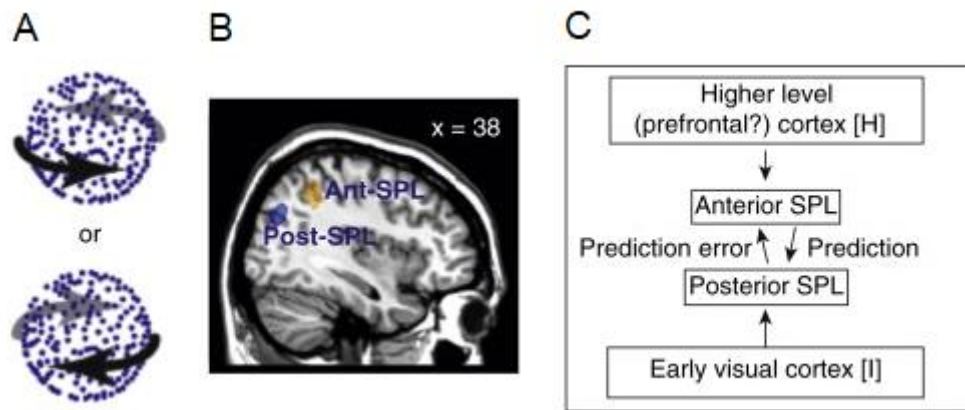
Figure 3.1 An illustration of the perceptual rivalry task (A), the parietal regions that are structurally related to rivalry alternation rate (B), and (C) the putative mechanism of perceptual prediction

The perceptual rivalry task (A) comprises an ambiguous rotating sphere that appears to alternate between two directions of rotation. The parietal cortex regions (B) that structurally predict rivalry alternation rate in Kanai and colleagues (2010, 2011); the yellow region is anterior SPL where greater GM volume predicts perceptual stability, the blue region is posterior SPL where greater GM volume predicts perceptual instability. The putative mechanism of perceptual prediction (C), where right anterior SPL is involved in generating stable perceptual predictions, whereas bilateral posterior SPL is proposed to update perceptual predictions based on the prediction error. Images taken from Kanai and colleagues (2011).

There are strong reasons to expect that the structure of the primary visual cortex (V1) will also predict individual differences in visual awareness. Functionally, the contents of VSTM can be decoded from patterns of V1 activity (Christophel, Hebart, & Haynes, 2012), suggesting it is a locus of held visual representations. In terms of structure, the anatomical properties of V1 may determine the quality of low-level visual features that contribute to complex scene representations. For instance, Bergmann and colleagues (2014) showed that individuals with greater V1 size, in volume, surface area, and cortical thickness, demonstrate greater VWM storage capacity. The authors suggest that anatomical differences of V1 may determine the richness or specificity of the representations encoded in VWM. A larger surface area or greater thickness of V1 may enable the individual to represent more information in their visual 'map' and this then

leads to less competition between items, which may allow the encoding and detection of new objects within complex scenes. The activation of V1 is argued to be causally involved not only in the encoding but also the maintenance stages of VSTM, evidenced by the finding that a single pulse TMS applied to occipital cortex affects both processes (Cattaneo, Vecchi, Pascual-Leone, & Silvanto, 2009). Additionally, Verghese and colleagues (2014) found that the functional size of V1, defined as the size of the central 12-degree visual field representation in V1, predicts the efficiency of top-down attention in visual search, assessed by RT slope differences for feature and conjunction search. Individuals with a larger V1 surface area may be able to allocate the top-down attentional 'spotlight' from parietal cortex priority maps to V1 more efficiently, perhaps due to greater connectivity between these areas. This attentional gating process would then facilitate the selected representations in V1 faster, especially in highly cluttered scenes. Consequently, we expect greater GM density in V1 will predict greater VSTM accuracy (given capacity is conditional on visual information load, Alvarez & Cavanagh, 2004) and lower attentional capture. Since encoding and maintenance of VSTM representations and attentional control are key mechanisms for change detection (Beck et al., 2005; Tseng et al, 2010; Andermane et al., 2019) we also hypothesise that greater GM density in V1 will predict superior change detection.

Table 3.1 The brain regions related to individual differences in visual awareness

The coordinates of the voxels previously shown to structurally predict individual differences in visual awareness (i.e., perceptual rivalry, distractibility) or areas found to be causally involved in visual awareness using TMS techniques (i.e., perceptual rivalry, distractibility, change blindness). All coordinates are in the MNI coordinate system.

Region and coordinates	Association
Right anterior SPL $(X = 36, Y = -45, Z = 51)$[2]	Greater GM density predicts perceptual stability in rivalry; disruption with TMS leads to increased instability[2]
Right posterior SPL $(X = 34, Y = -66, Z = 34)$[1]	Greater GM density predicts perceptual instability in rivalry, disruption with TMS leads to increased stability[1]
Left posterior SPL $(X = -21, Y = -63, Z = 61)$[1]	Greater GM density predicts perceptual instability in rivalry, disruption with TMS leads to increased stability[1]
$(X = -15, Y = -61, Z = 54)$[3]	Greater GM density predicts more self-reported distractibility, disruption with TMS leads to more attentional capture[3]
Right PPC $(X = 23, Y = -65, Z = 68)$[4,5]	Disruption with TMS leads to poorer change detection[4,5]

[1] Kanai, Bahrami, & Rees (2010), [2] Kanai, Carmel, Bahrami, & Rees (2011), [3] Kanai, Dong, Bahrami, & Rees (2011b), [4] Beck, Muggleton, Walsh, & Lavie (2005), [5] Tseng and colleagues (2010)

To investigate the structural basis of individual differences in visual awareness we administered four perceptual measures (i.e., CB task, attentional capture, VSTM, and perceptual rivalry tasks). This selection was motivated by our earlier work, where these measures loaded on a common 'visual stability' factor (Andermane et al., 2019). In our work, improved change detection was predicted by more accurate VSTM, less attentional capture, and lower alternation rate in perceptual rivalry. We expect that the correlations between GM density in the previously identified ROIs (see Table 3.1 for the regional coordinates and associations with visual awareness) will reflect this pattern of relationships between the tasks (see Table 3.2). We chose to investigate SBB

associations using separate measures, rather than looking at how the 'visual stability' factor relates to brain structure, as the former approach gives us more fine-grained and sensitive indices of the distinct mechanisms involved in change detection (e.g., VSTM and attentional control). We initially carried out a whole brain analysis (WBA) to find clusters of voxels that correlate with our measures and then adopted a ROI-based approach, investigating the relationship between average GM density in the *a priori* defined regions and our measures.

First, we predict that GM density in the right PPC will predict performance on the CB, VSTM, and attentional capture task, given it is causally involved in detection of visual changes (Beck et al., 2005; Tseng et al, 2010). However, the direction of this relationship is not specified, as increased GM occasionally is associated with poorer, rather than superior performance on tasks. Less GM in some regions may indicate efficiency in the function of the region due to developmental pruning (Kanai & Rees, 2011). For example, greater GM density in left posterior SPL has been shown to correlate with increased distractibility (Kanai et al., 2011b), whereas decreased GM in areas associated with sensorimotor function is related to increased expertise in musical training (James et al., 2014). As greater GM density in right anterior SPL predicts increased perceptual stability in rivalry (Kanai et al., 2011), we hypothesise it will predict better change detection, greater VSTM accuracy, and lower proneness to attentional capture. In contrast, as greater GM density in left and right posterior SPLs previously correlated with perceptual instability and distractibility (Kanai et al., 2010; 2011; 2011b), we hypothesise this will also predict poorer change detection ability, lower VSTM accuracy, and more attentional capture by distractors. Finally, we hypothesise that greater GM density in bilateral V1 will predict superior change detection, VSTM accuracy, and reduced proneness to attentional capture, due to the

suggestions it is a bottleneck for the fidelity of VSTM representations (Bergmann et al., 2014) and may affect the speed of allocating top-down attention to low-level representations (Verghese et al., 2014).

Table 3.2 The expected correlations between GM density in ROIs of the brain and the behavioural measures

The listed measures are as follows: the number of alternations in perceptual rivalry (i.e., the opposite measure of average dominance duration used elsewhere), CB task performance in terms of parameters α & β (i.e., both represent performance positively; greater α represents more changes are identified and greater β indicates changes are identified faster), attentional capture in milliseconds (i.e., represents performance negatively, as an increased value represents more attentional capture), and iconic, fragile, and robust VSTM percent accuracy (i.e., represents performance positively).

	Perceptual rivalry (N of alternations)	CB task (α, β detection rate)	Attentional capture (Mean RT increase with distractor)	VSTM accuracy (% correct)
Right anterior SPL ↑ GM density ↑ Perceptual stability H: generates predictions, aids perceptual stability[2]	Negative ↑ GM ↓ Rivalry	Positive ↑ GM ↑ CB α, β	Negative ↑ GM ↓ Capture	Positive ↑ GM ↑ VSTM
Right and left posterior SPL ↑ GM density ↓ Perceptual stability H: generates prediction errors[1]	Positive ↑ GM ↑ Rivalry	Negative ↑ GM ↓ CB α, β	Positive ↑ GM ↑ Capture	Negative ↑ GM ↓ VSTM
Right PPC TMS → ↓ Change detection H: causally involved in change detection[4,5]		Either ↑ GM ↑↓ CB α, β	Either ↑ GM ↑↓ CB α, β	Either ↑ GM ↑↓ VSTM

Primary visual cortex	Positive	Negative	Positive
↑ Surface size, thickness ↑ VWM capacity[6]	↑ GM	↑ GM	↑ GM
	↑ CB α, β	↓ Att. Capture	↑ VSTM
↑ Functional size ↑ Top-down attention[7]			
H: determines fidelity of visual representations[6,7]			

[1] Kanai, Bahrami, & Rees (2010), [2] Kanai, Carmel, Bahrami, & Rees (2011), [4] Beck, Muggleton, Walsh, & Lavie (2005), [5] Tseng and colleagues (2010), [6] Bergmann and colleagues (2014), [7] Verghese and colleagues (2014)
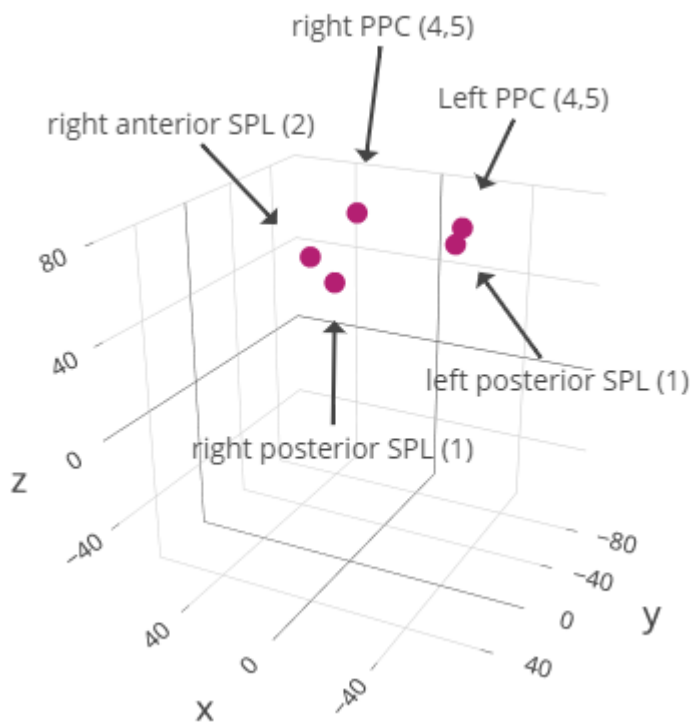
Figure 3.2 The MNI coordinates (X, Y, Z) of parietal regions of interest

The regions of parietal cortex with these coordinates are structurally related to or causally involved in initiating or stabilising visual awareness in the following studies: [1] Kanai, Bahrami, & Rees (2010), [2] Kanai, Carmel, Bahrami, & Rees (2011), [4] Beck, Muggleton, Walsh, & Lavie (2005), [5] Tseng and colleagues (2010).

3.3. Method

3.3.1 Participants

Forty-nine participants (Aged 18 – 46, Mean = 26.31, SD = 5.84; 30 female) with normal or corrected-to-normal vision and no reported colour vision deficiencies completed this study. No participants from the present study participated in the first study (*Chapter 2*), mainly because the CB task used in the present study was different in terms of timing (see Materials). This also enabled us to have an independent sample for replication of the associations between behavioural tasks observed *Chapter 2*. We recruited participants that had previously taken part in one (or more) imaging studies at the University of Sussex Clinical Imaging Sciences Centre (CISC) and consented to their structural MRI scans being analysed for the purposes of the present study. The participants were undergraduate and postgraduate students at the University of Sussex who received course credit and adults from the Brighton community who were reimbursed in cash. The study took 1h to complete and comprised only behavioural measures; CB, attentional capture, VSTM, and perceptual rivalry tasks. The study was approved by the Science and Technology Cross-Schools Research Ethics Committee (C-REC), at the University of Sussex.

3.3.2 Materials

The tasks administered in this study were identical to tasks 1, 3-5 from *Chapter 2*, the only difference being that in the CB task the flickering cycle of image presentation lasted 30s (instead of 60s) if no change was identified. Additionally, 60 images were presented instead of 30. These changes were introduced to maximise the number of trials, as the results of CB task from *Chapter 2* demonstrated that participants

do not need 60s to identify most of the changes (i.e., the average accuracy at 60s was 95%).

1. *Change blindness task*

The CB task was taken from Andermane and colleagues (2019) and required participants to find changing objects within flickering natural indoor scenes. Sixty image pairs were obtained from a CB database (Sareen et al., 2016); one image was an original indoor scene and in the other image one of the objects (e.g., a vase) was removed. Half of the object changes occurred on the left side of the image and half occurred on the right. The task was presented using Inquisit Millisecond software and consisted of one practice trial and 60 randomly intermixed experimental trials. On each trial the pre-change and post-change scenes alternated with a blank screen in between the two, creating a flickering cycle of image presentations lasting 30 seconds. Participants were instructed to use a mouse to click on the object that keeps appearing and disappearing. The next trial began after the mouse click or, in the case of no response, when the image cycle finished (after 30s). There was an inter-trial interval of 1000ms and a black screen with white fixation square was presented for 3000ms before each trial. To separate correct from incorrect responses, ROIs within each image were defined around the centre coordinates of the changed object (Mean radius = 1°), and mouse clicks with coordinates outside ROIs (Mean radius = 2°) were labelled as misses.

2. *Attentional capture task*

The attentional capture task was similar to that described by Kanai and colleagues (2011b). This task was presented using E-prime software and measures the extent to which participants are distracted by salient task-irrelevant stimuli. The task consisted of 12 practice trials and 300 experimental trials (4 blocks). A colour singleton

distractor was present on 140 of the trials and absent on 148 trials. On each trial participants were presented with 9 shapes: 8 diamonds and 1 circle. Each shape contained either a horizontal or a vertical line – this was assigned randomly. The colour of the shapes varied; when no colour singleton was present all shapes were either green or red, whereas when a colour singleton was present all shapes were either green or red, but one diamond was the opposite colour. Participants were instructed to report the orientation of the line inside the circle (e.g., horizontal or vertical) by keyboard responses as quickly and accurately as possible, whilst trying to ignore the diamonds. Attentional capture was estimated by subtracting the average correct RTs in the condition with no distractor from the condition with the distracting colour singleton.

3. *Visual short-term memory task*

The VSTM task measured three different VSTM processes; iconic, fragile, and robust. In this task, adapted from Sligte and colleagues (2008; 2009), participants detected changes in the orientation of cued rectangles. The VSTM task was presented using MATLAB (Mathworks Inc.) and the Psychophysics Toolbox extension (Brainard, 1997) and comprised 288 trials (48 trials x 6 blocks); an initial block was treated as practice. There were three types of trials with different cue onset times and after-cue intervals. In the iconic VSTM condition a cue was presented 100ms after the off-set of the memory array, followed by an 1800ms blank interval, targeting iconic VSTM store which has an unlimited capacity and largely relies on after-image. In the fragile VSTM condition a cue was presented 1000ms after the offset of the memory array followed by 900ms blank interval; this was designed to target fragile VSTM store thought to be relatively high capacity but prone to over-writing. In the robust VSTM condition a cue was presented 1000ms after the offset of the memory array simultaneously with the test

array; this was designed to target robust VSTM store thought to store about four items. Each of these trial types was presented 96 times randomly intermixed. The test array included the words 'same' and 'different' in the top right and left corners of the screen, respectively. This prompted participants to click the right mouse button if the orientation of the cued rectangle in the test array matched its orientation in the memory array and the left mouse button if it did not. During the inter-trial interval (1600ms) participants saw a green fixation point after a correct response and a red 'Error!' feedback after an incorrect response. Participants were instructed to respond as accurately as possible without prioritising speed. The measure of interest was percent accuracy in each of the three cue conditions.

4. *Perceptual rivalry task*

The stimulus used in this task was the ambiguous structure-from-motion rotating sphere described by Kanai and colleagues (2010). It was presented using MATLAB and the Psychophysics Toolbox extension (Brainard, 1997), and is typically experienced as an ambiguous sphere that appears to rotate either to the left or right, with the perceived direction of rotation alternating. The sphere consisted of 200 white dots moving sinusoidally with a red fixation cross in the middle and was presented against a black background. The sphere was continuously presented on the screen for two blocks of 2 minutes and participants responded by clicking the mouse whenever the sphere appeared to change its direction of rotation. The measure derived was the total count of the reported perceptual alternations over the 4-minute presentation of the sphere.

3.3.3 Design

The participants completed all four of the tasks (see Figure 3.3) in the lab in a fixed order. The design was correlational; associations between task performance and GM density were analysed. At first whole brain VBM analyses were run to look for significant associations between GM volume of clusters of voxels and performance on the behavioural measures. Following this, a more focused ROI approach was adopted, whereby the average GM density was calculated over the ROIs identified in previous research literature (see tables 3.1 and 3.2) and correlated with behavioural measures.
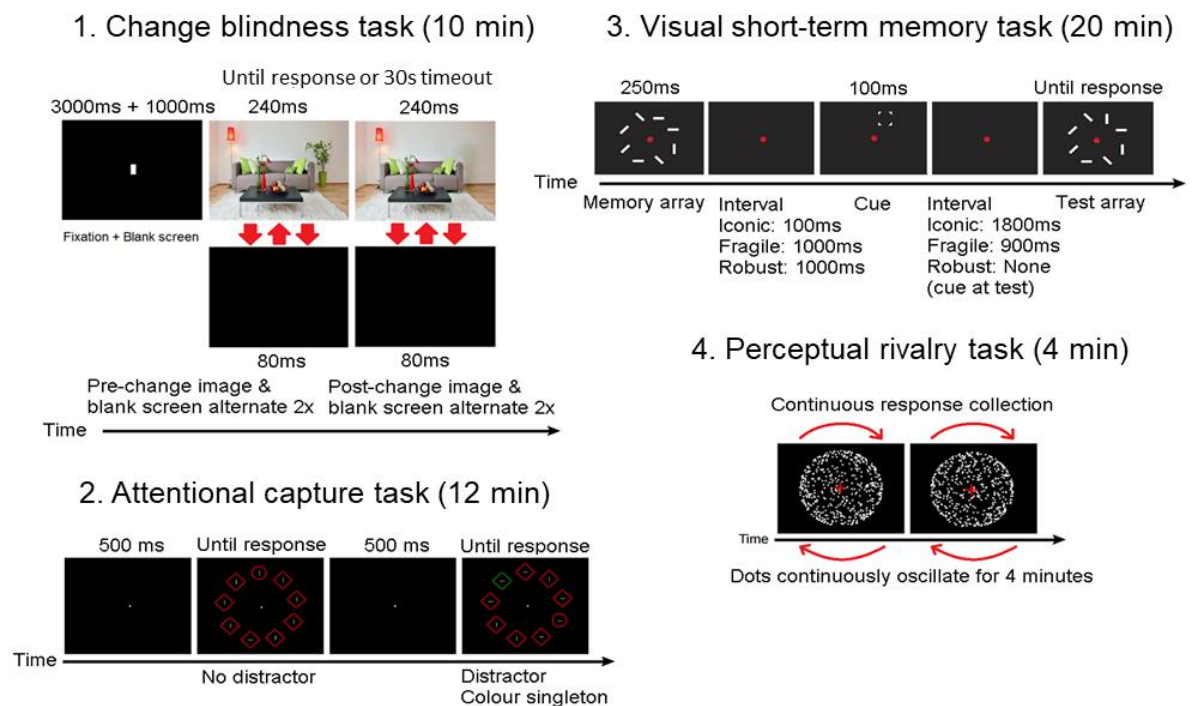
Figure 3.3 The stimuli and trial structure of the CB, attentional capture, VSTM, and perceptual rivalry tasks

3.3.4 Procedure

All participants signed informed consent before taking part and consented to their structural MRI scans, obtained from participation in previous research at the

University of Sussex, to be accessed and analysed for the purposes of the present study. After this, participants completed the CB task, attentional capture task, VSTM task, and perceptual rivalry task. The task and condition order were fixed for everyone to measure individual differences in performance holding all other variables constant, as recommended by Mollon and colleagues (2017). The perceptual rivalry, VSTM, and attentional capture tasks were completed seated 100cm from a CRT monitor (screen resolution = 1280 x 1024) which was surrounded by a black tunnel box, in a dark room with participants' heads resting on a chinrest. The CB task was completed seated comfortably 55 cm from the computer screen (screen resolution = 1920 x 1080) with the light on in the room.

3.4. Results

3.4.1 Data preparation

The data preparation for the tasks was identical to that in *Chapter 2*. For the CB task the coordinates of the reported change locations were analysed and responses with coordinates outside the ROI were considered a failure to detect the change and added to misses. The cumulative percentage of correctly identified changes was calculated at each time point (e.g., percentage correct with RTs of below 1s, 2s, 3s ... 30s). An inverse exponential function ($Y = \alpha e^{\beta / X}$) was then fit to this data, where Y is the cumulative percentage correct, X is the time in seconds, α is the asymptote, and β relates to steepness/curvature (see Andermane et al., 2019, for a more detailed discussion of this approach). A greater parameter α reflects that participants missed fewer changes overall, whereas a greater parameter β indicates that participants were more likely to reach asymptote quickly: i.e., detect changes faster.

In the perceptual rivalry task, the number of clicks was recorded in each of the two 2-minute blocks of rivalry display presentation and the total number of reported alternations was calculated by adding the scores. In the attentional capture task, for each participant the data was trimmed; we removed responses with RTs of below 200ms and over 2.5 SD. After this, we subtracted the average RT to target with distractor absent from the average RT to target with distractor present to obtain the attentional capture measure in milliseconds. In the VSTM task data was similarly trimmed per each participant, all responses with RTs of below 200ms and above 2.5 SD were removed, and the average percent accuracy was calculated in each of the three VSTM conditions – iconic, fragile, and robust.

Outlier diagnostics revealed two participants had very low parameter β values in the CB task that likely arose due to clicking on a random location in the scene out of impatience or boredom (as shown by error trials with short RTs and clicking coordinates greatly outside the ROI surrounding the object) instead of continuing to search for the changing object. These participants were excluded from the CB task analyses. In the VSTM task one participant was identified as an outlier in the boxplot; they scored below 50% in all three conditions, suggesting random responding and potentially not engaging with the task. This participant was removed from the VSTM task analyses. The summary statistics of the behavioural tasks are listed in Table 3.3.

Table 3.3 The summary statistics of the behavioural measures

The listed measures are as follows: CB parameters α and β, attentional capture in milliseconds, iconic, fragile, and robust VSTM percent accuracy, the number of alternations in perceptual rivalry, together with the associated N.

Measure	Mean	SD	N
CB α	1.06	.09	46
CB β	-5.87	1.05	46
Att. Capture	69.40	48.09	49
Iconic VSTM	83.39	.11	48
Fragile VSTM	73.43	.10	48
Robust VSTM	62.06	.08	48
Perceptual rivalry	32.14	18.74	49

3.4.2 Behavioural analyses

We first assessed the correlations between our behavioural measures for a confirmatory replication of our previous findings (Andermane et al., 2019). The significant correlations that emerged were as follows (see Table 3.4 for the correlation matrix and Figure 3.4 for the scatterplots). There was a negative correlation between CB parameter β and attentional capture, $r = -.30$, $p = .047$, indicating better change detection performance is associated with a lower proneness to be distracted by salient colour singletons. There was also a significant positive correlation between CB parameter β and fragile VSTM accuracy, $r = .38$, $p = .011$, demonstrating that possessing a more accurate fragile sub-component of VSTM predicts superior change detection. These relationships replicate the correlations found in our previous work (Andermane et al., 2019). The one exception was that the previously found significant negative correlation between perceptual rivalry and CB parameter β was not replicated

in this study. As this was a confirmatory replication of established and corrected

associations, no correction for multiple comparisons was needed.

Table 3.4 Pearson correlations between CB parameter β and the other measures

The correlated measures are as follows: CB parameter α, attentional capture, iconic, fragile, and robust VSTM percent accuracy, the number of alternations in perceptual rivalry, together with the associated significance values (2-tailed), lower and upper 95% bootstrapped confidence intervals, and N, respectively. The significant correlations are bolded.

	CB α N = 46	Att. Capture N = 49	Iconic VSTM N = 48	Fragile VSTM N =48	Robust VSTM N = 48	Perceptual rivalry N = 49
CB β						
r	-.18	**-.30**	.21	**.38**	.06	.07
p	.159	**.042**	.159	**.011**	.710	.649
Lower CI	-.46	**-.55**	-.10	**.09**	-.29	-.25
Upper CI	.17	**.01**	.53	**.61**	.38	.31
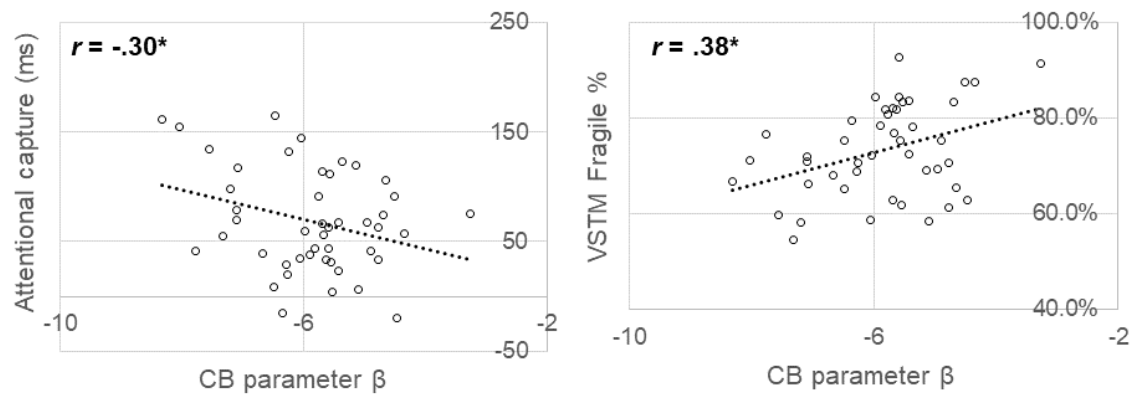
Figure 3.4 Scatterplots illustrating the significant correlations between CB parameter β, attentional capture, and fragile VSTM accuracy

The associated Pearson's *r* coefficient along with its two-tailed significance level (* *p* < .05, ** *p* < .01, *** *p* < .001) is provided on each panel.

3.4.3 Voxel-based morphometry analyses

Whole brain analyses

The voxel-based morphometry analyses were carried out on pre-processed structural T1-weighted MR images. The pre-processing steps were conducted using SPM12 and were as follows; the MR images were initially segmented into GM and white matter, subsequently the Diffeomorphic Anatomical Registration Through Exponentiated Lie Algebra (DARTEL) was performed, after which the images were transformed into MNI stereotactic space and smoothed with a Gaussian kernel (FWHM = 8mm). CAT12 was used to estimate total intracranial volume (TIV).

Initially a WBA was carried out on the segmented, spatially normalised, and smoothed GM images to explore correlations between the behavioural measures (CB task parameters α and β, attentional capture, the percent accuracy of iconic, fragile, and robust VSTM sub-components, and the number of alternations in perceptual rivalry) and GM volume in the different regions of the brain. TIV was entered as a global covariate, such that the means were adjusted to be proportional to TIV. Although various regions showed a peak-level correlation with behavioural measures at $p < .001$ (uncorrected), only two associations survived the Family Wise Error (FWE) correction at the cluster level. First, there was a significant negative association between robust VSTM accuracy and GM density at the cluster-level (k = 1148 voxels) coordinate of (x = 39, y = -38, z = -42, $p = .009$, FWE corrected), with a significant peak-level correlation ($t = 5.29$, Z = 4.65, $p = .046$, FWE corrected), a region that is located in the right cerebellum. Second, the CB parameter α was significantly negatively correlated with GM volume at the cluster level (k = 842 voxels) in the coordinate (x = -35, y = -23, z = -18, $p = .029$, FWE corrected), with a significant effect at the peak voxel when

uncorrected ($t = 4.65$, $Z = 4.17$, $p < .001$), which did not survive FWE correction ($p = .262$). This region is in the left hippocampus.

For the rest of the tasks, none of the uncorrected correlations at cluster-level were significant or those that were significant did not survive FWE correction. Some of the perceptual rivalry and GM density correlations with non-significant cluster correlations but significant peak effects were close (e.g., positive correlations at X = -47, Y = -36, Z = 62 and X = -36, Y = -38, Z = 53), to coordinates reported by Kanai and colleagues (2010; 2011). However, given the possibility that they represent noise, results that did not survive FWE correction at cluster level were not analysed in more detail. Next, we took a more specific ROI approach, focusing on the *a priori* hypothesised associations.

ROI-based analyses

We created masks using the MarsBaR region of interest toolbox (Brett, Anton, Valabregue, Poline, 2002) and the MNI coordinates identified in previous research literature (see Table 3.1); the masks were specified as a sphere with a radius of 5mm around the coordinate. The masks were then used to extract the mean GM densities (i.e., mean intensity or probability of the region containing GM) in the ROIs from the segmented, smoothed, and normalised GM images created in the previous steps, using MATLAB. To extract the mean GM density from V1, a bilateral mask was selected from SPM12 anatomy toolbox. This was done because previous studies on the relationships between V1 structure and attentional and short-term memory tasks tend to focus on whole V1 surface size, volume, cortical thickness, rather than focal regions within V1 (Bergmann et al., 2014; Verghese et al., 2014). The extracted GM density values of the ROIs were correlated with the behavioural measures. The significant

associations that emerged are summarised in Table 3.5 (see Figure 3.5 for the

scatterplots).

Controlling for gender, age, and TIV in ROI-based analyses

The performance of males (N = 19) and females (N = 30) did not significantly

differ on any of the behavioural measures or on the mean GM intensity values in any of

the pre-specified cortical ROIs. The two genders only differed in TIV, t (47) = 2.40, p =

.020, with males having greater mean TIV (Mean = 1624.53, SD = 131.58) than females

(Mean = 1534.57, SD = 125.32). The TIV did not correlate significantly with the

behavioural measures, the only exception being robust VSTM, which yielded a

marginally significant positive correlation (r = .26, p = .075). Additionally, TIV was

significantly positively related to mean GM intensity in all ROIs at the level of $p < .001$.

For these reasons TIV was controlled for in subsequent analyses using partial

correlations but gender was not used as a covariate. Age was significantly negatively

associated with iconic VSTM accuracy (r = -.43, p = .002), such that older participants

demonstrated poorer iconic memory accuracy, and positively correlated with attentional

capture (r = .31, p = .029), indicating older participants were more prone to distraction.

For this reason, age was also controlled for in subsequent analyses.

ROI-based correlations

The only predicted relationship that emerged between GM density in the

specified ROIs and behavioural measures was a marginally significant positive

correlation between GM density in left posterior SPL and the number of alternations in

perceptual rivalry (r = .26, p = .075). This correlation remained marginally significant

when controlled for age and TIV (r = .25, p = .095).

The other correlations that emerged were unexpected or opposite to our predictions. These included a significant positive correlation between GM density in left PPC and robust VSTM accuracy ($r = .42$, $p = .003$). This correlation remained significant when controlling for age and TIV ($r = .34$, $p = .022$). This relationship was unexpected in the sense that previous research has focused on the causal role of right not left PPC in change detection tasks.

The association that ran contrary to our predictions was a positive correlation between GM density in left posterior SPL and robust VSTM accuracy ($r = .35$, $p = .014$). This correlation became marginally significant when controlling for age and TIV ($r = .26$, $p = .088$). Note that this region is only a few voxels away from the ROI termed left PPC (see Table 3.1 and Figure 3.2), so essentially reflects the same effect. These close regions were called differently because the authors of the rivalry literature refer to this region differently (left posterior SPL, Kanai et al., 2010; 2011) to the authors of CB literature (left PPC, Beck et al., 2005; Tseng et al, 2010). Although CB literature did not suggest directional hypotheses, based on the rivalry literature increased GM density in this region was hypothesised to predict poorer VSTM accuracy. No significant relationships emerged between V1 average GM density and the behavioural measures.

Table 3.5 The observed relationships between the ROIs and the behavioural measures

The correlations that are the opposite valence of the predicted ones are marked with an asterisk. Non-significant associations are marked as n.s.

	Perceptual rivalry	CB task performance	Attentional capture	VSTM accuracy
Right anterior SPL	n.s.	n.s.	n.s.	n.s.
Bilateral posterior SPL	Positive ↑ left posterior SPL GM ↑ Rivalry	n.s.	n.s.	Positive* ↑ left posterior SPL GM ↑ robust VSTM
PPC	n.s.	n.s.	n.s.	Positive ↑ left PPC GM ↑ robust VSTM
Primary visual cortex	n.s.	n.s.	n.s.	n.s.
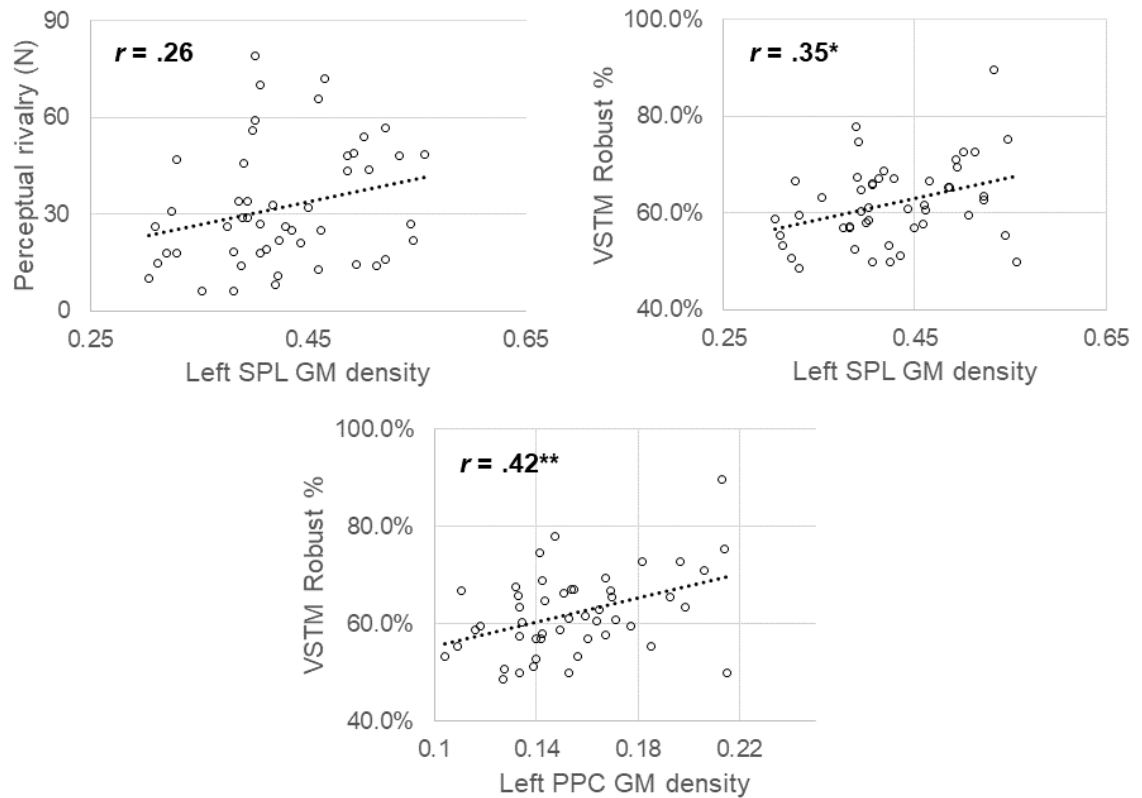
Figure 3.5 Scatterplots illustrating the significant correlations between GM density in the ROIs (left SPL and left PPC) and the behavioural measures; the number of alternations in perceptual rivalry and robust VSTM accuracy

The associated Pearson's *r* coefficient along with its two-tailed significance level (* $p <$ .05, ** $p <$ .01, *** $p <$ .001) is provided on each panel.

3.5. Discussion

3.5.1 Summary of findings

The present study aimed to investigate whether inter-individual variation in brain structure predicts individual differences in visual awareness, assessed by visual change detection. The measures of VSTM accuracy, attentional capture, and the number of alternations in perceptual rivalry were also selected, as they have been shown to predict detection and load onto a common factor we termed 'visual stability' (Andermane et al., 2019). Several candidate ROIs of the brain were chosen *a priori*,

based on the evidence that they are causally involved in or functionally or structurally related to the process of generating visual awareness. Specifically, the right PPC was selected based on its causal role in change detection (Beck et al, 2005; Tseng et al., 2010), bilateral SPLs were considered due to their opposing roles in perceptual rivalry (Kanai et al., 2010; 2011), and V1 was selected due to its functional and structural relationship to VSTM (Bergmann et al., 2014, Verghese et al., 2014). We aimed to replicate the relationships between the four behavioural tasks from Andermane and colleagues (2019), as well as to investigate whether regional GM density of parietal and visual cortices predicts individual differences in visual awareness. The direction of each SBB association was hypothesised based on existing findings (see Table 3.1. for the predicted correlations). We also conducted a WBA to look for SBB associations outside of the pre-specified regions.

We replicated the relationships between the behavioural measures observed in Andermane and colleagues (2019); greater accuracy of fragile VSTM and lower attentional capture predicted better change detection. An exception was the previously reported correlation between perceptual rivalry and change detection, which was not significant in this study. The ROI-based approach, whereby mean GM densities of pre-specified regions were extracted and correlated with our behavioural measures, largely yielded no significant associations in the hypothesised directions. An exception was a marginally significant positive correlation between GM density in the left posterior SPL and perceptual rivalry alternations, consistent with the work by Kanai and colleagues (2011). We also observed a significant positive correlation between GM density in the left PPC (aka left posterior SPL) and robust VSTM accuracy, which survived controlling for age and TIV. No significant associations emerged between mean GM density of V1 and our behavioural measures. The whole brain analysis (WBA)

additionally revealed two significant associations that survived FWE correction; a negative correlation between robust VSTM accuracy and GM volume in a region of the cerebellum, and a negative correlation between change detection and GM volume in the left hippocampus. In the following sections we review the functional role of the left PPC region that predicted VSTM accuracy in the present study, evaluate the results of the WBA, as well as consider the potential limitations and reasons for the general lack of predicted SBB associations below.

3.5.2 Structural predictors of individual differences in visual awareness

The key finding of the present research was that greater GM density in a left PPC region[1] predicted more accurate robust VSTM, a result that was unexpected and contrary to one of our hypotheses. Our initial literature review on the regions implicated in visual change detection suggested that disruption of the right (not left) PPC activity impairs change detection (Beck et al., 2005; Tseng et al., 2010). Additionally, the structure of left posterior SPL positively predicts instability in perceptual rivalry (Kanai et al., 2010) and self-reported distractibility (Kanai et al., 2011b; Sandberg et al. 2014). It has been proposed that the functional role of left PPC may be initiating shifts in visual awareness due to updating of perceptual predictions (Kanai et al., 2011). Our expectation therefore was that greater GM density in this region would predict a tendency to generate fleeting visual representations that are prone to overwriting. Accordingly, we anticipated greater GM density in left posterior SPL to be associated with poorer, not better, VSTM accuracy.

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[1] (MNI coordinates: X = -23, Y = -65, Z = 68)

However, a review of research exploring the neural basis of VSTM provides evidence that, consistent with our result, left PPC may be a central region for the short-term storage of visual representations. Todd and Marois (2004) found that the set size of VSTM display correlates with activity in left PPC on a group level. Additionally, the activity of left PPC[2] predicts individual differences in VSTM capacity (Todd & Marois, 2005). The activity in this region at encoding, maintenance, and retrieval significantly correlated with the maximum number of items an individual can store in VSTM, explaining 40% of the variance in VSTM capacity. Convergent evidence comes from an electrophysiological study by Vogel and Machizawa (2004) who measured event-related potentials (ERPs) and found the amplitude increase between sets of 2 and 4 items over posterior parietal and lateral occipital cortex sites was positively correlated with subject's VSTM capacity. These findings suggest that the process of encoding and maintenance of visual representations may greatly depend upon left PPC activation. Furthermore, using MVPA, Christophel and colleagues (2012) found that VSTM content is reliably decoded from activation patterns in early visual and parietal cortices. Right early visual cortex and left PPC were particularly highlighted as robustly predicting content across different types of stimuli; a left PPC cluster with a central coordinate close to ours[3] showed significant above chance classification in 97% of tests. This finding corroborates the evidence for left PPC as the central locus of VSTM representations, its activity not only reflecting capacity but the patterns of activity differentiating content. The observed structural relationship between left PPC and VSTM accuracy adds to this picture by showing that the more GM is available in this region, the more accurate VSTM representations can be.

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[2] (MNI coordinates: X = -17 to -29, Y = -85 to -61, Z = 21 to 49)
[3] (MNI coordinates: X = -26, Y = -66, Z = 56)

As the left PPC is in the dorsal stream, which is thought to be important for location information and action guidance rather than identity of objects, VSTM representations encoded there may involve information about salient regions of the object for guiding attention (Christophel et al., 2012). This is consistent with research by Soto and colleagues (2014) who performed a WBA looking for regions that structurally predict the extent to which visual items held in WM facilitate performance when the stimulus surrounding the target matches the WM held item (WM benefit), as well as hinders performance when a distractor matches the WM held item (WM cost). They found that GM volume in left superior PPC[4] positively predicts WM benefit in performance. Individuals with greater GM volume in this region benefited from facilitated selection of target due to WM cueing. Furthermore, the structure of this region also positively predicted recognition memory performance of the WM held item. The authors concluded that left PPC is involved in visual WM processes, specifically, in the guidance of attention to the items in the external world that match the visual representations currently held in WM. Thus, the size of left PPC may affect the quality of an 'attentional priority map' representation, which then guides attention to lower level areas such as visual cortex (Verghese et al., 2014) to activate the specific perceptual features of the VSTM representation.

Although our finding that greater GM density predicts VSTM accuracy is consistent with research highlighting the role of left PPC in VSTM content and capacity, it is still difficult to reconcile with evidence that greater GM density in this region also predicts distractibility (e.g., Kanai et al., 2011b[5]; Sandberg et al., 2014[6]). In fact, the discrepancy is even more puzzling given that individuals with high VWM

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[4] (MNI coordinates: $X = -32$, $Y = -55$, $Z = 52$)
[5] (MNI coordinates: $X = -15$, $Y = -61$, $Z = 54$)
[6] (MNI coordinates: $X = -20$, $Y = -61$, $Z = 54$)

capacity tend to be able to resist attentional capture better than low-capacity individuals (Fukuda & Vogel, 2009), due to faster recovery from capture (Fukuda & Vogel, 2011). Importantly, it is the contingent-capture, i.e., capture by previously relevant items, that correlates with lower WM capacity, not stimulus-driven capture. This effect is thought to reflect that high WM capacity allows the individuals to more effectively disengage from the distractors due to less competition. The overlap between regions structurally related to distractibility and high VWM capacity would need to be investigated further, as perceptual and attentional instability is not compatible with accurate VSTM.

In terms of the differing roles of left and right PPC, studies administering TMS to parietal regions have revealed that right PPC may automatically select salient stimuli, whereas left PPC may suppress salient distractors when a non-salient target needs to be prioritised. For example, the attentional capture effect of salient distractors is eliminated or reduced after rTMS to right PPC (Hodsoll et al., 2008). If the distractors were previously targets, the effect is reduced but a delay of 100ms remains, suggesting that right PPC partly (but not exclusively) encodes representations of previously encountered visual stimuli. In contrast, TMS to left PPC delays the disengagement from capture (Kanai et al., 2011b). The timescale of these effects was delineated by Mevorach, Humphreys and Shalev (2009); online rTMS administered to right PPC lead to poorer performance when the target was more salient than distractor and when disruption occurred after the onset of the target. In contrast, disruption of the left PPC lead to decreased ability to select low salience targets when presented with high salience distractors and the impairment was associated with pre-target administration of TMS. Together these results suggest that right PPC is causally involved in selecting salient visual stimuli in a reflexive manner, whereas left PPC is causally involved in the preparatory activity that sets the visual system up for ignoring salient distractors. Left

PPC may accomplish this by altering the attentional set or spatial window of attention using the VSTM representations for guidance (Mevorach et al., 2009). This may be the reason individuals with high WM capacity can avoid distraction (Fukuda & Vogel, 2009; 2011).

The finding that average GM density in V1 does not predict performance on any of our measures but especially VSTM accuracy is perplexing, given evidence that activity patterns in right early visual cortex predicts the content of VSTM (Christophel et al., 2012). Additionally, ERPs over lateral occipital sites correlate with individuals' VSTM capacity (Vogel & Machizawa, 2004) and activity in a ventral occipital region when maintaining items over a retention period positively predicts individual differences in VSTM capacity (Todd & Marois, 2005). Additionally, individuals with greater V1 volume, surface size, and cortical thickness have already been shown to possess greater VSTM capacity (Bergmann et al., 2014) and TMS administered to this region impairs encoding and maintenance of VSTM representations (Cattaneo et al., 2009). The evidence clearly suggests that, together with PPC, V1 is involved in the encoding and maintenance processes of VSTM representations. A possible methodological reason for observing a null effect regarding the VSTM and V1 structure may be operationalisation of structure as average density over the entire anatomical V1 mask. Previous studies show it is the functional V1 surface area size (defined for each participant individually), volume, and cortical thickness that predicts VSTM fidelity (Bergmann et al., 2014; Verghese et al, 2014) – average GM density may not capture these aspects well.

In our WBA, we additionally observed a negative correlation between GM volume in a region of the right cerebellum and robust VSTM. Imaging research reveals that cerebellar activation is predominantly associated with a range of motor functions,

notably motor control, coordination, and learning (Desmond & Fiez, 1998). However, in their meta-analysis Stoodley and Schmahmann (2009) argue that in addition to its sensimotor involvement cerebellum also has a 'cognitive' region related to WM and executive functions. For example, language-based tasks, articulatory rehearsal, and verbal WM are reliably related to cerebellum activity (Durisko, & Fiez, 2010; Chen & Desmond, 2005). Visual WM tasks also activate the cerebellum, albeit to a lesser degree than verbal WM (Thürling et al., 2012). Sobczak-Edmans and colleagues (2016) employed a visual WM task with abstract patterns and found that cerebellum activation contributes to the task during encoding and maintenance. Stoodley and Schmahmann's (2009) meta-analysis highlighted that cerebellum has strong links with parietal cortex and its activation is consistently associated with spatial processing. Interestingly, the cerebellum is also activated during visual change detection, along with the typical cortical activations (i.e., parietal and frontal) (Pessoa & Ungerleider, 2004). Previous VBM research reveals positive correlations between cerebellar GM volume and verbal WM but no associations with visuospatial WM (Cooper et al., 2012). Note that we found a negative correlation, which is contradictory to VBM research on cerebellum; a lower GM volume here is typically associated with functional impairment (e.g., in schizophrenia, Hirjak et al., 2015; in attention deficit hyperactivity disorder (ADHD), Stoodley, 2014). In sum, there is evidence linking cerebellar activity to the encoding, maintenance, and retrieval of visual representations from STM; however, our negative association between GM volume and VSTM accuracy is not easy to reconcile with previous findings where lower cerebellar volume is associated with impairment.

The WBA also revealed a significant negative association between GM volume in the left hippocampus and change detection. The link between medial temporal lobe (MTL) and long-term recognition memory is well-established, both in imaging literature

tracking activation and the observed effects of hippocampal damage (Olsen, Moses, Riggs, & Ryan, 2012). However, the hippocampus is also involved in recognition tasks that require maintaining visual information over short delays, i.e., VWM and change detection (Olson, Moore, Stark, & Chatterjee, 2006; Ranganath & D'Esposito, 2005). For example, individual neurons in human MTL that prefer a visual stimulus fire more strongly when it is present and consciously detected relative to when it is missed (with no differences between correct and incorrect detection for other stimuli) (Reddy, Quiroga, Wilken, Koch, & Fried, 2006). The role of hippocampus in visual awareness may involve binding representations of stimuli across space and time and comparing current input to stored representations (Olsen et al., 2012). Such a relational binding of objects with the context of the scene and comparison process would be crucial for detecting visual changes. Additionally, hippocampus activation is proportional to confidence regarding a perceptual change in scenes, so it could contribute to assessing the strength of a match or a mismatch to previous experience when viewing the current visual scene (Aly, Ranganath, & Yonelinas, 2013). However, again, the negative direction we find for the structural relationship with detection in our WBA is incongruent. If the activation level of representations in hippocampus contributes to confidence regarding visual change, then more GM should afford stronger signal and better change detection, but we found the opposite. The negative direction of both associations calls the WBA analysis of the present investigation into question.

3.5.3 Limitations

Apart from the observed association between robust VSTM accuracy and GM density in the left PPC, no other significant ROI-based SBB associations were found. The absence of hypothesised associations may stem from two possibilities: (1) the

limitations of the design lead to a lack of power and increased levels of noise, obscuring genuine relationships between the structure of parietal cortex, V1, and individual differences in visual awareness (i.e., Type II error); (2) the GM density of the ROIs does not predict individual differences in visual awareness, despite their functional involvement shown in imaging and TMS studies. I will consider the evidence for these two possibilities in turn.

One limitation of the present study may be that with a sample of 49 participants it is underpowered for detecting SBB associations. However, previous VBM studies reporting significant associations with visual awareness measures have used comparable samples. Significant effects using the same perceptual rivalry task were observed with a sample of 52 (Kanai et al., 2010; 2011). There are studies employing a smaller sample (e.g., 44 participants) and reporting correlations between parietal cortex regions and VWM performance even using WBA with correction (Soto et al., 2014). A recent study by Boekel and colleagues (2015) attempted to replicate 17 VBM effects using a ROI-based approach with a sample of 36 participants. Whilst most of the effects were not replicated in terms of significance, the Bayes factor indicated moderate to strong evidence supporting the null hypothesis for 8 out of 17 of the associations, suggesting VBM analyses can yield informative results with a limited sample. Thus, although our sample size may be modest, it is not unusual for VBM research. However, note that Masouleh and colleagues (2019) recently examined perceptual and attentional SBB associations with a substantial sample (N = 466), as well as assessed their replicability using different sample splits. The authors cautioned against using samples of less than 200-300 for VBM research in healthy populations, due to a high probability of obtaining spurious false positives and exaggerated effects sizes. In sum, our sample is

comparable to similar VBM research; however, there is a concern regarding the lack of power and replicability of associations observed in small samples such as these.

Another limitation may be the noise introduced in our data due to the interval between scanning and behavioural testing sessions. The retrieved brain scans vary in terms of the image acquisition date; in some cases, the scanning session took place recently before completing our behavioural tasks (e.g., a minimum interval of 6 days), in other cases participants were scanned several years prior (e.g., max. 7.80 years), with an average interval of 1.44 years (SD = 1.74). Aging-related GM volume reductions may begin during early adulthood (Giorgio et al., 2010) and neuroplasticity in adults is observed upon learning new skills (e.g., GM increases in mid-temporal area and left IPS after training a new motor skill, Draganski et al., 2004), due to mental illness such as major depression (e.g., reduction of GM volume in anterior cingulate cortex, Bora, Fornito, Pantelis, & Yücel, 2012), and after a sustained mindfulness practice (e.g., increased GM in temporo-parietal junction and left hippocampus, Hölzel et al., 2011ab). As the brain is structurally plastic throughout adulthood, there is some concern regarding the congruence between our participants' brain structure at the time of the imaging session and that at the time of data collection for our behavioural measures – the delay likely added noise to our data.

Even considering potential issues with power or noise, there is a possibility that there are no genuine effects; cortical macrostructure of healthy individuals may not be predictive of individual differences in visual awareness. In fact, there is a concern in recent research literature about the replicability of VBM findings. Boekel and colleagues (2015) assessed evidence for previously reported SBB associations and found confirmatory evidence for the null hypothesis (no relationship) for 16 out of the 17 effects ranging from anecdotal to strong, including the correlation between left PPC

and distractibility originally found by Kanai and colleagues (2011b). Additionally, Masouleh and colleagues (2019) recently investigated SBB associations using several psychometric measures (e.g., perceptual reasoning, attentional network, and colour-word interference tasks) with a large sample. The authors concluded that finding SBB associations in healthy individuals using WBA is highly unlikely, as the spatial overlap of significant associations is poor over different sample splits, and associations discovered through exploratory WBA are difficult to replicate via ROI-based approaches using significance testing and Bayes factor. In contrast, the authors found consistent and replicable negative associations between GM volume and age, as well as better replicability of SBB associations in clinical samples. Taken together, there seem to be indications that the GM volume of parietal regions predicts perceptual rivalry and general distractibility; however, the failures to replicate these effects in the present study and that of Boekel and colleagues (2015) calls their strength and generalisability into question.

Another limitation may be how we operationalised brain structure, as the average probability of a region containing GM may not be the most informative measure. Cortical thickness, cortical surface area, structural white matter connectivity are measures that additionally capture the full range of structural differences. Although cortical thickness and cortical surface area both contribute to the volume of a cortical region, they may affect neuronal response properties differentially and have opposite relationships with performance (Song, Schwarzkopf, Kanai, & Rees, 2015). Specifically, in early visual cortex (V1 and V2) a larger cortical surface area is associated with finer neural population tuning (higher selectivity) and perceptual discrimination of visual stimuli, whereas neural population tuning and perceptual discrimination was finer for visual field positions corresponding to thinner cortex (Song

et al., 2015). A larger V1 surface size may be the parameter that affords greater selectivity of individual cortical columns and thus a visual representation with greater fidelity. We only measured GM density over the entire anatomical V1 mask, whereas previous studies tend to estimate the surface area for each participant individually based on functional retinotopic activation (Verghese et al., 2014). It may very well be that average GM density in this region is not predictive of change detection ability, attentional capture or VWM capacity; however, the surface area or cortical thickness may be.

A further question pertains to whether structural brain differences influence the selection and maintenance of visual stimuli or whether it is primarily the neural activity patterns and functional interaction between regions that matters. For example, using electroencephalography (EEG) and magnetoencephalography (MEG) techniques, Palva, Monto, Kulashekhar, & Palva (2010) demonstrated that phase synchrony in alpha, beta and gamma bands between areas previously implicated in VWM, such as frontoparietal and visual cortex, increased with increased memory load. Importantly, individual differences in VWM capacity were predicted by the strength of interareal phase synchrony in the alpha and beta bands in a network with IPS as the central hub. The authors suggest long-range phase synchrony between cortical areas may be the mechanism supporting the maintenance of object representations in VWM and that IPS may have a special role in this process, potentially due its location between the lower representational areas and higher order areas involved in attention and executive processes. Additionally, whole brain functional connectivity of a network comprising multiple cortical and subcortical locations is a reliable neuromarker for sustained attention – this was assessed by measuring synchronous fluctuations in BOLD signal via functional MRI (Rosenberg et al., 2016). Performance on sustained attention task

could be predicted from strength of functional connectivity during resting state, and the strength of functional networks identified as high-attention and low-attention also predicted ADHD scores of children and adolescents from a novel sample, even after controlling for age and intelligence. The connectivity between motor, occipital, and cerebellar regions specifically predicted increased sustained attention, whereas connectivity between temporal, parietal, intratemporal, and intracerebellar regions were associated with poorer sustained attention. Interestingly, the prefrontal and parietal regions that have frequently been identified as locus of attentional mechanisms only involved a proportion of the relevant nodes – the authors suggest this may mean *a priori* hypotheses may miss information about the whole process.

3.5.4 Conclusion

In sum, although TMS studies have established that different regions in the parietal cortex (e.g., right anterior and bilateral posterior SPLs) have opposing roles in bistable perception (Carmel, Walsh, Lavie, & Rees, 2010; Kanai et al, 2010; 2011), the relationship between the structure of these regions and bistable perception was not fully replicated here (i.e., no significant associations emerged). Furthermore, the conclusion that these regions generate perceptual predictions and prediction error may not generalise to other perceptual tasks. The structure of the ROIs was not differentially related to our measures, except for robust VSTM, which yielded the opposite of the association predicted by the putative model illustrated in Figure 3.1. The underlying mechanisms of the previously reported parietal fractionation may indeed be rivalry-specific, as it has been shown that the opposing causal roles of anterior and posterior SPLs demonstrated in bistable perception does not extend to spatial and sustained attention tasks – TMS to the coordinates identified in rivalry tasks did not affect the

attentional tasks differently (Schauer, Kanai, & Brascamp, 2016). Predictive processing has been characterised as a hierarchical process, with predictions generated and prediction errors computed and transmitted by neurons at each level of the cortical hierarchy (Rao & Ballard, 1999; Clark, 2013). It may not be plausible that a specific cortical area is responsible for generating all classes of perceptual predictions, irrespective of the nature of the stimulus. It is more likely that the representations of visual stimuli are built by activation at multiple levels of visual hierarchy and the activated areas depend on the nature (e.g., identity and complexity) of the stimulus. Our results do not support a specific cortical area of perceptual prediction generation; rather, these may depend on the stimuli and task requirements (Tulver, Aru, Rutiku, & Bachmann, 2019).

Although right (not left) PPC is causally involved in change detection (Beck et al., 2005; Tseng et al., 2010), we observed a positive correlation between GM density in the left PPC and robust VSTM. This is consistent with research linking activity of the left PPC to content of VSTM representations (Christophel et al., 2012) and individual differences in capacity (Todd & Marois, 2005). Our finding suggests that increased GM in this region may enable individuals to form more accurate VSTM representations, which presumably then allows for enhanced allocation of top-down attention to low-level features of VSTM representations stored in V1 (Verghese et al., 2014; Cattenao et al., 2012). It could be that right and left PPC have complementary roles in visual change detection. Although disruption of right PPC typically causes CB (Beck et al., 2005; Tseng et al., 2010), the left PPC involvement needs to be investigated further, as there is evidence it may enable resisting task-irrelevant distractors through developing a VSTM-based attentional set (Mevorach et al., 2009; Kanai et al., 2011b; Soto et al., 2014). Imaging research shows bilateral PPC is involved in allocation of spatial attention in

accordance with task goals (Hutchinson, Uncapher, & Wagner, 2009). If left PPC activity carries content-specific VSTM representations, it is unlikely these do not have a causal effect on awareness.

In our whole brain analysis, we also found a correlation between VSTM accuracy and right cerebellum volume. Although there is evidence of cerebellar involvement in change detection (Pessoa & Ungerleider, 2004), this structural relationship is questionable because of its negative direction. The same can be said regarding the observed negative association between left hippocampus volume and change detection. An independent replication of these findings would be necessary, given recent concern regarding the poor replicability of SBB associations (Boekel et al., 2015), and cautions pertaining to VBM effects demonstrated in small samples (Masouleh et al., 2019). In healthy individuals the functional connectivity between different brain regions may be more informative regarding the processes involved in visual selection, maintenance, and awareness of stimuli rather than regional macrostructure (Palva et al., 2010; Rosenberg et al., 2016; Masouleh et al., 2019).

To conclude, greater GM density in left PPC was found to predict robust VSTM accuracy, suggesting it may afford more detailed representations. The nature of parietal VSTM representations is likely spatial and attentional – they may be crucial for guiding attention via functional connectivity to perceptual representations stored in early visual cortex. However, no other hypothesised regional associations were established, and WBA results were questionable due to the presence of negative associations. Future VBM examination of SBB associations in healthy populations should employ larger samples (e.g., > 300, Masouleh et al., 2019) to maximise power, reduce noise, and avoid spurious false positives. Additionally, other macrostructure measures may be needed to characterise the full range of structural predictors, such as the functional surface area of

V1 (Bergmann et al., 2014). Finally, individual differences in the functional connectivity between bilateral PPC, hippocampus, V1, and the cerebellum, as well as the content-specificity of patterns of activation, may reveal the mechanisms of encoding, maintenance, and awareness of visual stimuli. These functional parameters are likely to be more predictive of performance in healthy populations than brain macrostructure.

CHAPTER 4

Individual Differences in Reliance on Prior Knowledge

4.1. Abstract

There is evidence that possessing prior knowledge about visual stimuli aids their identification within ambiguous input. For instance, if images of people are converted to two-tone versions (Mooney images), detection of faces is relatively difficult; however, prior exposure to the original images can help individuals to disambiguate faces. Previous research has found that the level of reliance on this prior information in the Mooney task positively predicts psychosis-like traits in the general population (e.g., proneness to sensory hallucinations). This result is consistent with predictive processing theories that suggest visual perception emerges as learnt statistical regularities (priors or expectations) interact with sensory input. Recently, several authors have proposed that the balance between assigning weight to priors versus sensory evidence could be subject to stable individual differences that predict atypical perception. In the present study we aimed to replicate and extend this research by asking whether reliance on prior knowledge also predicts typical visual perception (e.g., change detection ability) and other atypical perceptual traits (e.g., attention to detail in the autism spectrum). We found that change detection ability was positively predicted by face detection in Mooney images per se (independently of prior exposure) and by the attention to detail aspect of the autism spectrum. This suggests that both cognitive styles (i.e., gestalt perception and focus on detail) can be beneficial for noticing visual changes. Reliance on priors predicted the experience of perceptual anomalies, but negatively – individuals less prone to perceptual anomalies showed increased Mooney face detection sensitivity after seeing the original images. Our findings motivate careful operationalisation of measures in order to establish a trait-like reliance on priors.

4.2. Introduction

The appearance and disappearance of an object within a scene is often not noticed when the transition between the scenes is disrupted (e.g., by a brief blank screen). This phenomenon, termed change blindness (CB), is of great theoretical interest, as it reveals a dissociation between the subjective experience of having a rich representation of the visual world and the ability to notice changes in our environment. The present study aims to investigate whether the balance between reliance on prior knowledge versus incoming sensory evidence can predict individual differences in change detection ability. According to the predictive processing framework (Hohwy, 2013; Clark, 2013), the brain utilises prior learning of environmental regularities to make top-down predictions about the causes of its sensory input. During this process, prediction errors are generated whenever the prior expectations do not match the incoming signal, and these are then fed forward in the visual hierarchy to update predictions. Within this framework, change detection relies on the ability to update visual predictions based on new sensory evidence.

Several authors have suggested that individual differences in the rate of perceptual alternation when viewing ambiguous bistable phenomena (e.g., the Necker cube) may reflect variability in how much weight individuals assign to their top-down predictions versus bottom-up prediction errors (Hohwy et al., 2008; Kanai et al., 2010; 2011). Such accounts offer the intriguing possibility that the inter-individual variability in the balance of predictive processing may affect other visual experiences as well. In a recent study we found that a slower perceptual alternation rate when viewing an ambiguous structure-from-motion rotating sphere predicts superior change detection performance (Andermane et al., 2019), suggesting that forming relatively stable, strong

perceptual predictions may be beneficial for detecting unexpected changes. The present research is motivated by the question of whether individuals reliably differ in the extent they rely on prior knowledge in visual perception, and can this tendency predict visual change detection.

Predictive processing imbalances have been associated with various psychopathologies such as schizophrenia and autism (see Figure 4.1 for an illustration of a bias in Bayesian inference). For example, Teufel and colleagues (2015) used a face detection task with degraded (and, hence, potentially ambiguous) images to demonstrate that individuals with early psychosis show an increased reliance on prior knowledge. In their study participants were asked to detect faces in two-tone degraded 'Mooney' images both before and after being exposed to the original colour photographs, which was their manipulation of prior knowledge. Prior knowledge conferred a greater benefit for face detection in individuals with early psychosis relative to controls despite similar performance at baseline. The magnitude of this face detection improvement was also positively correlated with schizotypy in the general population, as assessed by the Cardiff Anomalous Perceptions Scale (CAPS) (Bell, Halligan, & Ellis, 2006). The authors concluded that increased reliance on priors may underpin some of the positive symptoms of schizophrenia such as hallucinations; these experiences may result from forming predictions that are weakly constrained by sensory evidence. Others have observed that individuals with psychosis 'jump to conclusions' or form predictions with limited evidence faster than controls, as well as having higher confidence in these predictions and a greater bias against disconfirmatory evidence (Bentall, Kaney, Dewey, 1991; Garety & Freeman, 1999; Warman, 2008). Consistent with this, auditory hallucinations induced via expectancy-based conditioning are easier to create in individuals who report psychosis-like experiences (Powers et al., 2017).
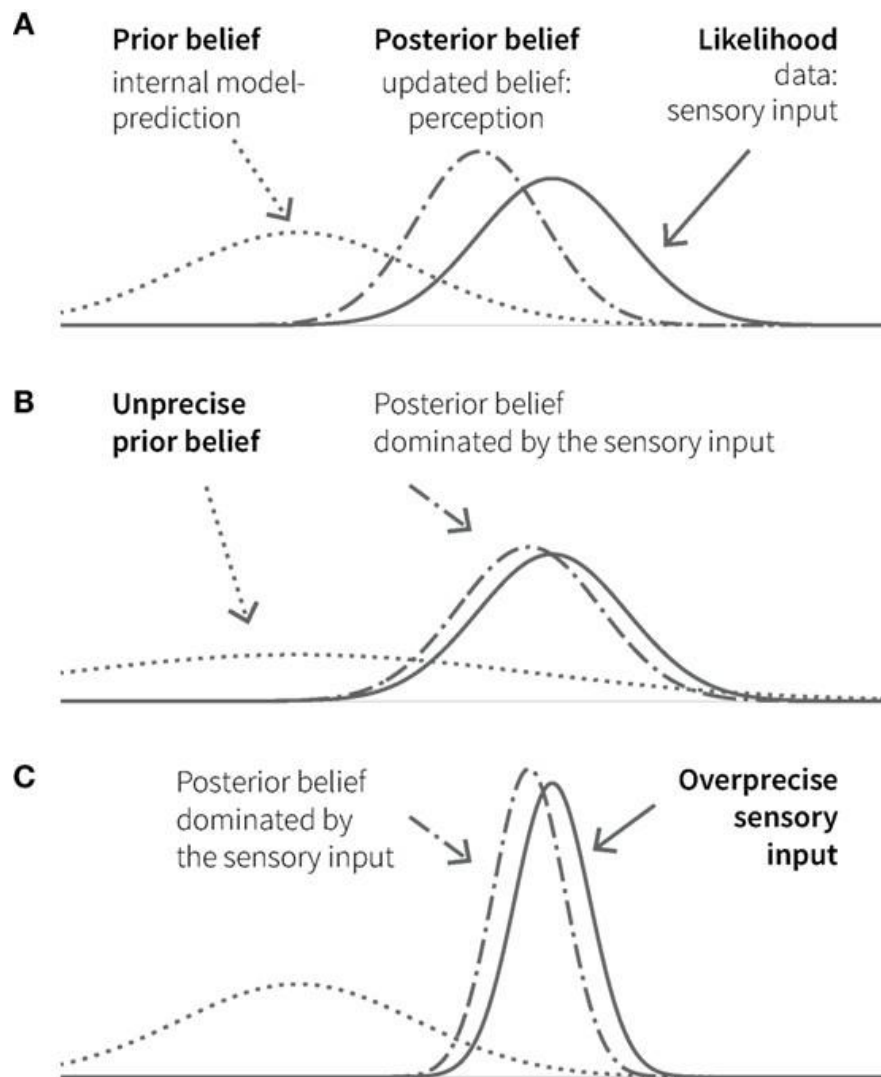
Figure 4.1 Example of a bias in Bayesian inference

Normal Bayesian inference is shown in panel A; the prior (expectation) and likelihood (sensory evidence) are combined, each weighted by their precision (inverse variance), to generate the posterior distribution, which corresponds to the current percept. An imprecise prior (panel B) or an overly precise likelihood (panel C) leads to a posterior (current percept) that is shifted towards the likelihood (sensory evidence). These are the predictive processing biases that have been implicated in the autism spectrum disorder. The opposite bias to assign greater weight to priors has been proposed in psychosis. Image taken from Haker, Schneebeli, & Stephan (2016).

Although most researchers implicate overly strong priors to be the underlying disturbance in psychosis, there are contradictory accounts (Adams et al., 2013) arguing that some symptoms of psychosis such as delusions are caused by an abnormally high

confidence in prediction errors, leading to the delusory state of assigning high salience (and thus importance) to neutral stimuli. A later compensatory mechanism is thought to downregulate the precision of sensory evidence and to increase the reliance on priors, which contributes to state abnormalities such as hallucinations. Nevertheless, in terms of perceptual alternations when viewing bistable stimuli, individuals with schizophrenia have not been shown to differ from controls in most studies (Hunt & Guilford, 1933; Hoffman, Quinlan, Mazure, & McGlashan, 2001; Miller et al., 2003). If slower perceptual rivalry truly reflects greater strength and stability of perceptual predictions (Kanai et al., 2011), then an unaffected alternation rate in psychosis is difficult to reconcile with the proposed predictive coding imbalances in schizophrenia.

The perceptual, cognitive, and social characteristics of individuals on the autism spectrum have also been described in terms of an imbalance in predictive processing mechanisms, and psychosis and autism have been linked in terms of their aetiology (Crespi & Badcock, 2008). Van de Cruys and colleagues (2014) suggest that autism is associated with inflexible assignment of high precision to any perceptual violation of expectation due to a limited ability to take into account the expected noisiness of the environment. That is, autistic individuals may form predictions that are too precise and do not allow for minor deviations, leading to impairments in tasks that require abstraction and benefits in perceptual discrimination tasks. However, others have proposed that possessing weak priors is the core deficit in autism (Pellicano & Burr, 2012). Kanai and colleagues (2010; 2011) suggest that increased alternation rate in perceptual rivalry reflects assigning greater weight to prediction error; however, people with autism have a similar alternation rate to controls (Said, Egan, Minshew, Behrmann, & Heeger, 2013) or in other cases an even slower rate, with more mixed percepts (Robertson, Kravitz, Freyberg, Baron-Cohen, & Baker, 2013). Robertson and

colleagues argue that the prevalence of mixed percepts in rivalry comes about from a poorer ability to form high-level predictions (i.e., autistic individuals stay true to the signal). The predictive processing framework can accommodate two conflicting hypotheses about effects of an increased weight to prediction error on perceptual alternation rate (e.g., faster and slower), which complicates interpretation. Given these contradictory accounts on the proposed predictive imbalances in autism and psychosis, the relationship between reliance on priors and atypical perception needs to be clarified.

In the present research we ask how individual differences in reliance on prior knowledge relate to typical perception (e.g., visual change detection) as well as atypical perceptual traits related to psychosis and the autism spectrum. To operationalize reliance on priors, we used a Mooney face detection task previously employed by Teufel and colleagues (2015). Mooney images were originally developed by Craig Mooney (Mooney, 1957) and initially appear as black and white blobs; however, these ambiguous images typically hide a coherent percept of a face (see Figure 4.2 for some examples). The performance in the Mooney task at baseline is thought to measure 'perceptual closure' – the ability to generate a coherent percept from seemingly disorganized and disparate elements carrying limited information (Thurstone, 1944; 1950). There are marked and reliable individual differences in perceptual closure, assessed via Mooney task, and these are predicted by genetic markers (Verhallen et al., 2014). The version of the Mooney task employed here mirrors that presented by Teufel and colleagues (2015) and measures the extent that prior exposure to colour images of people later improves detection of their faces in degraded two-tone versions of the original images. We also administered a perceptual rivalry task of ambiguous structure-from-motion sphere to measure individual differences in perceptual alternation rate, previously suggested to index predictive processing bias (Kanai et al., 2011). To assess

individual differences in everyday perception, we administered a flicker change

detection task (Rensink et al., 1997), where participants were asked to detect the sudden

appearance and disappearance of objects in naturalistic scenes. Finally, to measure

autism spectrum and psychosis-like traits, we administered two questionnaires that

assess atypical experiences related to these in the general population; the AQ (Baron-

Cohen et al., 2001) and the CAPS (Bell et al., 2006), respectively.

Figure 4.2 Examples of Mooney face images
Taken from the landmark study of Craig Mooney (1957).

We hypothesized that, in line with previous research on shizotypy and psychotic

traits (Teufel et al., 2015; Powers et al., 2017), a greater reliance on prior knowledge in

the Mooney task will predict more reported perceptual anomalies in CAPS. In contrast,

a lower influence of prior exposure to images in the Mooney task should predict more

autism spectrum traits, according to the weak priors account (Pellicano & Burr, 2012).

Finally, a greater reliance on priors in the Mooney task should also predict improved change detection performance. We previously observed that superior change detection is related to forming strong and stable visual representations (Andermane et al., 2019), as this may enable individuals to compare the change to the formed representation more efficiently. We ran two separate experiments; in Experiment 1 we conducted a lab-based study with all of the tasks but due to the difficulty level of our stimuli we ran a second online-based study (Experiment 2) to replicate the Teufel and colleagues (2015) finding with an improved set of Mooney images.

4.3. Experiment 1

4.3.1. Method

Participants

Fifty adult participants (Aged 18 – 43, Mean = 21.86, SD = 4.50; 39 female) with normal or corrected-to-normal vision, no reported colour vision deficiencies, no sensitivity to flashing lights or epilepsy, and no diagnosed mental disorders (e.g., depression or schizophrenia) took part in this study. The latter criterion was important, as we aimed to study reliance on priors in the general population, i.e., sub-clinical trait differences in predictive processing biases. The participants were undergraduate students at the University of Sussex who took part in return for course credit and adults from the Brighton community who were reimbursed for their time in cash. This research was approved by the Science and Technology Cross-Schools Research Ethics Committee (C-REC), at the University of Sussex.

Materials and Design

The study consisted of three computer-based visual tasks (perceptual rivalry, CB, and Mooney tasks) and two paper-and-pen questionnaires (CAPS (Bell et al., 2006) and AQ (Baron-Cohen et al., 2001)). All participants completed the tasks in the same order, outlined below.

1. *Perceptual rivalry task*

The stimulus used in this task was an ambiguous structure-from-motion sphere described by Kanai and colleagues (2010) (for an illustration see Figure 4.3). This stimulus was presented for a total of 4 minutes using MATLAB and Psychophysics Toolbox (Brainard, 1997) and is typically experienced as an ambiguous sphere that appears to rotate either left or right, with the perceived direction of rotation frequently alternating. The sphere consisted of 200 white dots moving sinusoidally with a red fixation cross in the middle and was presented against a black background. The sphere was continuously presented on the screen for two blocks of 2 minutes and participants had to respond by clicking the mouse whenever the sphere appeared to change its direction of rotation. The measure derived was the total count of the reported perceptual alternations over the 4-minute presentation of the sphere.

Continuous response collection

Time

Dots continuously oscillate for 4 minutes
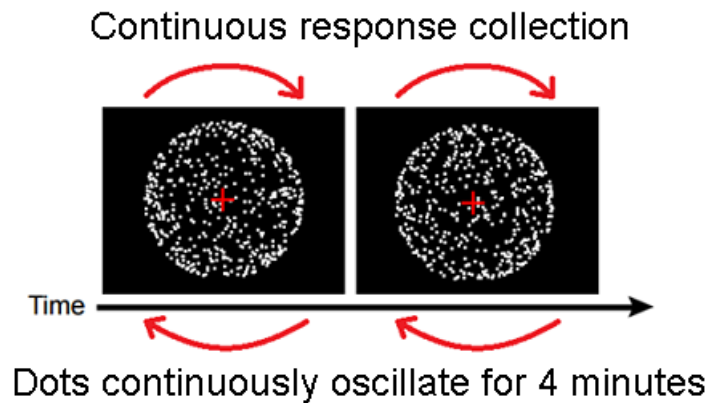
Figure 4.3 The ambiguous structure-from-motion sphere of the perceptual rivalry task

The moving dots create an illusion of a sphere, which alternately rotates clockwise and counterclockwise. The task is to click the mouse any time the direction of rotation subjectively changes.

2. *Change blindness task*

The CB task was adapted from the landmark study by Rensink and colleagues (1997), and required participants to find changing objects within flickering natural indoor scenes (see Figure 4.4). Sixty image pairs were obtained from a CB database (Sareen et al., 2016): one image was an original indoor scene and in the other image one of the objects (e.g., a vase) was removed. Half of the object changes occurred on the left side of the image and half occurred on the right side. The task was presented using Inquisit Millisecond software and consisted of one practice trial and 60 randomly inter-mixed experimental trials. On each trial the pre-change and post-change scene alternated with a blank screen in between the two, creating a flickering cycle or image presentation lasting 30s. Participants were instructed to click on the object that keeps appearing and disappearing. The next trial began after the mouse click or in the case of no response when the flicker cycle finished after 30s. To differentiate correct and incorrect responses, ROIs within each image were defined around the centre coordinates of the changed object and mouse clicks with coordinates outside ROIs (Mean radius =

2°) were labelled as misses. Response times (RTs) were collected for each trial, and the percentage of correctly identified changes was estimated at each point in time.
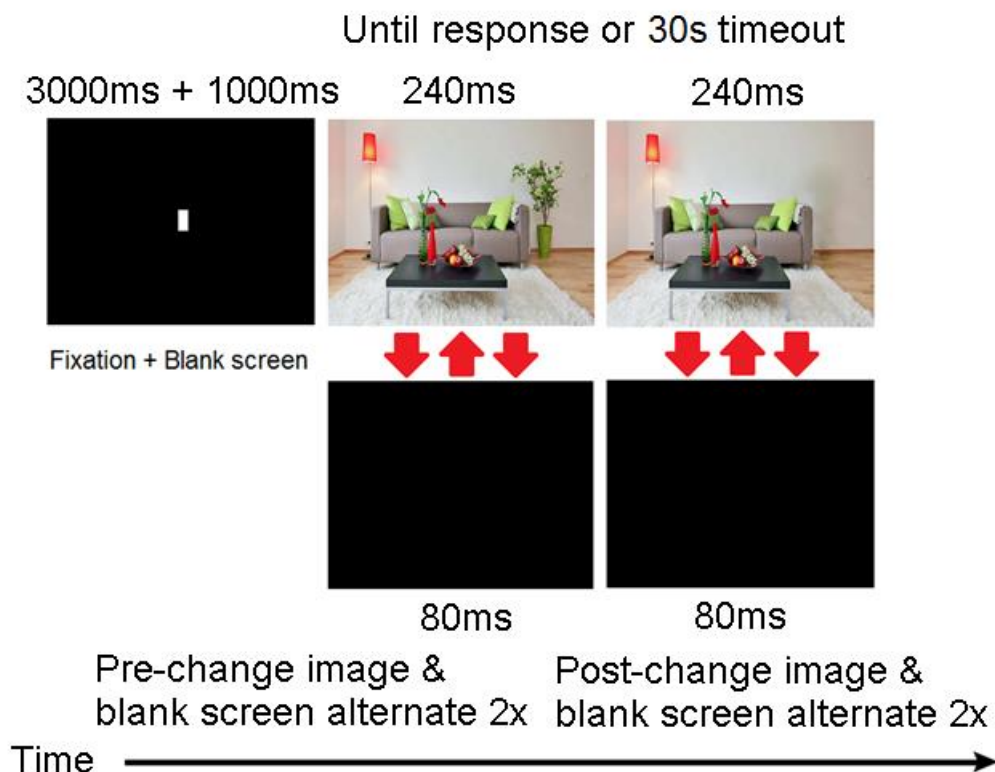
Figure 4.4 The stimuli appearance and trial structure of the CB task

The cycle of pre-change scene, blank screen, and post-change scene alternate for 30s or until a mouse click response. The task is to click on the object that keeps appearing and disappearing within the scene.

3. *Mooney task*

The Mooney task measures the ability to detect human faces in two-tone degraded images before and after the presentation of the original colour templates. The Mooney images were purposefully designed to be difficult to disambiguate before seeing the original colour templates; subjectively they appear as random black and white blobs. The improvement in face detection after seeing the original colour templates is thought to reflect reliance on top-down knowledge in visual perception (Teufel et al., 2015). To construct a set of stimuli for this task 150 colour images of

people were obtained via free online portrait database searches. The images were then smoothed and thresholded in black and white at various cut-offs using the image editing software PhotoScape. The Mooney images were cropped (234 x 312 pixels) to include the area of the face and remove most contextual cues which would aid identification of a human figure (e.g., clothing and surrounding objects). Half of the Mooney images were treated as target trials and the other half were converted into control stimuli by rotating the images by 180° and re-arranging some of the black and white blobs to disrupt face outlines (see Figure 4.5 for an illustration of targets and controls). After an informal pilot, 60 Mooney targets and 60 controls were selected and piloted on seven experimentally naïve participants who were asked to decide whether they see a face in each image. Based on analysis of the pilot data, 30 targets and 30 controls were selected for the main task. The selection criterion for the Mooney targets was that they should be sufficiently ambiguous; the faces should not be too obvious (no targets with average hits above 86%) but also not too difficult to detect (no targets with average hits of below 14%). The average hits for the 30 selected Mooney targets in the pilot study was exactly 50%. For the controls the selection criterion was that they should be similar to the targets (i.e., also include fluid blobs) so as to not make them stand out but that participants should not identify non-existent faces in them (i.e., no control images with false alarms of over 60% were selected). This was because we aimed to measure true identification of faces, rather than identification based on a guess (which may occur if controls were too face-like).
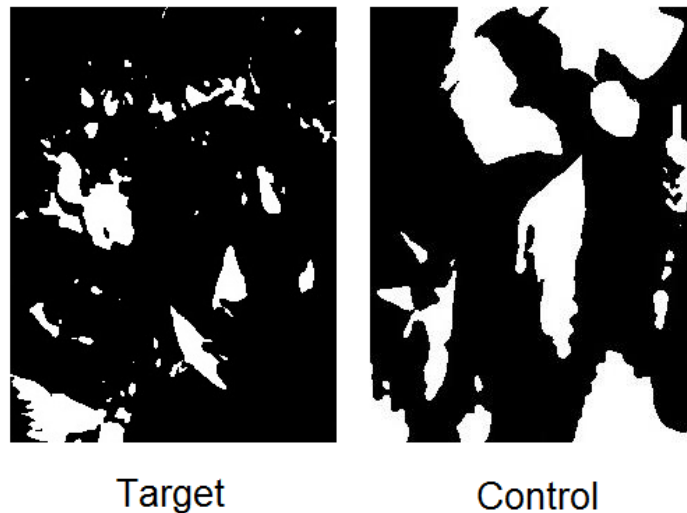
Figure 4.5 The target and control stimuli in the Mooney task

The target is a degraded black and white image of a human face, whereas the control comprises a meaningless arrangement of white blobs on a black background.

The main task was separated into 6 runs and started with two practice examples. Within each run a 'Before' block of 10 randomly presented Mooney images (5 targets, 5 controls) was shown. Subsequently, the participants saw three 'Template' blocks consisting of the original 10 colour templates that the Mooney images were created from, presented back-to-back, randomly intermixed and with a 5.5s break in between the blocks. Subsequently, the participants saw the 'After' block consisting of the same 10 Mooney images again in a random order. Each trial in the 'Before' and 'After' block started with a presentation of the Mooney image for 2s, followed by a Gaussian white noise for 300ms, a blank screen for 500ms, and a response window with the prompt 'Did you see a face in that image?' with the response options of '1 = yes, confident', '2 = yes, not confident', '3 = no, not confident', and '4 = no, confident'. Participants could respond at their own pace by pressing one of the four buttons on the keyboard, after which an intertrial interval of 1s was presented and the next trial began. On each trial in the 'Template' block the colour template was presented for 2s, and participants were

instructed to observe the images, but no response was required. Overall there were 120 experimental trials (half before seeing templates, half after), and 120 template trials. The performance was assessed by calculating the hits and false alarms on the experimental trials in the 'Before' and 'After' blocks; responses 1-2 were counted as hits for targets and false alarms for controls, responses 3-4 as misses for targets and correct rejections for controls. The pooling of responses was identical in the study by Teufel and colleagues (2015) – this was done in the original study because there was not enough middle (i.e., not confident) options. These measures were then used to calculate detection sensitivity (d') of faces in the Mooney images, as well as the criterion (C) or the bias to report a face as present.

Figure 4.6 An example of a colour template in the Mooney task

This image was used to generate a corresponding two-tone Mooney target image. After viewing this image for a while, it should be easier to disambiguate the same person's face in the target image shown in Figure 4.5 (left panel).
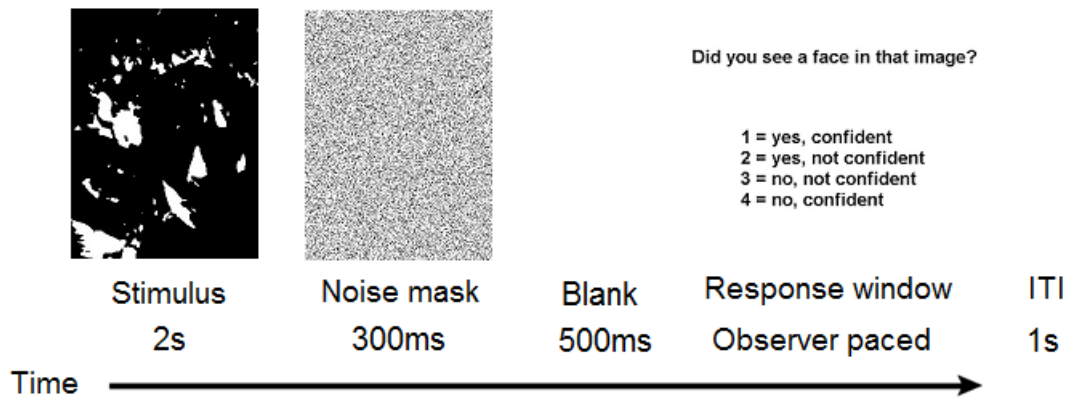
Figure 4.7 The trial structure of the Before and After blocks of the Mooney task

On each trial participants saw the Mooney stimulus (either a target or a control), followed by a noise mask, a blank, and a self-paced response window with four response options regarding the presence of a face in the Mooney image.

4. *The Cardiff Anomalous Perception Scale*

The Cardiff Anomalous Perceptions Scale (Bell et al., 2006) comprises 32 questions (with response options of 'Yes and 'No') and assesses experience of perceptual anomalies in all sensory modalities, such as hearing voices or experiencing visual or tactile hallucinations. An example of the items: "Do you ever see shapes, lights, or colors even though there is nothing really there?". The CAPS is thought to be a perceptual index of schizotypy in the general population and relates to a spectrum of experiences that occur in psychosis (Teufel et al., 2015). If participants answered 'Yes' to an item, they were additionally asked to evaluate the level of distress, intrusiveness, and frequency of the experience on a 5-point scale. Two scores were derived; a CAPS and CAPS total score, the latter was the CAPS score together with the distress, intrusiveness, and frequency scores.

5. *Autism-Spectrum Quotient*

The AQ (Baron-Cohen et al., 2001) is a questionnaire measuring autism spectrum traits within the general population. The AQ comprises 50 questions and uses a 4-point Likert response scale ranging from 'Definitely Agree' to 'Definitely Disagree'. The questionnaire is divided into five sub-scales pertaining to different perceptual, cognitive, and social aspects of the autism spectrum trait; social skill, attention switching, attention to detail, communication, and imagination. The total score, as well as the score on the attention to detail subscale was used in the analyses. The latter subscale includes items such as "I usually notice car number plates or similar strings of information".

4.3.2 Results

Data preparation

For the CB task the coordinates of the reported change locations were analysed, and responses with coordinates outside the ROIs were considered a failure to detect the change and thus added to misses. The cumulative percentage of correctly identified changes was calculated at each time point (e.g., % Correct with RTs of below 1s, 2s, 3s ... 60s); an inverse exponential function was then fit to this data, generating parameters α and β for each participant in each session, according to the function $Y = \alpha e^{\beta / X}$, where Y is the cumulative percentage correct, X is the time in seconds, α is the asymptote and β relates to steepness/curvature. Given that all participants should be able to detect the change, with infinite time, the asymptote should be around 1.0. A greater α therefore corresponds to more detected changes during the 30s presentation window. A smaller negative β indicates that participants are more likely to reach asymptote quickly: i.e., detect changes faster. The data preparation in the CB task was

identical to that in Andermane and colleagues (2019), more details on this can be found in *Chapter 2*.

The Mooney task performance was assessed by calculating the percentage of hits to Mooney targets and false alarms to Mooney controls in the 'Before' and 'After' blocks (e.g., responses 'yes, confident' and 'yes, not confident'). The detection sensitivity was then estimated by calculating d' values in 'Before' and 'After' blocks (formula: $d' = Z_{Hit} - Z_{FA}$). The response criterion (C) was also calculated to estimate the bias to report a face as present in the 'Before' and 'After' blocks (formula: $c = -1/2(Z_{Hit} + Z_{FA})$). We were primarily interested in how detection sensitivity changes from the 'Before' to the 'After' block and whether this predicts performance on other measures, as this was the measure Teufel and colleagues (2015) correlated with perceptual anomalies. However, we also wanted to assess if the response criterion changed after seeing the templates. Two participants had a false alarm rate of 0 in the Mooney task, so their d' values could not be accurately estimated – their Mooney task measures were marked as missing but the data from the rest of the tasks was used for analyses.

Analyses

The descriptive statistics of the perceptual tasks and questionnaires are presented in Table 4.1 and the correlation matrix with associations between the measures is presented in Table 4.2.

Table 4.1 The summary statistics of the measures

The listed measures are as follows: the d' in the Mooney task before seeing the colour templates, the d' after seeing the templates, the d' improvement due to seeing the templates, the response criterion before seeing the templates, the response criterion after seeing the templates, the change in response criterion due to seeing the templates, the total score of the AQ, the score in the attention to detail subscale of the AQ, the CAPS score, the total CAPS score including the distress, intrusiveness, and frequency subscales, the number of alternations in perceptual rivalry, CB parameter α, CB parameter β. All Mooney task measures N = 48, for the rest of the tasks and questionnaires N = 50.

Measure	Mean	SD
Mooney d' before	0.96	0.39
Mooney d' after	0.98	0.43
Mooney d' improvement	0.02	0.34
Mooney C before	0.40	0.40
Mooney C after	0.20	0.46
Mooney C change	-0.20	0.21
AQ	15.68	5.64
AQ AD	5.18	2.16
CAPS	10.24	6.37
CAPS total	83.74	56.91
Perceptual rivalry	44.50	22.37
CB α	1.04	0.12
CB β	-5.88	1.32

Table 4.2 Pearson correlations between the measures

The correlated measures are as follows: the d' in the Mooney task before seeing the colour templates, the d' improvement due to seeing the templates, the AQ score; the score in the attention to detail subscale of the AQ, the CAPS score, the CAPS total score including the distress, intrusiveness, and frequency subscales, the number of alternations in perceptual rivalry, the CB parameter α, and the CB parameter β. For all measures N = 50, except in the Mooney task where N = 48. The significant correlations are bolded. Only the AQ x AQ AD, CAPS x CAPS total correlations survived the Benjamini-Hochberg correction.

	d' before	d' improv.	AQ	AQ AD	CAPS	CAPS total	Rivalry	CB α	CB β
d' before	1	-.32	.07	-.11	-.05	-.14	-.21	-.02	**.33**
		(.027)	(.627)	(.477)	(.743)	(.335)	(.151)	(.901)	**(.021)**
d' improv.		1	.07	.13	**-.32**	-.24	.03	.13	-.24
			(.628)	(.370)	**(.026)**	(.097)	(.818)	(.399)	(.101)
AQ			1	**.46**	.09	.14	-.16	.09	.06
				(.001)	(.528)	(.320)	(.280)	(.530)	(.697)
AQ AD				1	.10	.07	-.03	**.39**	.08
					(.475)	(.621)	(.817)	**(.005)**	(.572)
CAPS					1	**.93**	.26	-.17	-.16
						(<.001)	(.065)	(.226)	(.275)
CAPS total						1	.26	-.14	**-.31**
							(.070)	(.338)	**(.029)**
Rivalry							1	-.15	.08
								(.294)	(.593)
CB α								1	-.09
									(.554)
CB β									1

The d' improvement due to seeing the colour templates was only 0.02.

Furthermore, the d' in the 'Before' block (0.96) was not significantly different from the

d' in the 'After' block (0.98), $t(47) = -0.50$, $p = .622$, Cohen's $d = 0.07$. Therefore, seeing the colour templates did not significantly improve the detection of faces in the Mooney task. There was no net improvement in detection sensitivity because as the correct identifications increased, so did the false alarms; there was a significantly higher rate of hits after seeing the templates (Mean = 59.13%, SD = 18.44%) relative to before (Mean = 51.87%, SD = 17.42%), $t(47) = -7.16$, $p < .001$, Cohen's $d = 1.01$, and there was also a significantly higher rate of false alarms after seeing the templates (Mean = 26.20%, SD = 15.82%) relative to before (Mean = 20.20%, SD = 12.46%), $t(47) = -4.56$, $p < .001$, Cohen's $d = 0.65$. The criterion; however, was smaller after seeing the templates (Mean = 0.20, SD = 0.46) relative to before (Mean = 0.40, SD = 0.40), $t(47) = 6.60$, $p < .001$, Cohen's $d = 0.95$, meaning that the response bias became more liberal after exposure to prior knowledge – this was also observed by Teufel and colleagues (2015). Although the detection sensitivity observed in the present study is comparable to and even greater than that found in Teufel and colleagues' (2015) experiment with healthy subjects (i.e., d' before of about 0.5 and after 0.9), their d' improvement was approximately 0.3. Our results demonstrate that on the group level, possessing prior knowledge of the faces did not confer a benefit for face detection in the Mooney images. This may mean that overall it was too difficult to disambiguate faces in the degraded stimuli of our study.
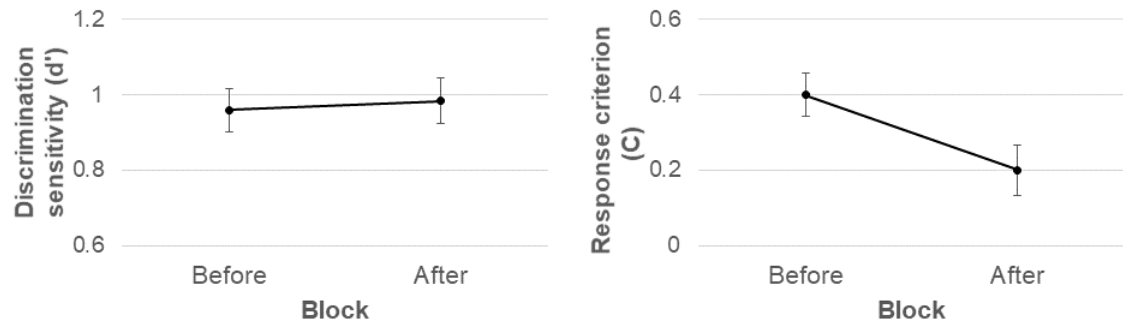
Figure 4.8 The average sensitivity (d') and response criterion (C) in the Before and After blocks of the Mooney task

N = 48 and the error bars represent 1 SEM.

Reliance on priors and atypical perception

There was a significant negative correlation between Mooney d' improvement and CAPS score, $r = -.32$, $p = .026$. This relationship was the opposite direction of that reported by Teufel and colleagues (2015) and indicates that the fewer perceptual anomalies participants reported, the greater their improvement in the Mooney face detection task after seeing the colour templates (see Figure 4.9 for scatterplots). However, given that the improvement in d' due to the exposure to colour templates was overall not significant, this result is not straightforward to interpret. Additionally, see Figure 7.4 in Appendix B for the relationships between CAPS and changes in hits and false alarms due to seeing the templates. There is a trend for hits to decrease and false alarms to increase for people with more reported perceptual anomalies. This would suggest individuals with high schizotypy have poorer discrimination sensitivity after obtaining prior knowledge. No correlations emerged between reliance on priors and autism spectrum traits.
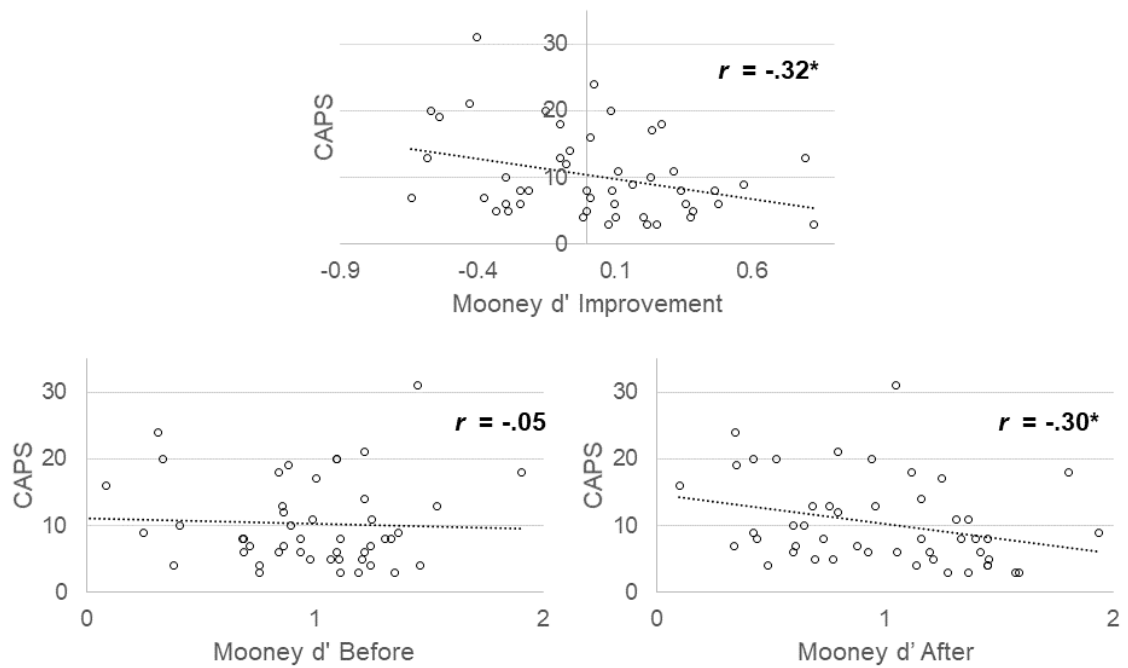
Figure 4.9 Scatterplots illustrating the relationship between reliance on prior knowledge and schizotypy

The upper scatterplot illustrates the correlation between the improvement in the Mooney face recognition task due to seeing the colour templates and the reported perceptual anomalies in the CAPS. Correlations between face detection in the Before and After blocks and CAPS are additionally provided in the lower panels demonstrating those with fewer perceptual anomalies tended to perform better only after seeing the templates. The associated Pearson's *r* coefficient along with its two-tailed significance level (* $p < .05$, ** $p < .01$, *** $p < .001$) is provided on each panel.

Reliance on priors and change detection

There was a significant positive correlation between CB parameter β and the d' value in the 'Before' block of the Mooney task, $r = .33$, $p = .021$. This indicates that participants who detected more faces in the Mooney targets at baseline (before seeing the templates) also detected changes more readily in the CB task (see Figure 4.10 for scatterplots). This positive correlation suggests that a superior perceptual closure ability when exposed to ambiguous visual information is associated with increased change detection rate. CB parameter β was also significantly negatively correlated with the CAPS total score, $r = -.31$, $p = .029$, suggesting that reporting fewer perceptual

anomalies and lower distress, intrusiveness, and frequency scores is associated with noticing visual changes at a faster rate. There was also a significant positive correlation between CB parameter α and the attention to detail subscale of the AQ, $r = .39$, $p = .005$, suggesting that greater self-reported attentiveness to detail predicts more identified changes in CB task. No significant relationship emerged between reliance on priors and change detection.

Teufel and colleagues (2015) did not report response criterion correlations and in our study the response criterion ('Before', 'After, change) did not correlate with any of the change detection or atypical perceptual measures.
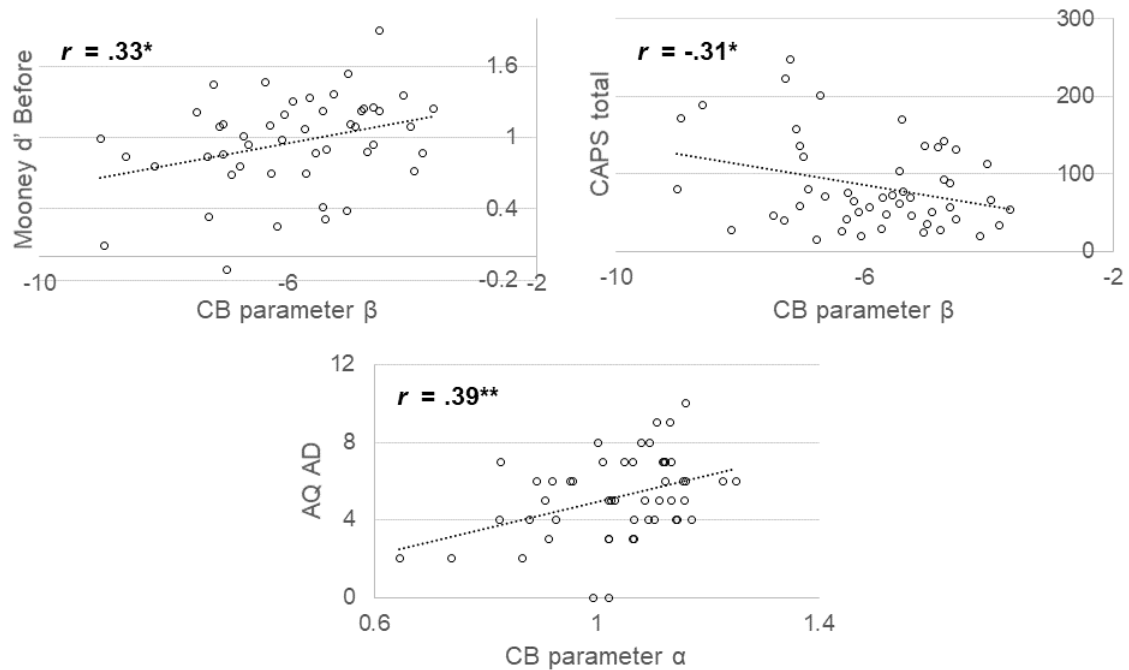
Figure 4.10 Scatterplots illustrating the correlations between CB parameters, perceptual closure, and atypical perception

The correlations between the CB parameters (β measuring the rate of change detection and α measuring the proportion of identified changes), face detection in the Mooney task at baseline reflecting perceptual closure, and atypical perception (CAPS and the AQ attention to detail subscale). The associated Pearson's *r* coefficient along with its two-tailed significance level (* $p < .05$, ** $p < .01$, *** $p < .001$) is provided on each panel.

4.3.3. Conclusion

In our first experiment we sought to measure individual differences in reliance on prior knowledge in visual perception. Reliance on priors was operationalized as the improvement in face detection in degraded two-tone Mooney images after seeing the corresponding colour templates. We aimed to discover if influence of priors could predict individual differences in everyday perceptual abilities, specifically, change detection in naturalistic scenes. We also aimed to investigate the relationship between reliance on priors and sub-clinical atypical perception, assessed by perceptual traits related to psychosis (e.g., perceptual anomalies) and the autism spectrum (e.g., attention to detail). A stronger effect of prior knowledge on visual perception was hypothesised to predict better change detection (Andermane et al., 2019), more perceptual anomalies (Teufel et al., 2015), and a lower number of autism spectrum traits (Pellicano & Burr, 2012).

We found that a better face detection ability in the Mooney task at baseline predicts a faster rate of change detection rate in naturalistic scenes. Although the Mooney task requires facial discrimination, it is primarily a test of perceptual closure, as it involves building a gestalt from disparate elements (Thurstone 1944; 1950; Mooney, 1957; Grützner et al., 2010; Verhallen et al., 2014). Wasserstein, Barr, Zappulla, & Rock (2004) report that baseline face detection in the Mooney task loads more highly onto a factor that underlies performance in various types of closure tasks (i.e., tasks that require developing an emergent gestalt) rather than tasks tapping face discrimination ability alone. Our finding therefore suggests that an improved perceptual closure when presented with ambiguous visual input predicts a better ability to detect visual changes. It may be that an ability to form high-level predictions more readily also aids detection of changes, as being able to rapidly build an internal representation or gestalt of the

scene may be necessary to detect changing objects within the scene. Binding of disparate elements into a whole representation is key for closure and relational binding of objects may also be important for detecting an appearance or disappearance of an object within the context of a scene (Aly et al., 2013; Olsen et al., 2012).

Change detection and Mooney face detection may be related because they share underlying neural substrates, as perceiving Mooney faces activates brain areas similar to those implicated in awareness of visual changes (i.e., the pulvinar, occipitotemporal and frontal areas, and PPC) (Grützner et al., 2010; Beck et al., 2001; Pessoa & Underleider, 2004). Early joint activation of inferotemporal gyrus and PPC in closure tasks is thought to match the current sensory input (i.e., shape and shading patterns) with representations held in long-term memory (i.e., face templates), which then help to disambiguate the signal (Grützner et al., 2010). This interpretation is consistent with the role of PPC in a wide range of recognition tasks; the PPC is consistently activated in episodic retrieval and may mediate the link between current visual input and long-term representations stored in the hippocampus (Wagner, Shannon, Kahn, & Buckner, 2005). Change detection and perceptual closure may both depend on the efficiency of these processes pertaining to matching current and stored visual representations. This is also in line with our previous research on individual differences in CB, which suggests that superior change detection ability is associated with an ability to form more accurate VSTM representations (Andermane et al., 2019).

Change detection in the present study was also significantly and positively predicted by the attention to detail subscale of the AQ, which agrees with earlier research showing that people with autism tend to outperform controls in change detection (Smith & Milne, 2009) and are faster in detecting marginal items in scenes (Ashwin, Wheelwright, & Baron-Cohen, 2017). Our result is also logical, given the

subscale consists of questions such as "I tend to notice details that others do not" and "I notice patterns in things all the time". The fact that the overall AQ score did not correlate with change detection indicates that being detail-focused predicts detection whether associated with the other spectrum traits or not. In contrast, schizotypy assessed by proneness to perceptual anomalies predicted poorer change detection. It is conceivable that experiencing greater departures from the sensory signal in the form of sensory hallucinations and the associated distress that they cause may disrupt the ability to quickly and accurately register visual changes that do occur. Note that both of these findings are contrary to the suggested role of predictive processing biases – we hypothesized individuals with high schizotypy would be better at change detection, whereas individuals on the spectrum would be worse, if they have an underlying bias of strong versus weak priors. Individuals on the autism spectrum may not have weak priors after all, because perceptual priors (even low-level ones) are needed for accurate perceptual discriminations (Teufel et al., 2013; Van de Cruys et al., 2014).

Our previous finding that greater perceptual stability when viewing the ambiguous structure-from-motion stimulus predicts superior change detection ability was not replicated in the present study (Andermane et al., 2019). In fact, perceptual rivalry alternation rate was not significantly related to any other of our variables. It is to be noted, however, that perceptual rivalry has as high a test-retest reliability so it captures reliable individual differences in cognitive mechanisms, but these may not predictive of other perceptual abilities. Thus, although conceptually perceptual rivalry alternation rate seems to index the frequency with which individuals update perceptual predictions (Kanai et al., 2011), behaviourally it reflects a distinct perceptual/cognitive process from reliance on priors or visual change detection.

Importantly, we did not replicate the original finding by Teufel and colleagues (2015) that schizotypal individuals benefitted more from exposure to colour templates in Mooney face detection. On a group level our participants did not significantly improve in the Mooney face detection task due to possessing prior knowledge, as the average improvement in detection sensitivity was close to zero. On an individual level, there was a significant negative correlation between the reported perceptual anomalies and improvement in Mooney face detection sensitivity. This meant that individuals less prone to perceptual anomalies actually benefitted from exposure to original photos more when disambiguating faces in the two-tone images. The failure to replicate the finding by Teufel and colleagues (2015) let alone finding a significant correlation between the measures in the opposite direction is challenging to interpret. Tulver and colleagues (2019) reported the same (negative) correlation as us, which could reflect that schizotypal individuals are in fact less sensitive when detecting faces in ambiguous displays, perhaps due to being more prone to false alarms (i.e., mistakenly seeing faces in the control images). However, as our participants on average did not improve after seeing the templates, it may be that our measures were not sensitive enough to detect genuine biases in the reliance on prior knowledge versus sensory evidence. Perhaps our Mooney stimuli were too complex, and participants could not easily disambiguate faces in them. Due to this, from Experiment 1 alone it is difficult to conclude whether a greater reliance on prior knowledge is predictive of the ability to detect changes, or of the traits associated with autism and psychosis.

A key difference between the Mooney stimuli used by Teufel and colleagues (2015) and us is that we presented the colour templates in their original size but cropped the Mooney targets and controls out of the templates to remove contextual information. This was done to make the Mooney targets maximally ambiguous, as described in the

Mooney face construction process by Verhallen and Mollon (2016). However, given the improvement in face detection sensitivity due to seeing the templates was not significant on the group level, it could be that the templates were not informative enough. It could be argued that when the template and target differ in size and when the context is removed in the target, it is more difficult to utilise the prior knowledge for finding a face. Our task may not be measuring reliance of prior knowledge as such but perhaps the ability to manipulate this knowledge to identify a fragment as a part of a previously seen whole. Consequently, we decided to conduct a second experiment, where the templates and targets were of the same size and cropped identically to mirror the stimuli of Teufel and colleagues (2015) more closely. This should make it easier for participants to make a link between the templates and targets and allow us to see whether the finding of Teufel and colleagues (2015) is replicable.

4.4. Experiment 2

4.4.1. Method

Participants

Fifty-four adult participants (Aged 23 – 68, Mean = 38.20, SD = 12.29; 24 female) with normal or corrected-to-normal vision, no reported colour vision deficiencies, no sensitivity to flashing lights or epilepsy, and no diagnosed mental disorders took part in this online experiment. The participants were adults of all ages from the global community who were recruited via Amazon Mechanical Turk and received monetary reward for their time.

Materials and Design

In this experiment we administered two questionnaires (the AQ and CAPS) and the Mooney task. The only difference between the Mooney task administered in Experiment 1 and Experiment 2 was that in the latter the colour templates were also cropped, such that the contextual information was removed in both the templates and targets, and they were identical in size and position (see Figure 4.11).

Figure 4.11 An illustration of the new cropped Mooney templates and targets

In Experiment 2 the colour templates, Mooney targets, and controls were all cropped identically and were of the same size.

4.4.2. Results

The data was prepared in the same manner as in Experiment 1. For the descriptive statistics of Experiment 2 see Table 4.3, for the correlation matrix with associations between the measures see Table 4.4.

Table 4.3 The summary statistics of the measures

The listed measures are as follows: the d' in the Mooney task before seeing colour templates, d' in the Mooney task after seeing colour templates, the d' improvement due to seeing the templates, the response criterion before seeing the templates, the response criterion after seeing the templates, the change in response criterion due to seeing the templates, the total AQ score, the attention to detail subscale score of the AQ, the CAPS score, the total CAPS score including the distress, intrusiveness, and frequency subscales (N = 54).

Measure	Mean	SD
Mooney d' before	0.79	0.44
Mooney d' after	0.94	0.58
Mooney d' improv.	0.15	0.45
Mooney C before	0.37	0.52
Mooney C after	0.14	0.52
Mooney C change	-0.23	0.22
AQ	18.63	8.74
AQ AD	5.15	2.76
CAPS	2.65	3.20
CAPS total	21.54	28.98

Table 4.4 Pearson correlations between the measures

The correlated measures are as follows: the d' in the Mooney task before seeing the colour templates; the d' improvement due to seeing the templates; the AQ score; the attention to detail subscale score of the AQ; the CAPS score; the total CAPS score including the distress, intrusiveness, and frequency subscales (N = 54). The significant correlations are bolded.

Measure	d' before	d' improv.	AQ	AQ AD	CAPS	CAPS total
d' before	1	-.16	.08	.002	.01	.001
		(.259)	(.588)	(.990)	(.933)	(.995)
d' improv.		1	-.06	-.20	-.07	-.12
			(.695)	(.147)	(.632)	(.395)
AQ			1	**.57**	.24	.24
				(<.001)	(.086)	(.087)
AQ AD				1	**.31**	.26
					(.024)	(.063)
CAPS					1	**.95**
						(<.001)
CAPS total						1

Reliance on priors and atypical perception

The Mooney task d' improvement due to templates was 0.15, which is comparable to that found by Teufel and colleagues (2015). Furthermore, the d' in the 'Before' block (0.79) was significantly different from the d' in the 'After' block (0.94), $t(53) = -2.42$, $p = .019$, Cohen's $d = 0.33$. As in Experiment 1, there was a significantly higher rate of hits after seeing the templates (Mean = 61.60%, SD = 16.84%) relative to before (Mean = 50.86%, SD = 18.35%), $t(53) = -8.34$, $p < .001$, Cohen's $d = 1.14$, and there was also a significantly higher rate of false alarms after seeing the templates (Mean = 30.31%, SD = 20.85%) relative to before (Mean = 25.56%, SD = 18.07%), t

(53) = -3.58, *p* < .001, Cohen's *d* = 0.49. The criterion was significantly smaller after seeing the templates (Mean = 0.14, SD = 0.52) relative to before (Mean = 0.37, SD = 0.52), *t* (53) = 7.73, *p* < .001, Cohen's *d* = 1.05, showing that, as previously reported, the criterion became more liberal. These results demonstrate that the colour templates did improve the detection of faces in the Mooney task in Experiment 2 and the task is comparable to that presented by Teufel and colleagues (2015).
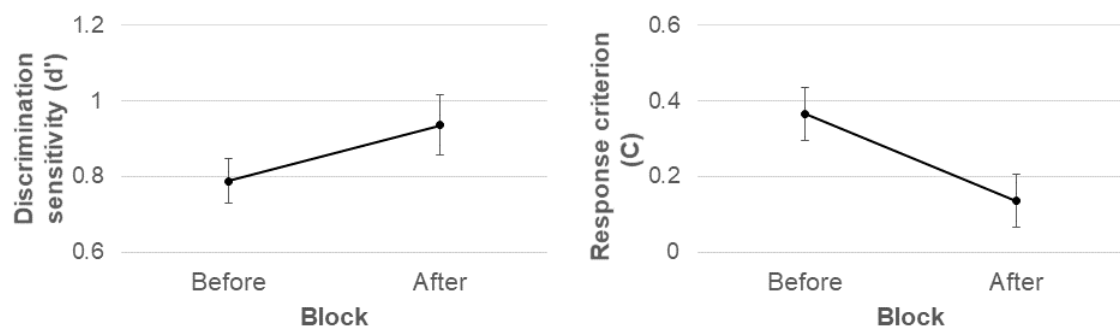
Figure 4.12 The average sensitivity (d') and response criterion (C) in the Before and After blocks of the Mooney task

N = 54 and the error bars represent 1 SEM.

However, the positive correlation between CAPS scores and d' improvement that was previously found by Teufel and colleagues (2015) could not be replicated in this experiment – a negative trend was present, as we observed in Experiment 1.

The only significant relationship that emerged was a positive correlation between the attention to detail subscale of AQ and CAPS score, *r* = .31, *p* = .024. This suggests that people who reported being more attentive to detail were also prone to report more perceptual anomalies (see Figure 4.13). Note that this relationship was not previously significant in the lab-based sample but correlations between AQ and CAPS have been noted before (Horder et al., 2014).
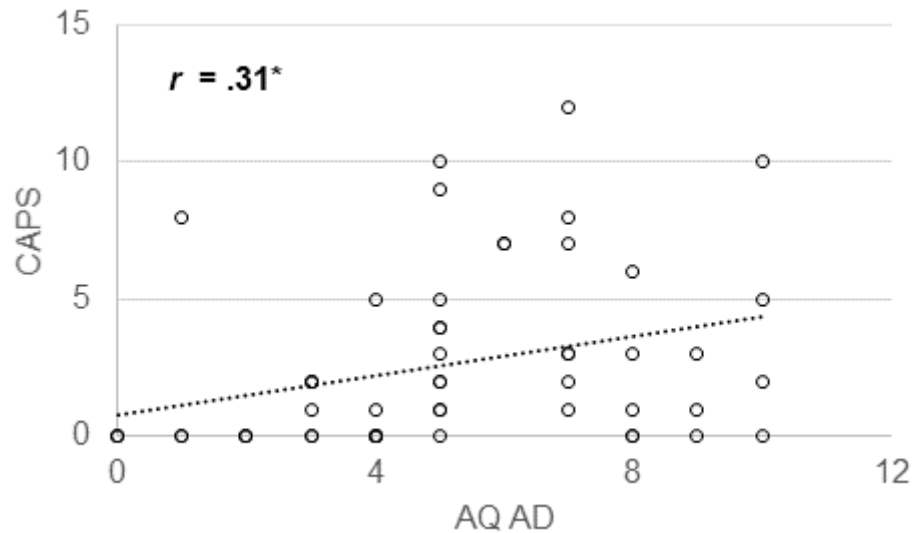
Figure 4.13 The relationship between the attention to detail subscale of the AQ and the CAPS score

The associated Pearson's *r* coefficient along with its two-tailed significance level (* $p <$ .05, ** $p < .01$, *** $p < .001$) is provided on the panel.

4.4.3. Conclusion

In our second experiment we improved the stimuli of the Mooney task by creating identically cropped and sized colour templates, targets, and controls. In doing so, we aimed to determine whether the relationship between reliance on priors and schizotypy (Teufel et al., 2015) can be replicated with an equivalent set of stimuli. On a group level we found a significant improvement in face detection sensitivity between the 'Before' and 'After' blocks, suggesting prior knowledge conferred a benefit in the detection of faces. However, this detection improvement did not yield any significant correlations with the CAPS or AQ scores, suggesting that reliance on prior knowledge in this paradigm is not associated with schizotypy or autism traits in the general population.

A positive correlation was observed between the attention to detail subscale of the AQ and reports of perceptual anomalies. This association may have emerged

because the statements of the subscale such as "I often notice small sounds that others do not" and "I usually notice small changes in a situation, or a person's appearance" have a thematic overlap with some of the experiences that schizotypal individuals typically report, as illustrated by the CAPS questions "Do you ever hear noises or sounds when there is nothing about to explain them?" and "Do you ever find the appearance of things or people seems to change in a puzzling way, e.g., distorted shapes or sizes or colour?". Similarly, the statement in the AQ subscale "I notice patterns in things all the time" is reminiscent of the reports that people high in shizotypy and people experiencing psychosis develop delusions whereby irrelevant stimuli are assigned high relevance and patterns of meaning are imposed on stimuli that are seemingly unconnected (Fletcher & Frith, 2009). Autism and schizophrenia have previously been conceptualised as existing on opposite ends of a spectrum (Crespi & Badcock, 2008) and our result is consistent with a study demonstrating a positive correlation between CAPS and AQ scores in a substantial sample from the general population (e.g., $r = .33$, N = 772, Horder et al., 2014). There are suggestions that ASD and psychosis may share common atypical information processing mechanisms in terms of how stimuli are assigned salience, and how this information is then utilised to develop internal probabilistic inferences and models of the world. It is suggested that individuals with autism and psychosis assign high weight to violations of expectations, albeit leading to different perceptual and cognitive consequences (Van de Cruys et al., 2014).

In autism, inflexibly high confidence for violations of perceptual predictions is thought to result in greater sensitivity to sensory information, and greater accuracy in some perceptual tasks requiring high sensory precision such as visual search (Keehn et al., 2009). However, this tendency may compromise the ability to form abstract

predictions due to a lower ability to ignore spurious or uninformative prediction errors, leading to the various observed difficulties in autism from sensory overload (Ward, 2018), lower susceptibility to visual illusions, reduced ability to process stimuli globally to problems in the social domain such as development of theory of mind (Van de Cruys et al., 2014). Similarly, trait abnormalities of psychosis are thought to be related to aberrant metacognition, in particular, overestimating the precision of prediction errors (Adams et al., 2013). However, Adams and colleagues (2013) argue that a later compensatory mechanism may be at work, where precision of sensory evidence is downregulated and reliance on priors increases, which may explain state abnormalities such as hallucinations, as well as the tendency to form predictions based on limited information that are resistant to disconfirmatory evidence (Bentall et al., 1991; Warman, 2008; Woodward et al., 2008). Our finding that in the general population greater attentiveness to detail of the AQ is predictive of more reported perceptual anomalies is consistent with the view that people with traits associated with psychosis tend to assign high precision to prediction errors, similarly to individuals on the autistic spectrum.

4.5 Discussion

Reliance on priors, assessed by improvement in Mooney face detection sensitivity due to seeing the original images, did not predict visual change detection ability with naturalistic scenes in the present study. However, the rate of change detection was predicted by perceptual closure in the Mooney task at baseline (before any knowledge of the faces). That is, participants who found it easier to disambiguate faces in the two-tone images also detected visual changes more readily. Individuals who are capable of fast perceptual closure may also notice visual changes faster because binding disparate elements into a coherent representation and matching current percept

to stored representations are key mechanisms in both detection tasks and both rely on similar neural substrates (Beck et al., 2001; Pessoa & Underleider, 2004; Aly et al., 2013; Olsen et al., 2012; Grützner et al., 2010). Change detection was also positively predicted by the attention to detail aspect the autism spectrum, consistent with previous work on autism showing it is associated with superior perceptual discrimination of novel stimuli, visual search, and change detection (Plaisted, O'Riordan, & Baron-Cohen, 1998; Keehn et al., 2009; Smith & Milne, 2009). The tendencies of easily forming a global gestalt versus being detail-focused appear to be rather opposite cognitive styles (Happé, & Frith, 2006) but both predicted change detection ability in the present study. It may be the case that successful change detection can be accomplished via different strategies or via a combination of both approaches (i.e., noticing a change in the relational aspects of the scene context versus focused scanning of the individual elements).

In two separate experiments (lab-based and online-based) we did not replicate the Teufel and colleagues' (2015) finding that schizotypal individuals demonstrate a shift towards reliance on priors. In fact, our lab-based experiment yielded a significant association in the opposite direction, whereby those less prone to sensory hallucinations benefitted more from exposure to prior knowledge in terms of their sensitivity (i.e., detected more faces and false alarmed less). Our online-based experiment improved upon the lab-based stimuli and although this time participants benefitted from seeing the templates, their performance improvement was not correlated with perceptual anomalies. This indicates that the previously reported relationship between reliance on priors and psychosis-like symptoms in the general population may not be replicable. If reliance on perceptual priors is a consistent trait-like tendency, then it should be possible to measure it allowing slight differences in the stimuli set. Moreover, we used a

comparable set of stimuli and sample to Teufel and colleagues (2015), so the lack of association (a) calls into question reliance on priors as a trait or (b) calls into question the relationship between reliance on priors and perceptual anomalies.

Given our findings, the proposal that people high on psychotic traits benefit from prior knowledge in perceptual discrimination sensitivity must be re-considered. From a conceptual point of view, if individuals are more likely to rely on prior knowledge in perception when the faces are present (hits), they would also do so when faces are absent (false alarms), therefore it is not clear why overall sensitivity would be enhanced. Indeed, when asked to detect faces in noisy displays individuals with high schizotypy have a reduced detection sensitivity and are more likely to see meaningful patterns in visual noise (i.e., false alarm) than those with low schizotypy (Partos, Cropper, & Rawlings, 2016). The authors explain this pattern of results as individuals with schizotypy having an increased neural noise, which makes it more difficult to detect genuine signal but also forces the system to attempt to fit internal models to noisy input, generating false alarms in the process. Consistent with this, individuals with psychotic traits are also more easily conditioned to hear auditory hallucinations (Powers et al., 2017). A bias to project priors onto ambiguous information may sometimes increase correct detection; however, it would be at the cost of increased false alarms, so it is arguable whether discrimination can truly increase in a visual system that is prone to sensory hallucinations. Our results seem to show that improvement in detection sensitivity due to priors is either unchanged (Experiment 2) or even reduced (Experiment 1) in people who experience more perceptual anomalies.

Neither the Mooney face detection at baseline, nor the improvement due to seeing the colour templates predicted autism spectrum traits. As the perceptual phenotype of autism spectrum is associated with staying true to the signal, we expected

to observe a tendency for seeing the disparate patterns rather than the whole face in Mooney images. This hypothesis was motivated by the weak priors account of the autism spectrum (Pellicano & Burr, 2012). Our result is contrary to ample behavioural evidence demonstrating individuals with autism prefer a local (i.e., detail-focused) rather than global processing style (Happé, & Frith, 2006) and observations that they have a lower Mooney face detection rate (Sun et al., 2012). However, associations with Mooney task are not always found when testing individuals below the threshold for ASD diagnosis (e.g., no association with AQ using a sample from general population of > 300 individuals by Verhallen et al., 2014). Van de Cruys, Vanmarcke, Van de Put, and Wagemans (2018) recently administered a Mooney task equivalent to that of Teufel and colleagues (2015) and found that even individuals with an ASD diagnosis performed as well to controls at baseline, and had a similar improvement in performance due to exposure to the original photos. Van de Cruys and colleagues (2018) also found the AQ did not predict reliance on prior knowledge in an experiment conducted with a large sample of healthy individuals. Our null result with autism spectrum was also mirrored by Tulver and colleagues (2019) who used and equivalent Mooney task. On the whole, our results and similar recent research challenge the idea that individuals with autism spectrum traits have weak priors or a poorer ability to use contextual knowledge.

Perceptual rivalry alternation rate did not correlate with reliance on priors, nor with any of our perceptual and questionnaire measures in this study. There are large and stable individual differences in perceptual and binocular rivalry alternation rate (Miller et al., 2010; Andermane et al., 2019), suggesting as a measure it indexes stable individual differences in perceptual/cognitive mechanisms. However, these may not tap predictive processing biases as such (Kanai et al., 2011) or predict typical (visual

change detection ability) or atypical perception (proneness to sensory hallucinations, autism spectrum traits).

To conclude, the operationalisation of reliance on priors/ predictive processing bias needs to be carefully considered in light of repeated failures to replicate hypothesised associations between this trait and atypical perception here and elsewhere. It may be the case that the improvement in the Mooney task does not sensitively measure an underlying trait of prior reliance. For example, it has been suggested that the improvement in performance can relate to two or more distinct processes, such as the strength of the encoded memory trace of the template versus the ability to apply this information to the Mooney image (i.e., matching) (Van de Cruys et al., 2018). Alternatively, it may be that there is no method-general trait of prior reliance and in turn this may depend on the type of stimuli and task. Participants may be more prone to rely on perceptual priors in some contexts but have no general tendency across the board. For example, the Mooney face detection ability at baseline does not predict performance on similar gestalt-based tasks, such as identifying objects and animals in incomplete figures (Foreman, 1991). Studies with different closure-related paradigms show that the ability to form a gestalt is not strongly unitary; the variance in gestalt-based perception is best explained by a multi-factorial structure, suggesting task-specific mechanisms (Wasserstein, Zappulla, Rosen, Gerstman, & Rock, 1987). This mirrors recent research demonstrating that a collection of tasks measuring reliance on priors including the Mooney task do not form a unitary factor-structure (Tulver et al., 2019). Tulver and colleagues argue that conclusions about priors should not be decoupled from the stimuli they are measured with as this may lead to misleading generalisations and, crucially, that the influence of priors may change depending on the context, task, stimuli (e.g., faces, objects, scenes) and their associated representation in the hierarchy of the visual

system. For these reasons, in future research it is important to employ a battery of tasks when measuring the effect that perceptual priors exert on awareness; one measure may not suffice and if it is operationalised as such, its convergence validity needs to be verified. Future research should aim to develop a comprehensive and robust measure of reliance on priors and to explore whether it has predictive power of typical and atypical perception.

CHAPTER 5
Individual Differences in the Tendency to See the Expected

5.1. Abstract

Research has established that possessing prior knowledge of visual stimuli facilitates their entry into awareness. However, different methods are used to manipulate priors. For example, expectations are induced via cueing, perceptual priming, predictive context, or mental imagery. In the present study, we adopted an individual differences approach to explore whether a tendency to 'see the expected' is general or method specific. We administered a binocular rivalry task with Gabor patches and manipulated *selective attention* (i.e., instructing participants to focus on a particular stimulus), as well as induced expectations via *predictive context* (i.e., presenting a sequence that predicts the next stimulus), self-generated *imagery* (i.e., asking participants to visualise the stimulus), *expectancy* cues (i.e., suggesting that a stimulus is probable), and perceptual *priming* (i.e., repeating a stimulus). All prior manipulations led to an increased tendency to see the biased percept in the binocular rivalry display, except presenting primes with strong signal, which led to adaptation. Correlations and an exploratory factor analysis revealed that the facilitatory effect of priors on visual awareness is closely related to attentional control. We also investigated whether expectation-based biases predict variability in the experience of the visual world. For example, could a tendency to 'see the expected' predict the ability to detect visual changes, distractibility, vividness of mental imagery, and the experience of perceptual anomalies? Some prior manipulations correlated with perceptual experiences and traits – adaptation predicted change detection in naturalistic scenes and priming predicted perceptual anomalies. Taken together, our results indicate that the common mechanism that underpins the facilitatory effect of priors may be selective attention but the tendency to 'see the expected' is method specific.

5.2. Introduction

Numerous studies have demonstrated that possessing prior knowledge of stimuli facilitates their entry into visual awareness (Pearson, Clifford, & Tong, 2008; Summerfield & Egner, 2009; Melloni et al., 2011; Denison et al., 2011; Pinto et al., 2015). This is consistent with predictive processing theories which propose that perceptual content emerges as the brain generates top-down predictions about the world that are then tested against sensory evidence (Hohwy et al., 2008; Clark, 2013). However, different methods are used to manipulate the priors; some researchers manipulate expectations via explicit or symbolic cues that indicate the probability of the stimulus occurring (Pinto et al., 2015), others induce priors via perceptual priming of the stimuli (Brascamp, Knapen, Kanai, Van Ee, & Van Den Berg, 2007), others manipulate the predictive context of the task so that it is possible to anticipate the stimulus based on the preceding sequence (Denison et al., 2011), yet others ask participants to self-generate visual imagery (Pearson et al., 2008).

Irrespective of the exact method of prior induction, possessing prior knowledge of a stimulus demonstrably increases the probability of seeing it and enables it to be detected faster and based on weaker sensory evidence. For example, in binocular rivalry paradigms where different visual stimuli are presented to each eye and then compete for perceptual selection, individuals report seeing a particular percept more often and respond to it faster after being primed by it either directly or via self-generated imagery (Pearson et al., 2008). Similarly, presenting a sequence of rotating gratings increases the probability and reduces the latency of seeing a grating that matches the sequence in binocular rivalry (Denison et al., 2011). In the paradigm of perceptual hysteresis, degraded stimuli are less subjectively visible in the ascending sequence (high to low

noise) relative to the descending sequence (low to high noise), as expectations have been generated regarding the identity of a stimulus in the latter (Melloni et al., 2011). Thus, awareness of a stimulus can not only be facilitated by expectations but can also be sustained with a lower signal to noise ratio if expectations are present.

The question therefore arises as to whether the facilitatory effects of priors are determined by a common mechanism, or whether the mechanisms are distinct depending on how the prior is induced (e.g., by priming, imagery, predictive context, cueing). For example, some authors argue that perceptual priming is a similar process to self-generated mental imagery (Pearson et al., 2008) in that both are argued to rely on formation (or activation in the case of imagery) of a memory trace of the stimulus. In other prior manipulations, the representation of the stimulus is not directly activated by physical presentation but can be inferred by the preceding context (Denison et al., 2011). Furthermore, manipulation of expectations via explicit or symbolic cues that indicate the probability of a stimulus or work by association is arguably also distinct from perceptual priming, as these effects may rely on the learning of statistical regularities (Pinto et al., 2015). Although there are apparent differences in how these methods induce priors, the common mechanism may be activation (whether direct or indirect) of the representation of the expected stimulus. For instance, using MEG multivariate decoding techniques, Kok, Mostert, and de Lange (2017) found that learned auditory cues activate pre-stimulus sensory templates of the associated visual stimulus in visual cortex. Crucially, the magnitude of sensory template activation predicted the expectation-based behavioural improvement. If the facilitatory effects of priors on awareness are underpinned a common mechanism, activation of the sensory template of the expected stimulus may be a likely candidate.

Attention is another process that boosts sensitivity to visual stimuli albeit expectation and attention seem to accomplish this via markedly opposing neurocognitive mechanisms (Summerfield & Egner, 2009). Imaging research reveals that whilst expectation attenuates the overall neural activity in V1 for expected relative to unexpected stimuli, the pattern of activation becomes more specific to the expected stimulus – the neural representation is sharpened (Kok et al., 2012). In contrast, selective attention seems to operate by enhancing neural activity in visual cortex (Martinez et al., 1999; Kastner et al., 1999) thus increasing the signal of the attended location, feature or object representation whilst reducing the activity of competitors (Carrasco, 2011). This enhanced signal then results in a greater sensitivity for conscious detection and discrimination of the attended visual stimuli. Expectation and attention work synergistically, as predicted stimuli are frequently also task relevant. In fact, it has been proposed that expectation-based facilitatory effects on awareness and the corresponding sharpening of neural representations may work via attention, as neural representations of expected and unexpected stimuli cannot be differentiated when unattended (Jiang, Summerfield, & Egner, 2013). Attention may increase the weight of sensory evidence for valid predictions, leading to an increased cortical activity for the representations of the predicted visual stimuli, which then promotes faster error-correction for these stimuli. Attention may also reverse the attenuation of activity that is observed for predicted but unattended stimuli (Kok et al., 2011).

Whether purely behaviourally, at a neurocognitive level, or from the point of view of theoretical accounts such as predictive processing, expectation and attention are intimately interlinked (e.g., attention is thought to adjust the precision weighting of prediction errors, Feldman & Friston, 2010; Friston, 2010). Thus, it is likely that if we discover individual differences in the effect of priors on visual awareness, attentional

abilities would also likely reflect these. Given their inter-dependence, it is difficult to investigate the effect of expectation on visual awareness completely independent from attention. In the present study we aimed to measure the influence of expectation and attention in separate conditions within the context of the same perceptual task. To this end, we selected the binocular rivalry paradigm, where a constant display of stimuli is presented (i.e., each eye is presented a different stimulus via a mirror stereoscope) but the awareness alternates between two interpretations (Blake & Logothetis, 2002). We considered this to be a relatively controlled paradigm to probe the effects of expectation on awareness, as the alternation rate is only weakly influenced by endogenous attention, relative to other forms of perceptual rivalry (Meng & Tong, 2004; Tong, Meng, & Blake, 2006).

In the present research we aimed to initially replicate and compare the facilitatory effects that different prior manipulation methods exert on visual awareness (Brascamp et al., 2007; Pearson et al., 2008; Denison et al., 2011). Second, by taking an individual differences approach and assessing correlations between the effects of these methods, we aimed to discover if there is a general bias towards reliance on priors. A third objective was to explore whether expectation-based biases manifest effects only with highly ambiguous and non-ecologically valid input such as binocular rivalry, or whether they also predict variability in the way individuals experience their visual world in naturalistic scenarios. For example, if someone is more prone to 'see the expected' in the binocular rivalry display, would this individual be more or less likely to detect visual changes, be more or less distractible, have a more or less vivid imagination, or be more or less prone to experience perceptual anomalies?

To address these questions, we administered a binocular rivalry task with Gabor patches comprising seven conditions (*baseline, free viewing, selective attention,*

predictive context, imagery, expectancy, perceptual priming, see Figure 5.1 for an

illustration). In these conditions we manipulated attention and expectation to measure

the tendency to see the biased percept in the rivalry display. In the *free viewing*

condition, the rivalry display was presented continuously, and we measured the

subjective binocular rivalry alternation rate, as it has been suggested to index

differences in predictive processing biases (Kanai et al., 2011). In the *selective attention*

condition, we measured the participants' ability to increase the dominance duration of

particular gratings via focusing selective attention (Meng & Tong, 2004; Tong et al.,

2006). In the *predictive context* condition participants viewed a rotating sequence of

gratings before seeing the rivalry display and indicating which grating they saw in the

display first. This condition measured the extent to which the anticipation of a stimulus

based on a previous sequence influences awareness and was adapted from Denison and

colleagues (2011). In the *imagery* condition participants were asked to imagine one of

the gratings before indicating what they see in the rivalry display. This assessed the

influence of internally generated representations on awareness and aimed to replicate

the effects observed by Pearson and colleagues (2008). In the *expectancy* condition,

participants saw a cue indicating the probability of seeing a particular grating; the cue

was uninformative, as both gratings were equally likely to appear. This condition

measured the bias of expectancy based on suggestion alone rather than induced by

statistical regularities. Finally, in the *perceptual priming* condition participants saw two

types of prime differing in signal strength before viewing the binocular rivalry display;

a low contrast prime presented briefly, and a high contrast prime presented for longer.

The rationale for including these two sub-conditions was that weak primes are known to

facilitate awareness of the matching percept (Pearson et al., 2008), whereas strong

primes lead to adaptation effects (Brascamp et al., 2007). Including both conditions may help to elucidate the relationship between priming and adaptation.

To explore how a tendency to 'see the expected' relates to individual differences in perceptual experiences and traits, participants additionally completed a battery of questionnaires. The battery comprised the AQ (Baron-Cohen et al., 2001), which estimates autism spectrum traits in the general population (including subscales such as attention to detail); the CAPS (Bell et al., 2006) measuring experiences of sensory anomalies such as hallucinations, as well as the distress levels associated with these; the CFQ (Broadbent et al., 1982) estimating everyday problems with attention and memory; and the Sussex Cognitive Styles Questionnaire (SCSQ) Imagery Ability subscale (Mealor, Simner, Rothen, Carmichael, & Ward, 2016), measuring the reported tendency for vivid mental imagery and its use for memory and planning. Finally, participants completed a CB task with naturalistic scenes, based on the 'flicker' CB paradigm introduced by Rensink and colleagues (1997). This paradigm was used to examine whether a tendency to 'see the expected' in the binocular rivalry task could predict the ability to notice visual changes in more ecologically valid conditions.

To test whether a common mechanism underlies observed patterns of perceptual bias across different methods of prior manipulation, we conducted a factor analysis. We hypothesised that if there is a general tendency to 'see the expected' most prior manipulation methods will correlate together and load onto the same factor in factor analysis. An alternative possibility is that some methods directly engage the representation of the stimulus in sensory cortex (e.g., perceptual priming and self-generated imagery), whereas others may rely on a more indirect processes of coding the probability or onset timing of a particular stimulus and/or activating the sensory template weakly (e.g., predictive context or expectancy cues). In this case, we

hypothesised that the different prior manipulation conditions will not correlate well and will load onto separate factors. Furthermore, given the intimate links between attention and prediction, we hypothesised that a greater attentional control over binocular rivalry dominance durations will also predict a greater effect of prior manipulations on awareness.

In terms of links to everyday perception, possessing strong priors should be adaptive as it may enable individuals to allocate attention effectively according to internal representations (i.e., a predictable stimulus is also expected to be more precise, Hohwy, 2012). Therefore, we hypothesised that reliance on priors will predict perceptual experiences and traits that reflect improved behavioural responses to the visual world; namely, superior change detection ability and lower distractibility. Nonetheless, it is conceivable that at some level the influence of priors can become too great to be adaptive. In fact, the condition of psychosis and the experience of hallucinations in the general population may stem from possessing overly strong perceptual priors. Individuals prone to psychotic experiences are more likely to utilise perceptual priors when presented with ambiguous input (Teufel et al., 2015) and the ease with which perceptual hallucinations can be induced is related to psychotic symptoms (i.e., proneness to voice-hearing) (Powers et al., 2017). Therefore, we anticipate that an increased tendency to 'see the expected' in the binocular rivalry display may also predict proneness to experience perceptual anomalies. Finally, as the pattern of perceptual experiences in autism has been argued to manifest the opposite bias; weak priors or, alternatively, inflexible assignment of high precision to prediction errors (Van de Cruys et al., 2014), we hypothesised that a weaker bias of expectation may predict ASD-related perceptual traits (e.g., attention to detail).

5.3. Method

5.3.1 Participants

Seventy-five participants (aged 18 – 46, mean = 21.47, SD = 5.18; 58 female) with normal or corrected-to-normal vision, normal binocular vision and no reported colour vision deficiencies completed this study. The participants were undergraduate students at the University of Sussex who received course credit and adults from the Brighton community who were reimbursed in cash. The study took 2h to complete and consisted of two parts; an online questionnaire (30 min) and a subsequent lab-based part involving the TNO test (BIB Ophthalmic Instruments, Stevenage) administered in order to assess problems with stereopsis (i.e., to identify and exclude participants with binocular vision problems), the binocular rivalry task, and the CB task (1h 30min). The study was approved by the Science and Technology Cross-Schools Research Ethics Committee (C-REC) at the University of Sussex.

5.3.2 Materials and Design

Participants completed the initial part of the study online and this included several questionnaires assessing a range of normal and anomalous perceptual experiences.

1. Online questionnaires

Four questionnaires were administered based on a rationale that the traits that they measure may be related to individual differences in attentional and expectation-based biases; the questionnaires are described in the order of presentation. The AQ (Baron-Cohen et al., 2001) comprises 50 items with a 4-point Likert scale ranging from

'Definitely Agree' to 'Definitely Disagree', and measures aspects of the autism spectrum trait, including social skill, attention switching, attention to detail, communication, and imagination. The whole AQ was administered and the total score was derived, as well as a score for the 'Attention to detail' subscale. The latter subscale includes items such as "I usually notice car number plates or similar strings of information".

The Cardiff Anomalous Perceptions Scale (CAPS) (Bell et al., 2006) comprises 32 items with two response options ('Yes' and 'No') and measures the experience of perceptual anomalies in all sensory modalities. These include distortions of sensory experiences, changes in their intensity, experiences with unexplained causes, and non-shared experiences (e.g., voice-hearing). The answer of 'Yes' to any item is followed by rating the associated distress, intrusiveness, and frequency of the experience on a 5-point Likert scale. An example of the items: "Do you ever see shapes, lights, or colours even though there is nothing really there?". Although perceptual hallucinations are considered symptomatic of psychosis, psychotic experiences may exist on a continuum in the general population as they are quite common (e.g., 11% of the general population score above the mean of a psychotic sample on CAPS) (Bell et al., 2006). The total score for the CAPS was derived, as well as a CAPS score without the additional distress scales.

The Cognitive Failures Questionnaire (CFQ) (Broadbent et al., 1982) consists of 25 items with a 5-point scale ranging from 'Very Often = 4' to 'Never = 0' (within the context of last six months), and it measures everyday cognitive failures of perception, attention, memory and motor function. These are characterised as cognitive lapses that interfere with the smooth running and completion of everyday tasks and items are found

to be underpinned by separate but related factors including distractibility (disturbance of focused attention), forgetfulness and blunders (slips of action) (Wallace et al., 2002).

The Sussex Cognitive Styles Questionnaire (SCSQ) Imagery Ability subscale was also administered (Mealor et al., 2016). This subscale consists of 17 items and, as in the whole questionnaire, uses a 5-point Likert scale ranging from 'Strongly Disagree' to 'Strongly Agree'. It comprises items measuring the strength of mental imagery (e.g., "My mental images are very vivid and photographic.") as well as its use in daily life for the functions of remembering, planning, thinking, and problem-solving (e.g., "I often use mental images or pictures to help me remember things.").

1. Baseline

Fixation Rivalry display

1s Left eye Right eye

Which seen first?
(80 trials)

2. Binocular rivalry

Fixation Rivalry display

1s Left eye Right eye

Which seen now?
(60s, 4 presentations)

3. Selective attention

Fixation Attention cue Rivalry display

1s Focus on
left-slanted Left eye Right eye

Which seen now?
(60s, 4 presentations)

4. Predictive context

Fixation Predictive rotation stream Rivalry display

1s Four item stream 1600ms
Item = 300ms grating
& 100ms blank Left eye Right eye

Which seen first?
(80 trials)

5. Imagery

Fixation Imagery cue Imagery window Rivalry display

1s 1s 5s Left eye Right eye

Imagine left-slanted **Which seen first?**
(40 trials)

6. Expectancy

Fixation Expectancy cue Blank Rivalry display

1s 1s 100ms Left eye Right eye

Expect left-slanted **Which seen first?**
(80 trials)

7. Priming

Fixation Prime Blank Rivalry display

1s **a) Weak prime:**
100ms, 20% contrast
b) Strong prime:
2.5s, 100% contrast 100ms Left eye Right eye

Which seen first?
(40 + 40 trials)

Figure 5.1 The stimuli and trial structure of the binocular rivalry task conditions

In conditions 1 and 4-7 on each trial participants indicated which grating they saw first in the rivalry display by clicking one of the two mouse buttons. After a response, a blank intertrial interval of 1s was presented, followed by the next trial. Fixation crosses, cues, and primes were shown to both eyes; only in the rivalry display were different stimuli presented to each eye. In 10% of the trials of conditions 1 and 4-7, catch trials were presented where both eyes were presented the same grating in the rivalry display. In conditions 2-3 participants continuously indicated how they perceived the rivalry display to alternate from one grating to the other during the 60s presentation window by clicking one of the two mouse buttons. All gratings except the strong primes in condition 7 were presented at 20% Michaelson contrast.

2. Binocular rivalry task

In this task participants viewed Gabor patches of right- and left-slanted sinusoidal gratings through a mirror stereoscope. The Gabor patches (diameter = 4.24º) were presented on a grey screen with a black square border around them (for full details on visual stimuli and monitor parameters see Table 7.2 in Appendix C). The Gabors were oriented at 45 degrees (right-slanted) or 135 degrees (left-slanted). The task comprised seven conditions designed to manipulate attention and expectations before presenting the binocular rivalry display (see Figure 5.1). The task was to use the left or right mouse button to indicate which grating the participant saw in the binocular rivalry display (e.g., left-slanted or right-slanted). Participants were verbally instructed before each condition, in addition to the instructions provided on the screen.

The task started by setting up the binocular rivalry display. We presented a different grating surrounded by a black square to each eye and asked participants to adjust a dial on the mirror stereoscope until the grating and the square comfortably aligned into one image. This was followed by a *practice* condition (12 trials), where the same grating was shown to each eye (6 left-slanted, 6 right-slanted trials) and participants indicated which grating they saw. The practice condition involved feedback

and assessed whether or not participants understood which grating was labelled left-slanted and which right-slanted.

Next, participants completed the *baseline* condition (80 total trials, 8 catch trials), where the binocular rivalry display was presented on each trial and participants indicated which grating they saw first. This condition estimated any eye dominance effects.

Next, participants completed the *free viewing* condition (4 presentations of 60s). During each presentation participants continuously viewed a binocular rivalry display for 60s and indicated any time their subjective experience changed from left-slanted to right-slanted grating or vice versa using the left and right mouse buttons. This condition was designed to measure the number of perceptual alternations in binocular rivalry.

Next, participants completed the *selective attention* condition (4 presentations of 60s); participants were informed that the rivalry display will alternate continuously, and they will need to try to see a particular grating in the display. Then they saw a cue (e.g., 'Focus on the LEFT SLANTED grating.') instructing them to bring and maintain either the left or right-slanted grating into awareness whilst viewing the binocular rivalry display for 60s. They indicated how their subjective experience changed during this time, similarly to the *free viewing* condition. This condition assessed participants' ability to increase the dominance of the cued percept using attentional control.

Next, participants completed the *predictive context* condition (80 total trials, 8 catch trials). This replicated the paradigm by Denison and colleagues (2011); each trial started with a rotating stream of gratings, which provided a context predicting the subsequent orientation of the grating in the stream. Participants were told that they will see a stream of rotating gratings before the rivalry display, but its purpose was not revealed. After the predictive stream, participants saw the rivalry display and indicated

which grating they saw first. This condition assessed to what extent participants are influenced by a predictive context.

Next, participants completed the *imagery* condition (40 total trials, 4 catch trials). On each trial participants saw a cue instructing them to vividly imagine one of the gratings ('L' or 'R'), followed by a 5s imagery window, followed by the rivalry display and reporting which grating they saw first. This condition assessed the influence of self-generated imagery on visual awareness.

Next, participants completed the *expectancy* condition (80 total trials, 8 catch trials). Participants were instructed that a cue will indicate which grating has a 75% chance of appearing first. On each trial of this condition, participants saw a cue ('L' or 'R'), then the rivalry display and they reported which grating they saw first. The cue had no predictive power in terms of statistical regularity, and thus induced an expectancy based on suggestion alone.

Finally, in the *priming* condition (80 total trials, 8 catch trials), participants saw a perceptual prime before seeing the rivalry display. There were two types of prime, each presented in a separated block; weak primes were presented first and were low contrast (20%) and presented briefly (100ms), whereas strong primes were high contrast (100%) and presented for longer (2.5s). The weak primes were designed to lead to facilitation of the same percept in rivalry, whereas strong primes to the suppression (e.g., adaptation) of the same percept.

For all conditions, trials were presented randomly intermixed and the identity of the gratings shown to each eye was counterbalanced, as was the cue/prime identity. Ten percent of the trials in conditions 1 and 4-7 were catch trials where the same grating was presented to both eyes (half of these were left and half right-slanted gratings). Catch trials were introduced to check if participants exhibited any response bias by responding

in line with prior manipulations even on unambiguous trials. In all conditions, participants were asked to indicate which grating they saw by clicking the left or right mouse button. In conditions 1 and 4-7 response was made only regarding the initial percept and the next trial started after response, whereas in conditions 2-3 clicking responses were made continuously to indicate how perception of the Gabors subjectively alternated throughout the 60s presentation window. In condition 3 the timing of clicks and the time interval between clicks was additionally recorded to enable calculation of average duration of each percept.

In the case of seeing a mixed percept, participants were instructed to report which grating is more dominant. If the mixed percept was too ambiguous, participants were asked to wait until one of the gratings became visibly dominant (e.g., covering more than half of the stimulus field). The gratings in the rivalry display were always presented at 20% contrast, and so were the other gratings in most of the prior manipulation conditions, except the strong primes of the priming condition, which were presented at 100% contrast.

3. Change blindness task

The CB task was adapted from Andermane and colleagues (2019) and required participants to find changing objects within flickering natural indoor scenes. Sixty image pairs were obtained from a CB database (Sareen et al., 2016); one image was an original indoor scene and in the other image one of the objects in the scene (e.g., a vase) was removed. In half of the images, object changes occurred on the left side, and in the other half they occurred on the right. The task was presented using Inquisit Millisecond software and consisted of one practice trial and 60 randomly intermixed experimental trials. On each trial the pre-change and post-change scenes alternated with a blank

screen in between the two, creating a flickering cycle of image presentations lasting 30s. Participants were instructed to use a mouse to click on the object that kept appearing and disappearing once they saw it. The next trial began after the mouse click or, in the case of no response, when the image cycle finished (after 30s). There was an intertrial interval of 1000ms and a black screen with a white fixation square of 3000ms before each trial. To separate correct responses from incorrect ones, ROIs within each image (image dimension: 1024 x 768) were defined around the centre coordinates of the changed object (Mean radius = 1°), and mouse clicks with coordinates outside ROIs (Mean radius = 2°) were labelled as misses.

5.3.3 Procedure

All participants gave informed consent prior to taking part in the study. The online questionnaires lasted 30 minutes and were completed before attending the lab-based session. The lab-based session took 1h and 30 minutes to complete and started with the TNO test to screen for any problems with stereopsis. The TNO test was administered to exclude any participants who had binocular vision problems or unusually strong eye dominance, which could prevent them from experiencing stimuli presented to the non-dominant eye and may therefore render the prior manipulations ineffective. If participants passed the selection criterion (i.e., correctly identifying shapes in plates I-V by stereopsis, the criterion being stereoacuity of at least 240 arcseconds), they were eligible to participate in the rest of the lab-based study, if not they were reimbursed for completing the questionnaires (3 out of 78 participants did not pass the TNO test and were excluded). Next, participants completed the binocular rivalry task (all conditions 1-7) and finally the CB task. The task and condition order were fixed for all participants to limit noise introduced by differences in task context

and maximise sensitivity to individual differences in performance (as suggested by Mollon et al., 2017). The binocular rivalry task was presented using MATLAB (Mathworks Inc.) and the Psychophysics Toolbox extension (Brainard, 1997) and completed seated 100 cm from a CRT monitor (screen resolution = 1280 x 1024), with a black tunnel box around the monitor, in a dark room with participants' heads resting on a chinrest and eyes looking through a mirror stereoscope. The CB task was completed seated comfortably 55cm from the computer screen (screen resolution = 1920 x 1080) with the light on in the room.

5.4. Results

5.4.1 Data preparation

In the binocular rivalry task, the *baseline* condition assessed any strong eye dominance effects. A strong tendency to suppress input from one eye could potentially obscure effects of priors on the experience of binocular rivalry, as it renders the rivalry display less ambiguous and priors are more likely to be utilised when input is ambiguous (de Lange et al., 2018). In addition, strong eye dominance could potentially induce correlations among conditions that do not reflect relationships between effectiveness of the prior manipulation, but rather represent eye dominance itself (due to how it influences the ambiguity of display). To control for such effects, the percentage of responses matching the grating shown in the left and right eye was calculated across all conditions. This led to exclusion of 6 participants who consistently reported the grating shown to either the left or right eye more than 85% of the time throughout the task (this value having been used by previous studies, e.g., Denison et al., 2011).

In the *free viewing* condition, the measure of interest was the total number of alternations throughout the four 60s binocular rivalry presentations. In the *selective attention* condition, the average duration of right and left-slanted responses was calculated on each trial and the average duration of the percept that did not match the attentional cue was subtracted from the average duration of the percept matching the cue. Two participants did not respond with enough clicks in this condition (e.g., total of 8 and 10 clicks over the four 60s presentation windows), presumably due to mixed percepts. Therefore, their percept durations could not be calculated; these responses were excluded. In the other conditions (*predictive context, expectancy, imagery, priming)*, the percentage of initial responses to the rivalry display matching the expected grating was calculated.

In the CB task the cumulative percentage of correctly identified changes was calculated at each time point (e.g., percentage correct with RTs of below 1s, 2s, 3s ... 30s) (this analysis is described in Andermane et al., 2019). An inverse exponential function (i.e., $Y = \alpha e^{\beta / X}$, where Y is the cumulative percentage correct, X is the time in seconds, α is the asymptote and β relates to steepness/curvature) was then fit to this data, generating parameters α and β for each participant in each session. A greater α indicates that participants missed fewer changes (see Figure 7.5 in Appendix C for the correlation between CB parameter α and the percentage of missed changes). A greater β indicates that participants were more likely to reach asymptote quickly: i.e., detect changes faster throughout the task in terms of RT.

5.4.2 Descriptive statistics

All attentional and prior manipulations led to significant moderate to large effects on the experience of binocular rivalry (the descriptive statistics, effect sizes, and inferential statistics are presented in Table 5.1), indicating the manipulations were effective. In the *selective attention* condition, voluntarily holding a particular grating in awareness significantly increased its dominance duration, relative to that of the competing grating (Cohen's d = 0.71). In the *predictive context, imagery, expectancy*, and *weak prime* conditions the percentage of initial percepts matching the biased grating significantly exceeded 50% (Cohen's d ranging from 0.43 to 0.84), suggesting that priors exerted a facilitatory effect on awareness in these conditions. In the *strong prime* condition, the percentage of initial percepts matching the biased grating was significantly lower than 50% (d = 2.23), suggesting that the high-contrast, long duration primes suppressed awareness of the primed grating.

Table 5.1 The summary statistics of the performance in the binocular rivalry task conditions

The listed measures are as follows (the numbering corresponds to Figure 5.1): (2) the number of alternations in binocular rivalry, (3) the difference in seconds between dominance duration of percepts matching versus not matching the attentional cue in the selective attention condition, and (4-7) the percentage of initial percepts matching the prior in the predictive context, imagery, expectancy, weak prime, and strong prime conditions, respectively. Statistics demonstrating the influence of attentional and prior manipulations are provided in the last two columns including the Cohen's d effect size and t-tests. The t-tests include: (3) a paired sample t-test comparison of the percept durations matching and not matching the attentional cue in the selective attention condition, and (4-7) one-sample t-test comparisons of percentage of initial percepts matching the cue and chance performance in the rest of the conditions. All t-tests survived the Holm-Bonferroni correction.

	Mean (SD, N)	Measure	Cohen's d	t-test (2-tailed)
2. Binocular rivalry	64.96 (25.99, 69)	N of alternations	N/A	N/A
3. Selective attention	1.05 (1.61, 68)	Diff in dominance duration (s)	0.71	$t(67) = 5.38$, $p < .001$
4. Predictive context	54.93 (5.87, 69)	% of responses matching prior	0.84	$t(68) = 6.97$, $p < .001$
5. Imagery	63.29 (16.47, 69)	% of responses matching prior	0.81	$t(68) = 6.70$, $p < .001$
6. Expectancy	56.10 (9.35, 69)	% of responses matching prior	0.65	$t(68) = 5.42$, $p < .001$
7. a) Weak prime	58.98 (21.09, 69)	% of responses matching prior	0.43	$t(68) = 3.54$, $p = .001$
7. b) Strong prime	17.67 (14.53, 69)	% of responses matching prior	2.23	$t(68) = -18.5$, $p < .001$

All prior manipulations had a significant effect on RTs in the binocular rivalry task (see Table 5.2). In all prior manipulation conditions (except *strong prime*) RTs to

percepts matching the induced prior were significantly faster, relative to percepts not matching the prior. In the *strong prime* condition, responses to percepts matching the prime were slowed, reflecting an adaptation effect. These results suggest that priors not only bias the probability of the corresponding percept entering into awareness but also facilitate the speed of the percept coming into awareness and becoming available for a response, unless the prior stimulus is presented physically and has a strong signal, in which case the effect is reversed.

Table 5.2 The summary statistics of response times in the binocular rivalry task conditions

The means and standard deviations of RTs for percepts matching and not matching the prior in the different prior manipulation conditions of the binocular rivalry task, along with the non-matching - matching percept RT difference, the associated Cohen's d effect size (calculated using pooled variance), and a paired samples t-test comparison of the non-matching and matching RTs. All prior manipulation conditions lead to a significant boost in RTs to the matching percept, except in strong prime condition, which lead to slower RTs to the matching percept. All t-tests survived the Holm-Bonferroni correction.

	Mean matching RT (SD)	Mean non-matching RT (SD)	Mean RT diff (SD, N)	Cohen's d	t-test (2-tailed)
Predictive context	1876 (976)	2138 (1601)	262 (919, 69)	0.20	$t(68) = 2.37$, $p = .021$
Imagery	1977 (1041)	2404 (1218)	428 (654, 69)	0.38	$t(68) = 5.43$, $p < .001$
Expectancy	1394 (664)	1489 (724)	95 (287, 69)	0.14	$t(68) = 2.76$, $p = .007$
Weak prime	1217 (493)	1452 (804)	235 (666, 67)	0.35	$t(66) = 2.89$, $p = .005$

Strong prime	2114	1413	-701	0.62	$t(66) = -4.56, p < .001$
	(1257)	(1000)	(1258, 67)		

5.4.3 Catch trial analyses

In order to assess whether the effect of the priors was indeed perceptual or whether it reflected a shift in the response bias, we analysed the catch trials (i.e., where the same grating was presented to both eyes). Three participants consistently responded incorrectly to these; their average accuracy on catch trials across the conditions was below 5%. Since these participants also responded incorrectly on catch trials in the *baseline* condition with no prior manipulations, it was concluded they responded with the opposite response keys and thus their responses were reversed (this was done prior to all main analyses). We found that on average participants were highly accurate on catch trials (Mean = 97.86%, SD = 4.52%). Accuracy on catch responses in the baseline condition (Mean = 97.06%, SD = 7.82%) did not significantly differ from any other prior manipulation condition (means ranging from 96.75% to 98.91%), suggesting the prior manipulations did not affect the veracity of responses on unambiguous trials (see Table 7.3 in Appendix C for the t-tests).

Next, we looked at the percentage of responses on catch trials matching the prior. Given counterbalancing, the percentages of responses matching and not matching the prior should be equal (i.e., 50%). By the same logic we also compared average RTs of responses matching versus not matching the prior, in all of the conditions. These analyses revealed that in most conditions the percentage of responses to catch trials matching the prior was not significantly different from 50% (see Table 5.3 for the summary statistics and t-tests). The only exception was the expectancy condition, with a

mean difference of 2.9% between the percentage of responses matching and not matching the prior (d = 0.36). Note that before the *expectancy* condition the experimenter verbally instructed the participants that if they see the cue 'L', the left-slanted grating has a 75% chance of occurring (and vice versa for 'R'). It could be argued that as there was no corresponding statistical regularity supporting this instruction, it may have worked (especially for highly suggestible people) as an imaginative suggestion (Lush et al., 2019), hence the response bias. Finally, the RTs to catch trials matching the prior were not significantly faster than responses not matching the prior (except in imagery condition, although not after FWE correction) (see Table 5.4). Overall, the analyses of the catch trials suggest that the experimental results summarised above reflect a genuine effect of priors on the contents of visual awareness, rather than a response bias. The two exceptions to the pattern (the *expectancy* and *imagery* conditions) were smaller in magnitude for the catch trials than the effects seen in the experimental trials.

Table 5.3 The summary statistics of accuracy on catch trials

The means and standard deviations for percent accuracy on catch trials, the percentage of responses matching the prior, as well as Cohen's d effect sizes and a one sample t-test comparing prior matching responses to 50% in each of the conditions (N = 69). Participants in the Expectancy condition reported significantly more prior-matching responses than 50% and this effect survived the Holm-Bonferroni correction.

	Mean % accuracy (SD)	Mean % matching prior (SD)	Cohen's d	t-test (2-tailed)
Predictive context	97.64 (5.78)	49.09 (5.39)	-0.17	$t(68) = -1.40$, $p = .167$
Imagery	98.91 (5.14)	50.36 (5.24)	0.07	$t(68) = .57$, $p = .567$
Expectancy	98.19 (4.92)	51.45 (4.03)	0.36	$t(68) = 2.99$, $p = .004$
Weak prime	97.83 (8.29)	51.45 (8.45)	0.17	$t(68) = 1.42$, $p = .159$
Strong prime	96.74 (12.80)	49.64 (5.24)	-0.07	$t(68) = -.57$, $p = .567$

Table 5.4 The summary statistics of response times on catch trials

The means and standard deviations of RTs for catch trial responses matching and not matching the prior, along with the non-matching - matching response RT difference, the associated Cohen's d effect size (calculated using pooled variance), and a paired sample t-test comparison of the non-matching and matching RTs. The RTs for responses matching and not matching the prior did not significantly differ for any of the conditions, except for the Imagery condition, which yielded a RT boost for matching responses. However, no t-tests survived the Holm-Bonferroni correction.

	Mean matching RT (SD)	Mean non-matching RT (SD)	Mean RT diff (SD, N)	Cohen's d	t-test (2-tailed)
Predictive context	1078 (1103)	1051 (625)	-27 (783, 69)	-0.03	$t(68) = -.29$, $p = .776$
Imagery	999 (549)	1391 (1598)	392 (1516, 69)	0.33	$t(68) = 2.15$, $p = .035$
Expectancy	850 (508)	943 (459)	94 (396, 69)	0.19	$t(68) = 1.95$, $p = .056$
Weak prime	851 (523)	765 (275)	-86 (522, 68)	-0.21	$t(67) = -1.36$, $p = .180$
Strong prime	1124 (882)	1132 (817)	8 (943, 69)	0.01	$t(68) = .07$, $p = .944$

5.4.4 Correlations between binocular rivalry conditions

There were several correlations between the different conditions of the binocular rivalry task (see Table 5.5 for the correlation matrix and Figure 5.2 for the scatterplots of the significant relationships), suggesting that some attention and prior manipulation methods are related and indeed may be reliant on a common mechanism. It must be noted that given the large number of correlations (21), the corrected alpha thresholds

using Holm-Bonferroni correction for FWE and Benjamini-Hochberg correction for

FDR were very low (Benjamini & Hochberg, 1995). As a result, none of the significant

associations survived correction for multiple comparisons with either of the methods.

However, the pattern or correlations in Table 5.5 demonstrates a positive manifold

(Verhallen et al., 2017; Mollon et al., 2017); all of the correlations that were

hypothesised to be positive, such as the associations between attentional and prior

manipulations, are in fact positive. The only two columns that have negative

coefficients include measures of adaptation (*strong prime*) and binocular rivalry

alternation rate (*free viewing*), which we anticipated given adaptation leads to

suppressive rather than facilitatory effect on awareness (Brascamp et al., 2007) and

frequent rivalry display alternation may reflect instability of perceptual predictions

(Kanai et al., 2011). Additionally, we subsequently conducted a factor analyses to look

at the relationships between variables holistically. All of the nominally significant

correlations are reported below.

A greater number of alternations in binocular rivalry predicted a weaker ability

to increase dominance durations of gratings in binocular rivalry by selective attention

(Spearman's rho = -.26, p = .032) and a greater suppression effect of strong primes

(Spearman's rho = -.29, p = .014). This suggests perceptual stability in binocular rivalry

may be related to greater attentional control and a lower sensitivity to adaptation effects.

A greater ability to increase dominance durations of gratings in binocular rivalry

by selective attention was associated with a stronger facilitatory effect of predictive

context (Spearman's rho = .30, p = .013), a stronger facilitatory effect of self-generated

imagery, (Spearman's rho = .34, p = .005), and a greater priming effect with weak

primes (Spearman's rho = .24, p = .044). These results point to the inter-connectedness

of the ability to exert attentional control and the strength of the effect exerted on visual awareness by different prior manipulations.

A greater facilitatory effect of predictive context on the initial percept in binocular rivalry was associated with a stronger adaptation effect of strong primes (Spearman's rho = -.27, p = .022). This is in line with a suggestion by Denison and colleagues (2011) that the influence of the preceding rotation stream of gratings consists of separate effects of adaptation and facilitation, the relative contribution and strength of which are dependent on the contrast and timing of the gratings in the stream. The opposite grating to the one that the stream sequence predicts is shown as the second to last stimulus in the stream (see Figure 5.1 condition 4) for 300ms. This may lead to stronger adaptation effects for those individuals who are more sensitive to adaptation and therefore suppress that percept and make the opposite grating (which is also predicted by the rotation stream) more visible.

Table 5.5 Spearman's correlations between the conditions of the binocular rivalry task

The associated p-values (two-tailed) are provided and the significant correlations are bolded. All conditions: N = 69, Selective Attention condition: N = 68. No correlations survived the Benjamini-Hochberg correction.

	Binocular rivalry	Selective attention	Predictive context	Imagery	Expectancy	Weak prime	Strong prime
Binocular rivalry	1	**-.26** **.032**	.09 .450	.13 .301	-.10 .419	-.14 .254	**-.29** **.014**
Selective attention		1	**.30** **.013**	**.34** **.005**	.11 .379	**.24** **.044**	.08 .523
Predictive context			1	.09 .483	.09 .485	.14 .261	**-.27** **.022**
Imagery				1	.07 .584	.19 .110	-.15 .206
Expectancy					1	.06 .608	.19 .114
Weak prime						1	-.17 .165
Strong prime							1
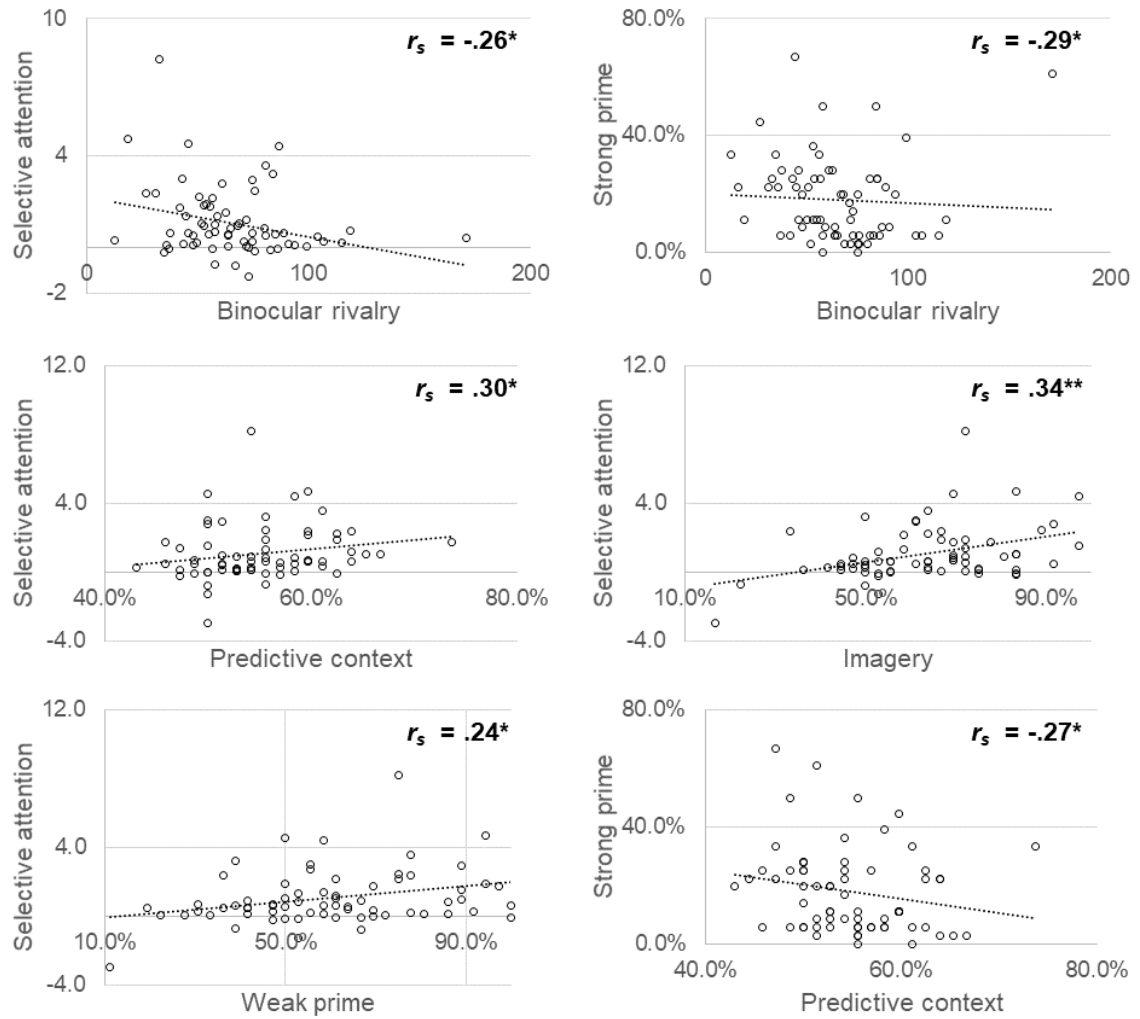
Figure 5.2 Scatterplots illustrating the nominally significant correlations between the binocular rivalry task conditions

The number of each condition corresponding to Figure 5.1 is provided in brackets: binocular rivalry refers to the total number of alternations in free viewing condition (2), selective attention refers to the increase in dominance of the attended grating measured in seconds (3), predictive context refers to percentage of initial percept reports matching the grating expected based on the rotation stream (4), imagery refers to percentage of initial percept reports matching the imagined grating (5), weak prime refers to the percentage of initial percept reports matching the low contrast short prime (7 a)), strong prime refers to percentage of initial percept reports matching the high contrast long prime (7 b)). The associated Spearman's rho coefficient along with its two-tailed significance level (* $p < .05$, ** $p < .01$, *** $p < .001$) is provided on each panel. None of the correlations survived the Benjamini-Hochberg correction.

5.4.5 Factor analysis

A principal axis factor analysis with a sample size of 69 participants was conducted on 9 measures (7 measures from the binocular rivalry task and the 2 parameters of CB task performance) in order to identify any underlying general or paradigm-specific dimensions of prior reliance. We used orthogonal rotation (varimax). The Kaiser-Meyer-Olkin measure indicated that the sample size was adequate for conducting factor analysis (KMO = .58, higher than the acceptable standard of 0.5 (Hutcheson & Sofroniou, 1999)). Bartlett's test of sphericity was significant ($p < .001$), thus the hypothesis that the correlation matrix is an identity matrix can be rejected. An initial factor analysis was run to identify the eigenvalues for each factor in the data and to analyse the Scree plot. Three factors had eigenvalues over Kaiser's of 1 criterion (Kaiser, 1958) and an inspection of the Scree plot confirmed that an inflection point was present at fourth factor (see Figure 7.6 in Appendix C). The first three factors in combination explained 55.12% of variance in the data. Table 5.6 shows the factor loadings after rotation.

Table 5.6 Exploratory factor analysis with the nine measures from the binocular rivalry task and two parameters of change detection

Varimax rotation was used and loadings above 0.3 are bolded (N = 69).

	Factor 1: Selective attention	Factor 2: Adaptation	Factor 3: Binocular rivalry
Binocular rivalry	-.21	.04	**.87**
Selective attention	**.68**	.02	-.14
Predictive context	.25	**.36**	.03
Imagery	**.55**	.29	.15
Expectancy	**.49**	-.07	.01
Weak prime	**.44**	.14	-.14
Strong prime	.04	**-.59**	-.02
CB α	.03	**.72**	-.13
CB β	.21	-.13	.21

The first factor we interpreted as 'selective attention', as it had the highest positive loading on the *selective attentio*n condition of the binocular rivalry task, which reflects the ability to increase dominance of a percept by attentional control. Other measures that loaded highly on this factor reflect the effect of prior knowledge on visual awareness. These include the tendency to see the initial percept that matches a previously imagined one (*imagery* condition), the tendency to see the percept that was suggested to be more likely (*expectancy* condition), and the tendency to see the percept that was previously seen as a brief low-contrast prime (*weak prime*). The loadings on

this factor suggest that attentional control and the tendency for prior manipulations to exert a facilitatory influence on visual awareness are closely related.

The second factor, which we interpreted as 'adaptation', loads highly and negatively on the tendency to see the matching percept after seeing a high contrast, long duration prime (*strong prime*). This suggests that this factor represents the extent to which visual representations are suppressed by adaptation. This factor also has a high positive loading on the CB parameter α, which reflects the percentage of identified changes in the CB task. A higher CB parameter α indicates better performance (i.e., detecting more changes). This indicates that proneness to adaptation may support improved change detection performance for naturalistic scenes. This factor also had a positive (albeit lower) loading on the tendency to see the percept matching a predictive rotating sequence of gratings (*predictive context* condition). It has previously been noted that performance in the predictive context task is related to both facilitatory effects of context and adaptation to individual items of the predictive stream (Denison et al., 2011), which may explain the loading of this measure.

The third factor was named 'binocular rivalry', as it had a large loading on solely the number of perceptual alternations when freely viewing the binocular rivalry display (i.e., with no prior manipulations). Although this suggests that binocular rivalry alternation rate may have separate mechanisms to the influence of prior knowledge or proneness to adaptation, this strong interpretation may not be fully warranted given the correlations reported earlier (e.g., faster alternation rate linked to greater adaptation to strong visual stimuli).

5.4.6 Correlations between expectation-based effects and perceptual experiences and traits

The descriptive statistics for the CB task parameters and the questionnaire (trait) measures are shown in Table 5.7. The scatterplots of the correlations between binocular rivalry task conditions and the perceptual measures and traits are shown in Figure 5.3.

Table 5.7 The summary statistics of the measures of typical and atypical perception

The means and standard deviations of the tasks and questionnaires measuring typical and atypical perceptual experiences and traits; CB parameter α, CB parameter β, the AQ score, the CAPS score, the total CAPS total score with the associated distress, frequency, and intrusiveness, the CFQ score, and the SCSQ Imagery Ability subscale score.

Measure	Mean (SD, N)
CB α	1.03 (0.11, 68)
CB β	-6.16 (1.48, 68)
AQ	16.87 (6.75, 69)
CAPS	4.83 (4.80, 69)
CAPS total	36.42 (41.07, 69)
CFQ	46.86 (13.29, 69)
SCSQ Imagery Ability	60.90 (9.09, 69)

We found that an increased adaptation to strong primes predicted higher CB parameter α (Spearman's rho = -.34, p = .005) (see Figure 5.3). This demonstrates that being more sensitive to adaptation effects may be beneficial for change detection, perhaps because adapting to the scene makes the visual transient of the changing object more salient. An increased facilitatory effect of self-generated imagery correlated with higher CB parameter α values (Spearman's rho = .26, p = .035) (see Figure 5.4). This

suggests that possessing stronger visual imagery predicts better change detection performance.
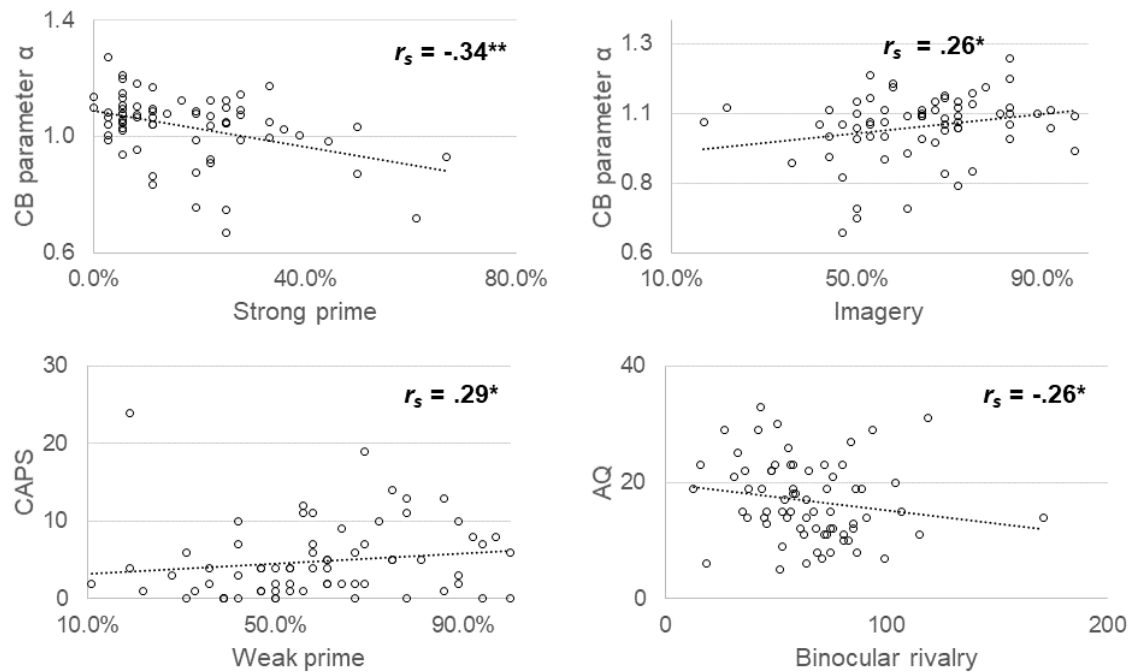
Figure 5.3 Scatterplots illustrating the significant correlations between the tendency to see the expected and typical and atypical perception

The correlations between the binocular rivalry task conditions and other perceptual measures: CB parameter α, CAPS, the AQ. The binocular rivalry conditions are as follows (with corresponding Figure 5.1 numbers provided in brackets): imagery refers to the percentage of initial percept reports matching the imagined grating (5), weak prime refers to the percentage of initial percept reports matching the low contrast short duration prime (7 a)), strong prime refers to percentage of initial percept reports matching the high contrast long duration prime (7 b)). The associated Spearman's rho coefficient along with its two-tailed significance level (* $p < .05$, ** $p < .01$, *** $p < .001$) is provided on each panel.

The facilitatory effect of weak primes on awareness in binocular rivalry significantly correlated with reports of perceptual anomalies in the CAPS (Spearman's rho $= .29$, $p = .016$), and CAPS together with associated distress (Spearman's rho $= .29$, $p = .017$). A lower number of alternations in binocular rivalry correlated with reporting more autism spectrum traits in the AQ (Spearman's rho $= -.26$, $p = .030$). Finally, the effect of expectancy cues in the binocular rivalry task correlated with CB task

performance in terms of β value (Spearman's rho = .24, p = .046), and poorer imagery ability (Spearman's rho = -.25, p = .042).

5.5 Discussion

In the present study we employed a binocular rivalry paradigm and used several methods of attentional and prior manipulation that have been shown to facilitate the entry of stimuli into visual awareness (e.g., Brascamp et al., 2007; Pearson et al., 2008; Denison et al., 2011). Our first aim was to replicate the effects that different prior manipulations exert on the subjective experience of binocular rivalry. Secondly, by adopting an individual differences approach, we asked whether the effects of these manipulations share a common mechanism, reflecting a general tendency for 'seeing the expected' along which individuals vary. Finally, we asked whether individual differences in expectation-based effects predict variability in visual change detection and perceptual traits (e.g., distractibility, proneness to perceptual anomalies, attention to detail, and mental imagery). We reasoned that if there are consistent trait-like differences in how readily individuals apply expectations to inform the contents of their awareness when confronted with ambiguous input (as in binocular rivalry), this should manifest in how they perceive and attend to their visual worlds more generally. The effects of attentional and expectation-based manipulations on awareness are discussed first, followed by their associations with change detection and perceptual traits.

5.5.1 Expectation-based and attentional effects on awareness

As hypothesised, our analyses showed that inducing expectations via predictive context (Denison et al., 2011), self-generated imagery (Pearson et al., 2008), expectancy cues, and weak perceptual primes (Brascamp et al., 2007; Pearson et al., 2008)

significantly increased the probability of the biased percept entering awareness, as well as speeded response latencies to the biased percept in the binocular rivalry paradigm. The effect sizes for the tendency to see the expected percept in the different conditions were moderate to large and there were small to moderate effects on response latencies. Together these results demonstrate that possessing an expectation of a visual stimulus, irrespective of the method of induction, results in a greater tendency for it to be consciously experienced and responded to faster. These effects are in line with extensive evidence that expectations facilitate perception (de Lange et al., 2018) and support predictive processing theories, which characterise visual perception as a predictive inference, constrained and guided by previously generated probabilistic models about the regularities of the visual world (Friston, 2010; Clark, 2013; Howhy, 2013).

We consider these results to reflect genuine effects of expectation on perception as opposed to biased responding because participants were not influenced by expectations on catch trials with unambiguous stimuli. Additionally, we replicated the finding that increasing the signal strength (i.e., the contrast and duration) of perceptual primes reverses facilitation and leads to suppression of the matching percept, reflecting a process of adaptation (Brascamp et al., 2007). In the weak and strong prime conditions, the same prior stimulus (differing only in signal strength) gives rise to differences in visual awareness – this would not be observed if participants had a bias to respond in line with the expectation. Note that the expectancy condition was an exception, as a slight response bias was observed on catch trials. Explicitly instructing participants that a stimulus is likely to appear (when this is not the case) may have worked as an imaginative suggestion in this case, leading suggestible participants to generate genuine effects on awareness even when viewing unambiguous catch trials

(Lush et al., 2019). However, on the whole expectations indeed resulted in a facilitated perception rather than a response bias.

As with priors, engaging selective attention also lead to a facilitatory effect on awareness. Attending a particular grating in the binocular rivalry display with the intention to hold it in awareness significantly increased its dominance duration relative to the unattended one. This replicates previous work on voluntary control of rivalry (Meng & Tong, 2004; Tong et al., 2006), although the attentional effects are typically smaller for binocular relative to perceptual rivalry and sometimes absent with low-level stimuli like gratings (Meng & Tong, 2004; van Ee et al., 2005). However, the dominance effect of selectively attending a percept in binocular rivalry, even using gratings, can be enhanced if attending to the features is task-relevant (e.g., using a counting task), highlighting the role of attention in motivational relevance and behaviour (Chong, Tadin, & Blake, 2005). Chong and colleagues (2005) also found that the selective attention effect is equivalent to increasing the physical contrast of the grating (i.e., 0.3 log units or more) when it is dominant so it may operate by boosting the apparent contrast. Indeed, attention does increase subjective contrast and the enhanced neuronal sensitivity due to attending resembles neuronal responses to increased contrast (Carrasco, Ling & Read, 2004; Carrasco, 2011). Our result is thus consistent with previous research on attentional control of binocular rivalry and theoretical accounts of selective attention enhancing the signal of sensory evidence for the attended stimulus (Jiang et al., 2013).

5.5.2 The tendency to see the expected – general or method-specific?

To explore whether individuals vary along a trait-like tendency for expectations to influence visual awareness, we first examined the correlations between attentional and expectation-based effects in the binocular rivalry task and then conducted an exploratory factor analysis. We reasoned that individual differences in the effects of prior manipulations may be underpinned by a common latent mechanism (e.g., activation of sensory templates, Kok et al., 2017) and hypothesised that if individuals consistently differ in the strength of this mechanism, the expectation-based effects should correlate together and load onto a common factor.

The strengths of most prior manipulation effects in the binocular rivalry task were predicted by the ability to use selective attention to influence the dominance durations of percepts at will. For instance, attentional control of percept dominance positively predicted the facilitatory effects of predictive context, self-generated imagery, and weak perceptual primes on awareness. The factor analysis further supported this pattern, as the first factor loaded strongly on the ability to voluntarily control dominance durations and on the influence of priors in three binocular rivalry conditions: self-generated imagery, expectancy, and perceptual priming with weak signal. We termed this factor 'selective attention'. These results support our hypothesis that individual differences in attentional ability and expectation-based biases are closely connected. Our findings are consistent with predictive processing frameworks, where attention is characterised as optimisation of expectations regarding the precision of priors, boosting the evidence for some prediction errors over others (Hohwy, 2012). Selective attention may be the mechanism that mediates the facilitatory effect of expectations on awareness

(Jiang et al., 2013). For example, inducing an expectation of a visual stimulus may result in attention selectively enhancing its sensory representation, which boosts the sensitivity to the stimulus and thus its visibility. However, whether the facilitatory effect of expectations on awareness is conditional on attentional abilities or vice versa is not possible to ascertain, given the correlational nature of our result.

In terms of the correlations between the different prior manipulation methods themselves, the influence of predictive context was associated with adaptation to strong sensory priors, both conditions also loading onto a separate factor we termed 'adaptation'. This result agrees with Denison and colleagues (2011) who show that responses in predictive context condition are influenced by a combination of facilitation due to the predictive sequence as well as adaptation to the individual items within it. Although the correlation matrix indicated a positive manifold (Verhallen et al., 2017), apart from the attentional and adaptation associations outlined above, most of the prior manipulation effects did not significantly correlate with one another. Without test-retest reliabilities it is not possible to conclude decisively about the meaning of small effects; however, the generally low correlation coefficients are against the idea that there is a consistent trait of 'seeing the expected'. Given we observed that on the group level all prior manipulations influenced awareness (with strong to moderate effects) and considering the large body of evidence regarding expectation effects on perception (de Lange et al., 2018), a lack of strong individual differences in prior reliance is surprising. This may indicate the different methods recruit somewhat distinct mechanisms that operate at different levels of the visual hierarchy (Tulver et al., 2019). As suggested, the methods may differ in the extent to which they activate sensory templates (Kok et al., 2017). Nonetheless, our analyses do demonstrate that selective attention may be a shared determinant of performance in the different prior induction conditions.

We also assessed binocular rivalry alternation rate, as the individual differences in this measure are large and stable (Miller et al., 2010) and have been suggested to index a tendency to assign weight to prediction errors (Kanai et al., 2011). Although alternation rate did not correlate with prior manipulations, a faster rivalry was predicted by an increased adaptation effect with strong primes and a weaker attentional control of binocular rivalry. These results are in line with the proposed neurocognitive basis of binocular rivalry which include mechanisms at low levels of visual hierarchy (e.g., inhibitory interactions of visual neurons and inter-ocular suppression), as well as high levels (e.g., competition of high-level representations and attentional selection) (Blake & Logothetis, 2002). At a low-level of processing, adaptation to the current percept coming from one eye increases whilst inhibition of the unexplained signal coming from the other eye diminishes until a threshold is reached where a perceptual switch is initiated (Tong et al., 2006; Hohwy et al., 2008). A greater sensitivity to adaptation would then lead to faster dynamics of the inhibition-adaptation cycle and consequently a faster alternation rate. The correlation with selective attention is consistent with the finding that attention can modify percept duration and alternation rate in binocular rivalry (van Ee et al., 2005; Chong et al., 2005). Individual differences in rivalry rate may be explained (but not exclusively) by a combination of both mechanisms (i.e., proneness to adaptation and endogenous attentional control). There may also be independent mechanisms involved, given rivalry loaded on a separate factor in our factor analysis. In sum, we show that individual differences in adaptation and attentional control predict the rate of binocular rivalry, in line with characterisation of rivalry as competitive interactions throughout the visual system in attempts to represent a single object in a single spatial position (Hohwy et al., 2008). However, there was no evidence that the strength of priors predicts rivalry rate, contrary to previous

suggestions that individual differences in rivalry rate index a predictive processing bias (Kanai et al., 2011).

5.5.3 Can attentional and expectation-based effects predict change detection and perceptual traits?

Finally, we examined whether expectation-based effects on awareness can predict perceptual experiences and traits (e.g., distractibility, anomalous experiences, tendency to use visual imagery). We found that the facilitatory effect of imagery in the binocular rivalry task predicted superior change detection. Rodway, Gillies, and Schepman (2006) also found that vivid imagers noticed more salient changes in a long-term change detection task (i.e., where the title of each image was shown before presentation to facilitate retrieval). The relationship between change detection and visual imagery could be explained by common dependence on a third variable, namely, VSTM. Accessing vivid representations internally may be conditional on storing high quality representations in the first place. Encoding and maintenance of scenes into VSTM is thought to be one of the key mechanisms causally involved in change detection (Tseng et al., 2010) and in our own work we showed that VSTM accuracy predicts improved detection of changes in naturalistic scenes (Andermane et al., 2019). Visual imagery strength also correlates with performance on VWM tasks (Keogh & Pearson, 2011) and both rely on representations encoded in the visual cortex (Pearson, Naselaris, Holmes, & Kosslyn, 2015; Albers, Kok, Toni, Dijkerman, & de Lange, 2013; Slotnick, Thompson, Kosslyn, 2005; Kosslyn et al., 1999). Future research could investigate the neurocognitive basis of VSTM representations in strong and weak imagers further.

Improved change detection was also predicted by stronger adaptation effects in the binocular rivalry task and both measures loaded onto the same factor. This finding supports the suggestion that the functional role of adaptation is to discount the expected perceptual properties and calibrate the sensitivity of the visual system for the detection of novelty (Clifford et al., 2007; Kohn, 2007; Webster, 2011). Adaptation is typically considered a low-level phenomenon, mainly occurring at the level of retina and visual cortex (Kohn, 2007) but the naturalistic scenes presented in our CB task are complex and explored freely via eye-movements, which would disrupt retinal adaptation. However, adaptation to low-level features at the level of visual cortex could contribute to later processing stages in the visual hierarchy. There is evidence of adaptation after-effects for abstract representations such as attractiveness and emotion in faces (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster, Kaping, Mizokami, & Duhamel, 2004). Furthermore, emotion after-effects are influenced by adaptation to location-specific low-level features (e.g., concave and convex lines at the location of the mouth) (Xu, Dayan, Lipkin, & Qian, 2008). Thus, it is conceivable that adaptation to low-level features affects higher-level representations of complex objects and naturalistic scenes. Adapting to the scene more rapidly may increase the sensitivity to novel scene elements faster. The object that keeps appearing and disappearing in the CB display is visible only half of the presentation window so its subjective contrast and salience might increase relative to the rest of the scene. The finding that individual differences in adaptation to low-level features (i.e., gratings) is predictive of complex visual change detection warrants further exploration, as proneness to adaptation may index a beneficial (adaptive) bias in visual perception.

Questionnaires were also assessed to determine if expectation-based biases could predict self-reported traits previously suggested to reveal predictive processing

imbalances (Teufel et al., 2015; Powers et al., 2017; Van de Cruys et al., 2014). A lower binocular rivalry rate predicted a greater number of autism spectrum traits, assessed by the AQ. This finding replicates earlier work by Robertson and colleagues (2013) who showed that perceptual alternations are slower in people with autism relative to controls. The authors interpreted this finding as reflecting that people with autism have atypical cortical dynamics; specifically, reduced inhibition of visual representations. Low alternation rate could be due to generation of more mixed percepts – it is suggested that this way individuals with ASD may stay true to the signal in binocular rivalry (utilising priors less to interpret the input). We also found that the facilitatory effect of weak primes predicted more reports of perceptual anomalies in the CAPS, with and without the associated distress scores. This is consistent with Teufel and colleagues (2015) who found that the facilitatory effect of prior knowledge on face detection in ambiguous Mooney images was positively associated with CAPS scores. The authors proposed that proneness to sensory hallucinations (i.e., sensing what is not there) in the general population and in psychosis may be the result of overly strong reliance on prior knowledge. The influence of perceptual priming with simple gratings on a subsequent ambiguous display is another measure of prior reliance. Our result supports the hypothesis that there may be a threshold at which residual activation of seen items no longer contributes to accurately representing the visual world.

5.5.4 Expectation, attention, and adaptation

The present research points to the close association between selective attention and the influence of priors on awareness; however, it is not possible to ascertain the direction of this relationship based on correlational results. One interpretation is that a greater ability to sustain attention throughout the binocular rivalry task boosts the

influence of prior manipulations. Attention is shown to enhance the neural activity of cortical areas representing particular locations or objects and increase visual sensitivity (Martinez et al., 1999; Kastner et al., 1999; Carrasco, 2011). Therefore, greater attentional focus upon the presentation of a perceptual prime (i.e., a grating in weak prime condition) should boost the baseline activity of the corresponding internal representation, amplifying its signal to noise ratio and easing its detection in the rivalry display. The role of selective attention is also clear in the process of self-generating visual imagery; attentional control may be required to access and re-activate the stimulus representation. Attention could also influence the strength of other prior manipulations; closely attending the sequence in predictive context and the letters in expectancy conditions may lead to allocating preparatory attention to the internal representation of the corresponding grating, easing its detection. Thus, the facilitatory effects of priors may (to a degree or wholly) represent enhanced neural activity of the corresponding representation due to selectively attending the expected grating.

An alternative interpretation is that developing strong priors of visual stimuli enable the individual to allocate selective attention more efficiently. There is evidence for this, as statistical regularities (e.g., temporal) implicitly attract spatial and feature-based attention, even when the regularities and the stimuli embedded in them are task-irrelevant (Zhao, Al-Aidroos, & Turk-Browne, 2013). Additionally, in visual search memory-guided orienting of spatial attention is more efficient than cue-based visual orienting (Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006). Individuals with high visual WM capacity are better at avoiding distraction via attentional capture (Fukuda & Vogel, 2009; 2011) and a greater capacity to encode VSTM representations leads to better control of attention in line with the stored representations and a better suppression of distractors (Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016).

Thus, it could be that perceptual priors facilitate awareness through attracting/biasing attention.

In sum, attentional control correlates with the strength of expectation-based biases but the direction of the influence (sustained attention boosting priors versus strong priors biasing attention) is not clear and could very well be bi-directional. To elucidate this, orthogonal manipulations of attention and expectation need to be employed and the neurocognitive basis of attended and unattended expectations examined. The time course of sensory cortex activation and representational specificity would also need to be investigated in this paradigm, to see whether attention amplifies the signal of a prior or whether a learnt prior or regularity draws attention.

We found that adaptation loaded on a separate factor from most attentional and prior manipulations and predicted naturalistic change detection, suggesting adaptation is distinct from facilitation by priors yet is an important mechanism for high-order perception. Surprisingly, adaptation to strong primes did not correlate with facilitation by weak primes, although the only difference between these conditions was the contrast and duration of the stimulus. Brascamp and colleagues (2007) argued that priming and adaptation is a part of one continuous neural process; however, our findings add a caveat. There may not be a correspondence between the individual differences in the magnitude of facilitation and adaptation effects. Future investigations could measure the threshold at which the facilitatory effect of priors on visual awareness shifts into a suppressive effect (Brascamp et al., 2007; Suárez-Pinilla, Seth, Roseboom, 2018), how this process is expressed in the visual pathway, and whether individual differences in this threshold predict perceptual experiences.

The relationship between priors and adaptation is further complicated by adding attention into the equation. Attentional effects on neuronal and visual sensitivity are

similar to that of increasing stimulus contrast (Carrasco et al., 2004; Carrasco, 2011) and in line with this full attention relative to partial attention is shown to increase the effects of adaptation (e.g., increasing motion after-effect, Rezec, Krekelberg & Dobkins, 2004; and strengthening contrast adaptation, Ling & Carrasco, 2006). The attentional effect can be best characterised as an initial boosting of visual sensitivity but sustained attention then leads to greater (and faster) adaptation over time (Ling & Carrasco, 2006). Diverted attention slows rivalry rate about as much as halving the contrast of the stimuli, so attention does seem to have the paradoxical property of simultaneously enhancing the visual signal and also facilitating a faster adaptation and error-correction (Paffen, Alais, & Verstraten, 2006; Jiang et al., 2013). Note also that viewers can voluntarily increase dominance durations of gratings (despite the idea that attending should speed adaptation) and even voluntarily slow down alternation in binocular rivalry (Meng & Tong, 2004), so it is likely different attentional strategies can be used to exert opposing effects on awareness, perhaps using saccades and fixation (Van Dam & van Ee, 2006ab). A future extension of this work should use stimuli of different signal strengths to investigate priming/adaptation curves (see Figure 7.7 in Appendix C for an example) when stimuli are fully versus partly attended. This may reveal individual differences in attentional enhancement of visual signal and its contribution to the facilitation and adaptation effects of primes. To conclude, it seems that expectation, attention, and adaptation interact synergistically – attention can facilitate the effects of priors but also speed adaptation. Our findings suggest that although the facilitatory effects of selective attention and priors on visual awareness are related, adaptation may be a somewhat distinct mechanism that warrants further exploration.

5.5.6 Conclusion

The present study demonstrates that different methods of manipulating attention and prior knowledge (e.g., selective attention, predictive context, imagery, expectancy, priming, and adaptation) are effective in exerting an influence on the subjective experience of binocular rivalry. This was evidenced by a significantly longer duration of the selectively attended percept and a higher percentage of (and shorter latencies for) initial percepts matching the prior in all manipulation conditions (primes with strong signal showing the reverse). Our correlational and factor analyses indicated that the effectiveness of most prior manipulations is connected to the ability to control the contents of visual awareness via selective attention. This suggests that the common mechanism of the influence of priors on awareness may be attentional. Whether attention increases the facilitatory effect of priors by increasing the sensory evidence for them (Jiang et al., 2013) or whether possessing strong priors increases effectiveness of attentional allocation and control (Zhao et al., 2013) is difficult to assess based on correlation alone. It is clear; however, that attention and expectation work synergistically and the causal correspondence between them needs to be investigated further. Our analyses also revealed that proneness to adaptation is a distinct tendency from facilitation by priors. The strength of adaptation predicted superior change detection in complex naturalistic scenes, supporting the notion that adaptation serves the purpose of increasing sensitivity to novelty.

It must be noted that the effects of different prior manipulations did not correlate together strongly – individuals did not show a consistent tendency for 'seeing the expected', suggesting that, apart from attentional effects, expectation-based biases may be method specific. Only perceptual priming predicted atypical perceptual experiences, such as experience of perceptual anomalies. It may be that prior manipulations differ in

the extent they activate the sensory representations of the expected grating, or the extent to which they recruit high-level mechanisms. Both possibilities are empirical questions that can be investigated further through MVPA during the binocular rivalry task. For example, the accuracy of decoding content-specific patterns of neural activity from early visual cortex during the different conditions could tell us about the extent that prior manipulations activate sensory templates, a technique previously employed by Kok and colleagues (2017). Assessing the priming/adaptation curves under full and partial attention could further reveal how attention influences the balance between facilitatory and suppressive effects of priors in different individuals. Individual differences in the interactions between expectation, attention, and adaptation, in terms of their effects on awareness and their neurocognitive basis, may then reveal different profiles of visual experience.

CHAPTER 6
GENERAL DISCUSSION

6.1. Summary of aims and results

How do people differ in their subjective experience of the visual world? Given the same visual environment, do individuals reliably differ in their awareness of change? What might drive individual differences in the ability to notice visual changes? These are the questions that motivated this thesis. I selected change blindness (CB) as the main paradigm to explore these questions, as it can be defined as a failure to become aware of a visual stimulus (Rensink et al., 1997; Simons & Rensink, 2005). Change blindness also reveals a startling limitation of the human visual system; in opposition to our intuitions, we may not possess an accurate and detailed internal image of the external world that we can access at any given moment. Considering large and salient changes in the environment can go unnoticed, our conscious access to visual representations may be limited. The interference of a highly salient mask or a disruption between the pre- and post-change scenes is key in CB paradigms, as without it the visual transient of the change easily attracts attention and enters awareness (Becker, & Vera, 2007). Although it was known that people are generally poor in CB tasks (Jensen et al., 2011), it was not known if people reliably differ in their noticing ability and what mechanisms could explain these differences. Visual change detection is thought to involve interactions between several processes; attentional selection and encoding of pre-change scene into the VSTM, attentional capture or interference due to the visual transient (e.g., flicker), allocation of endogenous attention to search for the change, comparison of the post-change scene to the one stored in VSTM, and conscious registration of the change. The failure of detection could lie at any one point of this likely recursive chain of processes. An investigation of individual differences in CB and its predictors could reveal the mechanisms that support visual awareness.

Predictive processing was the theoretical framework that informed the hypotheses about the mechanisms underlying individual differences in visual awareness (Friston, 2010; Feldman & Friston, 2010; Clark, 2013; Hohwy, 2012; 2013). This theory holds promise to provide an explanatory framework of visual awareness due to the simplicity and elegance of its purported mechanism. Prediction generation and updating is proposed to take place at all levels of the cortical hierarchy, blurring the lines between perception and cognition (Clark, 2013). Thus, a promising approach was to identify individual differences in predictive processing biases. A perceptual inference necessarily involves a combination of prior knowledge (learnt priors about the state of the world) and sensory evidence (sensory signal from the environment). The current content of visual awareness is the multi-level perceptual prediction that best explains the incoming sensory evidence. Importantly, mismatches between the perceptual prediction and sensory evidence generate prediction errors that propagate upwards in the visual hierarchy and dynamically adjust inferences. Attention is thought to be the mechanism that dynamically gates the access to awareness, by selectively changing the weight of some prediction error units over others, according to expected precision of a perceptual model (Feldman, & Friston, 2010; Howhy, 2012). Within this framework, CB can be defined as a failure to update the current perceptual prediction of the visual world.

Considering this, I hypothesised that individual differences in the awareness of visual stimuli may be determined by the balance between weighting prior knowledge versus sensory evidence. In the process of perceiving a visual scene, an observer could assign more weight to their prior expectations about the scene or to the incoming sensory signal. At the outset of this project, it was not clear how a predictive processing bias would manifest in visual experience in the general population, as these biases were mainly described in relation to psychopathology. For example, it has been proposed that

when the processing balance is shifted towards reliance on prior knowledge, individuals are more likely to experience sensory hallucinations and psychotic symptoms (Teufel et al., 2015; Sterzer et al., 2018). A bias towards weaker priors or weighting up sensory evidence may in turn manifest in conditions like the ASD, explaining the visual characteristics of such as fine perceptual discrimination coupled with sensory hypersensitivity and a poor ability infer abstract patterns such as complex social rules (Van de Cruys et al., 2014; Pellicano & Burr, 2012).

The initial hypothesis of this thesis was that attending to sensory evidence will result in an improved awareness of novel stimuli. Boosting the weight of sensory evidence should increase the signal of prediction error and therefore result in more frequent updating of perceptual predictions. However, the alternative hypothesis that increased weight to prior knowledge would manifest in better awareness was also considered. The fundamental principle of predictive processing is that having internal models makes the ambiguous and changing stimulation from the external world easier to parse and use for adaptive behaviour (Teufel et al., 2013; Clark, 2013; Hohwy 2013). Therefore, having strong perceptual models should be adaptive and facilitate optimal awareness of relevant visual stimuli. In this sense, the hypothesis was agnostic as to how the predictive processing bias will predict change detection, but it was hypothesised that there will be a relationship. To summarise, the overarching aim of the thesis was to investigate individual differences in visual awareness and to assess whether they are connected to a predictive processing bias.

6.2. Chapter-wise findings

The empirical work of *Chapter 2* characterises the individual differences in the flicker CB task with naturalistic scenes and identifies the strongest predictors of

noticing ability among a battery of perceptual and cognitive tests. The bottleneck of superior visual change detection could be high-order processes related to encoding and maintenance of visual representations or it could be low-level sensitivity to visual signal. By selecting tasks pertaining to high-order and low-level mechanisms *Chapter 2* aimed to get at the distinction between assigning greater weight to perceptual prediction versus prediction error. The perceptual rivalry task was also included, as the alternation rate in bistable perception has large and stable individual differences (Pettigrew, 2001; Miller et al., 2010) and the stability of perceptual interpretation (low alternation rate) versus frequent updating (high alternation rate) may reveal predictive processing biases (Hohwy et al., 2008; Kanai et al., 2010; 2011). The results summarised in *Chapter 2* revealed the flicker CB task has a good test-retest reliability, as did the other perceptual and cognitive measures. The CB task performance could be generalised to the more ecologically valid task of detecting continuity errors in video clips. Greater fragile VSTM accuracy, lower proneness to attentional capture, and lower self-reported distractibility predicted superior change detection, and all three of these measures, along with greater stability in perceptual rivalry loaded onto a common factor we termed 'visual stability'. I consider this to be high-order factor reflecting strength of visual representations or, in the terminology of predictive processing, perceptual predictions. The second factor that emerged reflected low-level visual sensitivity and was named 'visual ability'. This factor was related to superior performance on tasks requiring fine discrimination of temporal order, sensitivity to spatial frequency and contrast, as well as accurate iconic VSTM. The factor structure was not perfect, as a few measures contributed to both factors (i.e. TOJ and fragile VSTM). These tasks may correspond to intermediate stages, which require visual sensitivity, as well as involvement of higher order attentional and memory-based processes. The main conclusion of *Chapter 2* was

that change detection in flickering naturalistic scenes captures reliable individual differences in ability that are likely to affect individuals in everyday life. Possessing accurate VSTM representations and the ability to resist attentional capture by salient distractors may support faster change detection. These results are consistent with the processes thought to be involved in visual change detection, such as attentional control and VSTM encoding and maintenance (Beck et al., 2001; 2005; Tseng et al., 2010).

Having identified the behavioural predictors of visual change detection, the next aim was to investigate the neural basis of individual differences in CB. *Chapter 3* outlines voxel-based morphometry (VBM) analyses that explore whether variation in grey matter (GM) volume in the whole brain and the average density in ROIs, predict measures of visual stability identified in *Chapter 2* (CB task, VSTM task, attentional capture, and perceptual rivalry). As the right PPC is causally involved in visual change detection (Beck et al., 2005; Tseng et al., 2010), I centred the first ROI around this coordinate and hypothesised there will be correlations between GM density in the right PPC and the behavioural measures. The other ROIs in bilateral parietal cortex were selected based on previous work on perceptual rivalry (Kanai et al., 2010; 2011). Finally, V1 was also hypothesised to predict performance on our tasks, given its purported role in determining the fidelity of VSTM representations (Cattenao et al., 2012; Bergmann et al., 2014, Verghese et al., 2014). We replicated the behavioural correlations found in *Chapter 2*, with the exception of the negative association between CB and perceptual rivalry. A replication with an independent sample gives confirmatory evidence that lower fragile VSTM accuracy and greater attentional capture are reliable predictors of CB. The ROI-based analyses yielded a positive correlation between GM density in left PPC and robust VSTM accuracy. The structural relationship between left PPC and VSTM observed in our work is consistent with research literature

demonstrating VSTM representations can be decoded from left PPC (Christophel et al., 2012) and its activation correlates with VSTM capacity (Todd & Marois, 2004; 2005). Our result additionally suggests that the accuracy of VSTM representation may be dependent on how much GM is available in this region. The whole brain analyses (WBA) revealed negative associations between robust VSTM accuracy and the GM density in a cluster of voxels in the right cerebellum and left hippocampus. However, given lower GM volume in these regions is typically associated with impaired performance, I concluded these two WBA results may represent noise. It must be noted that no correlations that survived correction emerged between brain structure and change detection parameters. We also did not replicate the established findings of relationships between brain structure and perceptual rivalry although one association was approaching significance (Kanai et al., 2010; 2011). This failed replication casts doubt on the SBB associations discovered in VBM research with limited sample sizes. These methodological concerns are further addressed in the section *Evaluation: limitations and lessons learnt* of this chapter.

In *Chapter 4* I aimed to operationalise the strength of perceptual predictions in a more concrete way than in *Chapter 2*, where it was inferred from the pattern of correlations between high-order tasks and their loading on a common factor with perceptual rivalry. Additionally, I questioned whether the perceptual rivalry alternation rate measures a predictive processing bias at all. Given that the correlation between perceptual rivalry and CB did not survive correction for multiple comparisons in *Chapter 2* and that in *Chapter 3* the association was not present, I sought a more valid measure of the strength of perceptual predictions. A variant of the Mooney task (Mooney, 1957) administered by Teufel and colleagues (2015) offered this kind of measure. Here participants' detection of faces in degraded two-tone images is improved

after seeing the original colourful templates. This indicates participants can use the internal representation of the previously encountered face to disambiguate it in the degraded image. The difference between the detection sensitivity at baseline and after seeing the template is operationalised as reliance on prior knowledge. This measure has been shown to correlate with anomalous experiences in the general population (Teufel and colleagues, 2015), giving support to the notion expressed in predictive processing frameworks that excessive reliance on priors can result hallucinations (Fletcher, & Frith, 2009; Adams et al., 2013; Sterzer et al., 2018). In *Chapter 4*, consisting of a lab-based and an online experiment, we did not replicate the original finding by Teufel and colleagues (2015) that schizotypal individuals exhibit a shift towards reliance on prior knowledge. The lab-based study yielded a significant negative association; individuals who were less prone to sensory hallucinations actually improved in detection sensitivity more after seeing the Mooney templates. However, on a group level, participants did not benefit due to prior knowledge. This indicated the targets may have been too difficult to disambiguate even with knowledge of the templates. We amended this issue in the follow-up online study, as subjects experienced significant Mooney task improvement after seeing the templates with the corrected stimuli. However, the finding by Teufel and colleagues (2015) could still not be replicated, calling it into question. Furthermore, perceptual rivalry did not correlate with Mooney task performance, again suggesting it does not closely measure a bias to rely on perceptual predictions. We did find that Mooney face detection performance at baseline, which taps into the process of perceptual closure or formation of a gestalt (Thurstone, 1944; Mooney, 1957; Wasserstein et al., 2004), positively predicted change detection in naturalistic scenes. The latter finding points to the possibility that visual change detection and forming a coherent holistic representation from limited information may rely on similar

mechanisms, perhaps of relational binding of scene elements and matching current and stored representations.

After measuring reliance on priors using Mooney images and a failure to replicate its association with atypical perception, in *Chapter 5* I developed a more comprehensive and reliable way to measure the bias of expectations on visual awareness. In order to have a robust test that is amenable to influence of priors I chose the binocular rivalry task; the experience of the initial percept in rivalry has been shown to be affected by perceptual priming (Brascamp et al., 2007), mental imagery (Pearson et al., 2008), and the preceding context (Denison et al., 2011). The aim was to bias the perceptual experience of the rivalry display (i.e., the identity of initial percept) by inducing expectations in several different ways – through manipulating the preceding context, self-generated imagery, expectancy cues, and perceptual priming. Additionally, participants' normal binocular rivalry rate was assessed, and they were asked to use selective attention to control percept dominance durations at will. The latter manipulation was used to measure the extent to which selective attention influences awareness. The overarching aim of *Chapter 5* was to assess whether the prior manipulations significantly affected the awareness of the expected stimuli, whether the extent to which they do correlates, and whether these effects load onto a common factor. This would reveal whether there are reliable individual differences in a tendency to 'see the expected'. Finally, I explored whether the influence of priors predicts change detection performance, perceptual traits, and atypical perception. All prior manipulations exerted significant and strong effects on the initial percept in binocular rivalry. Expected stimuli were more likely to enter awareness when viewing the rivalry display and they were also responded to faster. Participants were also able to significantly increase the dominance duration of a selectively attended grating. There

were few correlations between the prior manipulation conditions themselves, but the strength of most prior manipulations was predicted by the ability to control binocular rivalry via selective attention. Change detection ability was predicted by the proneness to adaptation – the greater the strength of adaptation, the better the performance. The results of *Chapter 5* (as did *Chapters 2* and *3*) yet again highlighted the intimate links between endogenous attention and the strength of visual representation, in their influence on visual awareness. However, the mechanisms of the different prior-induction techniques may be somewhat method-specific.

The question after summarising the findings of the thesis is – what has become clearer about individual differences in visual awareness? Taking stock from these findings reveals several key areas of discussion; the mechanisms of CB, the relationship between VSTM and attentional control, and the existence of general versus method-specific predictive processing biases. Evaluation of the empirical work conducted here motivates improvement in operationalisation of predictive processing related constructs, as well as improving the methodology of individual differences research to uncover the neuropsychological basis of visual awareness. This thesis has provided some insight into these areas, but a lot remains unknown and there are still outstanding questions that are sparked by the current research findings. These will all be discussed in turn.

6.3. Change blindness – what do we know now?

Table 6.1 Measures that predicted better visual change detection in this thesis

The predictors are as follows: fragile visual short-term memory (VSTM) percent accuracy, attentional capture when a salient singleton distractor is present, the distractibility score of the Cognitive Failures Questionnaire (CFQ), temporal order judgement threshold (TOJ) (the smaller the threshold, the finer the temporal discrimination), the number of alternations during perceptual rivalry, robust visual short-term memory (VSTM) percent accuracy, baseline Mooney face detection sensitivity assessing perceptual closure without prior knowledge, the attention to detail subscale from the Autism-Spectrum Quotient (AQ), the total score of the Cardiff Anomalous Perceptions Scale (CAPS), including the distress, frequency, and intrusiveness scales, the facilitatory effect of strong signal primes on the initial percept in the binocular rivalry task (a score of below 50% indicates an adaptation effect), the facilitatory effect of self-generated imagery on the initial percepts in binocular rivalry. All effect sizes are Pearson's r, except in Chapter 5, where Spearman's rho was used. The associated two-tailed significance level (* $p < .05$, ** $p < .01$, *** $p < .001$) is noted. The associations that survived the Benjamini-Hochberg correction are noted. The associations that were not replicated (not rep.) in subsequent chapters are noted.

	Measure and relationship	Effect size
Chapter 2, Chapter 3	↑ Fragile VSTM accuracy	.33**, .38* (survived)
Chapter 2, Chapter 3	↓ Attentional capture	-.41**, -.30* (survived)
Chapter 2	↓ CFQ distractibility	-.30* (survived, not rep. in 5)
Chapter 2	↓ TOJ threshold	-.33** (survived)
Chapter 2	↓ Perceptual rivalry	-.28* (not rep. in 3, 4)
Chapter 2	↑ Robust VSTM accuracy	.26* (not rep. in 3)
Chapter 4	↑ Mooney task d'	.33*
Chapter 4	↑ AQ AD	.39** (not rep. in 5)
Chapter 4	↓ CAPS total	-.31* (not rep. in 5)
Chapter 5	↓ Strong prime	-.34**
Chapter 5	↑ Imagery	.26*
Chapter 5	↑ Expectancy	.24*

6.3.1. Individual differences in change blindness are predicted by the accuracy of visual short-term memory and attentional control

The present investigation demonstrated that the flicker CB paradigm with naturalistic scenes can be used to reliably estimate an individuals' ability to notice visual changes. In this paradigm change detection was predictive of participants' performance with realistic displays and correlated with self-reported distractibility. Furthermore, VSTM accuracy and the ability to resist or recover from attentional capture are capacities that predicted better detection. Note that the sub-stage of VSTM that consistently predicted change detection in *Chapters 2* and *3* was fragile VSTM, a processing stage that is information rich and of high capacity but decays after about 4s and is prone to over-writing by new visual information (Sligte et al., 2008; 2009). Fragile VSTM is probed by a cue to attend a particular location during the retention period before the presentation of the test array. Timing-wise the fragile stage of VSTM occurs after iconic VSTM, which is largely driven by retinal afterimage, and precedes the more commonly measured robust VSTM, which is known to hold about four items. Fragile VSTM is not affected by luminance masks but is affected by patterned (object-based) masks and is reduced to the capacity of robust VSTM after such interference. The neural basis of fragile VSTM is thought to involve persistent activation in visual and temporal cortex after the retinal activation supporting iconic VSTM ceases (Sligte et al., 2008; 2009). The present results suggest that the quality (e.g., richness or detail) of the representation of the visual scene encoded in fragile VSTM may be particularly important for noticing an object change within a scene. The stronger these representations are, the more resistant they may be to over-writing. Given the measures

of fragile and robust VSTM are correlated (e.g., in *Chapter 2, r = .55****), it is likely that individuals with stronger fragile representations can also transfer a greater number of integrated units into robust VSTM. This finding is consistent with other work showing correlations between VWM capacity using one-shot task and flicker change detection (albeit with simpler stimuli) (Pailian & Halberda, 2015). It is also in accordance the proposal that successful encoding of pre-change scene is a crucial determinant of detection (Beck et al., 2005; Tseng et al., 2010) and that having more time to encode the details of the pre-change objects may alleviate CB (Brady, Konkle, Oliva, & Alvarez, 2009). Individual differences in attentional strategy (e.g., selective attending) and brain activity at the encoding stage have been shown to predict change detection with simple stimuli before (Linke, Vicente-Grabovetsky, Mitchell, & Cusack, 2011). Together these findings highlight that building a strong internal model of the scene is key for change detection.

The mechanism of the relationship between VSTM and CB may be that individuals with high capacity VSTM store may have more detailed 'visual maps' and thus an ability to encode the scene more quickly, with a greater fidelity, and less competition between items (Bergmann et al., 2014; Verghese et al., 2014). People with a greater VWM capacity are also less susceptible to attentional capture and can disengage from capture easier (Fukuda & Vogel, 2009; 2011). This may be because larger functional V1 size enables better connectivity with prefrontal and parietal cortices and thus a more efficient allocation of attention (Verghese et al., 2014). Additionally, the flicker of the CB display may disrupt VSTM representations and attention, making it difficult to determine what to fixate on next. That is, the interference of the flicker may make it harder to predict the next saccade based on the representation held in VSTM (Friston, Adams, Perrinet, & Breakspear, 2012). Flicker is known to inhibit

saccades (i.e. increase latencies to peripheral targets) even when the saccades are not guided by memory (Baccino, Jaschinski, & Bussolon, 2001). Furthermore, increasing the background luminance during VWM tasks disrupts memory for those individuals with vivid mental imagery (e.g. users of sensory-based VWM strategies) (Keogh & Pearson, 2011). It has also been shown that priming effects of recently experienced stimuli can be disrupted by presenting an intervening neutral stimulus before test (Kanai, Knapen, van Ee, & Verstraten, 2007). Thus, the likely mechanism of CB is that the highly salient flicker disrupts the salience map which codes the naturalistic scene and its objects, therefore impairing the allocation of attention to the change. Consequently, recovering from the flicker interference may be easier if there are strong VSTM representations. People with strong representations (i.e. an accurate and/or large capacity VSTM store) may be able to recover from the interference and use VSTM-based salience maps to guide attention to search for the likely location of the change. In sum, CB may occur due to an adaptive process of dynamically re-calibrating the visual system to prioritise high salience stimuli; the flicker resets the VSTM salience maps but individuals with high capacity/fidelity VSTM may overcome this interference more easily.

The close correspondence between VSTM and attentional capture/control in this thesis and previous work (Fukuda & Vogel., 2009; 2011; Linke et al., 2011; Gaspar et al., 2016) highlight the intimate links between the strength of short-term visual representations and attentional ability. Many researchers have suggested that the process of VWM is best explained as allocation of internal attention to sustain certain perceptual representations over others (Theeuwes, Belopolsky, & Olivers, 2009; Chun, 2011; Machizawa & Driver, 2011). The filtering out of distracting external and internal information may allow particular VWM representations to be activated and maintained.

Correspondingly, a high VWM capacity can be understood as more efficient attentional filtering of sensory channels during the encoding stage and/or allocation of internal attention to the representation during maintenance. In predictive processing terms this ability would be equivalent to flexible allocation of high precision to some perceptual predictions over others. Whether attention and WM are separate processes or WM is equivalent to internally directed attention is debated but it is clear these processes are intimately linked (for a review see Kiyonaga & Egner, 2013). In sum, the ability to notice visual changes is consistently predicted by the accuracy of fragile VSTM representations (i.e., probed by retro-cue before the presentation of test display) and the ability to resist attentional capture by salient but irrelevant stimuli. These findings suggest CB is what happens when the link between phenomenal awareness (subserved by rich but fleeting visual representations, Block, 2005) and access consciousness is disrupted by irrelevant salience. Individuals with stronger phenomenal representations may be able to overcome attentional disruption more easily and allocate attention more efficiently.

6.3.2. Individual differences in change blindness are predicted by perceptual closure and adaptation

The two other behavioural measures that positively predicted change detection ability were the detection of faces in Mooney images and the strength of adaptation effects in binocular rivalry. As the disambiguation of briefly presented Mooney faces requires quickly building a gist of several disparate elements, performance could be mediated by VSTM capacity. However, since individuals could in principle quickly and accurately represent the elements of the Mooney image but not realise a face is present, an additional process is likely at work. This process may go beyond the speed or

accuracy of building a VSTM representation but rather require the ability to perceive the image in a relational and holistic manner, i.e., form perceptual closure (Thurstone, 1944; Mooney, 1957; Wasserstein et al., 2004). In terms of the neural basis of the processes causally involved in perceptual closure tasks, these largely overlap with regions involved in change detection, such as the parietal cortex (Giovannelli et al., 2010; Tseng et al. 2010). The mechanisms of Mooney task are proposed to involve binding the visually presented patterns into a coherent whole and matching it with long-term memory templates (Grützner et al., 2010). This may be the reason why change detection is predicted by perceptual closure, as relational binding and matching is also implicated in change detection (Aly et al., 2013). In addition to low-level scene properties such as contrast energy, coding the semantic and relational aspects of the scene is important for resolving CB, as semantically central (high importance) objects are detected more easily (Zuiderbaan, van Leeuwen, & Dumoulin, 2017). Our results indicate that high-level abilities such as building a gestalt of the scene may support faster detection of changing objects within naturalistic scenes. Future research could explore whether this process is dependent on VSTM capacity or fidelity.

The finding that adaptation to Gabor gratings predicts change detection in complex naturalistic scenes suggests that becoming aware of changes may involve a process of adapting to the constant elements of the scene. It is plausible that for individuals who adapt to the scene more rapidly the changing object gains salience faster. This finding supports the proposal that naturalistic vision is continuously guided by adaptation and that its functional role is noticing novel information (Clifford et al., 2007; Kohn, 2007; Webster, 2011). This result is also consistent with previous demonstrations that adaptation to the properties of a scene background improves visual search times for novel features on the adaptor background (McDermott, Malkoc,

Mulligan, & Webster, 2010; Wissig, Patterson, & Kohn, 2013). It is known that adaptation to orientation primarily occurs at the level of visual cortex although adaptation responses are also observed to object representations in extrastriate regions (Clifford et al., 2007). Whether change detection in naturalistic scenes is supported by purely low-level cortical adaptation to the features of the scene (e.g., contrast and orientation) or whether adaptation additionally occurs at the level of complex object representations (on top of the low-level contributions) is an open empirical question (Webster, 2011). Additionally, it could be investigated how adaptation-proneness is related to VSTM capacity. This is especially interesting, considering holding stimuli in VSTM and in mental imagery can lead to faciliatory and suppressive effects on visual awareness similar to that of direct priming and adaptation by a physical stimulus (Pearson et al., 2008; Saad & Silvanto, 2013; Dijkstra, Hinne, Bosch, & van Gerven, 2019). Perhaps stronger VSTM representations (i.e., in terms of activity level or specificity) also lead to faster adaptation, which then would improve detection of features that are novel relative to the representation.

A further question pertains to whether adaptation resolves CB due to adaptation to the scene, the flicker, or both. Note that presenting visual transients in the form of 'mudsplashes' in a one-shot change detection task leads to CB; however, individuals can recover from CB when the mudsplashes are shown several times before the onset of the post-change display (Becker & Vera, 2007). Importantly, Becker and Vera found that this recovery is not location-specific, as performance is improved even if the 'mudsplashes' changed location on each trial. The authors concluded that an attentional filter must be created to ignore the repeated uninformative visual transients and notice the smaller transient of the change. Even though the authors argue this is not a process of retinal adaptation, a higher-level adaption mechanism that is object not location-

specific could still support their results. Future research could elucidate if adaptation to the flicker or the scene (or both) resolves CB by manipulating the signal strength (e.g., contrast or luminance) of each. If adaptation to the scene resolves CB, object changes should be easier to notice in high-contrast scenes due to a faster adaptation rate with strong signal. If adaptation to the flicker is important, changing the luminance of the flicker should also affect performance.

6.3.3. No associations between change blindness and brain structure

In addition to the behavioural predictors of change detection, the neural basis of the individual differences in CB were also investigated. Although significant correlations emerged between robust VSTM accuracy and the average GM density in left PPC, there were no correlations between change detection with naturalistic scenes and brain structure. It is not clear whether this null finding means that brain structure does not predict CB or whether the relationship could be revealed with a high-powered study. Occipital (Vogel & Machizawa, 2004; Todd & Marois, 2005; Cattaneo et al., 2009; Bergmann et al., 2014; Verghese et al., 2014) and parietal regions (Todd & Marois, 2004; 2005; Vogel & Machizawa, 2004; Christophel et al., 2012; Soto et al., 2014) are functionally and structurally related to VTSM performance and VSTM is a consistent predictor of the ability to detect visual changes (Pailian & Halberda, 2015; Andermane et al., 2019). Thus, there are reasons to expect the macrostructure of these regions will affect visual detection. However, it may be that within healthy populations (e.g., with no neurodegenerative illness) brain structure is not a strong determinant of visual change detection with naturalistic stimuli (Masouleh et al., 2019). As discussed in *Chapter 3*, it may be the case that functional aspects of neural activity are stronger

determinants of detection – not which regions have a greater GM density, but which regions communicate with each other and in what temporal patterns. Some of the neural correlates of change detection that may reveal individual differences are functional connectivity patterns between the cerebellum, visual, parietal, and prefrontal regions of the cortex (Kuo, Rotshtein, & Yeh, 2011; Rosenberg et al., 2016). Activation level of PPC (Christophel et al., 2012), as well as the functional size of V1 (Verghese et al., 2014) have been shown to predict VSTM capacity so may also predict individual differences in visual change detection.

6.3.4. Wider implications of change blindness research

When discussing CB as a lab-based phenomenon, it is important to keep in mind how it relates to our experiences in naturalistic environments. In this paradigm a visual change is purposefully masked by a physical interference – this is equivalent to real life scenarios where a change occurs simultaneously with an occlusion or whilst looking away (e.g., when driving). People will be susceptible to CB in situations where they encounter a highly salient visual transient that masks a smaller but behaviourally more relevant change or where they must rely on VSTM representations of the recent state of the environment. In this thesis change detection predicted how easily individuals noticed continuity errors in videos and their self-reported distractibility, suggesting CB may indeed capture individuals' naturalistic experiences. It is known that distractibility is a stable trait and can be remedied through adjusting the environment; for example, increasing perceptual load during the task of interest (Forster & Lavie, 2016). It may be worthwhile to investigate whether distractibility could also be remedied via attentional and WM training. Distractibility is associated with poorer life outcomes such as accidents (Larson & Merritt, 1991; Larson, Alderton, Neideffer, & Underhill, 1997) so

reducing it could improve safety on roads and the life quality of distractible individuals. Mindfulness-based practices in particular hold promise as tools that could improve visual detection performance, among other gains in cognitive and well-being outcomes (Tang, Hölzel, & Posner, 2015). Mindfulness-based training is associated with neuroplasticity in brain regions engaged in spatial attention and memory such as the fronto-parietal areas and the hippocampus (Hölzel et al., 2011ab) and improvements in different aspects of attention such as alerting, orienting, and conflict monitoring (Jha, Krompinger, & Baime, 2007; Tang et al., 2015). There is already evidence from a substantial sample that the rate of inattentional blindness of unexpected distractors is lower after a brief mindfulness induction (Schofield, Creswell, & Denson, 2015). Further research on how different meditation practices (e.g., open monitoring versus focused attention) fosters visual awareness would be of great practical relevance and longitudinal studies on their structural and functional effects on the brain could reveal the markers supporting greater visual awareness.

6.4. Is there a trait-like predictive processing bias in the general population?

Through characterising individual differences in visual change detection and identifying its perceptual and cognitive predictors the present investigation also aimed to infer the existence of a trait-like predictive processing bias. The thesis asked whether the influence of expectation on perceptual content reliably predicts individual differences in visual awareness. The results are not conclusive in this regard – it is still not clear whether a unitary tendency to 'see the expected' exists. The search for a sensitive measure of a tendency to rely on perceptual priors has revealed that in healthy

individuals such a bias may be so subtle that it cannot reliably be assessed via perceptual rivalry alternation rate (*Chapters 2* and *3*), face detection improvement due to templates in the Mooney paradigm (*Chapter 4*), or expectation-based influences in the relatively controlled binocular rivalry task (*Chapter 5*). This is not to say that prior knowledge does not affect perceptual experience and performance on a group level. Significant improvements in detection sensitivity were obtained in the Mooney task after exposure to the original photos of faces (*Chapter 4*) and the initial percept and response latencies were significantly biased towards the expected grating in binocular rivalry, with moderate to large effect sizes (*Chapter 5*). However, there may not be a general tendency to 'see the expected' across different methods of inducing expectations. Some manipulations may be more effective than others and the effects of these may not correlate strongly. The influence of most prior manipulations on awareness; however, was positively related to the strength of selective attention, which may be the shared aspect in the facilitatory effect of expectations. With regards to the direction of the relationship between expectation and selective attention, it could be bi-directional. For example, expectation may facilitate visual awareness via attentional prioritisation of the expected stimulus. Alternatively, greater attentional focus during the induction of priors may have led to facilitated effects on perception. Some (but not all) expectation-based biases predicted the ability to notice visual changes and atypical perception. In *Chapter 4* the improvement in Mooney task performance due to templates did not consistently predict detection, perceptual anomalies or autistic traits, In *Chapter 5* the facilitatory effects of imagery, expectancy, and the suppressive effects of strong primes predicted visual change detection, whereas perceptual priming predicted the number of reported perceptual anomalies. Judging from these results, it could be questioned whether the metaphor 'reliance on priors' is helpful or accurate, or

whether it is best to consider the concrete measure itself (e.g., the effects of perceptual priming or VSTM-based effect) and interrogate its neural mechanism. The conclusions from the present investigation are similar to those made by Tulver and colleagues (2019) who found that there was no unified factor explaining performance on tasks designed to measure reliance on priors including the Mooney task. Tulver and colleagues argue that what can be defined as a prior is always relative, in the sense that there are different priors at different levels of cortical hierarchy, for different stimuli, tasks, and contexts. This may be the reason a general tendency for reliance on priors is elusive in individual differences research. Recently, McGovern, Walsh, Bell, and Newell (2017) observed that individual differences in one type of adaptation effect (e.g., orientation adaptation, such as the tilt after-effect) correlate only weakly with a different kind (e.g., adaptation to the direction of motion). In their study, individual differences in contrast adaptation did not correlate with the other adaptation effects (i.e., direction, tilt after-effects) at all. Research like this highlights that it is important to consider where the facilitatory and suppressive effects of recent perceptual experience operate in the visual processing hierarchy. For example, adaptation to contrast or tilt may recruit different neural populations (e.g., in V1) than motion after-effects (e.g., in area MT).

Rather than possessing strong and set predictive processing biases it is feasible that individuals dynamically shift the balance between reliance on priors and sensory evidence according to the context. This strategy appears to be more adaptive, as the system should be flexible enough to determine the expected precision of the sensorium in each context separately (e.g., a dark forest versus a bright, empty room). The extent to which one relies on prior knowledge when perceiving the visual world will likely depend on how variable each context is, and how much information the observer has gathered about it (Hohwy, 2013; de Lange et al., 2018). Given similar perceptual

regularities and rules encountered during development, individuals may not greatly differ in a general tendency to use expectations to inform visual awareness. An exception may be if there are pronounced differences in the perceptual experiences during the development and beyond. For example, the statistics of the visual environment that individuals are exposed to may influence their perception of colour (Webster, 2011; Bosten et al., 2015) and the faces individuals habitually see may affect perception of faces of own and other races (Kelly et al., 2007). In sum, this thesis adds to the research literature demonstrating that possessing expectations about visual stimuli results in powerful facilitatory effects on perception (de Lange et al., 2018). Although most of these effects are related to attentional control, expectation-based effects do not reliably correlate across different prior induction methods. Furthermore, only some prior manipulations predicted atypical perceptual traits associated with the autism spectrum and schizotypy. Therefore, strong conclusions regarding differential reliance on perceptual priors in visual change detection, the autism spectrum, and schizotypy are unwarranted, especially if only using one paradigm to infer these (e.g. Teufel et al., 2015). That being said, the relationships that did emerge between expectation-based biases and perceptual experiences and traits, especially the priming and adaptation effects would need to be investigated further.

6.5. Evaluation: limitations, lessons learnt

There are strengths as well as weaknesses of the experimental approach of this thesis and lessons learnt about investigating individual differences in visual awareness. A strength of this thesis is that it assesses the test-retest reliabilities of commonly used change detection paradigms, as well as other perceptual tasks – this is the first attempt to determine the reliability of the naturalistic flicker CB task and to assess its

generalisability. It is important to assess if a task measures moment-to-moment fluctuations in performance or inter-individual variability in the relevant construct. Administering naturalistic tasks is also important for drawing connections with the experience of visual stimuli encountered in everyday life. Another strength is the individual differences approach – by identifying the predictors of performance it is possible to interrogate the mechanisms underlying visual change detection. It was previously known that VSTM and attentional control are mechanisms implicated in change detection, but the finding that performance on these measures correlate and load onto the same factor with CB adds further support.

A limitation of the present research is that it is correlational – it cannot be determined if the perceptual, cognitive, and structural predictors are causally involved in change detection. However, considering these findings together with experimental research, it is very likely that they are. We know that disruption of areas associated with VSTM encoding and attentional control processes result in greater CB (Beck et al., 2005; Tseng et al., 2010; Mevorach et al., 2006; 2009; Hodsoll et al., 2008). This research is complementary to experimental methods, in that it demonstrates the strength of the mechanisms that are causal at the group level also predict performance of individuals. In addition to research that enables inferring causality, there is value in exploratory and correlational research, as it can help to gain support for existing hypotheses and to inform new research questions regarding the underlying mechanisms of visual perception (Vogel, & Awh, 2008; Mollon et al., 2017). Another strength of the present research is that it is an independent replication of previously found expectation-based effects on awareness, of which some were replicated here (e.g., priming, Brascamp et al., 2007; imagery, Pearson et al., 2008; predictive context, Denison et al., 2011) but in others were not (e.g., the relationship between face detection in the

Mooney task and schizotypy, Teufel et al., 2015). Given broad conclusions in the research literature about a general effect of reliance on priors based on a single measure without assessing test-retest reliabilities, it is necessary to conduct independent replications of such effects, as well as to verify whether a trait can indeed be inferred using different methods of prior induction.

Another limitation of the present research concerns the investigation of neural basis of CB described in *Chapter 3*. The sample size was comparable to existing VBM research on visual perception (Kanai et al., 2010; 2011) and the tasks were previously shown to have good test-retest reliabilities (Andermane et al., 2019); however, we did not find the majority of the hypothesised associations, neither at the whole brain level, nor using a priori defined ROIs. This is somewhat troubling and there is indication that poor replicability of VBM research is a wider problem (Boekel et al., 2015), possibly due to questionable research methods or inconsistencies in processing steps, but primarily due to the simple fact that samples of more than 300 are recommended for decent power (Masouleh et al., 2019). This raises the issue that significant SBB associations found here and elsewhere may stem from false positives with exaggerated effect sizes.

This brings us to the larger problem of replication crisis in psychology (Cumming, 2014) and the suggested research practices to remedy this issue. To avoid replication issues in the future, researchers should make the research process as transparent as possible by using pre-registered reports, assessing the effects sizes, and evidence for the null hypothesis through Bayesian analyses, as well as making the original stimuli available for other researchers upon request. The last point is not necessarily the crux, as strong effects should be replicable even with a new set of stimuli if the effects rely on underlying mechanisms instead of being an artefact of

specific type of method. Meta-analyses investigating the effect size of the influence of perceptual expectations in schizotypal individuals, as well as individuals on the autism spectrum are needed in order to have confidence about the claim that priors are weaker or stronger in the two conditions (Cumming, 2014).

Interpretations of individual differences research is somewhat complicated by the finding that tasks that should in principle measure the same underlying construct often do not correlate or correlate only weakly in reality – this is observed in the present thesis as well as elsewhere (Wasserstein et al., 1987; Foreman, 1991; Tulver et al., 2019). This may mean performance on apparently similar tasks recruit somewhat different mechanisms or it could be because existing correlations are obscured by noise introduced in the task (i.e., measurement error in the form of trial-by-trial variation) (Rouder, Kumar, & Haaf, 2019). It is important that researchers make the link between the specifics of the task and what it intends to measure as concrete as possible and ensure the measure is reliable and valid through piloting and assessing test-retest reliability. Operationalising abstract concepts such as prior reliance may be problematic; keeping the description at the level of the actual task is preferable. Research exploring the neural basis of expectation-based effects may be needed to ascertain if there is a shared mechanism. Additionally, when discussing individual differences research and magnitude of relationships between measures, it may be worth considering how to evaluate effect sizes and how large they can realistically be. It has been suggested that the traditional benchmark set by Cohen (0.1 as small, 0.3 medium, 0.5 as large) is arbitrary, too stringent, and may undervalue important effects (Funder & Ozer, 2019). After considering the effect sizes of landmark findings in psychology (e.g., Milgram's obedience data has r of about .4) and the average correlations yielded in social and

personality research (e.g., about .2), Funder and Ozer advise to select more realistic

benchmarks for evaluating effect sizes:

> "We offer, therefore, the following New Guidelines: Assuming that estimates are reliable (a critical concern, as already discussed), an effect-size r of .05 indicates an effect that is very small for the explanation of single events but potentially consequential in the not-very long run, an effect-size r of .10 indicates an effect that is still small at the level of single events but potentially more ultimately consequential, an effect-size r of .20 indicates an effect of medium size that is of some explanatory and practical use even in the short run and therefore even more important, and an effect-size r of .30 indicates an effect that is large and potentially powerful in both the short and the long run. A very large effect size (r = .40 or greater) in the context of psychological research is, we suggest, likely to be a gross overestimate that will rarely be found in a large sample or in a replication. Smaller effect sizes are not merely worth taking seriously. They are also more believable." (p.166)

6.6. Outstanding questions and future research directions

The results of the present investigation motivate further research on the nature of

expectation, VSTM representations, attention, and adaptation. The interactions between

these mechanisms on a group level, as well as the correlations of their effects in

individuals are of interest. For example, it is shown that VSTM interacts with

adaptation, such that holding representations of gratings in memory exhibit tilt after-

effects like those produced by sensory adaptation to a prolonged physical stimulus

(Saad & Silvanto, 2013). There is already evidence that there are large individual

differences in the facilitatory effects of imagery on visual awareness, ranging from

priming to adaptation (Dijkstra et al., 2019). Top-down influences of expectation and

attention evidently have profound facilitatory effects on visual awareness (de Lange et

al., 2018; Denison et al., 2011; Pearson et al., 2008; Pinto et al., 2015; Melloni et al.,

2011) but it is also apparent that these effects are at some point constrained by

adaptation, which has previously been cast as low-level process (Brascamp et al., 2007).

The results of *Chapter 5* and similar work (McDermott et al., 2010; Wissig et al., 2013)

suggest adaptation may be a central process for calibrating the visual system's

sensitivity to novel visual change. It is evident that in order to fully understand how

prior knowledge and visual memory contribute to visual awareness, we need a clearer

understanding on how and when their facilitatory effects shift into suppression and how

individuals differ in these effects.

Future behavioural research on individual differences in visual awareness should

aim to use more robust research designs – careful operationalisation of measures, large

sample sizes, pre-registration of studies and methodology, and Bayesian analyses to

evaluate evidence for null and experimental hypotheses. Additionally, behavioural

research should be supplemented by structural studies of the human brain and its

relation to individual differences in visual experience. Structural research should also

aim for substantial samples (i.e., N > 300, Masouleh et al., 2019), follow and clearly

outline common guidelines, make the original masks used for extraction of GM volume

available for replication of effects, and investigate not only GM volume and density, but

also assess other morphological characteristics such as cortical thickness, surface area

(i.e. functional surface area of V1, Verghese et al., 2014), and white matter integrity and

connectivity, in order to obtain a full picture of the structural differences (Song et al.,

2015). Importantly, an investigation of changes to these structural characteristics

longitudinally after a sustained mindfulness-based training may reveal the potential to

alter individual differences in visual awareness and reveal structural correlates of

greater visual awareness (Hölzel et al., 2011ab). Conducting meta-analyses and

publishing null findings is important to have a truthful consensus regarding the

relationship between brain structure and individual differences in perception and

cognition. There is promise in investigating inter-individual variability in functional aspects of neural communication between cortical regions, as these may be stronger predictors of visual awareness than structural markers (Palva et al., 2010; Rosenberg et al., 2016). Finally, exploring brain activity patterns through MVPA techniques may allow us to delineate the similarities and differences between the effects of perceptual expectations, VSTM representations, mental imagery, and attention on visual awareness (Kok et al., 2017).

Box 1. KEY RESEARCH AREAS OF INTEREST AND OUTSTANDING QUESTIONS

ADAPTATION AND VISUAL AWARENESS

- Does adaptation to the visual scene or the flicker (or both) drive change detection in naturalistic scenes?
- Are individual differences in the strength of adaptation related to the capacity of VSTM and attentional control?
- How does attention interact with the facilitatory and suppressive effects of perceptual primes, behaviourally and in terms of the underlying neural representations? At what point does priming become adaptation for different people and can the parameters of the priming-adaptation curve predict perceptual ability and atypical perception?

PERCEPTUAL CLOSURE AND VISUAL AWARENESS

- Are individual differences in perceptual closure related to the capacity of VSTM and attentional control?
- Do strong VSTM representations support the processes of relational binding and matching involved in perceptual closure or is perceptual closure an additional process?

THE NEURAL BASIS OF VISUAL MEMORIES, IMAGERY, AND EXPECTATIONS

- If VSTM is conditional on activity patterns in visual and parietal cortex, what are their distinct contributions to the VSTM representation?
- How do weak and strong imagers differ in the neural basis of their VSTM representations? Are strong imagers more likely to activate content-specific information in visual cortex?
- How do weak and strong imagers differ in the extent expectations influence their visual awareness and is this bias expressed differently in their brains?

IMPROVING CHANGE DETECTION ABILITY

- Can the ability to notice visual changes, VSTM capacity, and attentional control be trained via different mindfulness-based practices such as meditation (e.g., open monitoring and focused attention approaches)?
- Are the functional neural correlates involved in visual awareness and the structural aspects of the implicated brain regions altered by a sustained meditation practice?

6.7. Concluding remarks

Change blindness is typically viewed as a failure of the visual system, but it is also an illustration of its dynamic plasticity in representing salient stimuli. Given that the visual system has adapted to be optimal for its environment, the rules that govern CB are likely to be beneficial during perception in naturalistic environments. When confronted with a very salient visual transient such as an abrupt onset, the visual system may re-set the salience maps thus making the detection of any less salient object transitions difficult. However, CB may be overcome through exerting attentional control to search for the change and matching the scene elements to internal representations or adapting to the constant elements of the scene (including the flicker).

This thesis shows individual differences in CB reflects variability in high-level abilities such as attentional control, the strength of short-term visual representations, and the ability to build a coherent percept and match it to stored knowledge, as well as low-level capacities such as proneness to adaptation. Attention and VSTM are likely to work in tandem, such that those with stronger internal representations are also capable of allocating attention more efficiently and to filter out distractors. Although expectations powerfully shape visual awareness by increasing the tendency and lowering the latency to consciously perceive the expected stimulus, a trait-like bias to 'see the expected' may be method-specific. The present investigation motivates future research to understand how the facilitatory effect of recent perceptual experience on visual awareness shifts into an adaptation effect, how attention and expectation interact in visual awareness, and how the activation patterns and functional connectivity between different brain regions give rise to their effects. Another important outstanding question pertains to the comparison process of the pre-change and post-change scene; this thesis suggests it is likely to work via mechanisms of high-level matching and low-level adaptation. Change blindness may not imply that visual representations are impoverished, rather that they are rich but temporally fragile in order to dynamically support perception of the present moment in the visual world.

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CHAPTER 7 APPENDICES

Appendix A: Chapter 2

Table 7.1 Stimulus parameters for the CB, attentional capture, VSTM, perceptual rivalry, TOJ, and CS tasks

Task	Stimulus parameters
CB	Image length & width: 27.28° x 20.60°
Attentional capture	Eccentricity of circular array of shapes from fixation: 9°
	Diamond & circle diameter: 2.25°
	Line length x width: 0.68° x 0.1°
VSTM	Eccentricity of circular array of shapes from fixation: 4°
	Rectangle length x width: 1.56° x 0.39°
	Cue length x width (four white triangles): 0.9° x 0.9°
Perceptual rivalry	Red fixation cross length x height: 0.5° x 0.5°
	Sphere diameter: 3.5°
	White dot angular velocity: 151 deg/s
TOJ	Dot radius: 0.3°
	Stimulus to centre distance: 4.4°
CS	Gabor patch size: 2.86°
	The initial parameters (priors) for the model were set as peak gain (γmax) of 100, peak spatial frequency (fmax) of 2 cycles per degree, width (β) of 3 octaves, and reduced gain at low spatial frequency (δ) of 0.5 log units. The luminance of the grey background was 36.85 cd/m2.

Data preparation

In the CB task one participant had a particularly low β (-11.26) and was identified as an outlier in the boxplot, and subsequently excluded from further analyses. The remaining 62 participants had a mean α of 1.05 (SD = 0.06), and a mean β of -5.27, (SD = 1.15). Landmark studies using the CB task have estimated performance by measuring percentage correct with presentation time windows varying from 40 to 60 seconds (O'Regan 1999; Rensink et al., 1997). However, our analysis shows that the test-retest reliability of percentage correct fluctuates depending on the cut-off point in time used to determine which responses count as timeouts (see Figure 7.1). At 40s the test-retest reliability of percentage correct is only 0.22, at 60s the reliability is 0.47, but average accuracy with our set of stimuli after 60s is 95%, and thus most participants have reached ceiling performance and variability is driven by a small number of weaker performing participants. We propose that our measure of CB performance, parameter β, is more reliable and informative than percentage correct, as it captures detection rate throughout the task.
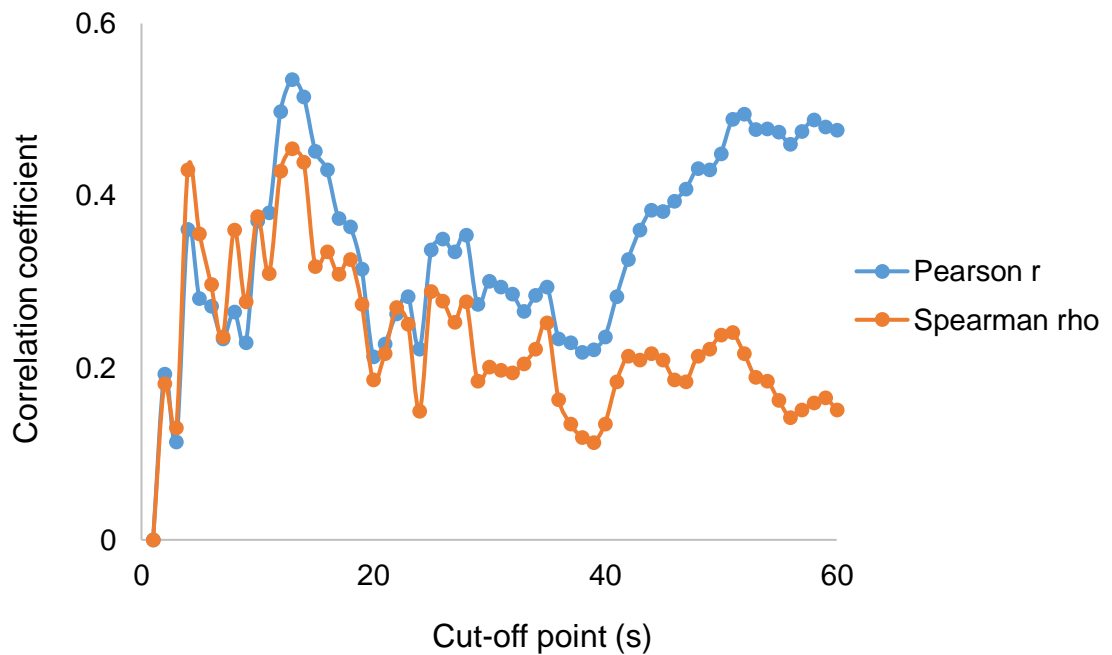
Figure 7.1 The test-retest reliabilities of percent correct in the CB task at different time points with a sample of 59 participants

In the continuity error video task, there were a number of control questions to ensure engagement with the task; 96.23% (SD = 3.99%) of these were answered correctly, indicating that participants were highly attentive. In the attentional capture task, incorrect responses, as well as responses with RTs that were less than 200ms or greater than 2.5 SD were removed from analyses; these constituted 6.39% (SD = 2.40%) of responses. For the VSTM task, responses with RTs of less than 200ms or greater than 2.5 SD were also removed; comprising 3.27% (SD = 1.20%) of responses. Outlier diagnostics of the average number of perceptual alternations in perceptual rivalry over the 4 min presentation revealed that one participant had an unusually high number of perceptual alternations (139); this outlier was removed from further analyses. In the contrast sensitivity task, participants (N = 7) with values of peak gain sensitivity (γmax) of under 0.5 were considered to be performing at the level of chance, possibly

due to inattentiveness, and therefore their contrast sensitivity data was not included in

analyses. In the matrix reasoning task, one participant failed to answer any of the

questions correctly, yielding a score of 0; this was also excluded, as in this case was

likely due to a failure of understanding the task instructions.

Figure 7.2 Pearson correlations between the measures of the full test battery

The measures are as follows: CB parameter β, percentage of correctly identified changes in continuity error videos, attentional capture in milliseconds, iconic, fragile, and robust VSTM percent accuracy, number of alternations in perceptual rivalry, TOJ threshold in milliseconds, CS parameters γmax, fmax, β, and δ, CFQ distractibility score, VVIQ score, and matrix reasoning task percent accuracy. Significance values (2-tailed), lower and upper 95% bootstrapped confidence intervals, and N values are provided below the correlation coefficients, respectively. The significant correlations are bolded. The correlation matrix is divided into three parts and continued on the next three pages.

Measure	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
CB β (1)	1	**.42** **.001** **.16** **.63** **(62)**	**-.41** **.001** **-.61** **-.16** **(62)**	.10 .420 -.18 .42 (62)	**.33** **.009** **.08** **.55** **(62)**	**.26** **.041** **-.02** **.51** **(62)**	**-.28** **.030** **-.52** **.01** **(61)**	**-.33** **.008** **-.53** **-.13** **(62)**	.22 .116 -.03 .45 (53)	.14 .319 -.17 .40 (53)	-.15 .292 -.48 .17 (53)	.03 .809 -.21 .26 (53)	**-.30** **.017** **-.51** **-.03** **(62)**	.17 .184 -.12 .45 (62)	-.05 .726 -.29 .19 (60)
CE % Correct (2)		1	-.01 .968 -.29 .26 (63)	.15 .249 -.13 .41 (63)	**.34** **.007** **.12** **.53** **(63)**	**.26** **.042** **.02** **.47** **(63)**	-.01 .920 -.27 .22 (62)	**-.26** **.041** **-.48** **-.04** **(63)**	.17 .207 -.07 .40 (54)	.05 .721 -.23 .33 (54)	-.01 .928 -.27 .26 (54)	.06 .643 -.22 .34 (54)	-.02 .871 -.29 .24 (63)	.06 .616 -.14 .27 (63)	-.10 .430 -.37 .15 (61)
Att. Capture (3)			1	-.11 .410 -.34 .10 (63)	-.24 .057 -.43 -.04 (63)	-.20 .120 -.42 .05 (63)	-.11 .379 -.32 .11 (62)	.17 .189 -.05 .39 (63)	-.10 .477 -.38 .17 (54)	-.10 .453 -.39 .17 (54)	.11 .413 -.19 .39 (54)	-.003 .981 -.23 .27 (54)	.20 .117 -.04 .41 (63)	-.09 .459 -.31 .14 (63)	.19 .143 -.12 .46 (61)
Iconic VSTM (4)				1	**.66** **<.001** **.51** **.77** **(63)**	**.29** **.023** **.07** **.47** **(63)**	-.07 .570 -.33 .18 (62)	**-.29** **.022** **-.52** **-.03** **(63)**	**.28** **.041** **-.01** **.55** **(54)**	.18 .203 -.07 .39 (54)	.19 .163 -.08 .41 (54)	.03 .835 -.25 .28 (54)	.06 .636 -.16 .26 (63)	.07 .605 -.22 .31 (63)	.14 .270 -.14 .39 (61)
Fragile VSTM (5)					1	**.55** **<.001** **.34** **.70** **(63)**	-.08 .516 -.28 .10 (62)	**-.41** **.001** **-.60** **-.20** **(63)**	.26 .057 -.03 .51 (54)	.01 .927 -.23 .25 (54)	.19 .175 -.06 .43 (54)	.12 .394 -.15 .35 (54)	-.01 .943 -.25 .24 (63)	.18 .168 -.06 .43 (63)	.10 .431 -.14 .31 (61)
Robust VSTM (6)						1	-.01 .958 -.23 .20 (62)	**-.29** **.022** **-.47** **-.07** **(63)**	.11 .408 -.16 .35 (54)	.07 .595 -.18 .33 (54)	.07 .621 -.23 .34 (54)	**.30** **.049** **.02** **.51** **(54)**	-.08 .510 -.34 .17 (63)	.09 .472 -.20 .38 (63)	-.01 .941 -.31 .27 (61)

Measure	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Perceptual rivalry (7)							1	-.01	.01	-.01	.11	-.08	.10	-.06	.16
								.948	.964	.966	.434	.564	.424	.619	.218
								-.23	-.21	-.35	-.27	-.35	-.18	-.34	-.11
								.23	.22	.33	.44	.19	.35	.19	.41
								(62)	(53)	(53)	(53)	(53)	(62)	(62)	(60)
TOJ (8)								1	**-.39**	-.20	.02	.06	**.32**	-.16	-.20
									.003	.139	.876	.660	**.011**	.217	.131
									-.67	-.43	-.23	-.21	**.08**	-.41	-.44
									-.01	.05	-.29	.31	**.53**	.09	.10
									(54)	(54)	(54)	(54)	**(63)**	(63)	(61)
CS vmax (9)									1	.07	.24	-.17	-.12	-.03	**.31**
										.598	.082	.229	.399	.809	**.024**
										-.25	-.001	-.41	-.40	-.30	**.08**
										.38	.45	.08	.18	.22	**.52**
										(54)	(54)	(54)	(54)	(54)	**(54)**
CS fmax (10)										1	.01	.02	**-.29**	-.07	.11
											.999	.911	**.031**	.608	.447
											-.30	-.26	**-.52**	-.30	-.22
											.27	.25	**.04**	.18	.41
											(54)	(54)	**(54)**	(54)	(54)
CS β (11)											1	.13	-.01	-.14	.22
												.364	.939	.330	.105
												-.16	-.30	-.38	-.10
												.38	.25	.10	.50
												(54)	(54)	(54)	(54)
CS δ (12)												1	.12	.08	-.03
													.403	.553	.833
													-.11	-.23	-.32
													.33	.34	.23
													(54)	(54)	(54)

Measure	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
CFQ (13)													1	.01 .966 -.20 .23 (63)	.17 .201 -.09 .42 (61)
VVIQ (14)														1	.02 .883 -.22 .27 (61)
Matrix (15)															1

Figure 7.3 The Scree plot for the exploratory factor analysis showing an inflection point at 3rd factor, justifying the extraction of 2 factors
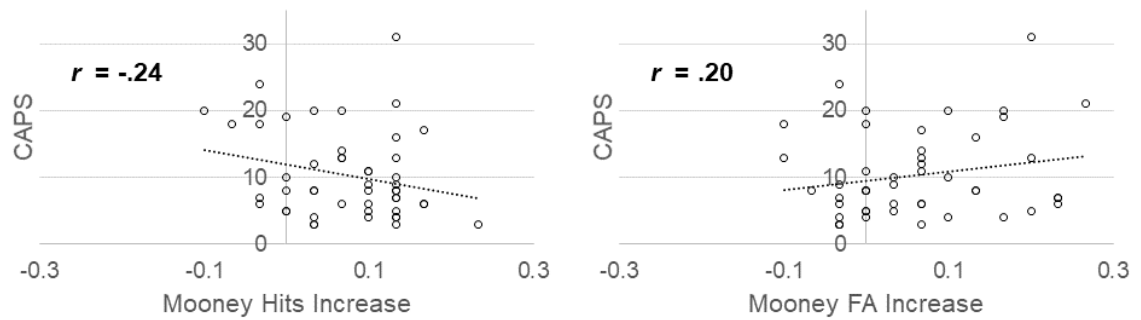
Appendix B: Chapter 4

Figure 7.4 Scatterplots illustrating the correlations between the change in the Mooney task hits and false alarms after seeing the templates and CAPS.

The associated Pearson's *r* coefficient is provided on each panel. These correlations are not significant (two-tailed) but there is a trend for hits to decrease and false alarms to increase for people reporting more perceptual anomalies in the CAPS.

Appendix C: Chapter 5

Table 7.2 Stimulus parameters of the binocular rivalry task

Parameters
<u>CRT monitor parameters</u>
Resolution: 1024 x 768, Refresh rate: 85 Hz, Colour: 32 Bit, Gamma correction: R: 2.341, G: 2.245, B: 2.245, L: 2.468
<u>Stimulus parameters</u>
Background colour: RGB (128, 128, 128), Background luminance: 3.60 cd/m^2
Gabor box visual angle: 4.24° x 4.24°, Gabor box border colour: RGB (0, 0, 0), Gabor box border visual angle: 0.06°, Gabor box luminance: 0.01 cd/m^2
Gabor patch diameter: 4.24°, Gabor patch spatial frequency: 15 cycles per pixel, Gabor patch orientation: Right-slanted: 45º, left-slanted: 135º, Gabor patch luminance at 20 % contrast: 4 cd/m^2, at 100% contrast: 5.90 cd/m^2
Fixation and cue visual angles: Fixation (Height: 0.23°, Width: 0.23°, Line thickness: 0.17°); Cues 'L' and 'R' (Height: 0.92°, Width:0.46°, Line thickness: 0.17°), Fixation and cue colour: RGB (255, 255, 255), Fixation and cue luminance: 6.80 cd/m^2

Table 7.3 The summary statistics of catch trial accuracy in the binocular rivalry task

The mean percentage accuracy difference between catch trials in the baseline and prior manipulation conditions, as well as Cohen's d effect size (calculated using pooled variance), and a paired samples t-test comparison of the two accuracies (N = 68). The prior manipulations did not significantly alter the accuracy on catch trials, relative to the baseline condition.

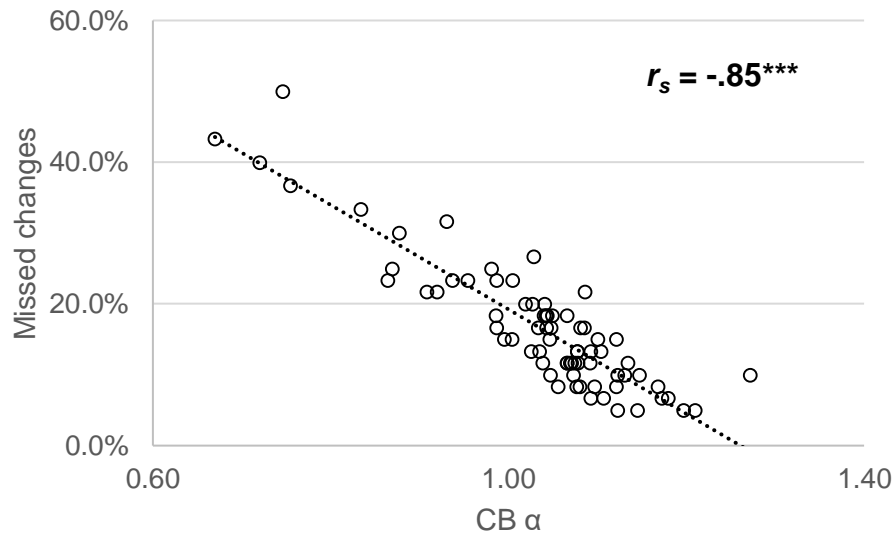|	Mean % accuracy difference (SD)	Cohen's d	t-test (2-tailed)
Predictive context	0.55 (9.52)	0.08	$t(67) = 0.48$, $p = .634$
Imagery	1.84 (9.23)	0.27	$t(67) = 1.64$, $p = .105$
Expectancy	1.10 (9.09)	0.17	$t(67) = 1.00$, $p = .321$
Weak prime	0.74 (11.61)	0.08	$t(67) = 0.52$, $p = .603$
Strong prime	-0.37 (15.72)	0.04	$t(67) = -0.19$, $p = .848$

Figure 7.5 A scatterplot illustrating the correlation between CB parameter α and the percentage of missed changes in the CB task

The associated Spearman's rho coefficient along with its two-tailed significance level (* $p < .05$, ** $p < .01$, *** $p < .001$) is provided on the panel.
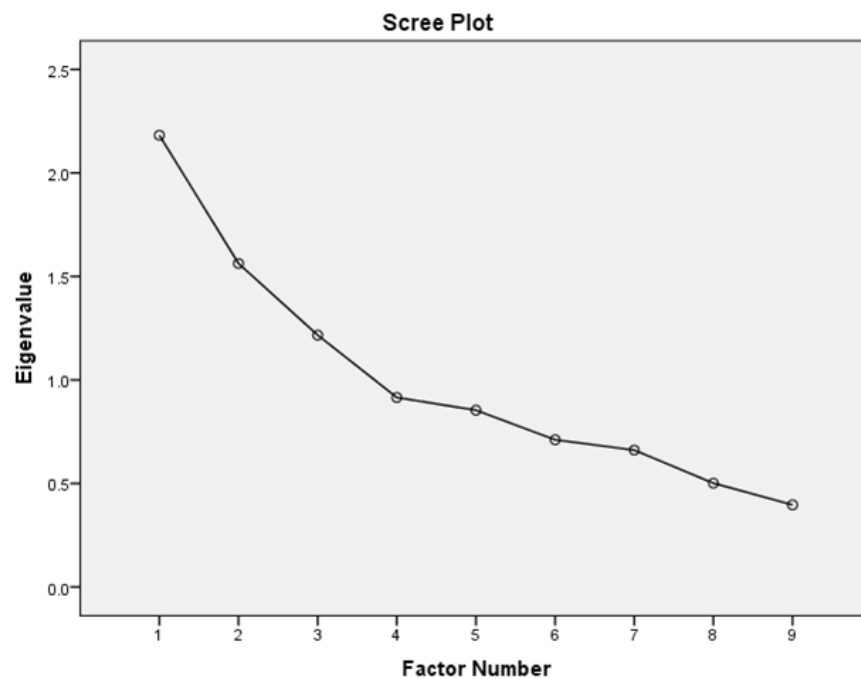

Figure 7.6 The Scree plot for the exploratory factor analysis showing an inflection point at 4th factor, justifying the extraction of 3 factors
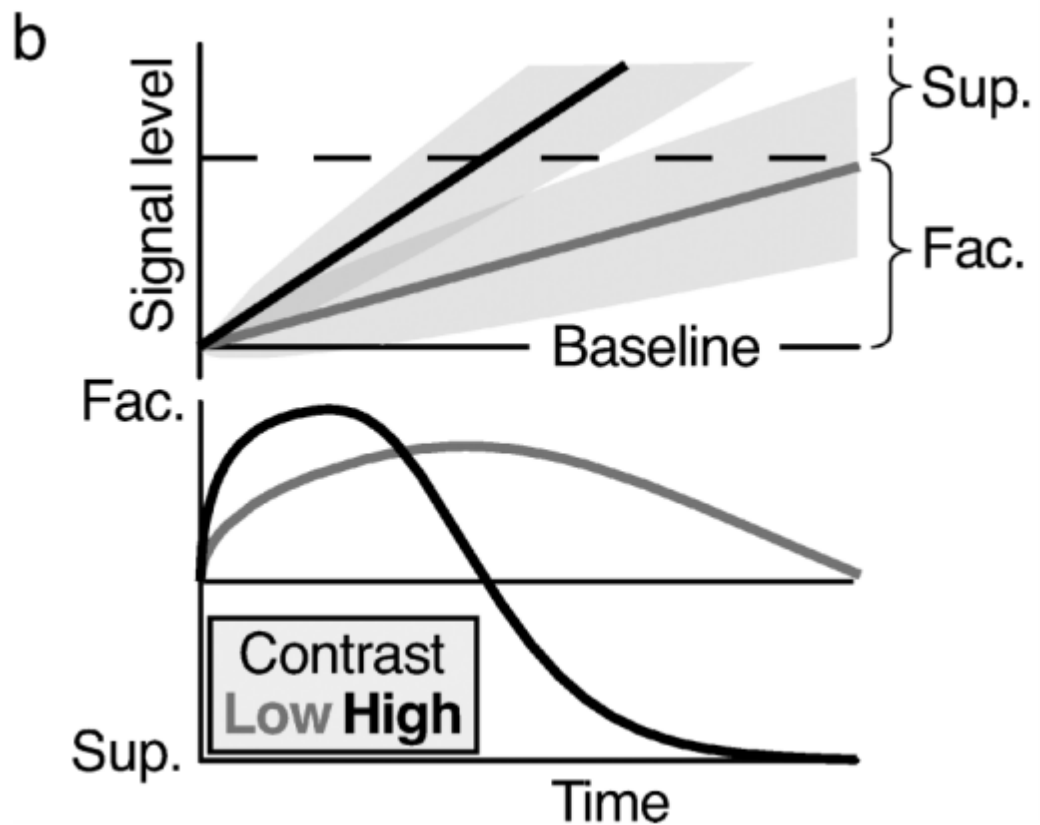
Figure 7.7 An illustration of the facilitatory (Fac.) and suppressive (Sup.) effects of weak and strong signal primes over time

Weak primes facilitate the awareness of the primed visual stimuli in a binocular rivalry display, whereas strong signal primes initially facilitate but then suppress awareness of the primed stimuli. Signal strength is determined by contrast and duration of the prime. Image taken from Brascamp and colleagues (2007).