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Article (Accepted Version)

Andermane, Nora, Bosten, Jenny M, Seth, Anil K and Ward, Jamie (2020) Individual differences in the tendency to see the expected. *Consciousness and Cognition*, 85. a102989 1-20. ISSN 1053-8100

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Individual Differences in the Tendency to See the Expected

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Manuscript submitted to: Consciousness and Cognition

Running Head: individual differences

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Abstract

Research has established that prior knowledge of visual stimuli facilitates their entry into awareness. 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 and manipulated *selective attention*, as well as induced expectations via *predictive context*, self-generated *imagery*, *expectancy* cues, and perceptual *priming*. Most prior manipulations led to a facilitated awareness of the biased percept in binocular rivalry, whereas strong signal primes led to a suppressed awareness, i.e., adaptation. Correlations and 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 perceptual abilities. Adaptation to strong primes predicted improved naturalistic change detection and the facilitatory effect of weak primes predicted the experience of perceptual anomalies. Taken together, our results indicate that the facilitatory effect of priors may be underpinned by an attentional mechanism but the tendency to 'see the expected' is method-specific.

Keywords: individual differences; visual awareness; attention; expectation; predictive processing; binocular rivalry

1. 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, Schwiedrzik, Müller, Rodriguez, & Singer, 2011; Denison, Piazza, & Silver, 2011; Pinto, Van Gaal, De Lange, Lamme, & Seth, 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, Roepstorff, & Friston, 2008; Clark, 2013). However, different methods are used to manipulate perceptual 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 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 the binocular rivalry paradigm where different visual stimuli are presented to each eye and then compete for perceptual selection, individuals report seeing a particular percept more often after being primed by it either directly or via self-generated imagery (Brascamp et al., 2007; 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 is not only facilitated by expectations but is also sustained with a lower signal to noise ratio if expectations are present.

The question therefore arises as to whether the facilitatory effects of perceptual 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, or 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 rely on formation (or activation in the case of imagery) of a memory trace of the stimulus. In other prior manipulations, the stimulus representation 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 cue-based effects may rely on learning 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 magnetoencephalography (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 seemingly distinct neurocognitive mechanisms (Summerfield & Egner, 2009). Imaging research reveals that expectation attenuates the overall neural activity in primary visual cortex for expected relative to unexpected stimuli and the pattern of activation becomes more specific to the expected stimulus – the neural representation is sharpened (Kok, Jehee, & De Lange, 2012). In contrast, selective attention seems to operate by enhancing neural activity in visual cortex (Martinez et al., 1999; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999) thus increasing the signal of the attended location, feature or object representation. 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 expected and unexpected representations cannot be differentiated using decoding techniques 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. Attention may also reverse the attenuation of activity that is observed for predicted but unattended stimuli (Kok, Rahnev, Jehee, Lau, & De Lange, 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 selectively increase the precision weighting of some prediction errors over others, 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 will also reflect these. Given their inter-dependence, it is difficult to investigate the effect of expectation on visual awareness completely independently from attention and we did not aim to dissociate the two in the present study. Instead, we aimed to measure the influence of attention and expectation on awareness 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 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). We operationalised the effect of selective attention as the change in percept dominance in the rivalry display due to voluntarily attending one rivalry stimulus over another, whereas the effect of expectation as the influence of recent perceptual experience on the initial percept in the rivalry display.

The aim of the present research was 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 gratings comprising seven conditions (*baseline*, *free viewing*, *selective attention*, *predictive context*, *imagery*, *expectancy*, and *priming*; see Figure 1 for an illustration). In these conditions we first manipulated attention or perceptual expectations and then measured the tendency to see the biased grating in the rivalry display. First, in the *free viewing* condition we measured the binocular rivalry alternation rate without any manipulations, as it has been suggested to index differences in predictive processing biases (Kanai, Carmel, Bahrami, & Rees, 2011). In the *selective attention* condition we measured participants’ abilities to increase the dominance duration of a particular grating via focusing attention (Meng & Tong, 2004; Tong et al., 2006). In the *predictive context* condition participants viewed a rotating sequence of gratings. This condition was adapted from Denison and colleagues (2011) and measured the extent to which the anticipation of a stimulus based on a previous sequence influences awareness. In the *imagery* condition participants were asked to imagine one of the gratings. This condition assessed the influence of internally activated 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. This condition measured the bias of expectancy based on suggestion alone rather than induced by statistical regularities. Finally, in the *priming* condition participants saw two types of prime differing in signal strength; a brief low contrast prime and a longer high contrast prime. 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). Note also that authors using the binocular rivalry paradigm with naturalistic images have found increased dominance of the unexpected stimulus after a predictive sequence has been well-learned via sequence repetition (Denison, Sheynin, & Silver, 2016). The amount of exposure to prior information (in terms of signal strength, duration, and statistical learning) may determine if predictable or novel stimuli lead to perceptual selection. Thus, including both conditions with weak and strong perceptual primes in the present study may help to elucidate the relationship between facilitatory and suppressive effects of recent perceptual experience. To measure perceptual traits, participants additionally completed a ‘flicker’ change blindness (CB) task (Rensink, O’Regan, & Clark, 1997) with naturalistic scenes and battery of questionnaires assessing their distractibility, visual imagery ability, and atypical perceptual experiences pertaining to psychosis and the autism spectrum.

To test whether a common mechanism underlies observed patterns of perceptual bias across different methods of prior manipulation, we assessed correlations between different expectation-based effects and conducted a factor analysis. We hypothesised that if there is a general tendency to ‘see the expected’

most expectation-based effects 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 visual cortex (e.g., perceptual priming and self-generated imagery), whereas others may rely on more indirect processes of coding the likelihood 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 expectation-based effects will not correlate well and will load onto separate factors. Furthermore, given the intimate links between attention and expectation, we hypothesised that a greater attentional control over binocular rivalry dominance durations will also predict a greater effect of prior manipulations on awareness.

Possessing strong perceptual 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, Mathys, & Corlett, 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).

2. Method

2.1 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 Brighton 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 of stereoacuity (Laméris Ootech, Nieuwegein, The Netherlands) 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.

2.2 Materials and Design

Participants completed the initial part of the study online; this included several questionnaires assessing a range of normal perceptual abilities and traits, as well as anomalous perceptual experiences.

2.2.1 Online questionnaires

Four questionnaires were administered based on the rationale that the traits that they measure may be related individual differences in attentional and expectation-based biases. The questionnaires are described in the order of presentation.

The Autism-Spectrum Quotient (AQ) (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 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, Halligan, & Ellis, 2005) 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., 2005). 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, Cooper, FitzGerald, & Parkes, 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), measuring everyday 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, Kass, & Stanny, 2002).

The Sussex Cognitive Styles Questionnaire (SCSQ) Imagery Ability subscale (Mealor, Simner, Rothen, Carmichael, & Ward, 2016) consists of 17 items and, as the rest of this 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

2. Binocular rivalry

3. Selective attention

4. Predictive context

5. Imagery

6. Expectancy

7. Priming

Figure 1. The stimuli and trial structure of the binocular rivalry task. In all conditions the trials started with a 1s fixation cross and ended with a blank 1s inter-trial interval. 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. Participants reported which grating (left-slanted or right-slanted) appeared dominant and, in case of a mixed percept, waited until one grating became visibly dominant. Responses were self-paced, with no time limit. After a response, an inter-trial interval 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 the two mouse buttons. All gratings except the strong primes in condition 7 were presented at 20% Michelson contrast.

2.2.2 Binocular rivalry task

In this task participants viewed right- and left-slanted sinusoidal Gabor gratings through a mirror stereoscope. The Gabors were presented on a grey screen with a black square border around them (for full details on visual stimuli and monitor parameters see Table A.1 in the Appendix). 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 1 for trial structure and timings). The task was to use the left or right mouse button to indicate which grating the participants saw in the binocular rivalry display (e.g., left-slanted or right-slanted). In the case of seeing a mixed percept, the instruction was to wait until one of the gratings became visibly dominant, i.e., covered more than half of the rivalry display field, before selecting a response. In all conditions each trial was preceded by a 1s fixation point and followed by a 1s blank inter-trial interval. Participants were instructed verbally before each condition, in addition to the written instructions provided on the screen.

The task started by setting up the binocular rivalry display. We presented a different grating (left- and right-slanted) 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 (i.e., the gratings overlapped in perceptual space). 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 trials, 8 catch trials). The binocular rivalry display was presented on each trial and participants indicated which grating they saw first. This condition was designed to estimate 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 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 of the rivalry display changed during this time using the left and right mouse buttons, similarly to the *free viewing* condition. As in the other conditions, in case of seeing a mixed percept participants were instructed to wait until one grating became visibly dominant before making a response. This condition assessed participants' abilities to increase the dominance of the cued grating using attentional control.

Next, participants completed the *predictive context* condition (80 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 orientation of the next 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 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 trials, 8 catch trials). Participants were instructed that a cue would 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 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 trials, 8 catch trials) participants saw a perceptual prime before the rivalry display. There were two types of prime, each presented in a separated block; weak primes were presented first, were low contrast (20%), and presented briefly (100ms), whereas strong primes were presented last, were of high contrast (100%), and had a longer duration (2.5s). The weak primes were designed to lead to facilitation of awareness of the same grating in rivalry, whereas strong primes to the suppression (e.g., by adaptation) of the same grating.

Within each condition 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 Gabors). Catch trials were introduced to check if participants exhibited any response bias by responding in line with prior manipulations even on perceptually unambiguous trials. In all conditions participants were asked to indicate which grating they saw in the rivalry display 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. In conditions 2-3 clicking responses were made continuously to indicate how perception of the gratings subjectively alternated throughout the 60s presentation window (e.g., click the left button when the left-slanted grating becomes dominant and vice versa). In condition 3 the timing of the clicks and the time interval between clicks was additionally recorded. This data was used to calculate for how long on average each grating (e.g., left- and right-slanted) was dominant during each rivalry display presentation window. Since mixed percepts were not recorded in this task, we define percept dominance as a period that started with the report of the specific percept and during which the competing grating did not enter awareness.

In the case of seeing a mixed percept, participants were instructed to report which grating was 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% Michelson 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% Michelson contrast.

2.2.3 Change blindness task

The CB task was adapted from Andermane, Bosten, Seth, and Ward (2019) 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 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 the 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 inter-trial interval of 1s and a black screen with a white fixation square of 3s before each trial. To separate correct responses from incorrect ones, ROIs within each image (image dimension: 1024 x 768 or 27.7° x 20.9°) were defined around the centre coordinates of the changed object, and mouse clicks with coordinates outside ROIs (Mean radius = 2°) were labelled as misses. The ROIs were liberal to avoid mislabelling imprecise mouseclicks as misses, i.e., to allow for responses that are not directly on the object but are closely next to it.

2.3 Procedure

All participants gave informed consent prior to taking part in the study. The online session comprising the questionnaires lasted 30 minutes and was completed before attending the lab-based session. The lab-based session lasted 1h and 30 minutes 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 therefore render the prior manipulations ineffective. If participants passed the selection criterion (i.e., correctly identifying shapes in plates I-V by stereopsis, demonstrating 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 (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, Bosten, Peterzell, & Webster, 2017). The binocular rivalry task was presented using MATLAB (Mathworks Inc., Natick, MA) and the Psychophysics Toolbox extension (Brainard, 1997). For this task participants were seated 100cm 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. Participants completed the CB task seated comfortably 55cm from the computer screen (screen resolution = 1920 x 1080) in a well-lit room.

3. Results

3.1 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 obscure the effect of priors on binocular rivalry, as it would render the rivalry display less ambiguous and priors are more likely to be utilised when input is ambiguous (De Lange, Heilbron, & Kok, 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). For most participants, eye dominance changed slightly throughout the task, thus the baseline condition was not representative of their average eye dominance. To control for such effects, the percentage of initial responses matching the grating shown to the left and right eye was calculated across all conditions (i.e., 1, 4-7). 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 cut-off value was previously used by Denison et al., 2011).

In the *free viewing* condition, the measure of interest was the total number of perceptual alternations reported 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., a 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*, and *priming*), the percentage of initial responses to the rivalry display matching the expected grating was calculated.

Mean response times (RTs) to target trials were also estimated in all prior manipulation conditions to determine whether the prior stimuli speeded response latencies to matching percepts. For the purpose of these analyses, RTs of over 10 seconds were excluded, leading to an exclusion of 0.5% trials overall (0.9% in the *predictive context*, 0.8% in the *imagery*, 0.1% in the *expectancy*, 0.04% in the *weak prime*, and 0.5% in the *strong prime* condition, respectively). This was done to prevent a few overly long responses affecting the mean RTs in the prior manipulation conditions differentially. However, long trials were not excluded from calculations of percentage of responses matching versus not matching the prior. This was done in order to keep the balance of possible trials equal (e.g., those preceded by a left-versus right-slanted prior). Since participants were given an instruction to only respond when one percept becomes dominant in the rivalry field, long responses likely resulted from a prolonged experience of a mixed percept.

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., $\alpha Y = e^{\beta/X}$, 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 A.1 in the Appendix 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.

3.2 Descriptive statistics

All attentional and prior manipulations led to significant moderate to large effects on the subjective experience of binocular rivalry (the descriptive statistics, effect sizes, and inferential statistics are presented in Table 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 0.44 to 0.86), 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% ($d = 2.45$), suggesting that the high-contrast, long duration primes suppressed awareness of the primed grating.

Table 1. The summary statistics of the performance in the binocular rivalry task. The listed measures are as follows (the numbering corresponds to Figure 1): the number of alternations in binocular rivalry (2), the difference in seconds between dominance duration of percepts matching versus not matching the attentional cue in the selective attention condition (3), and the percentage of initial percepts matching the prior in the predictive context, imagery, expectancy, weak prime, and strong prime conditions, respectively (4-7). 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 a paired sample t -test comparison of the percept durations matching and not matching the

attentional cue in the selective attention condition (3), and one-sample *t*-test comparisons of percentage of initial percepts matching the cue and chance performance in the rest of the conditions (4-7). 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)	Number of alternations	N/A	N/A
3. Selective attention	1.04 (1.61, 68)	Difference in duration (s)	0.71	$t(67) = 5.36$, $p < .001$
4. Predictive context	55.01 (5.81, 69)	% of responses matching prior	0.86	$t(68) = 7.17$, $p < .001$
5. Imagery	63.45 (16.33, 69)	% of responses matching prior	0.83	$t(68) = 6.84$, $p < .001$
6. Expectancy	56.26 (9.24, 69)	% of responses matching prior	0.68	$t(68) = 5.63$, $p < .001$
7. a) Weak prime	59.22 (20.98, 69)	% of responses matching prior	0.44	$t(68) = 3.65$, $p = .001$
7. b) Strong prime	17.19 (13.38, 69)	% of responses matching prior	2.45	$t(68) = -20.36$, $p < .001$

All prior manipulations had a significant effect on RTs in the binocular rivalry task (see Table 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. These results are consistent with previous observations of speeded response latencies to predicted percepts (Dension et al., 2011). In the *strong prime* condition, responses to percepts matching the prime were significantly slowed, reflecting an adaptation effect. Together these results suggest that priors not only bias the probability of the corresponding percept entering 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 2. The summary statistics of response times in the binocular rivalry task. The means and standard deviations of RTs (in milliseconds) 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 manipulations resulted in significantly faster RTs

to the matching percept relative to the non-matching one, except in the 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 <i>d</i>	<i>t</i> -test (2-tailed)
Predictive context	1766 (775)	1911 (924)	145 (272, 69)	0.17	<i>t</i> (68) = 4.44, <i>p</i> < .001
Imagery	1900 (842)	2307 (1033)	407 (558, 69)	0.43	<i>t</i> (68) = 6.06, <i>p</i> < .001
Expectancy	1381 (648)	1467 (678)	86 (249, 69)	0.13	<i>t</i> (68) = 2.88, <i>p</i> = .005
Weak prime	1218 (506)	1430 (726)	212 (597, 67)	0.34	<i>t</i> (66) = 2.91, <i>p</i> = .005
Strong prime	2143 (1183)	1268 (544)	-875 (935, 67)	0.95	<i>t</i> (66) = - 7.66, <i>p</i> < .001

3.3 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 A.2 in the Appendix 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 to 50% (see Table 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 the imagery condition, although not after correction for multiple comparisons) (see Table A.3 in the Appendix). We also pooled the catch trial responses across all five prior manipulation conditions (resulting in 28 trials per participant, 1932 trials altogether) and calculated the average percentage of catch trials matching the priors. This was done to ensure greater sensitivity for detecting a response bias, given the few catch trials (i.e., 4 to 8 trials per condition). However, this analysis also indicated that participants were not likely to respond in line with the prior information on unambiguous trials (see Table 3). Overall, the analyses of the catch trials suggest that the experimental results summarised above reflect genuine effects 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 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, as well as averages for all conditions pooled (*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 <i>d</i>	<i>t</i> -test (2-tailed)
Predictive context	97.64 (5.78)	49.09 (5.39)	0.17	<i>t</i> (68) = -1.40, <i>p</i> = .167
Imagery	98.91 (5.14)	50.36 (5.24)	0.07	<i>t</i> (68) = .57, <i>p</i> = .567
Expectancy	98.19 (4.92)	51.45 (4.03)	0.36	<i>t</i> (68) = 2.99, <i>p</i> = .004
Weak prime	97.83 (8.29)	51.45 (8.45)	0.17	<i>t</i> (68) = 1.42, <i>p</i> = .159
Strong prime	96.74 (12.80)	49.64 (5.24)	0.07	<i>t</i> (68) = -.57, <i>p</i> = .567
Pooled (all conditions)	97.86 (4.52)	50.40 (2.25)	0.17	<i>t</i> (68) = 1.47, <i>p</i> = .146

3.4 Correlations between binocular rivalry conditions

There were several correlations between the different conditions of the binocular rivalry task (see Table 4 for the correlation matrix and Figure 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 family wise error and Benjamini-Hochberg correction for false discovery rate 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 of correlations in Table 4 demonstrate a positive manifold (Verhallen et al., 2017); all of the correlations that are hypothesised to be positive, such as the associations between attentional and prior manipulations, are in fact positive. The only two columns that have mostly 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 perceptual alternations in binocular rivalry predicted a weaker ability to increase dominance durations of gratings by selective attention (Spearman's $\rho = -.25$, $p = .041$) and a greater suppression effect of strong primes (Spearman's $\rho = -.29$, $p = .016$). 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 $\rho = .29$, $p = .016$), a stronger facilitatory effect of self-generated imagery, (Spearman's $\rho = .34$, $p = .005$), and a marginally greater priming effect with weak primes (Spearman's $\rho = .24$, $p = .052$). These results point to the interconnectedness of the ability to exert attentional control and the strength of the expectation-based effects on visual awareness.

A greater facilitatory effect of predictive context on the initial percept in binocular rivalry was associated with a greater adaptation effect to strong primes (Spearman's $\rho = -.25$, $p = .042$). 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 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.

Finally, a greater facilitatory effect of expectancy on the initial percept in rivalry was associated with a weaker adaptation effect to strong primes (Spearman's

$\rho = .24, p = .047$). Participants who responded more strongly to the suggestion of expectancy were less likely to adapt to the matching percept after seeing the strong signal primes.

Table 4. Spearman's correlations between the conditions of the binocular rivalry task. The associated *p*-values (two-tailed) are provided and the nominally 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	Expect-ancy	Weak prime	Strong prime
Binocular rivalry	1	-.25 .041	.07 .558	.11 .375	-.12 .312	-.16 .201	-.29 .016
Selective attention		1	.29 .016	.34 .005	.08 .495	.24 .052	.07 .549
Predictive context			1	.06 .623	.05 .661	.11 .349	-.25 .042
Imagery				1	.03 .797	.17 .159	-.13 .281
Expect-ancy					1	.04 .773	.24 .047
Weak prime						1	-.15 .222
Strong prime							1

Figure 2. Scatterplots illustrating the nominally significant correlations between the binocular rivalry task conditions. The number of each condition corresponding to Figure 1 is provided in brackets: binocular rivalry refers to the total number of alternations in the free viewing condition (2), selective attention refers to the increase in dominance of the attended grating measured in seconds (3), predictive context refers to the percentage of initial percept reports matching the grating expected based on the rotation stream (4), imagery refers to the percentage of initial percept reports matching the imagined grating (5), expectancy refers to the percentage of initial percept reports matching the expectancy cue (6), weak prime refers to the percentage of initial percept reports matching the low contrast short prime (7 a)), strong prime refers to the 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.

3.5 Factor analysis

A principal axis factor analysis with a sample size of 67 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 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 ($KMO = .57$, 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 criterion of 1 (Kaiser, 1958) and an inspection of the Scree plot confirmed that an inflection point was present at fourth factor (see Figure A.2 in the Appendix). The first three factors in combination explained 54.57% of variance in the data. Table 5 shows the factor loadings after rotation.

Table 5. 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 ($N = 67$).

	Factor 1: Selective attention	Factor 2: Adaptation	Factor 3: Binocular rivalry
Binocular rivalry	-.20	-.02	.90
Selective attention	.69	-.04	-.13
Predictive context	.27	.29	.03
Imagery	.59	.22	.16
Expectancy	.45	-.17	-.04
Weak prime	.42	.10	-.16
Strong prime	.05	-.65	-.02
CB α	.13	.66	-.05
CB β	.15	-.23	.16

We interpreted the first factor as ‘selective attention’, as it had the highest positive loading on the *selective attention* condition of the binocular rivalry task, which measures 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 suggests that proneness to adaptation may support improved change detection in naturalistic scenes.

The tendency to see the percept matching a predictive rotating sequence of gratings (*predictive context* condition) had lower and approximately equal loadings on the first two factors. 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 loadings 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 be underpinned by a mechanism unrelated 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).

3.6 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 6. The scatterplots of the correlations between binocular rivalry task conditions and the perceptual measures and traits are shown in Figure 3. Note that the significant correlations between the expectation-based effects and the perceptual measures and traits reported below did not survive the Benjamini-Hochberg correction. For the full correlation matrix between all measures, visit https://osf.io/9827b/?view_only=16be1cdb84a44b4ba9860f900b253df6.

Table 6. 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 abilities and traits; change blindness (CB) parameters α and β , the Autism-Spectrum Quotient score, the Cardiff Anomalous Perceptions Scale (CAPS) score,

the total CAPS score with the associated distress, frequency, and intrusiveness ratings, the Cognitive Failures Questionnaire (CFQ) score, and the Sussex Cognitive Styles Questionnaire (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	60.90 (9.09, 69)

We found that increased adaptation to strong primes predicted a higher CB parameter α (Spearman's $\rho = -.34$, $p = .005$) (see Figure 3). This demonstrates that being more sensitive to adaptation effects may be beneficial for change detection in complex naturalistic scenes. An increased facilitatory effect of self-generated imagery correlated with higher CB parameter α values (Spearman's $\rho = .24$, $p = .045$). This suggests that a stronger influence of visual imagery on perception predicts better change detection.

Figure 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: change blindness (CB) parameter α , Cardiff Anomalous Perceptions Scale (CAPS), and the Autism-Spectrum Quotient (AQ). The binocular rivalry conditions are as follows (with corresponding Figure 1 numbers provided in brackets): imagery refers to the percentage of initial percepts matching the imagined grating (5), weak prime refers to the percentage of initial percepts matching the low contrast short duration prime (7 a)), strong prime refers to percentage of initial percepts 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 = .31, $p = .010$), and CAPS together with associated distress (Spearman's rho = .31, $p = .010$). Notice that despite an overall facilitatory effect of weak primes at the group level, some participants may have experienced suppressed awareness of the matching grating (adaptation) even with weak stimuli (see Figure 3). A lower number of alternations in binocular rivalry predicted reporting more autism spectrum traits in the AQ (Spearman's rho = -.26, $p = .030$). Finally, the

facilitatory effect of expectancy cues in the binocular rivalry task negatively correlated with imagery ability assessed by the SCSQ (Spearman's $\rho = -.24$, $p = .049$).

4. Discussion

In the present study we employed a binocular rivalry paradigm and used several methods of attentional and prior manipulation that have previously 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 visual change detection ability and perceptual traits (e.g., distractibility, visual imagery, proneness to perceptual anomalies, attention to detail). We reasoned that if there are consistent trait-like differences in how readily individuals apply expectations to inform the contents of visual 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.

4.1 *Expectation-based and attentional effects on awareness*

As hypothesised, 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 seeing the expected stimulus in the binocular rivalry display, as well as speeded response latencies to this stimulus. The effect sizes for the tendency to see the expected percept were moderate to large and there were small to moderate effects on response latencies. Together these findings 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; Hohwy, 2013). We consider these 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 opposite effects on visual awareness – this would not be observed if participants had a bias to respond in line with the expectation. All of our prior manipulations were presented for sufficient time to be consciously perceived, although priors differed in how long they were processed for (ranging from a minimum of 100ms for weak

primes and a maximum of 5s in the imagery condition). Therefore, the effects described here pertain to explicit (i.e., consciously perceived) rather than implicit representations of prior information. Indeed, it has been suggested that recent perceptual experience only affects perceptual judgements about subsequent stimuli in a facilitatory way when the prior stimulus is consciously perceived (e.g., in positive serial dependence, Kim, Burr, Cicchini, & Alais, 2020). Similarly, valid expectations about a subsequent target stimulus only lead to a facilitated awareness of it when the associated cue stimulus is consciously experienced (e.g., within the attentional blink paradigm, Meijs, Slagter, de Lange, & van Gaal, 2018).

Engaging selective attention also lead to a facilitatory effect on awareness, as attending a particular grating in the binocular rivalry display significantly increased its dominance duration relative to an unattended one. Previous work has also demonstrated 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, Van Dam, & Brouwer, 2005). However, the dominance effect of selectively attending a stimulus in binocular rivalry, even using gratings, can be enhanced if attending to stimulus features is task-relevant (e.g., using a counting task), suggesting that motivational relevance may modulate the magnitude of attentional effects (Chong, Tadin, & Blake, 2005). Chong and colleagues (2005) also found that the attentional effect was equivalent to increasing the physical contrast of the grating (i.e., by 0.3 log units) when it was dominant. Indeed, attention has been found to 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 therefore 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).

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

The strengths of most prior manipulation effects on the first percept in binocular rivalry were predicted by the ability to use selective attention to influence the dominance durations of percepts at will. Attentional control 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 perceptual priors in three conditions: self-generated imagery, expectancy, and perceptual priming with weak signal. 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).

Although present research points to the close association between selective attention and the influence of priors on awareness, it is not possible to ascertain the direction of this relationship based on correlational results. On the one hand, a greater ability to sustain attention throughout the task may have increased the influence of prior manipulations. Attention is known to enhance the neural activity of

cortical areas representing particular locations or objects and to increase visual sensitivity (Martinez et al., 1999; Kastner et al., 1999; Carrasco, 2011). Therefore, greater attentional focus upon the presentation of a prime or cue should boost the activation level of the corresponding internal representation, amplifying its signal to noise ratio and easing its detection in the rivalry display. Similarly, strong attentional control may facilitate self-generation of imagery by activating the internal representation and filtering out internal and external distractors. On the other hand, possessing strong perceptual priors may determine subsequent attentional prioritisation of stimuli. There is evidence for this, as statistical regularities 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, memory-guided orienting of spatial attention is more efficient than cue-based orienting in visual search (Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006). Individuals with high visual WM capacity tend to be better at avoiding distraction via attentional capture (Fukuda & Vogel, 2009; 2011) and a greater capacity to encode visual short-term memory (VSTM) representations leads to better control of attention in line with stored representations and ability to suppress distractors (Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016). Thus, perceptual priors may facilitate awareness through attracting/biasing attention. Indeed, multivariate decoding analyses have demonstrated that the neural representations of expected and unexpected visual stimuli can only be distinguished when attended – attention sharpens the representation of the expected stimulus (Jiang et al., 2013). Given the intimate links between expectation and attention, identifying their independent contributions to visual awareness may be challenging but future studies can aim to orthogonalise them and delineate the time course of neural events that occur as a perceptual expectation is formed and acts to facilitate awareness.

In terms of the relationships between the different prior manipulation effects themselves, the influence of predictive context was associated with adaptation to strong sensory priors. This result supports the conclusions of Denison and colleagues (2011) who show that responses in the 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. The strength of expectancy predicted less perceptual suppression due to strong primes, which may indicate that individuals prone to expectancy effects experienced weaker visual adaptation. Although the correlation matrix indicated a positive manifold (Verhallen et al., 2017), apart from the attentional and adaptation associations outlined above, the rest of the expectation-based effects did not correlate significantly 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 do not support 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 moderate to strong effects) and considering the large body of evidence regarding expectation-based effects on perception (De Lange et al., 2018), a lack of consistent 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. Recent attempts to observe relationships between commonly employed perceptual paradigms mirror our conclusions – a general factor of reliance on perceptual priors is elusive (Tulver, Aru, Rutiku, & Bachmann, 2019). Nonetheless, our analyses do demonstrate that selective attention may be a shared determinant of facilitatory effects across different methods of inducing perceptual priors. Future

research should explore whether these methods differ in the extent to which they activate sensory templates (Kok et al., 2017).

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 perceptual prediction errors (Kanai et al., 2011). Although alternation rate did not correlate with prior manipulations, a faster rivalry correlated with increased adaptation due to 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.

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

Finally, we examined whether expectation-based effects on awareness predict perceptual experiences and traits (e.g., distractibility, visual imagery, anomalous experiences). 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, as accessing vivid internal representations 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 change detection in naturalistic scenes (Andermane et al., 2019). Performance on visual working memory (VWM) tasks also correlates with visual imagery strength (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 should investigate the neurocognitive basis of VSTM representations and attentional abilities in strong and weak imagers further to understand the mechanisms and benefits of possessing vivid imagery.

Stronger adaptation effects in the binocular rivalry task also predicted improved change detection and both measures loaded onto the same factor. This supports the proposal that naturalistic vision is continuously guided by adaptation and that its functional role is to discount the constant perceptual properties to calibrate the visual system for the detection of novelty (Clifford et al., 2007; Kohn, 2007; Webster, 2011). Our 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). 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, there is evidence that adaptation to low-level features at the level of visual cortex contributes to later processing stages in the visual hierarchy. For example, high-level after-effects for representations such as attractiveness and emotion in faces (Rhodes, Jeffery, Watson, Clifford, & Nakayama, 2003; Webster, Kaping, Mizokami, & Duhamel, 2004) 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, faster adaptation to low-level features of naturalistic scenes may increase the salience of complex object changes more rapidly, speeding up their detection. Our result suggests that proneness to adaptation may index a beneficial (adaptive) bias in visual perception.

Questionnaires were also assessed to determine if expectation-based biases 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. 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 reasoned that autistic individuals may have atypical cortical dynamics; specifically, reduced inhibition of visual representations, which then leads to more mixed percepts and an overall stabilising effect on rivalry. We also found that the facilitatory effect of weak primes predicted more reports of perceptual anomalies. This finding appears to be consistent with Teufel and colleagues (2015) who found that the facilitatory effect of prior knowledge on face detection in ambiguous Mooney images predicted schizotypy. There are suggestions 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 (Teufel et al., 2015; Powers et al., 2017). Our result supports the hypothesis that there is a threshold at which residual activation of seen items no longer contributes to accurately representing the visual world. However, this conclusion is tentative, as it must be noted that perceptual anomalies did not correlate with any other of our expectation-based effects. Strong conclusions about prior reliance in autism spectrum and schizotypy are unwarranted, given these effects are not always replicated (Tulver et al., 2019). 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).

5. Conclusions, limitations, and future directions

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 a 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 effect). We conclude that possessing perceptual expectations led to effects on conscious perception rather than a bias to respond in line with the manipulation, given that our catch trials were largely unaffected and strong primes had a suppressive effect on responses. In addition, previous neuroimaging work on the neural correlates of expectancy-based effects gives support to our conclusion. Comparable methods of inducing perceptual expectations of gratings have been shown to activate stimuli-specific templates in the visual cortex (Kok et al., 2017). Additionally, there is evidence that positive serial dependence effects operate directly on perceptual representations in the visual cortex (John-Saaltink, Kok, Lau, & De Lange, 2016; Cicchini, Mikellidou, & Burr, 2017). That is, it is the conscious percept of a prior stimulus, rather than its sensory input or response category, that is carried over and influences judgements of a subsequent stimulus (John-Saaltink et al., 2016). Considering our results in conjunction with previous literature gives us confidence that our expectancy-based effects are perceptual in nature. However, there is a possibility that priors also affected post-perceptual decision strategies, for example, the threshold at which a grating was considered to be visibly dominant within a mixed percept. A replication of our work with a neuroimaging component is necessary to ensure that our manipulations led to prime-specific changes in sensory activation. Altering the ambiguity of the rivalry display (e.g., by changing its contrast) could also reveal how the prior manipulations interact with different levels of sensory evidence.

One limitation of our work is that we did not record mixed percept responses in the binocular rivalry task. These responses would have indicated how the different perceptual priors affected the ambiguity of the rivalry display. Systematic differences of this kind may explain why there were apparent response time differences between the conditions. Tracking mixed percepts may also enable us to determine if people accomplish attentional control of the rivalry display via maintaining perceptual dominance of the attended grating or via preventing the rivalrous grating entering awareness by remaining in a mixed perceptual state. Note also that to reduce contextual differences, we presented all tasks in a fixed order (as suggested by Mollon et al., 2017); however, future replications with a random order of presentation would be needed to limit possible carry-over effects. Finally, exploring when facilitatory effects shift into adaptation (Brascamp et al., 2007) may be useful, given evidence that even weak perceptual primes led to adaptation in some participants. Thus, future studies should further break down and inspect the conditions under which recent perceptual experience shapes awareness, both in terms of facilitation and suppression.

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 expectation-based effects 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 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 these processes 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.

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. Prior manipulations may differ in the extent that they activate 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 multivariate decoding of neural activity during the binocular rivalry task (Kok et al., 2017). Assessing the priming/adaptation curves (see figure A.3 in the Appendix) under full and partial attention could further reveal how attention influences the balance between facilitatory and suppressive effects of perceptual priors in different individuals. Individual differences in the effects of expectation, attention, and adaptation on awareness and their neurocognitive basis may then reveal the contribution of these processes to visual experience.

Acknowledgements

We would like to thank Mariyana Kirilova for helping with the data collection for this study.

Funding

This research was funded by the School of Psychology, University of Sussex, and enabled in part by a donation from the Dr Mortimer and Theresa Sackler Foundation, which supports the Sackler Centre for Consciousness Science. A.K.S. is also supported by the Canadian Institute for Advanced Research (Azrieli Programme in Mind, Brain and Consciousness).

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Appendix

Table A.1. Stimuli parameters of the binocular rivalry task

Parameters
<u>CRT monitor parameters</u>
Resolution: 1024 x 768, Refresh rate: 85 Hz, Gamma correction: R: 2.341, G: 2.245, B: 2.245
<u>Stimuli parameters</u>
Background colour: RGB (128, 128, 128), Background luminance: 23 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 grating spatial frequency: 3.53 cycles per degree, Standard deviation of the Gaussian envelope: 0.57°, Gabor grating orientation: Right-slanted: 45°, left-slanted: 135°, Gabor grating contrast: 20% and 100% Michelson contrast
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)

Table A.2. 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 diff (SD)	Cohen's <i>d</i>	<i>t</i> -test (2-tailed)
Predictive context	0.55 (9.52)	0.08	<i>t</i> (67) = 0.48, <i>p</i> = .634
Imagery	1.84 (9.23)	0.27	<i>t</i> (67) = 1.64, <i>p</i> = .105
Expectancy	1.10 (9.10)	0.17	<i>t</i> (67) = 1.00, <i>p</i> = .321
Weak prime	0.74 (11.61)	0.08	<i>t</i> (67) = 0.52, <i>p</i> = .603
Strong prime	-0.37 (15.72)	0.04	<i>t</i> (67) = -0.19, <i>p</i> = .848

Table A.3. The summary statistics of response times on catch trials. The means and standard deviations of RTs (in milliseconds) 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	998 (549)	1391 (1598)	393 (1516, 69)	0.33	$t(68) = 2.16$, $p = .035$
Expectancy	850 (509)	943 (460)	93 (397, 69)	0.19	$t(68) = 1.95$, $p = .056$
Weak prime	851 (522)	765 (275)	-86 (522, 68)	0.21	$t(67) = -1.36$, $p = .179$
Strong prime	1124 (882)	1132 (818)	8 (944, 69)	0.01	$t(68) = .07$, $p = .946$

Figure A.1. 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 A.2. The Scree plot for the exploratory factor analysis showing an inflection point at fourth factor, justifying the extraction of three factors.

Figure A.3. 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).