Introduction

Binocular rivalry occurs when two conflicting images are presented in the same retinal location to each eye. This inter-ocular conflict leads to an unusual conscious percept, as observers see an alternation between the two images.

This oscillation in perceptual awareness is thought to be driven by mutually inhibitory connections between pools of neurons which respond to each of the two images (Tong et al., 2006). One percept gains dominance and suppresses the other one. Activity in these neurons then gradually reduces via adaptation, and eventually the suppression becomes weakened to the point where a perceptual switch occurs.

These processes likely take place at many stages of visual processing. Both imaging and single-cell evidence show that eye-selective neurons in V1 show activity that rises and falls with perceptual dominance of the image presented to that eye (Tong and Engel, 2001; Xu et al., 2016). However, binocular rivalry is not completely resolved at early, eye-selective stages, as psychophysical evidence shows that perceptual dominance can endure even when the input to the two eyes is swapped (Logothetis et al., 1996), demonstrating that perceptual dominance is not tied to monocular processing. Indeed, computational and conceptual models of binocular rivalry now always include multiple binocularly integrated levels of visual processing where rivalry occurs (for examples, see Hohwy et al., 2008; Said and Heeger, 2013; Tong et al., 2006; Wilson, 2003).

The neural competition occurring during binocular rivalry is likely mediated by the main inhibitory neurotransmitter in the brain, gamma-amino-butyric acid (GABA). This is indicated by the correlation of rivalry dynamics with GABA measured by MRS (Lunghi et al., 2015; Robertson et al., 2016; van Loon et al., 2013), and different rivalry dynamics in autism spectrum conditions, where GABA signalling is suspected to be altered (Freyberg et al., 2015; Robertson et al., 2013, 2016). Recent computational, psychophysical and electrophysiological studies have established that this inhibition is not simple divisive normalisation, but is instead mediated by neurons who specifically compute conflict between the two eyes, and indiscriminately inhibit the opposing eye (Katyal et al., 2016; Said and Heeger, 2013).

The mechanism or cause of rhythmic alternations between percepts is more difficult to assess. Various models ascribe it either to unexplained prediction error (Hohwy et al., 2008), noise (Moreno-Bote et al., 2007), adaptation (Lehky, 1988; Shpiro et al., 2007; Wilson, 2003), or a combination of noise and adaptation (Shpiro et al., 2009). While psychophysical evidence points towards a role of adaptation in switches (Kang and Blake, 2010), stochastic variation in the length of percepts during rivalry also indicate that noise impacts when an alternation occurs (Brascamp et al., 2006). Most computational models include both adaptation and stochastic noise (Lehky, 1988; Said and Heeger, 2013; Wilson, 2007).

Given that binocular rivalry has been proposed to be involved in psychiatric conditions (Miller et al., 2003; Nagamine et al., 2009; Robertson et al., 2013; Said et al., 2012), it may be beneficial to assess the impact of adaptation on rivalry, particularly since atypical adaptation dynamics have been implicated in autism (Lawson et al., 2015; Pellicano et al., 2007; Turi et al., 2015). Given that adaptation dynamics can be abnormal at various levels of the visual hierarchy, we also wanted to develop a method to selectively probe different levels of visual processing.

We studied the effects of adaptation on the first few seconds of binocular rivalry, also known as onset rivalry. Onset rivalry is often biased towards specific percepts in ways in which continuous rivalry is not (for a review, see Stanley et al., 2011a). This bias is determined by stimulus properties such as visual field location (Carter and Cavanagh, 2007; Leat and Woodhouse, 1984), contrast (Song and Yao, 2009), and luminance (Stanley et al., 2011b). It is also affected by task properties such as context (Denison et al., 2011), task relevance of the stimuli (Chopin and Mamassian, 2010), and attention (Chong and Blake, 2006).

It has also been established that adaptation likely affects onset rivalry. Carter and Cavanagh performed an experiment in which two subjects were exposed to one of the rivalling stimuli for 60 seconds in 4 locations of the visual field (Carter and Cavanagh, 2007). They found that this biased onset rivalry in that location towards the non-adapted image. However, they also found significant variation in the duration of this effect between their participants. This fits with the role of adaptation in binocular rivalry proposed by models. However, others have argued that adaptation exposures of this length are far longer than the average dominance duration of a percept during rivalry (around 2-3 seconds, Kang and Blake, 2010). This limits the conclusions we can draw from such exposures.

Here, we establish that onset rivalry is also affected by shorter adaptation. We also selectively adapt binocularly integrated levels of the visual hierarchy, and demonstrate that this impacts onset rivalry, but that this effect is smaller than that of adaptation of the whole visual stream.

We then employ this paradigm to study the effects of adaptation on rivalry in individuals with autism spectrum conditions (ASC), a group which we have previously demonstrated to have reduced perceptual exclusivity during binocular rivalry (Freyberg et al., 2015; Robertson et al., 2013, 2016). The effects of adaptation on rivalry are equally large in both groups, consistent with the hypothesis that shifts in the balance of excitation and inhibition underpin rivalry dynamics in autism.

Methods

Participants & Psychometric Testing

Initially, 40 participants (23 with ASC) took part in this study. The two groups were age- and IQ-matched (STATS). To characterize autistic symptomatology, ASC participants were also assessed using the ADOS-II. Participants also completed the Autism-Spectrum Quotient (AQ), the Sensory and Perception Questionnaire (SPQ), and the Glasgow Sensory Questionnaire (GSQ).

We later recruited an additional sample of control participants (n = 14), with similar age to the first control group (STAT). All participants had normal or corrected-to-normal vision, and did not have epilepsy or Attention-Deficit/Hyperactivity Disorder diagnoses.

Materials

Participants viewed a calibrated Dell LCD monitor (width: 43.5 cm; resolution: 1600x900; refresh rate: 60 Hz) from a distance of 60 cm through a mirror stereoscope. The stereoscope reflected the left/right sides of the screen into the participants' left/right eyes, respectively. Stimuli were presented with custom scripts using the Psychtoolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

Stimuli

Stimuli consisted of grayscale images taken from a bank of standard, non-social images (e.g. a baseball and a broccoli). Each image (average height: 2.31°, width: 2.79°) was presented on a coloured square (width: 3.5°). A black circle surrounded the tinted squares (radius: 4.95°) and a black fixation cross was set in the centre of the circle to provide vergence cues.

There were three types of trials: trials without adaptation preceding rivalry, same-eye adaptation trials, and opposite-eye adaptation trials. On same-eye trials, the adaptor (one of the two stimuli, i.e. the red-tinted object) was presented to the same eye that would then go on to view that stimulus during rivalry. On opposite-eye trials, the adaptor was presented to the opposite eye, which would then go on to view the other stimulus during rivalry. Trials without adaptation were not preceded by an adaptor.

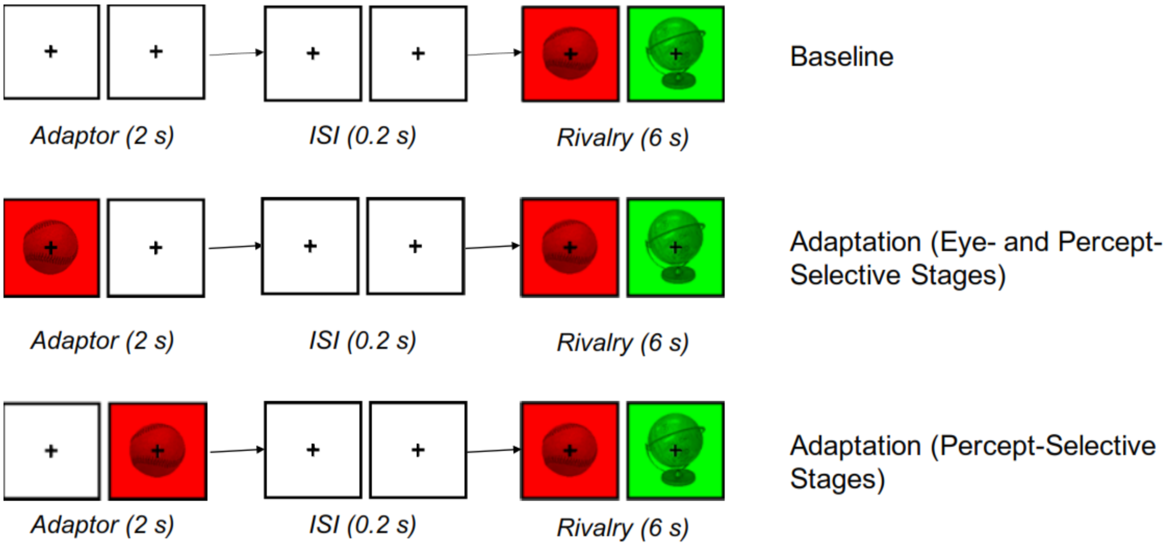

Figure 1: Stimuli and trial types. Rivalry periods were 6 seconds long, and were preceded by an inter-stimulus-interval (ISI) of 0.2 seconds. This ISI was preceded either by no adaptor in the baseline condition, an adaptor in the same eye as in the rivalry trial in the eye- and percept-selective adaptation stages, and an adaptor in the opposite eye as in the rivalry trial in the percept-selective adaptation condition.

The adaptation period was chosen to be 2s, based on piloting and its equivalence to the timescales of dominant periods during rivalry (on average 2-3s with these stimuli, Freyberg et al., 2015). Between adaptation and rivalry, a brief blank interval in which only the vergence cues were on the screen was presented (ISI: 0.2s). The rivalry period was preceded by an auditory cue which indicated participants should respond to the coming stimuli.

Procedure

Before the experiment began, fusion was established for each participant by moving two boxes (white/black, width: 4.95°) towards each other along the screen's horizontal meridian until the participant first reported their inner edges to touch. The two boxes were then moved by half the box width.

Participants were then given practice with the task, performing twelve 6s binocular rivalry trials, counterbalanced for adaptation and no-adaptation trials. The 6s trial duration was selected to allow participants enough time to go through more than two percepts, and to avoid perceptual memory effects often seen with shorter trial durations. Participants then began the main experiment, performing 92 6s binocular rivalry trials (20 no-adaptation, 36 Same-eye adaptation, 36 binocular adaptation, all counterbalanced for left/right presentation and red/green adaptation). There was an inter-trial interval of 2s, and after 30 and 60 trials participants were given a break of 30s which they were free to extend.

On each trial, participants were instructed to continuously press either the Left, Right, or Up Arrow on the keyboard to report their perceptual state ("the red image, the green image, or a mixture of the two", respectively). In Experiment 2, we reversed the arrows used for the red image and the green image, to test whether the bias towards green images was driven by a bias to use the index finger.

Analysis

Key presses throughout a trial were parsed into percepts. Rivalry usually starts with an initial period of fusion, or ambiguity, between the two images. For each trial, we determined what the first dominant, or unambiguous image was. We also determined how long it took participants to reach this percept. Across different types of trials, we determined what the median duration of percepts experienced by a participant was. For adaptation trials, we categorised percepts based on whether they matched the adaptor or not. Percepts shorter than 50ms were excluded from the analysis.

We performed a One-Way ANOVA with Diagnosis as between-subject factor on the proportion of trials which individuals reported as either green or red first in non-exposure trials to determine whether the two groups were similarly biased towards one of the two percepts.

Because of individual variation in biases of onset rivalry towards specific percepts, we subtracted the proportion of first percepts reached in adaptation trials by the proportion an individual reached that percept first in no-adaptation trials.

Much of this analysis focused on the first dominant percept reached, so we excluded individuals for whom the proportion of trials on which they did not achieve a dominant percept was more than 2 standard deviations above the mean for both groups combined (n = 4, all ASC). We further excluded three participants who responded during the adaptation stage and the ISI stage in more than 20% of all trials, for misunderstanding the task (n = 3, one with ASC).

We then analysed the proportion of trials on which the first percept was the adapted image in a 2x2 ANOVA, with Diagnosis of ASC as between subject factor, and Adaptation Type (Same-eye and Opposite-eye) as within subject factor.

We further analysed the time it took to reach the first percept in a 2x3 ANOVA, with Diagnosis of ASC as between subject factor, and Adaptation Type (No Adaptation, Same-eye Adaptation, and Opposite-eye) as within subject factors.

Finally, we analysed the median duration of a given percept across trials. All of these parameters were analysed in separate 2x2x2 ANOVAs, with Diagnosis of ASC as between subject factor, and Adaptation

Type (Same-eye and Opposite-eye) and Stimulus Type (Adapted or Non-adapted) as within subject factors.

Given that the analysis yielded many non-significant results as well as p-values around the threshold of significance used ($p < 0.05$), we post-hoc decided to add Bayesian analyses to test evidence for the null hypothesis. These analyses were conducted using JASP (JASP Team, 2016), and used default priors alongside robustness analyses.

Results

Equal Bias of Onset Rivalry in Autism

To test whether onset rivalry was biased towards one of the two percepts, we determined the proportion of trials in which the green percept was the first percept reported. We compared the two groups with an independent-sample t-test. There was no significant difference between the two groups ($t(32) = 0.811$, $p = 0.423$), indicating that the two groups experienced similar bias.

We then performed post-hoc one-sample t-tests with 50% Green as test value to determine whether the two groups were statistically different from an equal division between the red and the green image to be perceived first. The difference from 50% Green was significantly positive for the Control group ($t(15) = 14.78$, $p < 0.001$, green bias: 65.8% ± 17.8%) and the ASC group ($t(17) = 15.431$, $p < 0.001$, green bias: 61.0% ± 16.8%), indicating both groups were biased towards perceiving the green image first. The green image may have been more salient than the red, which could explain this bias of onset rivalry.

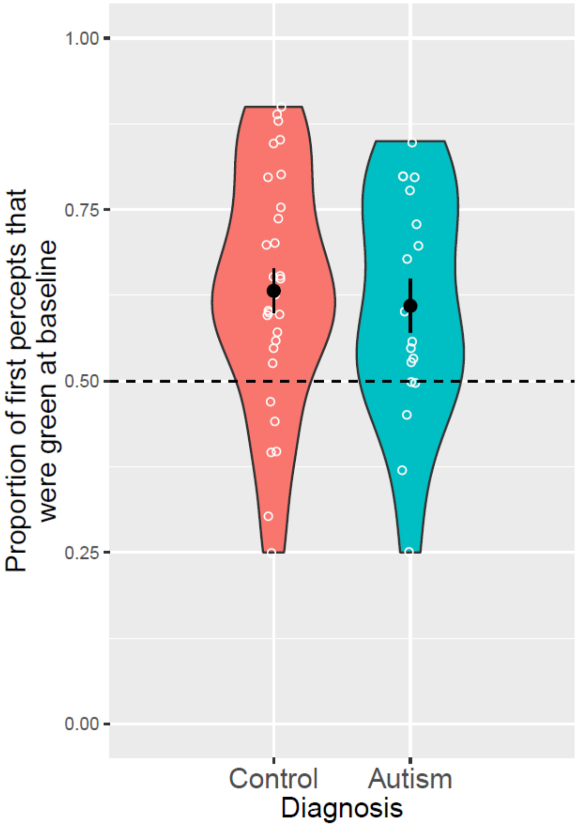

Figure 2: Percentage of baseline trials in which participants resolved to the green image first. Both groups saw the green image first significantly more often than the red image. This bias was not different between the two groups. This bias may reflect a greater luminance or otherwise greater saliency of the green image.

Given that participants reported the green percept with the “Left Arrow”, or the index finger, and the red image with the “Right Arrow”, or the fourth (ring) finger. To test whether the bias of onset rivalry towards the green percept was driven by a finger preference, we tested an additional group of 14 control participants and reversed the arrows for reporting the dominant percepts.

We found a bias towards the green percept of a similar magnitude, which was statistically significant in a one-sample t-test ($t(12) = 12.764$, $p < 0.001$, green bias: 59.8% ± 16.9%). This indicated the previous bias was not due to a preference for the index finger, but a bias towards the green percept. Given that there were no differences between the two groups on reporting bias, we included these participants in all subsequent analyses.

Adaptation biases towards the non-adapted image

We then tested how the first percept perceived was influenced by adaptation. To account for individual differences in overall bias towards a percept, we calculated the difference scores between the proportion of trials on which a person perceived a particular image in the Adaptation conditions and at baseline.

We analysed these difference scores in a 2x2 repeated measures ANOVA, with Adaptation Condition (Same-eye and Opposite-eye) as within-subject factor, and Diagnosis as between-subject factor. There was a significant main effect of Adaptation Condition ($F(1, 44) = 11.68$, $p = 0.001$, $\eta_p^2 = 0.210$), as both groups reported the adapted percept less frequently in the Same-eye Adaptation Condition.

There was no significant main effect of Diagnosis ($F(1, 44) = 0.514$, $p = 0.477$, $\eta_p^2 = 0.012$) and no significant interaction between Diagnosis and Adaptation Condition ($F(1, 44) < 0.001$, $p = 0.998$, $\eta_p^2 < 0.001$). The additional reduction in report of the adapted percept when adapting both monocular and binocular parts of the visual hierarchy was therefore similar in both groups.

To confirm that both adaptation conditions caused a statistically significant reduction in the proportion the adapted percept was perceived, we performed post-hoc one-sample t-tests with 0 as test value on the combined difference scores of both groups. Participants perceived the adapted percept significantly less frequently after same-eye adaptation ($t(46) = -5.144$, $p < 0.001$, Cohen’s $d = 0.750$) than after opposite-eye adaptation ($t(46) = -3.394$, $p = 0.001$, Cohen’s $d = 0.495$).

To test whether the difference between ASC and Control participants was simply not statistically significant, or whether there was in fact evidence for the null hypothesis, we repeated the ANOVA using Bayesian analysis. There was in fact only anecdotal evidence against the null hypothesis that Diagnosis has no impact on the shift in the first percept perceived ($BF_{Inclusion} = 0.426$).

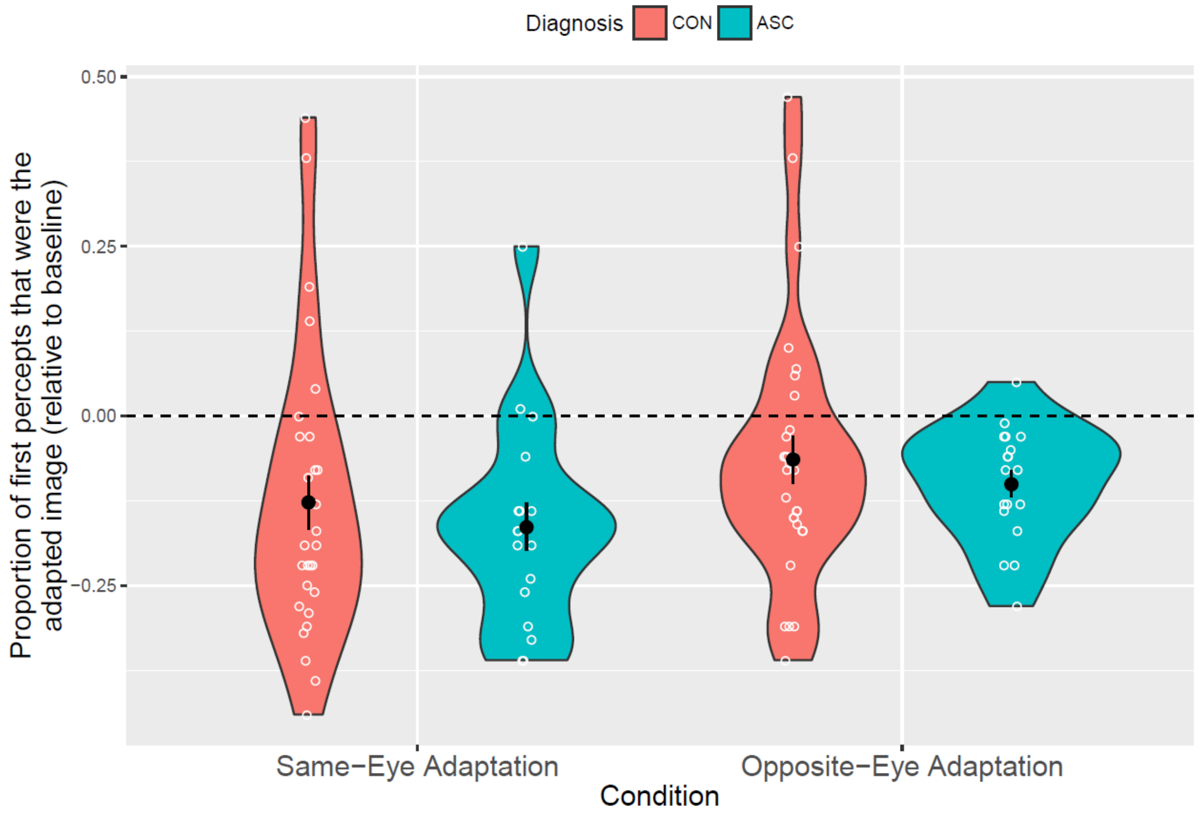

Figure 3: Difference between how often a percept was perceived first at baseline and when it was adapted. In both conditions, both groups showed an equally large shift towards perceiving the adapted image first less frequently. This shift was significantly larger in the same-eye adaptation than in the opposite-eye adaptation condition.

Non-adapted percepts are perceived for longer

We calculated the median duration of each percept – red, green and mixed – in order to test the effect of adaptation on the strength of percepts.

Despite the bias towards green images in onset rivalry, we did not find evidence for a significant difference in the median duration for which participants perceived either the red or the green image in the Non-adapted condition in a 2x2 ANOVA with Image Type (Red or Green) as within-subject factor and Diagnosis as between-subject factor (main effect of Image Type: F(1, 33) = 1.918, p = 0.175, $\eta_p^2 = 0.055$).

We then compared the changes in percept duration after opposite-eye adaptation and same-eye adaptation. To do so, we calculated the difference between the median duration of percepts in the adaptation conditions, and the median percept duration at baseline. We analysed this difference score in a 2x2x2 ANOVA, with Image Type (Adapted or Non-adapted) and Adaptation Type (Same-eye or Opposite-eye) as within-subject factors and Diagnosis as between-subject factor.

There was a significant main effect of Image Type, with the non-adapted image being perceived for longer than the adapted image (F(1, 44) = 13.985, $p < 0.001$, $\eta_p^2 = 0.241$). There was also a significant main effect of Adaptation Type, with the shift in percept duration being larger in the same-eye condition (F(1, 33) = 5.539, $p = 0.025$, $\eta_p^2 = 0.139$).

Additionally, we found a significant interaction between Image Type and Adaptation Type (F(1, 44) = 13.750, $p < 0.001$, $\eta_p^2 = 0.238$), demonstrating that the difference between adapted and non-adapted images was larger in the Same-eye adaptation condition than in the Opposite-eye condition.

There was no significant main effect of Diagnosis (F(1, 44) = 0.001, $p = 0.970$, $\eta_p^2 < 0.001$) and no interactions of Diagnosis with either Adaptation Type (F(1, 44) = 0.098, $p = 0.755$, $\eta_p^2 = 0.002$) or Image Type (F(1, 44) = 1.349, $p = 0.252$, $\eta_p^2 = 0.030$). We again repeated this ANOVA using Bayesian methods to test the evidence for the null hypothesis, and found that there was moderate evidence against an effect of Diagnosis on the shift in percept durations ($BF_{Inclusion} = 0.181$).

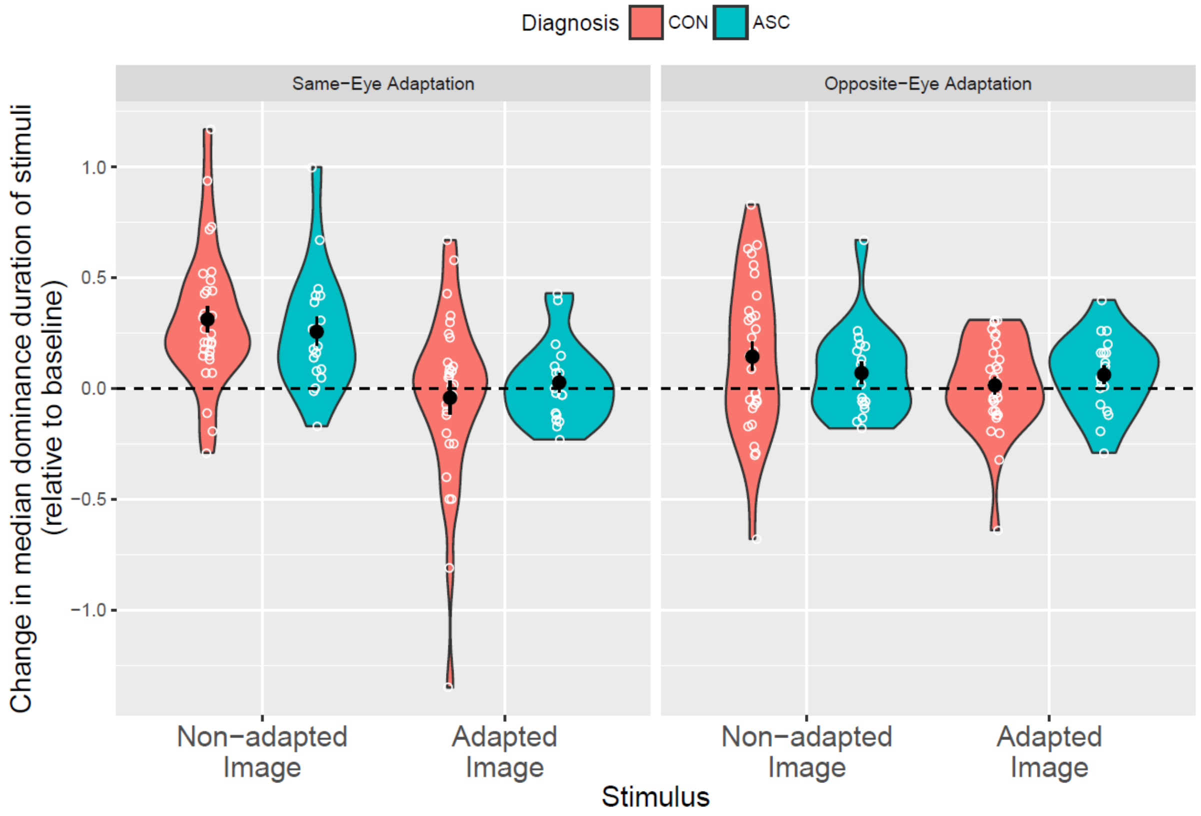

Figure 4: Difference in the median duration of percepts between baseline and adaptation conditions. We subtracted the median dominance duration at baseline from the median dominance durations after adaptation, for both the adapted and the non-adapted image.

Motivated by the interaction between Image Type and Adaptation Type, we tested which condition produced shifts significantly different from zero using one-sample t-tests. This yielded a significant increase in the median duration of the non-adapted image after same-eye adaptation ($t(46) = 6.773$, $p < 0.001$, Cohen's $d = 0.988$), and after opposite-eye adaptation ($t(46) = 2.667$, $p = 0.011$, Cohen's $d = 0.389$). The adapted image experienced no significant shift after same-eye adaptation ($t(46) = 0.299$, $p = 0.767$, Cohen's $d = 0.044$), and after opposite-eye adaptation ($t(46) = 1.189$, $p = 0.241$, Cohen's $d = 0.173$).

Discussion

We aimed to develop a paradigm which would allow us to test the effects of adaptation on onset rivalry. We also aimed to demonstrate the differential effects of adaptation of different levels of the visual hierarchy. Lastly, we tested whether differences in the effects of adaptation on onset rivalry were different between Control participants and participants with ASC, a group that exhibits atypical dynamics of rivalry during sustained rivalry.

Our results indicate several important facts about onset rivalry. First, we demonstrate that adaptation of both binocular and monocular areas of the visual hierarchy can affect the first percept. Previous studies have identified that this first percept is often determined by idiosyncratic biases which can vary in location and magnitude between individuals (Carter and Cavanagh, 2007). This bias is likely largely produced by idiosyncrasies in binocularly segregated areas of the visual hierarchy. This is demonstrated by the fact that when stimuli matched in luminance and contrast are switched between the two eyes on successive trials, the bias is reversed (Carter and Cavanagh, 2007). Here, we demonstrate that onset rivalry is also affected by binocularly integrated areas of the visual system, as adaptation to a stimulus reduced the likelihood of that stimulus being seen first – regardless of whether the stimulus was shown to the same or the opposing eye during adaptation and rivalry.

Additionally, while we find an effect of binocular adaptation on onset rivalry, we also find that adaptation of both monocular and binocular areas is stronger. While this may seem unsurprising, it confirms that adaptation of multiple levels of the visual hierarchy contributes to binocular rivalry. We demonstrate that neither none, nor all of the effects of adaptation on binocular rivalry originate at binocularly integrated areas.

We were also able to investigate the effect of adaptation on the duration of dominant percepts. Levelt's original laws of binocular rivalry (Brascamp et al., 2015; Levelt, 1965) stated that changing the strength of one stimulus does not affect the average duration for which a person perceives the stimulus. We found that adaptation of one stimulus increases the percept duration of the other stimulus. This matches what Levelt proposed, and indicates that adaptation of a stimulus is similar to weakening the strength of that stimulus. Again, we show contributions from both binocularly segregated and integrated areas to this stimulus strength.

Lastly, our results have important implications for our understanding of binocular rivalry in autism spectrum conditions. Individuals with ASC are likely to exhibit atypical dynamics of binocular rivalry (Robertson et al., 2013), and this was also true for this group of subjects (results published elsewhere). However, we found strong evidence for typical effects of adaptation on rivalry in autism. This indicates that the reduced speed of alternation and higher proportion of mixed percepts observed in individuals with an autism spectrum condition are likely to stem from sources other than adaptation. An imbalance between excitation and inhibition has been hypothesised to be a fundamental element of autism neurobiology. The imbalance between excitation and inhibition is predicted to produce the rivalry dynamics observed in autism, and here, we find evidence that there is likely to be no contribution of adaptation to rivalry dynamics in autism.

In sum, we present a method for testing the effects of adaptation on binocular rivalry. We show that selectively adapting binocular areas of the visual system affects binocular rivalry to a limited degree, and that short trials of binocular rivalry provide a method for comparing the contribution of binocular areas and monocular areas to binocular rivalry. With the increased focus on the use of binocular rivalry in clinical populations, this method may make it possible to identify the elements of the visual hierarchy which contribute to a clinical group's rivalry dynamics.