

# ***Reduced Perceptual Exclusivity during Object and Grating Rivalry in Autism***

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# Abstract

1 **Background:** The dynamics of binocular rivalry may be a behavioural footprint of excitatory and  
2 inhibitory neural transmission in visual cortex. Given the presence of atypical visual features in Autism  
3 Spectrum Conditions (ASC), and evidence in support of the idea of an imbalance in  
4 excitatory/inhibitory neural transmission in ASC, we hypothesized that binocular rivalry might prove a  
5 simple behavioural marker of such a transmission imbalance in the autistic brain. In support of this  
6 hypothesis, we previously reported a slower rate of rivalry in ASC, driven by reduced perceptual  
7 exclusivity.

8 **Methods:** We tested whether atypical dynamics of binocular rivalry in ASC are specific to certain  
9 stimulus features. 53 participants (26 with ASC, matched for age, sex and IQ) participated in binocular  
10 rivalry experiments in which the dynamics of rivalry were measured at two levels of stimulus  
11 complexity, low (grayscale gratings) and high (coloured objects).

12 **Results:** Individuals with ASC experienced a slower rate of rivalry, driven by longer transitional states  
13 between dominant percepts. These exaggerated transitional states were present at both low and high  
14 levels of stimulus complexity, suggesting that atypical rivalry dynamics in autism are robust with  
15 respect to stimulus choice. Interactions between stimulus properties and rivalry dynamics in autism  
16 indicate that achromatic grating stimuli produce stronger group differences.

17 **Conclusion:** These results confirm the finding of atypical dynamics of binocular rivalry in ASC. These  
18 dynamics were present for stimuli of both low and high levels of visual complexity, suggesting an  
19 imbalance in competitive interactions throughout the visual system of individuals with ASC.

## Introduction

20 The visual system often receives ambiguous information about the external world. Typically, this  
21 ambiguity can be resolved through contextual information and prior expectations (Bayerl & Neumann,  
22 2004; Scholl & Nakayama, 2002). However, when two interpretations of the input are equally viable, a  
23 phenomenon known as bistable perception occurs: the two percepts compete for perceptual  
24 dominance, alternating back and forth in perceptual awareness.

25 Binocular rivalry is a striking example of bistable perception, occurring when conflicting monocular  
26 images are presented to the same retinal location of each eye. During rivalry, observers report a  
27 perceptual experience that alternates between the two images. This oscillation is thought to be  
28 facilitated by competitive interactions between populations of neurons that code for the two possible  
29 percepts at various levels of visual processing (Tong, Meng, & Blake, 2006).

30 This role of inhibition in rivalry is highlighted in many models of binocular rivalry (Blake, 1989; Hohwy,  
31 Roepstorff, & Friston, 2008; Klink, Brascamp, Blake, & Van Wezel, 2010; Moreno-Bote, Rinzel, &  
32 Rubin, 2007; Said & Heeger, 2013; Wilson, 2003). While some models posit top-down signals (Hohwy  
33 et al., 2008) or neural noise (Moreno-Bote et al., 2007) as the primary triggers of rivalry alternations,  
34 these models often still include inhibition between percept-selective neuronal pools as a key element  
35 of rivalry dynamics (Hohwy et al., 2008; Moreno-Bote et al., 2007). The role of inhibition in binocular  
36 rivalry is supported by the strong relationship between binocular rivalry dynamics and the inhibitory  
37 neurotransmitter GABA in the visual cortex (Lunghi, Emir, Morrone, & Bridge, 2015; van Loon et al.,  
38 2013). Two recent computational models of binocular rivalry offer specific predictions about how  
39 alterations in inhibitory signalling would affect rivalry dynamics, specifically positing a relationship  
40 between the inhibitory connection strength and the perceptual exclusivity of the two rivalling percepts  
41 (Klink et al., 2010; Said, Egan, Minshew, Behrmann, & Heeger, 2012).

42 As a result, binocular rivalry can be thought of as a behavioural marker of the balance of excitatory  
43 and inhibitory neural transmission in the brain (the E/I ratio). We and others have proposed that  
44 binocular rivalry can serve as a tool to study a clinical population in which this ratio might be altered  
45 (Robertson, Kravitz, Freyberg, Baron-Cohen, & Baker, 2013; Said et al., 2012), such as Autism  
46 Spectrum Conditions (ASC, Rubenstein & Merzenich, 2003). There is converging evidence from  
47 animal models (Chao et al., 2010; Gogolla et al., 2009; Tsai et al., 2012; Yizhar et al., 2011), genetic  
48 findings (Bundey, Hardy, Vickers, Kilpatrick, & Corbett, 1994; Menold et al., 2001; Buxbaum et al.,  
49 2002; Kim et al., 2008; Warrier, Baron-Cohen, & Chakrabarti, 2013) and post-mortem studies (Fatemi,  
50 Reutiman, Folsom, & Thuras, 2009b) suggesting an alteration in E/I neurotransmission in the autistic  
51 cortex. Such an alteration could explain a wide array of autistic symptoms (Rubenstein & Merzenich,  
52 2003), as well as the elevated co-morbidity between autism and epilepsy (Canitano, 2007). Therefore,  
53 a behavioural test of the integrity of E/I dynamics in the autistic brain would significantly help our  
54 understanding of the condition.

55 Two studies have examined binocular rivalry in individuals with ASC (Robertson et al., 2013; Said et  
56 al., 2012). One study, from our lab, reported a slower rate of rivalry in ASC with longer mixed percept

57 durations (Robertson et al., 2013); the other did not examine the overall rate of rivalry, and reported  
58 only a statistical trend towards a larger proportion of mixed percepts in ASC (Said et al., 2012). This  
59 pattern of results warrants further investigation. It is possible that these studies, taken together, point  
60 towards a fundamental perturbation in binocular rivalry dynamics in ASC.

61 The difference in the effect sizes of these two studies might arise from a difference between the  
62 stimuli used in each study, which could offer insight into the nature of the putative I/E imbalance in the  
63 autistic cortex. The study showing the greatest difference between ASC and controls used complex  
64 coloured object stimuli to test binocular rivalry dynamics (Robertson et al., 2013), while the study  
65 reporting a trend towards reduced perceptual exclusivity in ASC used simple grayscale gratings (Said  
66 et al., 2012). These different stimulus categories are thought to recruit competitive interactions at  
67 different levels of the visual hierarchy. Specifically, grayscale grating rivalry is thought to involve  
68 mutual inhibition between eye and orientation-selective neuronal populations in early visual cortex  
69 (Haynes & Rees, 2005; Menon, Ogawa, Strupp, & Uğurbil, 1997), while coloured objects are thought  
70 to recruit additional levels of competitive interactions between object-selective neuronal populations in  
71 higher-level visual cortex (Logothetis & Sheinberg, 1996) and colour-selective neuronal populations.  
72 The difference between the results of the two previous investigations of binocular rivalry in ASC might  
73 therefore indicate that atypical rivalry dynamics are only evident with chromatic object stimuli, which  
74 engage relatively more levels of competitive cortical interactions across which an E/I imbalance could  
75 accumulate.

76 The aims of the present study were therefore twofold. First, we tested whether our previous finding of  
77 a slower rate of binocular rivalry with longer mixed percepts in ASC would replicate in a new, larger  
78 sample of participants with and without ASC. Second, we tested whether this finding was selective for  
79 stimuli with the particular visual properties shown to elicit atypical rivalry dynamics in ASC in prior  
80 work: we intermixed trials using achromatic gratings and coloured images in order to assess whether  
81 stimuli varying on multiple dimensions differentially affect rivalry dynamics in ASC. Our results  
82 demonstrate an overall slower rate of rivalry in ASC with longer mixed percept durations and reduced  
83 perceptual exclusivity, which cannot be accounted for by group differences in decision criteria or  
84 motor latencies. These effects were evident, and stronger, with achromatic grating stimuli. These  
85 findings are consistent with the E/I imbalance hypothesis in autism, and indicate that atypical  
86 binocular rivalry is a robust behavioural marker in autism with respect to stimulus choice.

## Methods

### 87 *Participants and Psychometric Testing*

88 53 participants took part in the study (26 with ASC). The two groups were matched for mean age  
89 (Controls: 28.7±9.8; ASC: 32.0±11.0;  $p \geq 0.26$ , Table 1) and performance (non-verbal) IQ  
90 (Controls: 114.0±12.9; ASC: 118.2±11.2  $p \geq 0.22$ , Table 1), assessed using the Wechsler  
91 Abbreviated Scale of Intelligence (WASI). Participants were recruited from the Cambridge Autism  
92 Research Database (CARD), and online adverts, and there was no overlap between participants  
93 recruited for this study and Robertson et al., (2013). Participants with ASC all had clinical diagnoses  
94 of an ASD (DSM-IV criteria), as evaluated by a qualified clinical psychologist or psychiatrist in a  
95 recognized clinic. To quantify autistic symptoms, participants with ASC were also assessed using the  
96 ADOS-II (ASC: 9.6±3.1). Participants also completed the Autism-Spectrum Quotient (AQ, Controls:  
97 16.6±6.7, ASC: 37.5±7.1, Table 1) (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), the  
98 Sensory and Perception Questionnaire (SPQ, Controls: 113.5±27.0, ASC: 87.3±24.2) (Tavassoli,  
99 Hoekstra, & Baron-Cohen, 2014), and the Glasgow Sensory Questionnaire (GSQ, Controls:  
100 40.9±17.1, ASC: 74.9±20.9) (Robertson & Simmons, 2012). All participants had normal or corrected-  
101 to-normal vision, and were free of epilepsy or Attention-Deficit/Hyperactivity Disorder diagnoses. 6  
102 participants (5 with ASC) were on psychiatric medication (3: antidepressant, 1: antianxiety, 2:  
103 antipsychotic). Exclusion of these participants did not qualitatively alter our results: all effects involving  
104 Diagnosis remained significant.

### 105 *Materials and Procedure*

106 We conducted two experiments: one natural binocular rivalry experiment, and one control experiment  
107 in which binocular rivalry was simulated. In both experiments, participants viewed a calibrated Dell  
108 LCD monitor (width: 43.5 cm; resolution: 1600x900; refresh rate: 60 Hz) from a distance of 60 cm  
109 through a mirror stereoscope. The stereoscope reflected the left/right sides of the screen into the  
110 participants' left/right eyes, respectively.

111 Before the experiment began, fusion was established for each participant by moving two boxes  
112 (white/black, width: 4.95°) towards each other along the screen's horizontal meridian until the  
113 participant first reported their inner edges to touch. The two boxes were then moved by half the box  
114 width. Participants were then given practice with the task, performing four 20s binocular rivalry trials  
115 (2 for each stimulus condition). Finally, participants began the main experiment, performing 12 40s  
116 binocular rivalry trials (6 for each stimulus condition; see *Stimuli: Rivalry Experiment*) and 24 40s  
117 control trials (6 for each transition type and stimulus condition; see *Stimuli: Control Experiment*). All 36  
118 trials were presented in random order. A 20s pause occurred between trials, and a 15-minute break  
119 was taken every 12 trials.

120 On each trial, participants were instructed to continuously press either the Left, Right, or Up Arrow on  
121 the keyboard to report their perceptual state ("the red image, the green image, or a mixture of the

122 two”, respectively). Participants were instructed to define a “mixed image” as a perceptual state in  
123 which neither the green nor the red object was perceptually dominant.

#### 124 Stimuli: Rivalry Experiment

125 Two sets of stimuli were used, Objects and Gratings. Object stimuli consisted of grayscale images  
126 taken from a bank of standard, non-social images (e.g. a baseball and a broccoli) and were identical  
127 to those used in our previous study (Robertson et al., 2013). A random, non-repeating sequence of  
128 six image pairs was generated for each participant, which was used for both the Rivalry and Control  
129 experiments. Each image (average height: 2.31°, width: 2.79°) was presented on a coloured square  
130 (width: 3.5°). A black circle surrounded the tinted squares (radius: 4.95°) and a black fixation cross  
131 was set in the centre of the circle to provide vergence cues. On each trial, one eye viewed a red  
132 square, and one eye viewed a green square.

133 Grating stimuli consisted of sinusoidal luminance gratings (spatial frequency: 3 cycles/degree;  
134 Michelson contrast: 60%), displayed in a circular aperture (diameter: 3.5°). A black box surrounded  
135 the gratings (width: 4.95°) and a fixation cross was set in the centre of the box to provide vergence  
136 cues. On each trial, one eye viewed gratings tilted +45 degrees, and the other -45 degrees.

#### 137 Stimuli: Control Experiment

138 The stimuli used in the control experiment were identical to those used in the rivalry experiment.  
139 However, the same image was consistently presented to both eyes throughout the trial, and rivalry  
140 was simulated by presenting the two stimuli in alternation on the screen, separated by simulated  
141 transitions which were created by blending the two images (OpenGL blending, Brainard, 1997).

142 There were two trial types in the control experiment: smooth and sudden (Figure 1). In both trial types,  
143 the displayed stimulus alternated between the two dominant images. In the sudden transition trials,  
144 alternations were abrupt: either a dominant (e.g. 100% baseball) or a mixed image (e.g. 50%  
145 baseball, 50% broccoli) was displayed at any one time. In smooth transition trials, alternations were  
146 dynamic: a linear transition was placed between the two dominant images. The proportion of the  
147 images displayed at each pixel was determined by placing 15 two-dimensional Gaussian curves  
148 (average extent: 0.4°) in random positions in the alpha layer and increasing their amplitude  
149 throughout a transition. To simulate onset ambiguity, a mixed image was displayed at the start of all  
150 trials, which transitioned sinusoidally in the smooth trials around the 50% mixture point (Figure 2).

151 Stimulus durations for the Object condition were drawn from a distribution of percept durations  
152 obtained in a previous rivalry study (Robertson et al., 2013). In half the trials, durations were drawn  
153 from those of the control group means (dominant/mixed: 2.0s/1.5s). In the other half, durations were  
154 drawn from those of the ASC group means (dominant/mixed: 2.0s/2.0s). Durations for the Grating  
155 condition were drawn from the same distribution, adjusted so that the mean matched the means  
156 obtained in a previous study of rivalry using grating stimuli (ASC-matched dominant/mixed:

157 2.3s/1.73s, Control-matched dominant/mixed: 1.73s/1.3s (Said et al., 2012)). All stimulus durations  
158 were a minimum of 0.5s.

#### 159 *Performance Analysis: Rivalry Experiment*

160 Key presses throughout a trial were parsed into a sequence of perceptual transitions. Perceptual  
161 transitions during binocular rivalry can be broadly classified into “switches” (when the percept  
162 changes from one image to the other, typically via an intermediate mixed percept) and “reversions”  
163 (when the percept changes from one image to a mixed percept, but then returns again to the original  
164 percept). We excluded responses shorter than 150 ms and periods when no button was pressed.  
165 These occurrences were rare, 1.3% (ASC) and 1.5% (Con) of button presses, and were matched for  
166 the two groups ( $p > 0.93$ ).

167 We calculated the frequency of transitions, switches, and reversions, the average duration of mixed  
168 and dominant percepts, and the perceptual exclusivity, defined as the proportion of dominant  
169 percepts, for each participant and trial. These measures were analysed in separate 2x2 ANOVAs,  
170 using Stimulus Condition (gratings or images) as a within-subject factor, and diagnosis as a between-  
171 subject factor. Participants were excluded from all subsequent analyses if their percept durations  
172 were more than two standard deviations above or below the mean of both groups combined ( $n = 5$ , 2  
173 with ASC). Including these participants in the analysis did not change the outcome of any statistical  
174 tests. One further participant (Control) was excluded who continuously reported a mixed percept,  
175 indicating that stable binocular viewing was not achieved. All results reported below remained  
176 significant when repeated while co-varying for age, gender, and IQ.

#### 177 *Performance Analysis: Control Experiment*

178 Control experiment analyses allowed us to assess whether any differences in rivalry performance  
179 between groups were due to slower reactions or different perceptual criterion levels in either group by  
180 measuring participants’: 1) task understanding, 2) motor-response latencies, and 3) decision-criteria  
181 to judge the boundary between a mixed and dominant percept. To assess reaction time, we  
182 calculated the mean RT of a subject in the sudden-onset trials. Finally, to assess perceptual decision-  
183 criteria, we calculated the stimulus composition at the time-point at which participants reported a  
184 percept in the smooth-transition trials (e.g. 60% baseball, 40% broccoli), corrected for each  
185 participant’s mean reaction time in the sudden-onset trials.

## Results

186 We tested whether individuals with ASC evidence atypical dynamics of binocular rivalry, and whether  
187 such differences are specific to high or low levels of stimulus complexity. In addition, to explore  
188 participants' response latencies and response criteria, we ran two control rivalry stimulation  
189 experiments. We first present the results of the binocular rivalry experiment, followed by the results of  
190 the control experiment. In short, these results indicate atypical dynamics of binocular rivalry in ASC  
191 with both achromatic gratings and coloured objects, which cannot be accounted for by differences in  
192 response latencies or response criteria.

### 193 *Overall Slower Rate of Binocular Rivalry in ASC*

194 Participants with ASC demonstrated fewer perceptual transitions during binocular rivalry than controls  
195 (main effect of Diagnosis:  $F(1, 45) = 8.715$ ,  $p < 0.005$ ,  $\eta_p^2 = 0.178$ ), reporting on average 9.3  
196 transitions per trial, compared to 12.3 in controls, across both stimulus conditions (Figure 3). This  
197 replicates our previous result of slower binocular rivalry dynamics in ASC (Robertson et al., 2013),  
198 demonstrating that the rate at which two percepts compete for perceptual awareness is reduced in  
199 individuals with ASC. To further characterize these dynamics, we next analysed the two possible  
200 types of perceptual transitions: switches and reversions separately.

### 201 *Overall Slower Rate of Switches in ASC*

202 Again confirming our previous report (Robertson et al., 2013), participants with ASC switched  
203 between percepts significantly less frequently than controls (main effect of Diagnosis:  $F(1,$   
204  $45) = 8.717$ ,  $p < 0.005$ ,  $\eta_p^2 = 0.176$ ), reporting on average 8.0 switches per trial, compared with 11.1  
205 in controls across both stimulus conditions (Figure 3). Reversions were equally frequent in both  
206 groups (ASC: 1.2, CON: 1.2,  $F(1, 45) = 0.004$ ,  $p < 0.947$ ), and although the proportion of transitions  
207 that resulted in reversions, rather than switches, was numerically higher in the ASC group (ASC:  
208 15.1%, Con: 11.9%), no main effect of Diagnosis was observed ( $F(1, 45) = 1.795$ ,  $p < 0.187$ ). These  
209 findings confirm slower overall dynamics of binocular rivalry in individuals with ASC.

### 210 *Overall Longer Mixed Percepts in ASC*

211 In order to test whether the slower rate of rivalry observed in ASC was driven by a disproportionate  
212 amount of time spent reporting dominant percepts, mixed percepts, or both, we calculated the mean  
213 duration of dominant and mixed percepts. To calculate the duration of dominant percepts, we  
214 collapsed across clockwise/counter-clockwise and red/green responses, as we observed no response  
215 biases for any percepts for either group or stimulus type (all  $p > 0.77$ ).

216 Overall, individuals with ASC experienced significantly longer mixed percepts than controls (ASC: 4.0  
217 s, CON: 1.36 s, main effect of Diagnosis:  $F(1, 45) = 11.855$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.289$ ) (Figure 4).  
218 However, the durations of dominant percepts were comparable between the two groups (ASC: 2.34 s,



219 CON: 2.42 s, main effect of Diagnosis:  $F(1, 45) = 0.099$ ,  $p < 0.754$ ), attributing the slower rate of  
220 rivalry in ASC to a disproportionately long transitional (mixed) state between two dominant percepts.  
221 Indeed, the proportion of time participants spent in a mixed state, as opposed to a dominant  
222 perceptual state, was significantly larger in ASC as compared to controls ( $F(1, 45) = 9.674$ ,  $p < 0.003$ ,  
223  $\eta_p^2 = 0.231$ ), and this proportion strongly correlated with the rate of perceptual switches in both  
224 stimulus conditions ( $p < 0.002$ ). This replicates our previous finding (Robertson et al., 2013), and  
225 confirms a key prediction of how an E/I imbalance would alter the dynamics of binocular rivalry in  
226 models of rivalry (Klink et al., 2010; Said et al., 2012).

### 227 *Effects of Stimulus Type on Rivalry Dynamics in ASC*

228 No effect of Stimulus Type was observed on switch rate ( $F(45, 1) = 2.795$ ,  $p < 0.10$ ), indicating that  
229 the level of stimulus complexity did not significantly impact rivalry rate overall. However, an interaction  
230 between Stimulus Type and Diagnosis was observed (Switches:  $F(1, 45) = 9.084$ ,  $p < 0.004$ ,  
231  $\eta_p^2 = 0.157$ ), driven by a particularly slower rate of switches in ASC as compared to controls in the  
232 grating condition ( $U(23, 24) = 97.5$ ,  $p < 0.001$ ,  $12.46 \pm 4.64$  (Control),  $9.57 \pm 4.01$  (ASC), Cohen's  
233  $d = 0.67$ ), as opposed to the object condition ( $U(23, 24) = 230.5$ ,  $p < 0.34$ ,  $11.61 \pm 4.76$  (Control),  
234  $6.88 \pm 5.28$  (ASC), Cohen's  $d = 0.94$ ). No interactions or main effects involving Stimulus Type were  
235 observed for reversions.

236 As expected from previous literature (Brascamp, Klink, & Levelt, 2015), both groups demonstrated  
237 shift towards longer mixed and shorter dominant percepts in the grating condition, as evidenced by a  
238 main effect of Stimulus Type (mixed percepts:  $F(1, 45) = 11.069$ ,  $p < 0.002$ ,  $\eta_p^2 = 0.194$ ; dominant:  
239  $F(1, 45) = 19.402$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.280$ ). Individuals with ASC were disproportionately affected by  
240 this shift, resulting in a significant interaction between Stimulus Type and Diagnosis for mixed  
241 ( $F(1, 45) = 4.201$ ,  $p < 0.046$ ,  $\eta_p^2 = 0.105$ ) but not dominant ( $F(1, 45) = 0.003$ ,  $p < 0.957$ ) percepts.  
242 Critically, this exaggerated duration of mixed-percepts in ASC was observed at both levels of stimulus  
243 complexity (objects,  $U(23, 24) = 173$ ,  $p < 0.028$ ,  $1.19 \pm 0.71$  s (Control),  $1.93 \pm 1.5$  s (ASC), Cohen's  $d =$   
244  $0.63$ ; gratings,  $U(23, 24) = 110$ ,  $p < 0.001$ ,  $1.57 \pm 0.86$  s (Control),  $4.09 \pm 3.14$  s (ASC), Cohen's  $d =$   
245  $1.09$ ), suggesting that longer mixed percepts during binocular rivalry are a stable signature of atypical  
246 competitive dynamics in the autistic brain which replicates across levels of visual processing.

### 247 *Change of Rivalry Dynamics over Time*

248 As has previously been observed (Hollins & Hudnell, 1980), the rate of perceptual switches declined  
249 over the course of a 40s trial. To test whether the rate of this decline differed between individuals with  
250 and without ASC, switches were parsed into 4s time-bins, the first of which began with the first  
251 dominant button-press in each trial. A  $2 \times 2 \times 9$  repeated-measures ANOVA of this binned data, using  
252 Time Bins and Stimulus Type as a within-subject factors, revealed that switch rate fell significantly  
253 during a trial (main effect of Time  $F(8, 360) = 78.724$ ,  $p < 0.001$ ,  $\eta_p^2 = 0.904$ ). We observed no  
254 interaction between Time and Diagnosis ( $F(8, 360) = 0.766$ ,  $p < 0.633$ ), indicating that this decline  
255 was comparable between the two groups. There was, however, an interaction between Time and

256 Stimulus Type ( $F(8, 360) = 4.040, p < 0.001, \eta_p^2 = 0.383$ ), reflecting a steeper decline of switch rate in  
257 the object condition in both groups (Figure 5).

### 258 *Comparable Response Latencies and Criteria between ASC and Controls*

259 The results of our control experiment demonstrate that the atypical dynamics of binocular rivalry  
260 evidenced in ASC cannot be attributed to any non-perceptual differences between the two groups,  
261 such as response latency or response criteria. During the control experiment, when there were  
262 physical changes in the stimuli simulating rivalry alternations, individuals with and without ASC  
263 reported a similar proportion of image transitions and no group differences in the duration of dominant  
264 or mixed-images were observed (all  $p > 0.53$ ).

265 Overall, the two groups responded to a comparable proportion of simulated rivalry alternations  
266 (Control,  $87 \pm 15\%$ ; ASC,  $88 \pm 13\%$ ,  $p < 0.71$ ). Critically, individuals with and without ASC also  
267 exhibited comparable response latencies to report both single and mixed-image stimuli. During our  
268 sudden-onset control experiment, both groups exhibited comparable response latencies to report the  
269 onset of single ( $F(1, 45) = 0.217, p < 0.64$ ) and mixed-image stimuli ( $F(1, 45) = 0.4, p < 0.53$ ). No  
270 other main effects or interactions were observed (all  $p > 0.64$ ). These results indicate that both groups  
271 evidence similar motor latencies to detect sudden stimulus onsets. Likewise, during our smooth-onset  
272 control experiment, no differences were observed between the two groups' response criteria to report  
273 the onset of single ( $F(1, 45) = 3.3, p < 0.076$ ) or mixed-image ( $F(1, 45) = 1.145, p < 0.29$ ) stimuli, and  
274 no other main effects or interactions were observed (all  $p > 0.64$ ). These results indicate that both  
275 groups also exhibit comparable perceptual response criteria to judge the borders between simulated  
276 perceptual transitions. In sum, this demonstrates that any differences in the dynamics of binocular  
277 rivalry in autism do not arise from simple differences in the speed or criteria of report.

### 278 *Correlation with Autistic Traits*

279 We tested whether rivalry dynamics predicted two measures of autistic traits: the AQ and ADOS  
280 scores. AQ significantly predicted switch rates (Pearson's  $r = -0.299, p < 0.031$ ) and mixed percepts  
281 (Pearson's  $r = 0.387, p < 0.005$ ) in the grating condition. However, these correlations did not hold in  
282 each group individually (all  $p > 0.078$ ), and therefore were likely driven by the group differences in AQ  
283 and rivalry dynamics. There was no significant correlation between ADOS scores and any variables.

284 There was also a significant correlation between the GSQ Visual Subscale and switches (Pearson's  
285  $r = -0.334, p < 0.030$ ), mixed-percept durations (Pearson's  $r = 0.331, p < 0.037$ ) and overall mixed  
286 percept proportion (Pearson's  $r = 0.323, p < 0.042$ ) in the grating condition when the two groups were  
287 combined. Again, when analysed separately for each group, no correlation was statistically significant  
288 in each group individually (all  $p > 0.09$ ). The GSQ also correlated with the AQ ( $r = 0.789, p < 0.001$ ),  
289 replicating previous reports in the literature of a strong relationship between autistic symptoms  
290 measured on perceptual and social processing levels (Robertson & Simmons, 2012).

## Discussion

291 Our findings indicate that the dynamics of binocular rivalry are robustly altered in ASC. Specifically,  
292 individuals with high-functioning ASC demonstrate a slower rate of binocular rivalry with  
293 disproportionately long periods of transitional states between dominant percepts (mixed percepts).  
294 These results replicate our previous findings (Robertson et al., 2013), and lend support to a  
295 computational model of how a perturbation in the ratio of excitatory/inhibitory transmission in the  
296 autistic brain would alter binocular rivalry dynamics (Said et al., 2012). These findings occur with both  
297 coloured object stimuli and achromatic grating stimuli, indicating that they are not specific to a  
298 particular type of visual complexity. Importantly, interactions between stimulus properties and group  
299 suggest that achromatic gratings, which produce longer mixed percepts overall in typical populations,  
300 also produce larger group differences between individuals with and without ASC.

301 An increase in the E/I ratio has been proposed as a neurophysiological explanation for a wide range  
302 of symptoms associated with ASC. First described by Rubenstein and Merzenich (2003), this  
303 hypothesis was inspired, in part, by the observation that individuals with classic autism exhibit a high  
304 co-morbidity with epilepsy, estimated as high as 20-25% (Canitano, 2007). Since the original proposal  
305 of this hypothesis, converging genetic (Bundey et al., 1994; Menold et al., 2001; Kim et al., 2008;  
306 Buxbaum et al., 2002; Warrier et al., 2013), animal (Chao et al., 2010; Gogolla et al., 2009; Tsai et al.,  
307 2012; Yizhar et al., 2011), computational (Vattikuti & Chow, 2010), and neuroanatomical (Fatemi et  
308 al., 2009b; Oblak, Gibbs, & Blatt, 2011; Yip, Soghomonian, & Blatt, 2007) findings have further  
309 supported the role of altered E/I signalling in the neurobiology of ASC. In particular, subunits of  
310 receptors for GABA, the primary agent of inhibitory neurotransmission in the adult brain, have been  
311 reported to be under-expressed in histological studies of autism (Fatemi, Folsom, Reutiman, &  
312 Thuras, 2009a; Fatemi et al., 2009b).

313 An alteration in GABAergic signalling would likely have wide-reaching implications for many neural  
314 computations, as GABA plays a formative role during development, particularly during the critical  
315 period (Ben-Ari, 2002). Recent reports of architectural alterations of the autistic visual system are  
316 consistent with this hypothesis, demonstrating weaker surround suppression (Foss-Feig, Tadin,  
317 Schauder, & Cascio, 2013), larger population receptive fields (Schwarzkopf, Anderson, de Haas,  
318 White, & Rees, 2014), and atypical responses to motion stimuli in early visual cortex (Robertson et al.,  
319 2014). Therefore, a replicable behavioural marker of autistic symptomatology that would be predicted  
320 to directly couple with GABAergic signalling would greatly enhance our understanding of autistic  
321 neurobiology. Here, we confirm atypical dynamics of binocular rivalry in ASC using two very different  
322 sets of stimuli (coloured objects and achromatic gratings). This finding may be a simple behavioural  
323 index of a pervasive imbalance in E/I interactions in the autistic visual cortex.

324 Previous studies have investigated the dynamics of binocular rivalry in other clinical populations.  
325 Typical rivalry rates have been reported in individuals with schizophrenia (Miller et al., 2003).  
326 However, in bipolar disorder, a slower rate of rivalry is found with drifting (Pettigrew & Miller, 1998)  
327 and stationary gratings (Miller et al., 2003; Nagamine, Yoshino, Miyazaki, Takahashi, & Nomura,

328 2009). Crucially, the atypical rivalry dynamics reported in bipolar disorder were found to be specific to  
329 bipolar I, and are driven by longer dominant percepts (Nagamine et al., 2009). This is an important  
330 distinction from our findings in autism, where rivalry dynamics are marked by longer mixed percepts.  
331 These findings highlight the importance of characterizing the duration of perceptual states in binocular  
332 rivalry in clinical populations, rather than just the rate of alternation.

333 Computational descriptions of binocular rivalry further emphasize this importance of characterizing  
334 percept durations during binocular rivalry. Two recent computational models of binocular rivalry  
335 specifically predict that an E/I imbalance in the visual system would affect the ratio of mixed and  
336 dominant percepts during binocular rivalry (Klink et al., 2010; Said et al., 2012; Said & Heeger, 2013).  
337 Specifically, while neither model makes predictions about the absolute duration of percepts, they both  
338 predict that a reduction in inhibitory connection strength reduces exclusivity of the two percepts, or  
339 raises the proportion of mixed percepts, due to incomplete mutual suppression between pools of  
340 neurons coding for the opposing percepts. It should be noted that in one model, the same increase in  
341 mixed percepts occurs when excitatory connection strength amongst pools of neurons coding for the  
342 same percept is reduced (Said et al., 2012), indicating that atypical rivalry dynamics may be agnostic  
343 to the direction of an E/I imbalance. Future work linking the duration of mixed percepts to E/I balance  
344 in the brain is required to resolve these computational predictions.

345 A previous experiment did not confirm atypical dynamics of binocular rivalry in ASC using low-level  
346 stimuli. However, the reported results were consistent with the direction of our findings: the authors  
347 reported a higher proportion of mixed percepts in ASC ( $t(22) = 1.76$ ,  $p = .09$ , Said et al., 2012). We  
348 therefore suggest that the current literature, as a whole, supports the hypothesis of atypical dynamics  
349 of binocular rivalry in autism across multiple levels of stimulus complexity. However, we highlight one  
350 aspect of our stimulus parameters that may have contributed to the strength of the observed effects in  
351 the current study, which future work should explore. The proportion of mixed percepts reported during  
352 rivalry is known to increase with stimulus size (Blake, O'Shea, & Mueller, 1992), and our stimuli were  
353 larger than those used by Said and colleagues in order to match our object stimuli ( $3.5^\circ$ , as opposed  
354 to  $1^\circ$ ). This difference may have increased the dynamic range of rivalry dynamics measured in our  
355 experiments, and allowed for a group difference to become evident. It should also be noted that larger  
356 stimuli could also lead to larger eye movements, which are known to trigger perceptual switches  
357 during bistable perception (Bonneh et al., 2010; van Dam & van Ee, 2006). However, our results are  
358 not consistent with the concern that a clinical population might show a higher frequency of eye  
359 movements, as we report fewer perceptual switches in ASC.

360 Our primary motivation in comparing the grating and object rivalry in ASC was to explore whether  
361 atypical rivalry dynamics in ASC would generalize across various types of visual stimuli. Binocular  
362 rivalry between complex stimuli is thought to employ competitive interactions between pools of  
363 neurons at both early (eye-selective) and late (percept-selective) stages of visual processing  
364 (Freeman, 2005; Said & Heeger, 2013; Wilson, 2003). Consistent with these models, rivalry  
365 oscillations are mirrored in fluctuations in activity across levels of the visual hierarchy (Tong & Engel,  
366 2001; Tong, Nakayama, Vaughan, & Kanwisher, 1998). Our findings of reduced perceptual exclusivity

367 in ASC with both grating and object rivalry suggest that an E/I imbalance may affect multiple types of  
368 competitive interactions in the autistic visual system.

369 Although our results demonstrate that atypical rivalry dynamics in ASC are robust with respect to  
370 stimulus choice, they also indicate an interaction between stimulus type and diagnosis. Consistent  
371 with previous studies of binocular rivalry (Klink et al., 2010), we observed a main effect of Stimulus  
372 Type on percept durations: in both groups, coloured object stimuli elicited more perceptual exclusivity  
373 than grayscale grating stimuli, although this may also be influenced by luminance contrast (Brascamp  
374 et al., 2015). Interestingly, this effect interacted with Diagnosis: although mixed percepts were longer  
375 for ASC participants in both stimulus conditions, this difference between groups was exaggerated with  
376 the grating stimuli. Additionally, although we find an overall slower switch rate in ASC, this effect was  
377 particularly driven by grating trials in this study, as the numerically lower switch rate in ASC on object  
378 trials did not statistically differ between ASC and controls. Our two stimulus types were chosen to  
379 match the stimuli of prior studies (Robertson et al., 2013; Said et al., 2012), and therefore differed on  
380 many dimensions: colour (chromatic/achromatic), spatial frequency variation (varied/uniform),  
381 orientation variation (varied/uniform), shape (objects/lines), and contrast. As a result, it is impossible  
382 to establish whether differences in autistic visual processing on a particular one of these dimensions  
383 could explain the observed interaction between Stimulus Type and Diagnosis, or whether these  
384 findings reflect an increase in sensitivity to the diminished number of levels of cortical competition  
385 between object and grating stimuli. There is some evidence to suggest that stimulus complexity may  
386 be processed differently in ASC (Bertone, Mottron, Jelenic, & Faubert, 2003, 2005), but future work is  
387 needed to explore the influence of stimulus strength as modulated by, for example, colour contrast,  
388 luminance contrast or spatial frequency on mixed percepts in ASC.

389 In summary, these findings demonstrate a reliable perturbation in the dynamics of binocular rivalry in  
390 individuals with ASC. This replicable difference between individuals with and without ASC in such a  
391 fundamental aspect of vision, and across a diverse range of stimuli, suggests that an E/I imbalance  
392 may be pervasive in the autistic visual system, and might be predicted to occur in other sensory  
393 modalities. Rivalry may therefore have the potential to serve as a behavioural marker of atypical  
394 function in a canonical neural computation in the autistic brain.

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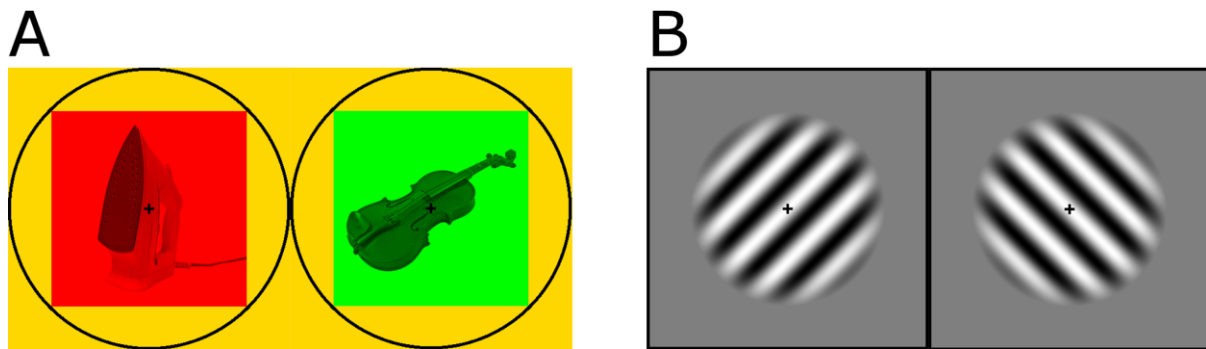
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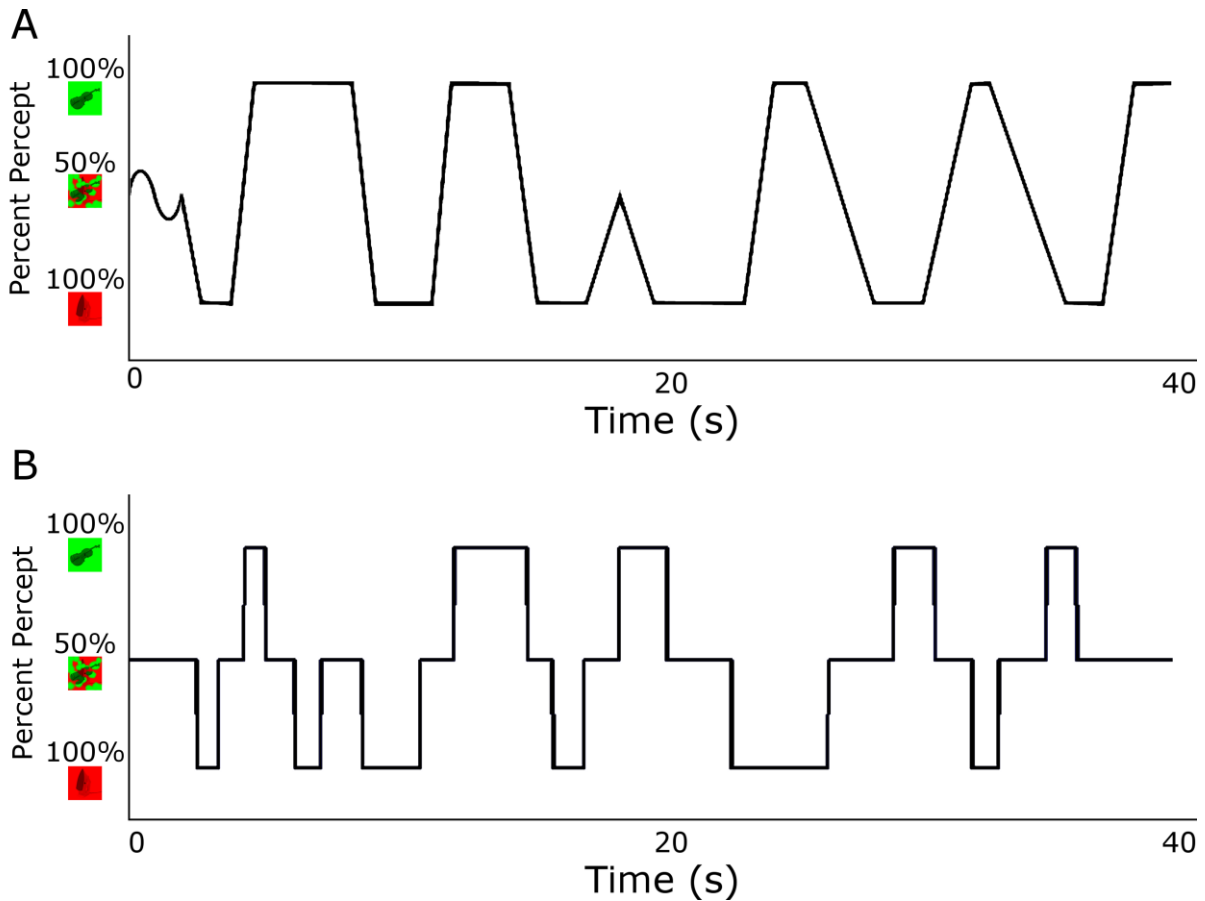
## Figures



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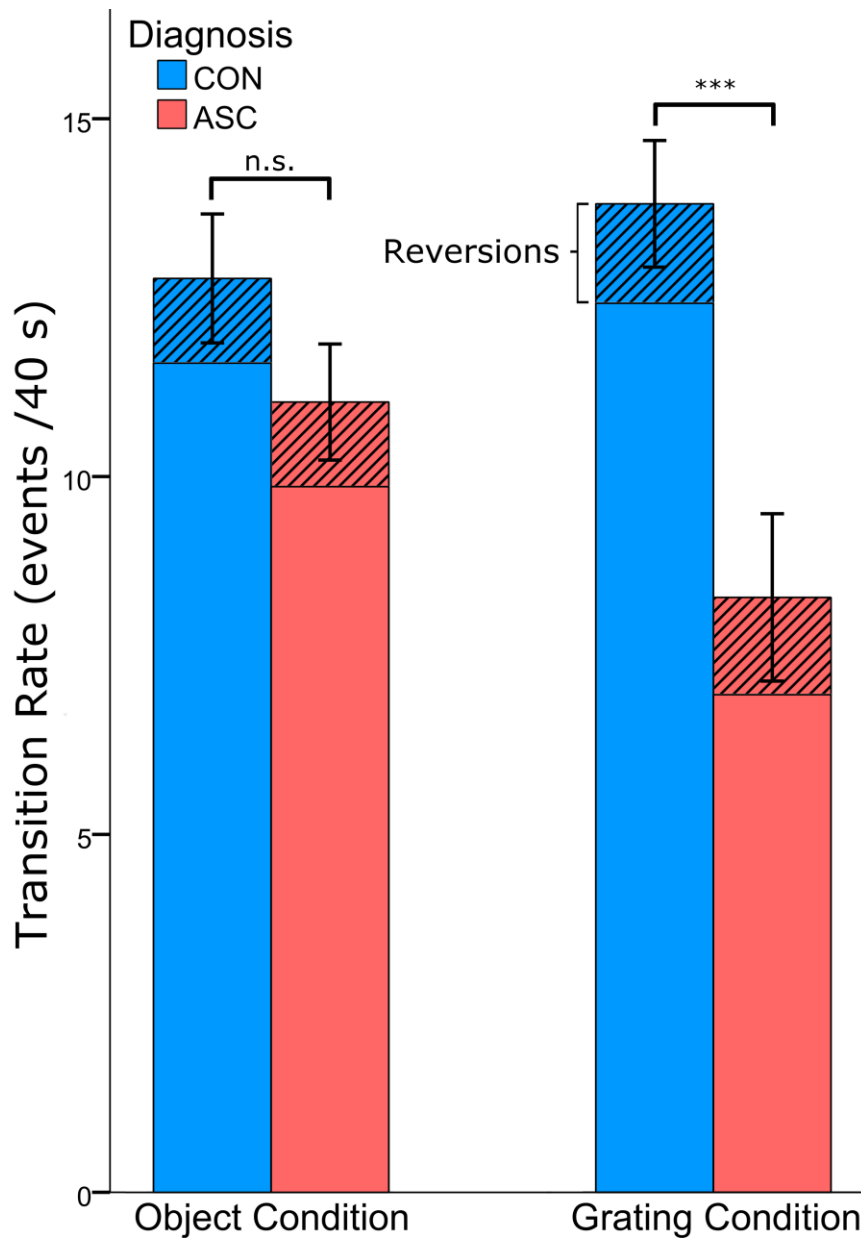
551 **Figure 1: Stimuli used in the binocular rivalry experiment.** A. Example stimuli for the object  
552 condition. Object stimuli consisted of grayscale images taken from a bank of standard, non-social  
553 images (e.g. a baseball and a broccoli). Each image (average height:  $2.31^\circ$ , width:  $2.79^\circ$ ) was  
554 presented on a coloured square (width:  $3.5^\circ$ ). A black circle surrounded the tinted squares (radius:  
555  $4.95^\circ$ ) and a black fixation cross was set in the centre of the circle to provide vergence cues. On each  
556 trial, one eye viewed a red square, and one eye viewed a green square. B. Example stimuli for the  
557 grating condition. Grating stimuli consisted of sinusoidal luminance gratings (spatial frequency: 3  
558 cycles/degree; Michelson contrast: 60%), displayed in a circular aperture (diameter:  $3.5^\circ$ ). A black box  
559 surrounded the gratings (width:  $4.95^\circ$ ) and a fixation cross was set in the centre of the box to provide  
560 vergence cues. On each trial, one eye viewed gratings tilted  $+45$  degrees, and the other  $-45$  degrees.

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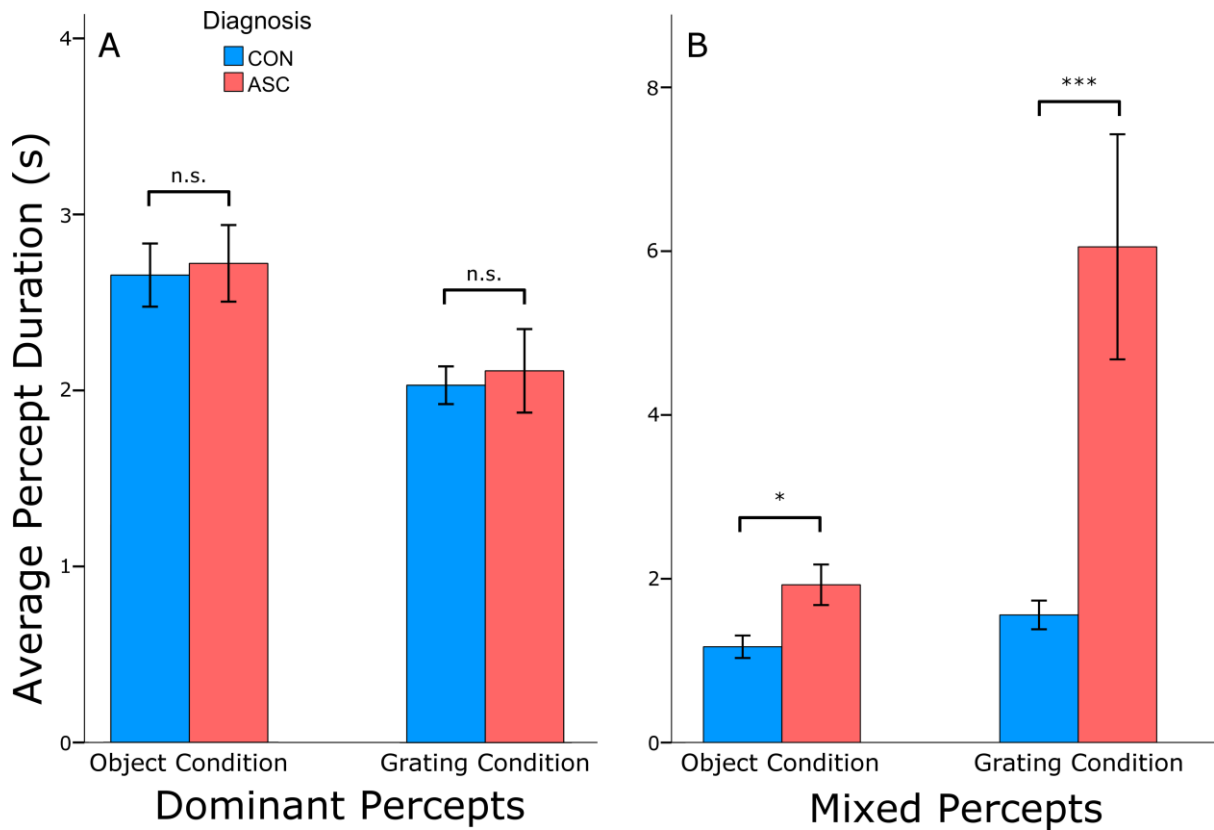
563 **Figure 2: Example time courses of control experiment stimulus presentation.** A. Smooth, linear  
 564 transitions between images, designed to measure participants' response criteria to judge the  
 565 boundary between a mixed and dominant image. Stimuli simulated natural rivalry, starting with a  
 566 mixed image (Object Condition: 50% green/red; Grating Condition: 50% 45°/-45°) and thereafter  
 567 smoothly oscillating between the two percepts (Object Condition: 100% green or 100% red; Grating  
 568 Condition: 100% 45° or 100% -45°). B. Sudden transitions between images, designed to measure  
 569 participants' motor latencies to report the onset of a mixed or dominant image. Trials began with a  
 570 mixed image, after which stimuli abruptly alternated between three states (Object Condition: 100%  
 571 green, 100% red, and 50% red/green; Grating Condition: 100% 45°, 100% -45°, and 50% 45°/-45°).



572

573 **Figure 3: Slower rate of binocular rivalry in ASC.** ASC subjects demonstrated overall fewer  
 574 perceptual transitions between the images presented to their right and left eyes (main effect of  
 575 Diagnosis:  $F(1, 45) = 8.717, p < 0.005$ ) The mean number of these transitions which were switches or  
 576 reversions is marked (stripes) for each group. Error bars represent one standard error of the mean  
 577 and \*\*\*  $p < 0.001$  difference between the two groups.

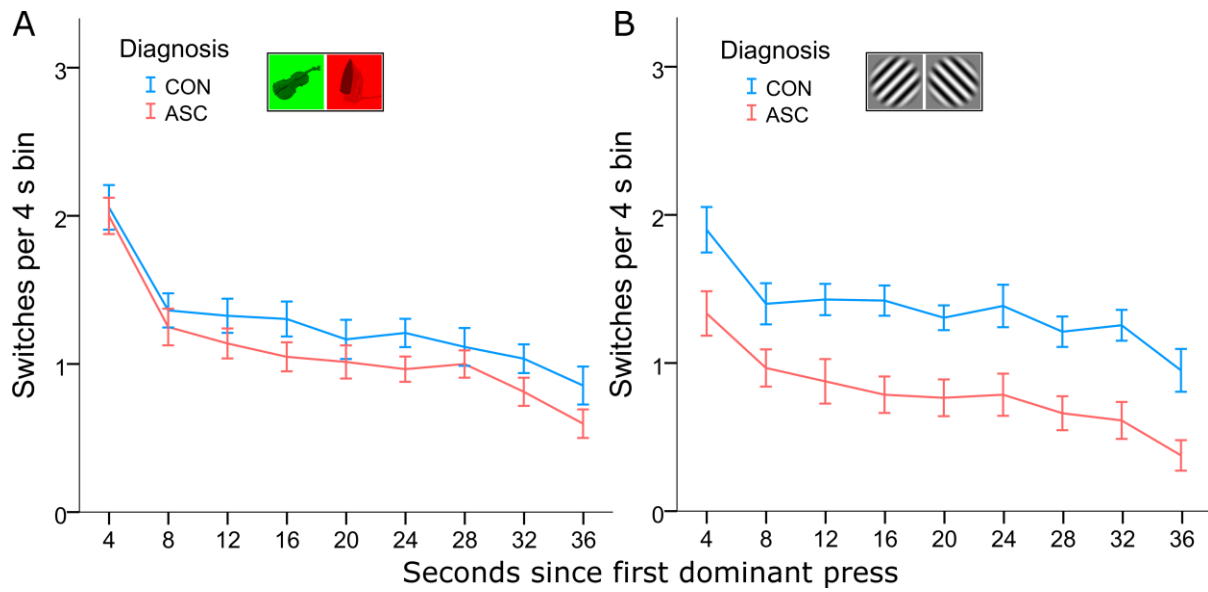
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579

580 **Figure 4: Lengthened mixed percepts in ASC.** A. The durations of dominant percepts were  
 581 equivalent between the two groups in both stimulus conditions. Both groups experienced longer  
 582 dominant percepts in the object condition than in the grating condition. B. The ASC group  
 583 experienced overall longer mixed percepts than the control group in both stimulus conditions (main  
 584 effect of Diagnosis:  $F(1, 45) = 11.855, p < 0.001$ ). Both groups experienced shorter mixed percepts in  
 585 the object condition than in the grating condition. In both plots, error bars represent one standard error  
 586 of the mean and \*  $p < 0.05$ , \*\*\*  $p < 0.001$  difference between the two groups.

587



588

589 **Figure 5: Decline of rivalry rate over time.** For both groups, the frequency of perceptual switches  
 590 declined throughout the trial. The rate of this decline was comparable between the two groups in both  
 591 the Object Condition (A) and the Grating Condition (B), with individuals with ASC reporting overall  
 592 fewer perceptual transitions (main effect of Diagnosis:  $F(1, 45) = 8.717, p < 0.005$ ).



## Tables

593 **Table 1: Descriptive Statistics and tests of equality between the two groups.**

	<b>Age</b>	<b>IQ</b>	<b>Gender</b>	<b>AQ</b>	<b>ADOS (A+B)</b>	<b>GSQ</b>	<b>SPQ</b>
<b>Controls</b>	28.7 ± 9.8 (21-72)	114.0±12.9 (87-135)	M:F 17:10	16.6±6.7 (6-33)	-	40.9±17.1 (9-81)	113.5±27.0 (72-148)
<b>ASC</b>	32.0±11.0, (17-56)	118.2±11.2 (99-139)	M:F 17:9	37.5±7.1 (23-47)	9.6±3.1 (5-16)	74.9±20.9 (41-120)	87.3±24.2 (56-141)
<b>p-value</b>	p >= 0.26	p >= 0.22	p >= 0.85	p < 0.001	-	p < 0.001	p < 0.001

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595 Table 1. Psychometric Data. Means +/- 1 standard deviation, as well as the range of data, are  
 596 reported for each group. Groups were matched for age, IQ, and gender.