

## 1 Title

## 2 Adaptation to transients disrupts spatial coherence in binocular 3 rivalry

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## 9 Short title

## 10 Adaptation to transients mixes perception in binocular rivalry

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## 13 Abstract

14 When the two eyes are presented with incompatible images, the visual system fails to create a single,  
15 fused, coherent percept. Instead, it creates an ongoing alternation between each eye's image; a  
16 phenomenon dubbed binocular rivalry (BR). Such alternations in awareness are separated by brief,  
17 intermediate states during which a spatially mixed (incoherent) pattern of both images is perceived. A  
18 recent study proposed that the precedence of mixed percepts positively correlates with the degree of  
19 adaptation to conflict between the eyes. However, it neglected the role of visual transients, which  
20 covaried with the degree of conflict in the stimulus design. We here study whether the presence of visual  
21 transients drive adaptation to interocular conflict and explain incidence rates of spatially incoherent BR.  
22 Across three experiments we created several adaptation conditions in which we systematically varied  
23 the frequency of transients and the degree of conflict between the eyes. Transients consisted of grating  
24 orientation reversals, blanks, and plaids. The results showed that the pattern of variations in the fractions  
25 mixed percepts across conditions was best explained by variations in the frequency of visual transients,  
26 rather than the degree of conflict between the eyes. We propose that the prolonged presentation of  
27 transients to both eyes evokes a chain of events consisting of (1) the exogenous allocation of attention  
28 to both images, (2) the increase in perceptual dominance of both rivalling images, (3) the speed up of  
29 adaptation of interocular suppression, and eventually (4) the facilitation of mixed perception during BR  
30 after adaptation.

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## 33 Author summary

34 When one eye is presented with an image that is distinct from the image presented to the other eye, the  
35 eyes start to rival and suppress each other's image. Binocular rivalry leads to perceptual alternations  
36 between the images of each eye, during which only one of the images is perceived at a time. However,  
37 when the eyes exert weak and shallow mutual suppression, observers tend to perceive both images  
38 intermixed more often. Here we designed an experiment and a model to investigate how stereoscopic  
39 stimuli can be designed to alter the degree of interocular suppression. We find that prolonged and  
40 repeated observations of strong visual transients, such as sudden changes in contrast, can facilitate the  
41 adaptation to suppression between the eyes, resulting in that observers report more mixed percepts.  
42 This novel finding is relevant to virtual- and augmented reality for which it is crucial to design  
43 stereoscopic environments in which binocular rivalry is limited.

44

## 45 Keywords

46 Exclusive dominance; piecemeal; binocular rivalry; adaptation; orientation conflict; interocular  
47 suppression

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59 **Additional Information**

60 Author Contributions

61 All authors designed the experiments. Author YdK collected the data. MN, SS, and YdK programmed  
62 the experiments and analyzed data. Author MN & CP wrote the concept paper and all other authors  
63 contributed to the final paper.

64

65 Competing Financial Interest

66 The authors declare no competing financial interests.

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## 1. Introduction

70 1.1 Studying the dynamics of visual awareness with binocular rivalry

71 Binocular rivalry (BR) is a primary method in the scientific fields of cognitive psychology and  
72 neurosciences to study visual awareness. It consists of the presentation of separate images to each eye.  
73 When the two images are distinct, the visual system is unable to fuse them into a coherent percept.  
74 Instead, the distinct mental representations of both eyes compete for priority to visual awareness. This  
75 results in the perception of unending perceptual alternations between the two images over time, a purely  
76 internally (mentally) driven process because the physical environment is kept stable.

77 BR has been heavily exploited by psychologists, neuroscientists, and philosophers for a variety of  
78 reasons. One reason is that the dynamic properties of BR provide information on what type of images  
79 dominate more strongly or break into visual awareness faster (e.g., 1, 2). Such research is necessary in  
80 order to understand why people sometimes fail to notice objects (e.g., in traffic), how image-parts are  
81 grouped into ensemble objects (i.e., Gestalt principles), and why certain objects in the visual  
82 environment receive sensory priority (e.g., advertisements). BR is also the primary method used to study  
83 the interaction between the sensory processing of stimulus properties and other cognitive high-level  
84 functions such as attention, numerosity and emotions (3-7). Furthermore, studies have revealed that a  
85 variety of brain regions and processes underlie changes in the content of visual awareness during BR  
86 (8-11). Using BR to find the neural loci of consciousness and to identify the distinct processing stages  
87 of the stream of consciousness remains an ongoing line of research. Lastly, BR serves as a tool to  
88 examine to what degree information, that falls outside the scope of awareness, is processed and affects  
89 behavior (e.g., 12). Following the iceberg-mind analogy in the sense that most of what an iceberg's  
90 constitutes is submerged under water, most stimuli in a visual environment are not consciously perceived  
91 but may still have a determinative effect on decision-making (13). In sum, BR has been shown to be a  
92 valuable method to examine perceptual selection, the neurobiological underpinnings of awareness, and  
93 unconscious processing (14). However, there is more to be learned from BR. While often overshadowed  
94 by discussions surrounding consciousness, BR also reflects how the eyes interact and strive for a stable,  
95 coherent percept. It is therefore necessary to understand under which circumstances dichoptic images

96 fuse and when they engage in binocular rivalry (e.g., 15, 16-18). Especially now, with the rise of virtual  
97 and augmented reality goggles, it is of importance to understand how images can be best designed to  
98 prevent BR, enhance the fusion of representations of both eyes, and create realistic depth perception.  
99 The experience of a coherent percept is important for effort-free viewing and the feeling of immersion  
100 when wearing stereoscopic goggles (19). BR may thus also be utilized to determine the level of  
101 “cooperation” between the eyes.

102 1.2 Exclusive versus nonexclusive, mixed episodes in binocular rivalry

103 How can BR serve as a tool to determine to what degree information of both eyes integrates rather than  
104 competes? To answer this question, it helps to focus on the spatio-temporal dynamics rather than merely  
105 the temporal dynamics of BR. Temporal dynamics include the rate at which switches in awareness occur  
106 and the ratio of left versus right eye dominance durations in perception. These measures indicate when  
107 and how often a change in awareness occurs and how strong, conspicuous, and relevant each image is  
108 to the visual system. Spatio-temporal dynamics embrace the local nature of binocular conflict and  
109 include episodes in which BR is in an intermediate, unstable state, in which perception exists of a  
110 mixture of the images of both eyes across image locations (i.e., piecemeal or non-exclusive rivalry).  
111 This latter measure indicates to what degree information of both eyes is integrated. However, this aspect  
112 of BR has received relatively little scientific attention, mainly because the spatio-temporal dynamics of  
113 binocular rivalry are typically operationalized as stemming from a discrete on-off process (i.e., the image  
114 of the left or right eye is visible) by means of measurements of binary responses (i.e., press either one  
115 of two buttons to report dominance of the two images). Only a handful of papers have looked at the non-  
116 binary properties of rivalry. For example, Naber et al. (20) instructed observers to report mixed percept  
117 episodes of moving gratings with a joystick and observed that the reported spatio-temporal dynamics  
118 matched the same dynamics measured objectively with the optokinetic nystagmus. Other studies  
119 examined so-called traveling dominance waves, described best as the gradual emergence of a suppressed  
120 image as it flows over the other, dominant image within a relatively short time span (21-23). These  
121 waves tend to have a local starting point in the visual field and move with a certain velocity (24-29). A  
122 few more studies inspected what type of images proliferate mixed percepts during rivalry (30-32). For

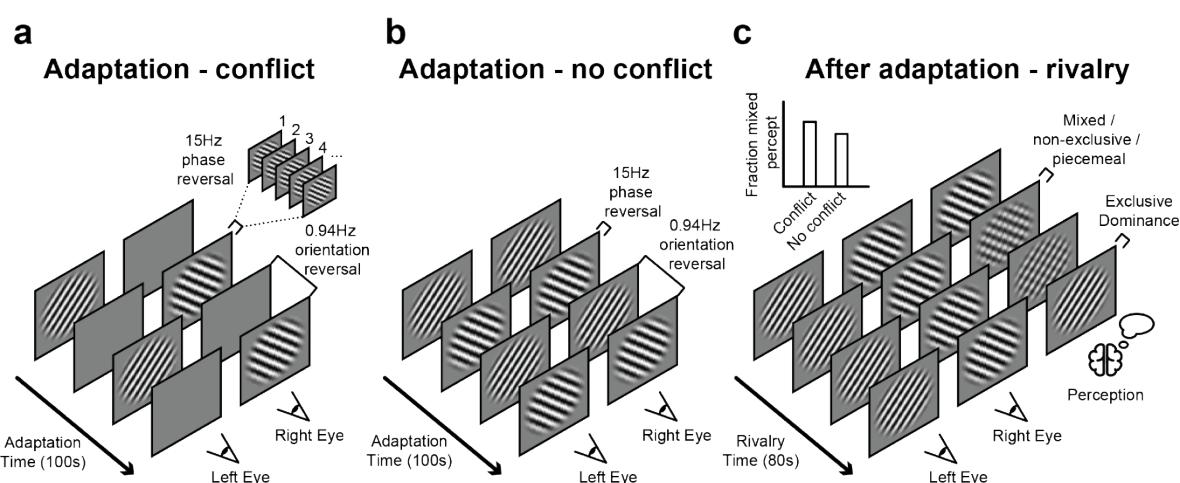
123 example, the more similar the images are across the eyes, the weaker the interocular suppression and  
124 the higher the chance of observing mixed rivalry (31). Similarly, gratings which are relatively similar  
125 with locally overlapping features, exhibit more mixed percepts as compared to complex, coherent  
126 objects such as houses and faces, which are more dissimilar (32). This means that when images mutually  
127 exert weak, shallow interocular suppression (i.e., a weak competition between the eyes) due to a local  
128 overlap of features between both eyes, exclusive (monocular) percepts are rarer and mixed episodes last  
129 longer. A recent adaptation study additionally showed that the durations of mixed episodes can be  
130 lengthened by first adapting observers to episodes of strong interocular conflict in orientation (33). The  
131 explanation for this finding is that the visual system includes neurons that detect conflict between the  
132 eyes and drive interocular suppression (34). When these conflict detectors become less responsive due  
133 to adaptation, interocular suppression presumably becomes weak (i.e., shallow), resulting in more or  
134 longer episodes of mixed rivalry. However, adaptation to interocular conflict may not be the only  
135 plausible explanation for the reported effects on mixed percepts during rivalry. The current study  
136 investigates whether the weaker suppression (reflected by a larger incidence of mixed percepts)  
137 following adaptation in the study of Said and Heeger was due to adaptation to conflict, or whether other  
138 factors contribute to weaker suppression following adaptation.

139       1.3 Binocular conflict detectors versus visual transients

140       Although Said & Heeger (33) elegantly applied the method of adaptation to support their model  
141 including conflict detectors, the authors may have overlooked the possibility that additional or  
142 alternative mechanisms may drive the occurrence of mixed episodes. Here we propose that the presence  
143 of strong transients affects binocular rivalry and, in the context of the findings of Said and Heeger, could  
144 be the principal underlying factor for the facilitation of mixed percepts in rivalry after adaptation. To  
145 clarify, let us first describe how visual transients affect binocular rivalry: It is known that an intermittent  
146 stimulus presentation (i.e., interleaving content-rich image presentations with content-absent blanks)  
147 strongly reduces the alternation rate of binocular rivalry. Depending on the duration of the blank  
148 episodes, an image of one eye can remain dominant for minutes rather than seconds (35, 36). Such  
149 changes in the temporal domain of rivalry dynamics suggest that intermittent presentation enhances

150 interocular suppression. We here propose that intermittent presentation (i.e., a strong visual transient)  
151 also affects the spatio-temporal rivalry dynamics. As for the study of Said & Heeger (33), their conflict  
152 condition (producing strong adaptation) included an intermittent presentation paradigm while their weak  
153 adaptation condition did not (see Figure 1, a modification of Figure 6 in Said & Heeger). In other words,  
154 the implementation of blanks, and thus of transient onsets and offsets of the images, may have facilitated  
155 adaptation to interocular suppression rather than conflict.

156 In three separate experiments we demonstrate that the presence of visual transients during adaptation  
157 explains the degree of mixed percepts better than the presence of orientation conflict between the eyes.  
158 By manipulating the rate of changes in monocular contrast and changes in orientations, we are able to  
159 show that these transients affect interocular suppression, resulting in decreased spatio-temporal stability  
160 of binocular rivalry.



162 **Figure 1. Procedural design by Said & Heeger.** In the design of Said & Heeger's (33), a single trial  
163 consisted of an adaptation period (a-b) that lasted for 100s and a rivalry test period (c) that lasted 80s.  
164 Observers experienced regular binocular rivalry and indicated the onsets of exclusive and non-exclusive  
165 percepts with keyboard buttons during the subsequent test period (c). During the preceding adaptation  
166 period, observers passively viewed alternations in oriented gratings (a-b). The gratings' phase reversed  
167 at a rate of 15Hz to prevent local brightness adaptation. More importantly, the perceived orientation  
168 alternated (counter-)clockwise at a rate of 0.94 times per second. According to Said & Heeger (33),  
169 prolonged presentation of different orientations to the eyes (a) adapt opponency neurons that detect

170 interocular conflict and drive interocular suppression (i.e., the degree the left eye's image is inhibited  
171 by the right eye's image and vice versa). However, when identical orientations are presented to both  
172 eyes at any point in time (b), they argue that no conflict between the eyes is present and neural conflict  
173 detectors do not adapt. Adaptation and therewith weaker interocular suppression subsequently leads to  
174 unstable perception, that is, a higher precedence of mixed (nonexclusive, piecemeal) percepts. A mixed  
175 percept consists of the presence of parts of two images from both eyes rather than a single exclusive  
176 image of one eye (c).

177

178      **2. Experiment 1**

179      2.1 Introduction

180      As described in the introduction, incoherent rivalry after adaptation (i.e., more mixed percepts) may be  
181      caused by the presence of transients, rather than the presence of interocular conflict. Such transients can  
182      be of any type, including changes in contrast and orientation. Here we extended the original conflict and  
183      no conflict conditions of Said & Heeger with novel conditions that either included or excluded the  
184      different transient types described above (see **Figure 2a**; for details, see *Stimulus and conditions*), and  
185      investigated their individual contributions to the degree of mixed percepts following adaptation.

186      2.2 Methods

187      2.2.1 *Participants*

188      Twenty-six human individuals, all right-handed, young students (age:  $M = 23.4$ ,  $SD = 4.5$ ; 21 females)  
189      and with normal or corrected-to-normal vision, participated in Experiment 1. Participants were naïve to  
190      the purpose of the experiment, gave informed written consent before participation, and received either  
191      study credit or money (€6 per hour; Experiment lasted approximately 3 hours) after participation. The  
192      experiments conformed to the ethical principles of the Declaration of Helsinki and were approved by  
193      the local ethical committee of Utrecht University.

194      2.2.2 *Apparatus*

195      Stimuli were generated on two 24-inch ASUS VG248QE monitors (AsusTek, Taipei, Taiwan) with a  
196      dell computer (Dell, Round Rock, TX, USA) operating Windows 7 (Microsoft, Redmond, WA, USA)  
197      and MatLab version r2010a (Mathworks, Natick, MA, USA). The presentation monitors displayed 1920  
198      by 1080 pixels at a 60-Hz refresh rate. Each screen size was 53cm in width and 30cm in height (51 by  
199      29 visual degrees), and the participant's viewing distance to the screen was fixed with a chin and  
200      forehead rest at 57cm. Each eye of an observer was presented with stimuli through a Wheatstone-  
201      inspired (37) mirror stereoscope (for details, see (38)). Observers used the arrow buttons on a Logitech  
202      keyboard (Logitech International S.A., Lausanne, Swiss) to report their percept (left for exclusive

203 dominance of counter-clockwise-oriented gratings, down for non-exclusive dominance, and right for  
204 exclusive dominance of clockwise-orientated gratings).

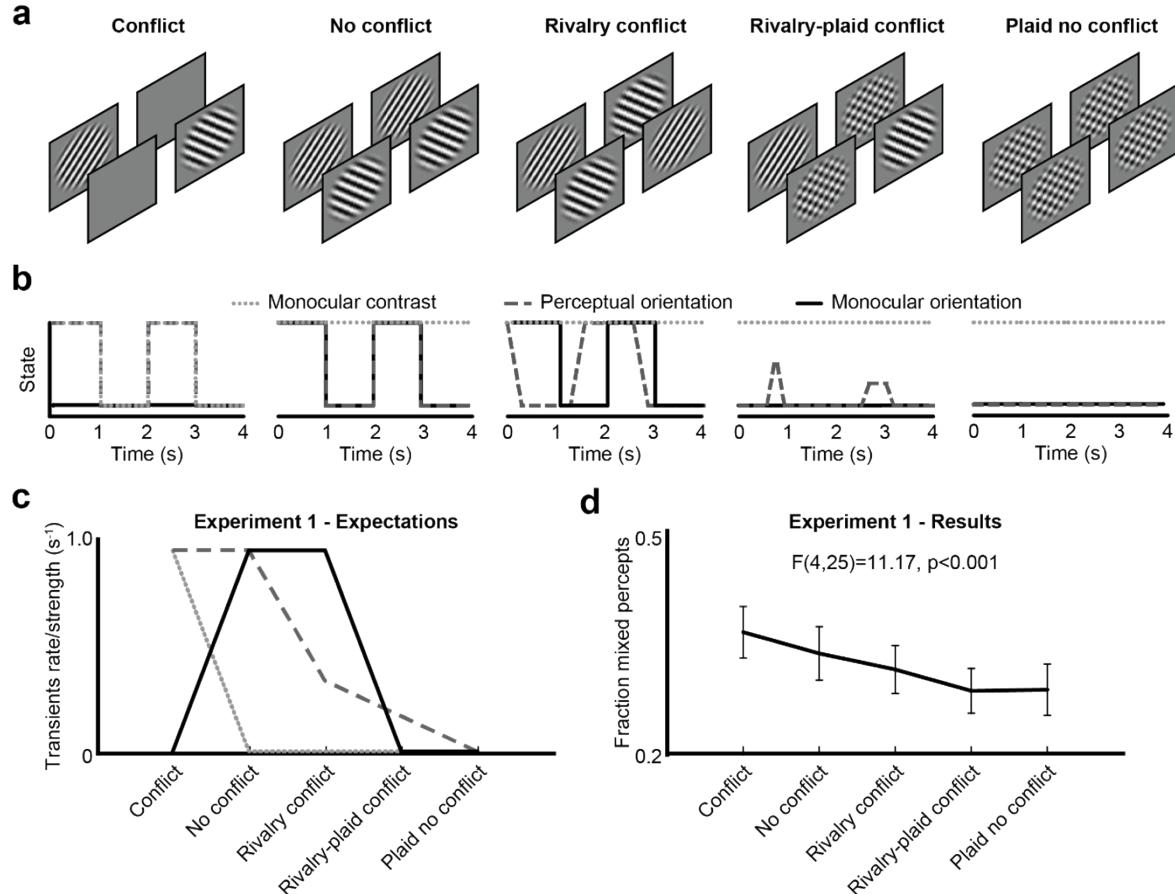
205 *2.2.3 Stimuli and conditions*

206 We used stimuli and conditions similar to those of Said & Heeger (33) by including an adaptation phase  
207 (**Figure 1a-b**) to affect perceptual stability in a subsequent rivalry phase (**Figure 1c**). Stimuli had a 0.6°  
208 radius in visual angle, a spatial frequency of 6.6 cycles/°, and edges softened by a cosine ramp of 0.1°  
209 in width. To prevent ocular vergence responses and thus to promote binocular fusion (i.e., to achieve  
210 perception of two spatially overlapping images), the stimuli were surrounded by a fusion stimulus. The  
211 fusion stimulus consisted of a 0.3° wide annulus (not shown in the figures) with a random noise pattern  
212 that was identical for each eye's image and located at 2.25° eccentricity.

213 Besides incorporating Said and Heeger's two original adaptation conditions in our design (first two  
214 panels from the left in **Figure 2a**), we added an adaptation condition called "rivalry conflict" (panel  
215 three in **Figure 2a**). In contrast to the conflict condition (panel one in **Figure 2a**), this condition did not  
216 include monocular contrast transients (i) but did include monocular orientation transients (ii) and could  
217 potentially adapt opponency neurons due to the conflicting information between the eyes.

218 Note that both the conflict and no conflict condition produce clearly visible transients in orientation at  
219 a fixed rate of approximately one reversal per second. However, the rivalry conflict condition also  
220 induces alternations between the eyes at a rate dependent on the perception of the observer. This  
221 condition thus adds another research opportunity, namely to investigate to what degree the rate of  
222 perceived, binocular transients affect the stability of binocular rivalry. Therefore, to manipulate and  
223 weaken conflict between the eyes even further in an incremental manner, and therewith the rate of  
224 perceived orientation alternations, we added two more conditions with plaids (see panel four and five in  
225 **Figure 2a**). These conditions serve as a baseline in which hardly any transients in terms of contrast and  
226 orientation are produced.

227



228

229 **Figure 2. Adaptation conditions, transient profiles, predictions, and results of Experiment 1.**

230 Experiment 1 tested five adaptation conditions with different stimuli (a). Each condition induced  
231 changes in stimulus states as a function of time (b), including monocular (solid black) and perceptual  
232 orientation (dashed dark gray) transients, and contrast transients (dotted light gray). We included the  
233 original conditions of Said & Heeger in which orientation and contrast (first panel from left) or only  
234 orientation (second panel) changes at a rate of 0.94Hz (solid black lines at (b)). We extended the original  
235 design by including a rivalry condition (third panel) with less frequently perceived orientation reversals  
236 (dashed dark gray lines at (b)) and a continuous orientation conflict between the eyes that excludes a  
237 monocular contrast conflict (dotted light gray lines at (b)). Another condition similar to the first panel  
238 was added but with a plaid rather than a blank screen in the other eye (fourth panel). A fifth condition  
239 with plaids presented to both eyes and thus no transients served as a baseline. Note that the perceptual  
240 orientation transients (dashed dark gray) are visible to the observer while the monocular transients  
241 (dotted light gray and solid black) are not (b). The pattern of expected fraction mixed percepts across

242 conditions per feature (c) is based on the number and strength of transients within a normalized time  
243 interval (for legend, see panel b). The actual pattern of fraction mixed percepts as indicated by observers  
244 (d) did not perfectly match the patterns predicted by each individual adaptation type but matched a  
245 combination of monocular contrast and perceptual orientation factors (c).

246

247 While the rate of *physical* stimulus changes was kept constant at 0.94Hz in the original two conflict and  
248 no conflict conditions, the three novel conditions were expected to differ in the number of evoked  
249 *perceptual* changes in orientation. Specifically, the rivalry conflict condition (third panel in **Figure 2a**)  
250 should evoke perceptual rivalry as probed in the test phase. The rivalry-plaid conflict condition (fourth  
251 panel) should cause even fewer perceptual reversals because the images of the plaid and the oriented  
252 grating are typically merged in a single percept during binocular rivalry (16). Note that the rivalry-plaid  
253 condition was similar to the original conflict condition of Said and Heeger but included the presentation  
254 of a plaid rather than a blank screen to the other eye as the oriented grating. The plaid no conflict  
255 condition (fifth panel) should cause no rivalry (16, 33). As the observers did not report alternation rates  
256 during the adaptation phase, authors MN and YdK independently confirmed that the orientation reversal  
257 rate and perceptual appearances were indeed manipulated as intended. In addition to the perceptual  
258 orientation transients, the five conditions also differed with regard to the presence of monocular contrast  
259 transients. Only the original conflict condition included intermittent blank presentations. The other four  
260 conditions thus contained no contrast transients (i.e., second-order, nonluminance contrast).

261 As shown in **Figure 2b**, the frequency and strength of each type of transient should differ considerably  
262 across the five conditions. For each transient type we plotted a hypothetical pattern of results (**Figure 2c**)  
263 assuming that each specific transient type independently affected the fraction mixed percepts during the  
264 test phase. Later in this paper we modelled weighted combinations of multiple transient types to  
265 investigate which of these best explain the fraction across all conditions and experiments (see last result  
266 section).

267 2.2.4 *Procedure*

268 The task for an observer was to attentively view the stimuli during the adaptation phase. Next they  
269 indicated their percept during the binocular rivalry phase as either exclusive (i.e., the majority of the  
270 surface of a single image was dominant) or mixed. The observers knew when to start reporting  
271 perceptions because the start of the rivalry test phase was marked by a sudden offset of phase reversals  
272 (i.e., the stimuli were contrast reversed at a rate of 15Hz during the adaptation phase to prevent local  
273 brightness adaptation; see **Figure 1a-b**). The observers kept their gaze on the fixation point at the center  
274 of the stimuli and screen.

275 Each condition was tested with six trials. The conditions were counterbalanced and the trials were  
276 divided into two experimental sessions held at different days, because the experiment took more than 3  
277 hours in total. Both sessions of the experiment started by having the observers align the stimuli on the  
278 screens to achieve best fusion, that is, the observers made sure the rivaling stimuli overlapped when  
279 viewed through the mirror stereoscope. Next, observers performed one rivalry test trial during which  
280 the contrast of the gratings was adjusted with the goal to counterbalance eye dominance by annulling  
281 between eye differences in dominance durations. Next, participants performed 30 trials and initiated the  
282 start of each trial with a button press.

283 2.2.5 *Analysis*

284 We refer to the independent variable as *adaptation type*. The dependent variable was the *fraction mixed*  
285 *percepts*, that is, the fraction of the total duration of perceptual episodes consisting of mixed dominance,  
286 as indicated by the observer. To investigate whether the factor adaptation type significantly affected the  
287 fraction mixed percept, we conducted a repeated measures ANOVA as a statistical test of significance  
288 (see figures for statistical outcomes). As post-hoc tests, we compared the fraction mixed percepts  
289 between each possible pair of conditions with two-tailed dependent t-tests (see tables in supplementary  
290 materials for statistical outcomes). We also examined the significance of effects of three transient types,  
291 namely that of (i) the presence versus absence of *monocular contrast* transients, (ii) the frequency of  
292 *perceptual orientation* transients, and (iii) the presence versus absence of *monocular orientation*  
293 transients.

294 2.3 Results & Discussion

295 We first aimed to test whether the adaptation type in the preceding adaptation phase affected the spatial  
296 stability of rivalry in the test phase. Indeed, the fraction mixed percepts during rivalry significantly  
297 varied across adaptation types (**Figure 2d**; repeated measures ANOVA:  $F(4,25) = 11.17, p < .001$ ).  
298 Qualitative inspection of the pattern of results suggested that the original conflict adaptation condition  
299 produced the highest fraction mixed percepts while the conditions with a plaid produced the lowest  
300 fraction.

301 Next, we determined whether we statistically replicated the findings by Said & Heeger (33). While the  
302 direction of the effect appeared similar to these previous findings, the conflict and no conflict conditions  
303 did not differ significantly according to a two-sided t-test (see **Supplementary table 1**). A one-sided t-  
304 test, which can be argued to be appropriate in case of a prediction based on previous findings, *did* result  
305 in a significant effect ( $t(25) = 1.870, p = .037$ ). Not surprisingly, the fraction mixed percepts in the first  
306 half of the test phase, that is directly after the adaptation phase when effects of adaptation are typically  
307 strongest before fading off (39), differed significantly between the conflict and no conflict condition,  
308 when tested with a two-sided t-test ( $t(25) = 3.726, p = .001$ ).

309 Next we continued to examine all conditions, including the novel three conditions, in order to determine  
310 which transient types drove the adaptation effects. When comparing the patterns of **Figure 2c** and **2d**,  
311 the decrease in perceptual orientations and monocular contrast across conditions matched the decrease  
312 in mixed percepts. To explore their individual significance of contribution to the pattern of results, we  
313 compared the effects of the presence versus absence of each transient type across conditions on the  
314 fraction mixed percepts. The first two conditions were the only conditions that included frequent and  
315 repetitive perceptual orientation transients and when pooled together they produced significantly higher  
316 fraction mixed percepts than the other three conditions, which included less frequent to no orientation  
317 transients (Difference:  $M = 0.054, SD = 0.051; t(25) = 5.389, p < .001$ ) The first conflict condition was  
318 the only condition that included monocular contrast transients and it produced significantly higher  
319 fractions mixed percepts than the other four conditions, which did not include monocular contrast  
320 transients (Difference:  $M = 0.059, SD = 0.075; t(25) = 3.986, p < .001$ ). The second and third conditions

321 were the only conditions which included monocular orientation transients and they did not produce  
322 higher fractions mixed percepts than the other conditions without monocular orientation transients  
323 (Difference:  $M = 0.013$ ,  $SD = 0.044$ ;  $t(25) = 1.480$ ,  $p = .151$ ). Lastly, the first, second, and fourth  
324 conditions were the only conditions which included an orientation conflict between the eyes and they  
325 *did* produce higher fractions mixed percepts than the conditions without orientation conflict, but the  
326 effect was ~50% weaker than that of perceptual orientation and monocular contrast transients  
327 (Difference:  $M = 0.028$ ,  $SD = 0.036$ ;  $t(25) = 3.908$ ,  $p = .001$ ).

328 To summarize the results of Experiment 1, the pattern of destabilization rates across all conditions is  
329 best explained by adaptation to both monocular contrast and perceptual orientation transients. Note that  
330 the third and fourth conflict rivalry(-plaid) conditions exhibited a conflict between the eyes but produced  
331 a lower fraction mixed percept than the first conflict condition. This latter finding cannot be explained  
332 by the conflict detector model of Said & Heeger (33) because conflict was clearly present in the rivalry(-  
333 plaid) conditions, predicting an increase rather than the observed decrease in the fraction mixed percepts.  
334 Because the manipulations of perceptual transients and monocular contrast (and conflict) were to some  
335 degree correlated across conditions, our next goal was to further disentangle the transient types and  
336 measure their individual contributions. As such, we continued to test the effects of monocular contrast  
337 transients independently from the other transient types in Experiment 2.

338 **3. Experiment 2**

339 **3.1 Introduction**

340 We have learned from Experiment 1 that it is likely that the presence of both perceptual orientation and  
341 monocular contrast transients in the adaptation phase disrupted the spatial coherency in binocular rivalry  
342 (i.e., increased the fraction mixed percepts) in the subsequent test phase. However, these two transients  
343 types co-varied across the conditions of Experiment 1. In Experiment 2 we manipulated the strength of  
344 contrast transients in isolation to further assess to what degree they contributed to incoherent perception  
345 during rivalry. We took a slightly different approach as compared to Experiment 1 by manipulating the  
346 contrast of the rivalling gratings rather than adding distracting information in the other eye. Based on

347 the findings in Experiment 1, we predicted that a low, compared to a high, grating contrast leads to  
348 relatively weak monocular contrast transients during adaptation, eventually resulting in relatively weak  
349 adaptation and more coherent rivalry, as characterized by less mixed percepts.

350 3.2 Methods

351 All aspects of the methods were identical to Experiment 1, except for the participants, duration of the  
352 rivalry test phase, and adaptation type conditions. A new group of twenty individuals (age:  $M = 21.9$ ,  
353  $SD = 2.3$ ; 14 females) participated in Experiment 2. The rivalry test phase was shortened from 80s to  
354 40s, because of the prominent effects of adaptation in the first 40s. We again included the original two  
355 adaptation conditions of Said & Heeger (33) in the conditional design as a reference (see outmost left  
356 and right panel in **Figure 3a**), as well as two novel conditions for which the contrast of tilted gratings  
357 were set at 50% and 25% (see second and third panel in **Figure 3a**). These two conditions specifically  
358 affected the degree of perceptual orientation and monocular contrast transients (see dotted and dashed  
359 lines in **Figure 3b**) and, based on the findings in Experiment 1, we predict that the decrease in contrast  
360 should weaken adaptation and decrease the fraction mixed percepts (**Figure 3c**).

361 3.1 Results & Discussion

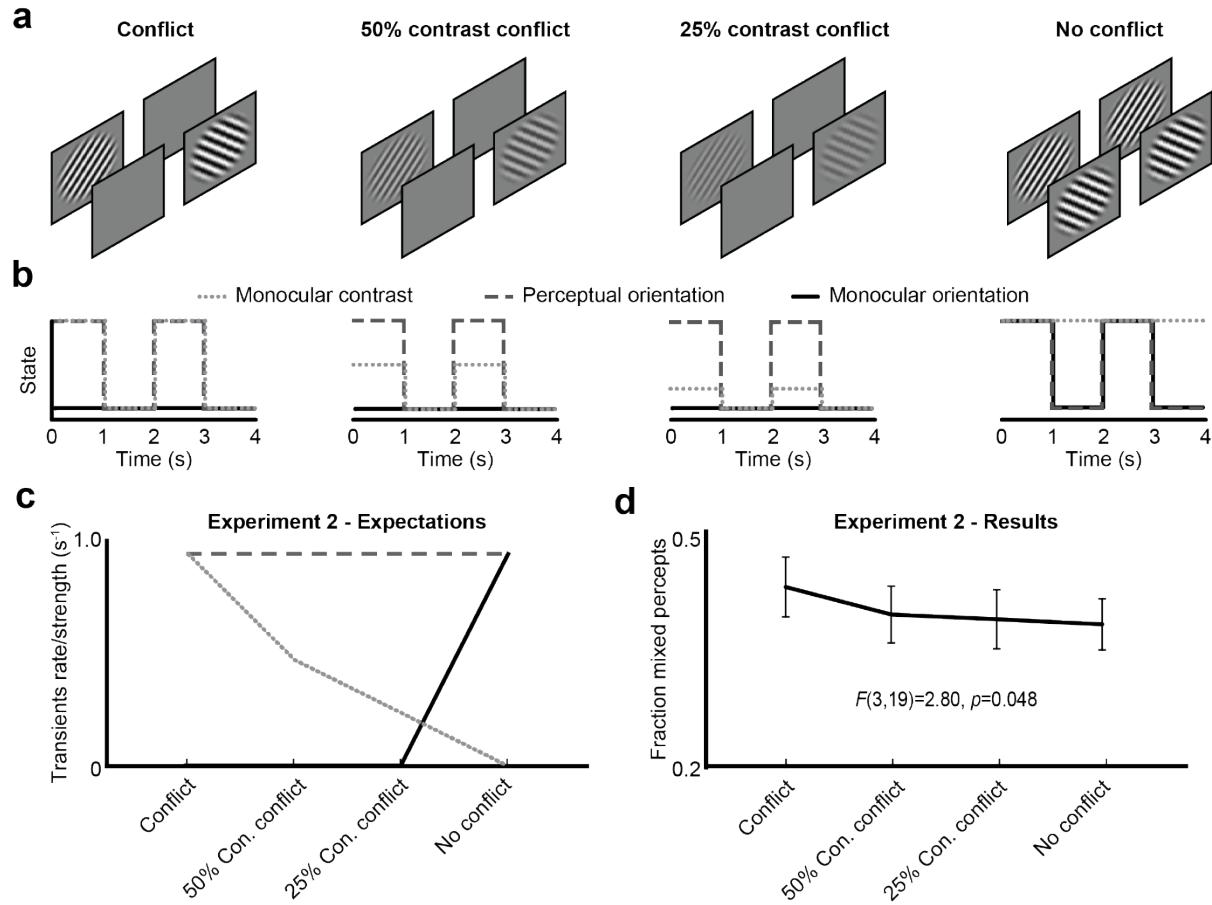
362 The fraction mixed percepts significantly differed across the four adaptation types ( $F(3,19) = 2.80$ ,  
363  $p = .048$ ), showing a decreasing pattern across conditions (**Figure 3d**; for post-hoc tests, see  
364 **Supplementary Table 2**). The original conflict adaptation condition produced the highest fraction  
365 mixed percepts ( $M = .43$ ,  $SD = .17$ ) while the other conditions with a lower grating contrast or no  
366 monocular contrast produced significantly lower fractions ( $M = .39$ ,  $SD = .15$ ;  $t(19) = 2.529$ ,  $p = .020$ ).

367 Furthermore, the first conflict condition was the only condition that included 100% monocular contrast  
368 transients and it produced significantly higher fractions mixed percepts than the other four conditions  
369 (Difference:  $M = 0.041$ ,  $SD = 0.073$ ;  $t(19) = 2.529$ ,  $p = .020$ ). The first three conditions were the only  
370 conditions which included an orientation conflict between the eyes (and monocular orientation  
371 transients) and they did *not* produce higher fractions mixed percepts than the fourth condition without  
372 orientation conflict (Difference:  $M = 0.022$ ,  $SD = 0.066$ ;  $t(19) = 1.516$ ,  $p = .146$ ).

373 In sum, we replicated the findings by Said & Heeger and in addition observed that a weaker adaptation  
374 contrast decreased the occurrence of mixed percepts during rivalry. The pattern of results of  
375 Experiment 2 most closely matched the pattern predicted by the monocular contrast transients, although  
376 the flatter and higher pattern than in Experiment 1 suggested that adaptation was again driven by a  
377 weighted combination of perceptual orientation transients and monocular contrast transients (i.e., an  
378 average of the dotted and dashed line in **Figure 3c**).

379 The results of Experiment 1 and 2 together favor a model that combines the effects of perceptual  
380 orientation and monocular contrast transients. It remains, however, unclear which of these transient  
381 types affects adaptation most. The final Experiment 3 was designed to extract the individual effects of  
382 monocular contrast versus perceptual orientation transients.

383



384

385 **Figure 3. Adaptation conditions, transient profiles, predictions, and results of experiment 2.** The  
386 design of Experiment 2 contained two original adaptation (first and fourth panel from the left) conditions  
387 and two novel conditions (second and third panel) with different time functions of monocular contrast  
388 (b). The new conditions varied the strength of monocular contrast transients (c) and the pattern of results  
389 followed this manipulation (d).

390

391        4. Experiment 3

392        4.1 Introduction

393        Experiment 3 disentangled the effects of monocular contrast transients and perceptual orientation  
394        transients by manipulating their presence and absence in opposite manners across conditions.

395        4.2 Methods

396        All aspects of the methods were identical to Experiment 2, except for the participants and adaptation  
397        type conditions. A new group of twenty human individuals (age:  $M = 21.4$ ,  $SD = 2.8$ ; 16 females)  
398        participated in experiment 3. The original conflict condition of Said & Heeger again served as a baseline  
399        (first panel from the left in **Figure 4a**) as well as the rivalry-plaid conflict condition from Experiment 1  
400        (second panel in **Figure 4a**). One novel condition consisted of a rivalry-plaid conflict condition in which  
401        the grating's contrast was lowered by 50% (see third panel in **Figure 4a**). This manipulation created  
402        monocular contrast transients but decreased the frequency of perceived orientation reversals. If both  
403        transient types equally strong adapt interocular suppression, both factors should cancel each other and  
404        no difference is expected between the full and 50% rivalry-plaid conflict.

405        We further disentangled the effects of perceptual orientation and monocular contrast transients by solely  
406        removing perceptual orientation transients in the last condition (see fourth panel in **Figure 4a**). This  
407        condition consisted of the presentation of a single, non-rotating tilted grating that switched between eyes  
408        over time.

409        The latter three conditions affected the degree of perceptual orientation and monocular contrast  
410        transients in opposite manners (see lines in **Figure 4b**) and each transient type predicted a different  
411        pattern of results (**Figure 4c**).

412        4.1 Results & Discussion

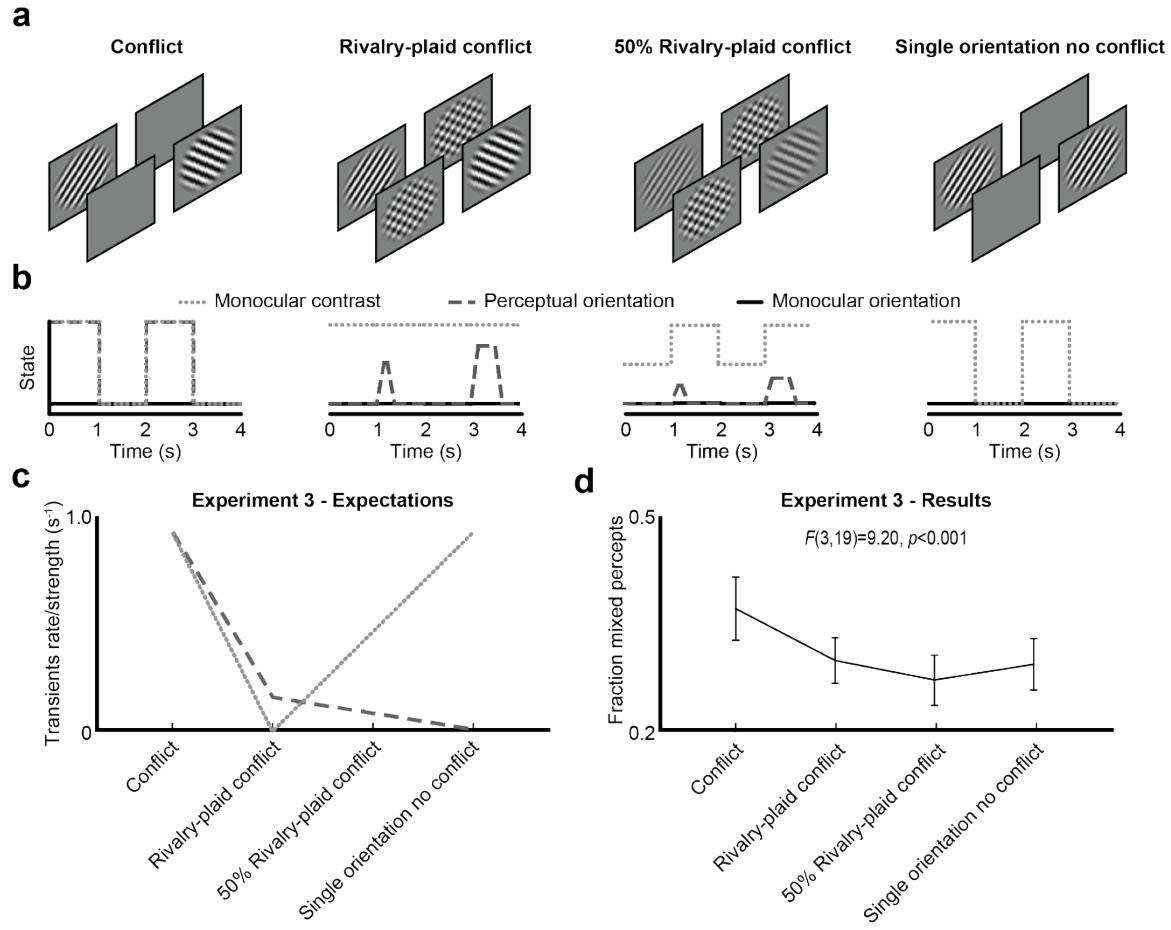
413        The fraction mixed percepts significantly differed across the four adaptation types ( $F(3,19) = 9.20$ ,  
414         $p < .001$ ), showing a U-shaped pattern across conditions (**Figure 4d**). The original conflict adaptation  
415        condition produced the highest fraction mixed percepts, the rivalry-plaid conflict and single orientation  
416        no conflict conditions scored medium fractions, and the 50% rivalry-plaid had the lowest fraction (for

417 post-hoc tests, see **Supplementary Table 3**). The pattern of results most closely matched a pattern  
418 predicted by the combination of perceptual orientation and monocular contrast transients. However, the  
419 effects of a weaker perceptual orientation transients and stronger monocular contrast transients in the  
420 50% as compared to 100% rivalry-plaid condition did not cancel each other out. In fact, the 50% contrast  
421 rivalry-plaid condition resulted in a significantly lower fraction mixed percepts than the 100% contrast  
422 rivalry-plaid condition ( $t(19)=1.787, p = .045$ ), indicating that the weakening of perceptual orientation  
423 transients had a stronger effect than the strengthening of the monocular contrast transients. In line with  
424 this finding, the full removal of perceptual orientation transients with the single orientation no conflict  
425 condition decreased the fraction mixed percepts (compared to conflict condition:  $M = .10, SD = .14$ ) to  
426 a similar degree as the removal of half the monocular contrast transients ( $M = .07, SD = .10$ ;  
427  $t(19) = 1.524, p = .144$ ).

428 Furthermore, the first and fourth condition were the only conditions that included 100% monocular  
429 contrast transients and they produced significantly higher fractions mixed percepts than the other two  
430 conditions (Difference:  $M = 0.045, SD = 0.066; t(19) = 3.045, p = .007$ ). The first condition was the  
431 only conditions that included frequent perceptual orientation transients and it produced significantly  
432 higher fractions mixed percepts than the other conditions (Difference:  $M = 0.080, SD = 0.100;$   
433  $t(19) = 3.584, p = .002$ ). The first three conditions were the only conditions which included an  
434 orientation conflict between the eyes and they did *not* produce higher fractions mixed percepts than the  
435 condition without orientation conflict (Difference:  $M = 0.020, SD = 0.048; t(19) = 1.817, p = .085$ ).

436 In sum, the results of Experiment 3 suggest that mainly adaptation to perceptual orientation transients  
437 and to some extent adaptation to monocular contrast transients cause higher fractions of mixed percepts,  
438 indicating more non-exclusive dominance and spatially incoherent rivalry. Note again that almost all  
439 conditions included orientation conflict but did not produce similar fractions of mixed percepts. This is  
440 in contrast with suggestions by Said & Heeger (33).

441



442

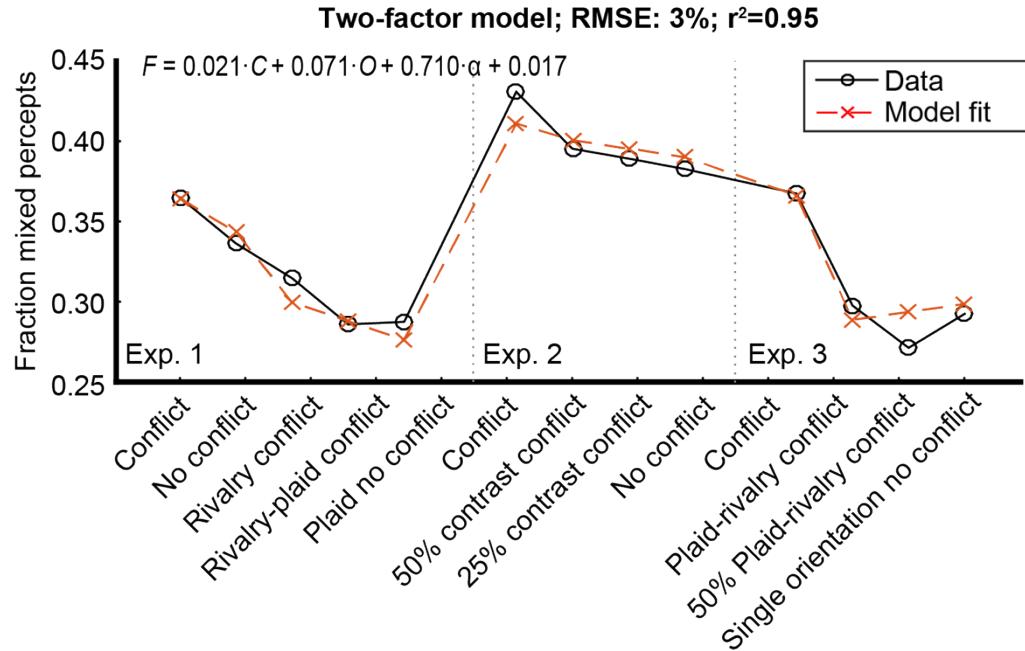
443 **Figure 4. Adaptation conditions, transient profiles, predictions, and results of Experiment 3.** Same  
444 plots as in **Figure 2 and 3** but now for Experiment 3 with two novel conditions (panel 3-4 at plots (a)  
445 and (b)). The pattern of results again reflected a combined weight of monocular contrast and perceptual  
446 orientation transients.

447

448        **5. Model – Weighted combinations of transient types**

449        The patterns of results in Experiment 1-3 indicated that the spatial instability of rivalry, measured as the  
450        fraction mixed percepts, is most likely enhanced after adaptation to a combination of monocular contrast  
451        transients and perceptual orientation transients, but not by monocular orientation transients and not by  
452        the presence of orientation conflict between the eyes. To further support this interpretation and to  
453        determine the degree of contribution of each individual transient type, we created a step-wise general  
454        linear model with the three transient types (monocular contrast, perceptual orientation, and monocular  
455        orientation) as well as conflict as predictors of the fraction mixed percepts. The model also included an  
456        experiment-dependent intercept  $\alpha$  to take into account variance created by differences in the groups of  
457        participants across experiments. The fraction mixed percept of the conflict condition, which was  
458        included in each experiment, served as the intercept  $\alpha$  (Experiment 1:  $M = .36$ ; Experiment 2:  $M = .43$ ;  
459        Experiment 1:  $M = .37$ ). The fitted model predicted the results very well, with a root mean squared error  
460        (RMSE) of 3% and an  $r^2$  of .95 (**Figure 5**). The betas (i.e., slopes) of the factors monocular orientation  
461        transients ( $\beta = 0.004, p = .824$ ) and conflict ( $\beta = 0.005, p = .657$ ) were not significant and therefore  
462        removed from the model. The final model's betas for monocular contrast ( $\beta_c = 0.021, p = .041$ ),  
463        perceptual orientation ( $\beta_o = 0.071, p < .001$ ) transients, and experiment-dependent intercept ( $\beta_g = 0.710,$   
464         $p = .001$ ) were significant. We conclude from this model that the presence of transients during the  
465        adaptation phase, whether produced by a change in grating orientation or contrast, and whether  
466        perceived or not, adapted and weakened interocular suppression, and disrupted the spatial coherence of  
467        the percept in subsequent binocular rivalry.

468



469

470 **Figure 5. General linear model results.** Modelled fraction mixed percepts (dashed red crosses) across  
471 the conditions for all experiments as compared to ground truth results (solid black circles) with the  
472 factors monocular contrast and perceptual orientation (and an intercept per experiment). The formula is  
473 the result of a general linear model with  $F$  as fraction mixed percepts,  $C$  as the presence (1) or absence  
474 (0) of monocular contrast,  $O$  as the presence or absence of perceptual orientation transients, and  $\alpha$  as the  
475 fraction mixed percepts of the conflict condition per experiment (see most left panels in plots (d) in  
476 Figure 2-4) that served as an intercept to take into account group differences across experiments.

477

478      **6. General discussion**

479      With a set of three experiments we have assessed whether the precedence of mixed percepts during BR  
480      is affected by adaptation to the frequency and strength of stimulus transients or to the degree of  
481      interocular conflict as suggested by previous research. The visual transients during adaptation consisted  
482      of changes in monocular contrast, perceptual (binocular) orientation, and monocular orientation as a  
483      function of time. The fraction mixed percepts, used as a proxy of the degree of the weakening of  
484      interocular suppression and spatial destabilization of BR, showed a pattern across a total of 9 distinct  
485      conditions that was almost perfectly explained by incidence rates of monocular contrast and perceptual  
486      orientation transients. Monocular orientation transients and the presence of a conflict between the eyes  
487      as defined in previous work (33) did not explain variance in the pattern of fraction mixed percepts to  
488      that degree. We conclude that visual transients affect the depth of interocular suppression during  
489      adaptation, resulting in weak, shallow, spatially incoherent binocular rivalry thereafter. Even though  
490      monocular contrast transients were inherent to conflict between the eyes in one critical condition (i.e., a  
491      blank in one eye and an oriented grating in the other eye), the fact that perceptual orientation transients  
492      affected the fraction mixed percepts in the absence of conflict, deems the explanation of visual transients  
493      the most parsimonious.

494      The question remains how transients relate to interocular suppression. We suggest that exogenous,  
495      involuntary attention may mediate the link between transients and the adaptation of interocular  
496      suppression. Even subtle transients (i.e., cues) to one eye automatically draw attention and can bias  
497      perceptual dominance towards that eye (3, 40-44). Similarly, subtle difference between the eyes also  
498      attract attention, as demonstrated with a change blindness (45) and visual search paradigm (46-48). As  
499      dominance of both eyes is strengthened when attention is drawn to both eyes, the mutual, reciprocal  
500      suppression between the eyes is also strengthened (49). Our suggestion therefore is the following: the  
501      (visual) transients during the adaptation phase attract attention towards the images and, as a result,  
502      increase their mutual inhibition (and thus the amount of interocular suppression). As a result, the strength  
503      of mutual inhibition is decreased after adaptation, leading to more shallow rivalry (and hence more  
504      mixed percepts) during the following adaptation phase.

505 An alternative explanation is related to working memory. Sterzer & Rees (50) identified a brain network  
506 including parietal and prefrontal areas involved in working memory to become active when dominance  
507 in binocular rivalry was temporally stabilized using intermittent blank presentations as strong transients.  
508 In line with this knowledge and an initial proposal (35), they suggested that the sudden disappearance  
509 of an image during binocular rivalry activates mnemonic processes dedicated to hold the previously seen  
510 image in memory and prioritize it for visual awareness the moment it reappears. This memory process  
511 is not restrained to only the most recent image but likely holds and biases perception based on images  
512 that are observed for at least the last sixty seconds (51). As an image is prioritized, it will also exert  
513 stronger suppression to the rivalling image. As the case in the current study, when both images are  
514 subject to transients, both will be prioritized and will mutually inhibit each other, that is strengthen  
515 interocular suppression and proliferate its adaptation.

516 It is not unlikely that the effects of working memory and attention on interocular suppression interact.  
517 The sudden aspect of transients may (involuntarily and unconsciously) both draw attention and  
518 strengthen the (mnemonic) representations of previously seen images, therewith enhancing their  
519 inhibitory influence on competing images. However, neither explanation requires adaptation of a  
520 specialized conflict detection mechanism. In the model put forth in Said & Heeger, this mechanism is  
521 based on the idea of ocular opponency neurons (34, 52, 53). Although such neurons appear likely  
522 candidates for involvement in binocular rivalry, and the initial prediction of the model by Said & Heeger  
523 that included a conflict detection mechanism explained their data well, the results reported here cannot  
524 be unified under that model. As such, we currently see no evidence that mechanisms based on ocular  
525 opponency neurons should be included in models of binocular rivalry.

526 It is important to note that in our study the intermittent presentation of blanks had a stronger effect on  
527 adaptation than the intermittent presentation of plaids. A similar effect has been reported before (54),  
528 showing that the presentation of interleaved blanks enhanced the temporal stabilization of rivalry more  
529 than plaids. As blanks are more distinct from the orthogonal images and therefore more conspicuous, it  
530 makes sense that intermittent presentation of blanks adapted interocular suppression stronger than  
531 plaids. This conclusion may appear at odds with our observation that the monocular contrast transients

532 (i.e., blanks) disrupted the spatial coherence of rivalry slightly weaker than perceptual orientation  
533 transients. Note however that the monocular contrast transients were not visible but the perceptual  
534 orientation transients *were* visible to the observer. As the visibility of transients is positively linked to  
535 the degree of drawing attention exogenously (55) and the suppressive strength of an evoked traveling  
536 dominance wave (26), it is not unexpected that the perceptually visible orientation transients adapted  
537 interocular suppression most. Our observation that a relatively high rate of orientation transients (e.g.,  
538 see rivalry condition) increased the fraction mixed percepts more than a relatively low rate (e.g., see  
539 plaid-rivalry condition) further confirms the modulatory effect of transient visibility on the adaptation  
540 of interocular suppression. Although out of the scope of the current study, it would be interesting to  
541 investigate whether perceptual (and thus visible) contrast transients adapt interocular suppression to a  
542 similar degree as the perceptual orientation transients that we investigated here. A useful paradigm to  
543 test this would be intermittent presentation in which conflicting gratings disappear and appear as a  
544 function of time (35, 56),  
545 To conclude, perceptual stability as expressed in the precedence of mixed percepts and traveling waves  
546 during rivalry is weakened when the eyes are stimulated beforehand with many, strong transients. Future  
547 work may shed light on the effect of visible and invisible transients on maintaining and adapting to  
548 visual representations.

549 **7. Acknowledgments**

550 Not applicable

551        8. References

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667

668

669 9. Supplementary materials

670 **Supplementary Table 1.** Post-hoc, paired, two-tailed t-test comparisons of fraction mixed percepts  
671 between conditions for Experiment 1.

	No conflict ( $M = 0.34$ ; $SD = 0.18$ )	Rivalry conflict ( $M = 0.31$ ; $SD = 0.16$ )	Rivalry-plaid ( $M = 0.29$ ; $SD = 0.15$ )	Plaid no conflict ( $M = 0.29$ ; $SD = 0.17$ )
Conflict	$t = 1.870$ , ( $M = 0.36$ ; $SD = 0.18$ )	$t = 3.291$ , $p = .003$	$t = 4.350$ , $p < .001$	$t = 4.443$ , $p < .001$
No conflict		$t = 1.924$ , $p = .066$	$t = 4.013$ , $p < .001$	$t = 4.088$ , $p < .001$
Rivalry conflict			$t = 2.231$ , $p = .035$	$t = 1.908$ , $p = .068$
Rivalry-plaid				$t = -0.140$ , $p = .890$

672

673 **Supplementary Table 2.** Post-hoc, paired, one-tailed t-test comparisons of fraction mixed percepts  
674 between conditions for Experiment 2.

	50% Contrast ( $M = 0.39$ ; $SD = 0.16$ )	25% Contrast ( $M = 0.39$ ; $SD = 0.17$ )	No conflict ( $M = 0.38$ ; $SD = 0.15$ )
Conflict	$t = 2.065$ , ( $M = 0.43$ ; $SD = 0.17$ )	$t = 1.874$ , $p = .038$	$t = 2.695$ , $p = .007$
50% Contrast		$t = 0.433$ , $p = .335$	$t = 0.821$ , $p = .211$
25% Contrast			$t = 0.315$ , $p = .378$

675

676 **Supplementary Table 3.** Post-hoc, paired, one-tailed t-test comparisons of fraction mixed percepts  
677 between conditions for Experiment 3.

	100% Rivalry plaid conflict ( $M = 0.30$ ; $SD = 0.14$ )	50% Rivalry plaid conflict ( $M = 0.27$ ; $SD = 0.15$ )	Single orientation no conflict ( $M = 0.29$ ; $SD = 0.15$ )
Conflict	$t = 2.700$ , ( $M = 0.37$ ; $SD = 0.19$ )	$t = 4.079$ , $p < .001$	$t = 3.446$ , $p = .001$
100% Rivalry- plaid conflict		$t = 1.787$ , $p = .045$	$t = 0.400$ , $p = .347$
50% Rivalry- plaid conflict			$t = -1.524$ , $p = .072$

678

## Two-factor model; RMSE: 3%; $r^2=0.95$

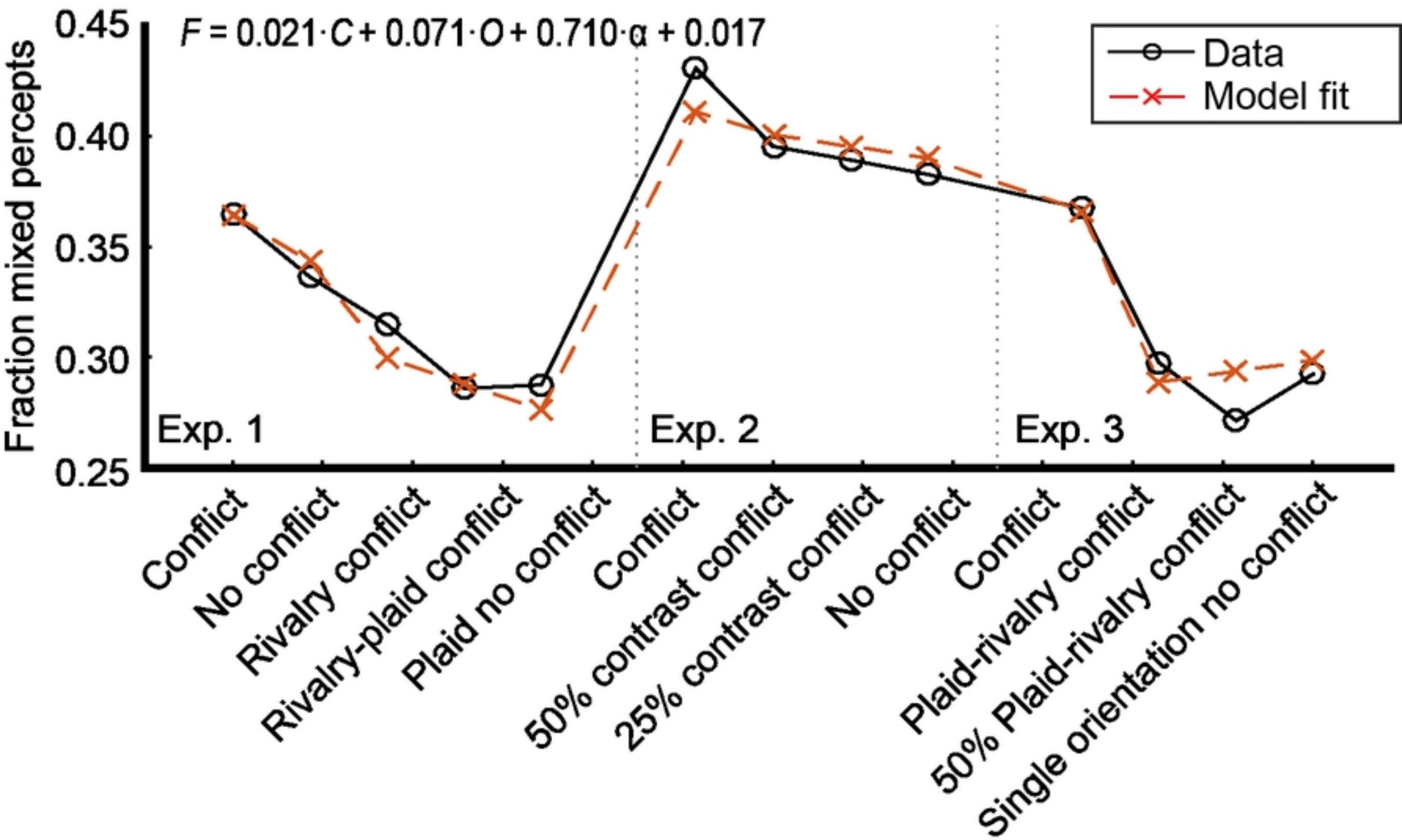
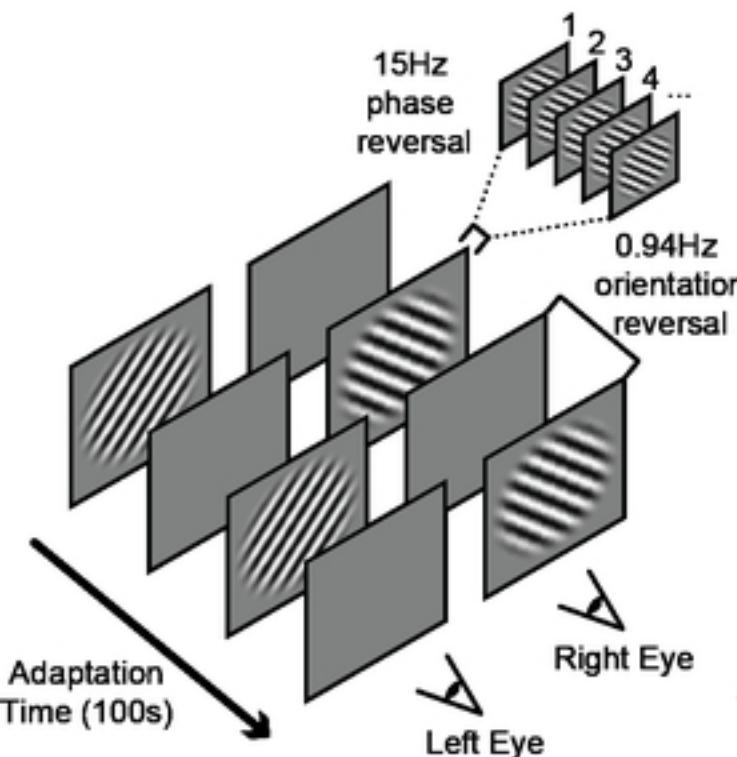
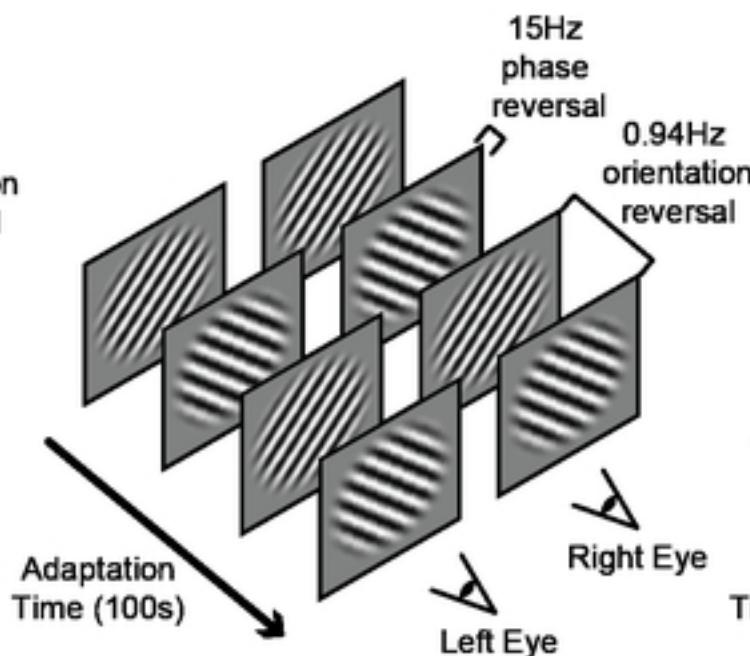
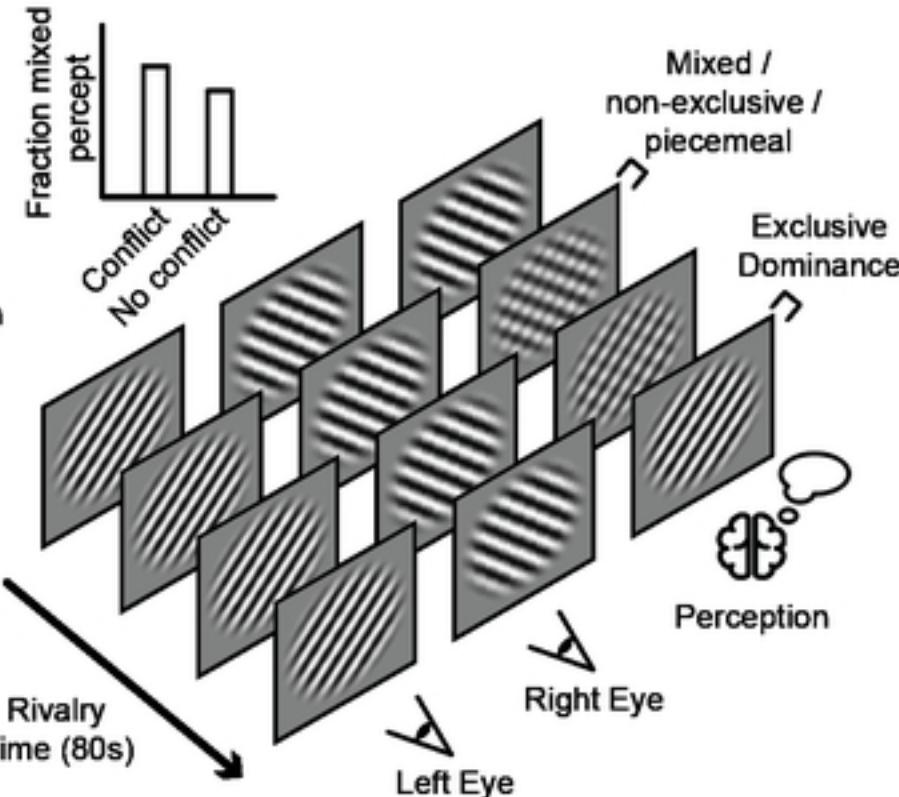


Figure 5

**a****Adaptation - conflict****b****Adaptation - no conflict****c****After adaptation - rivalry****Figure 1**

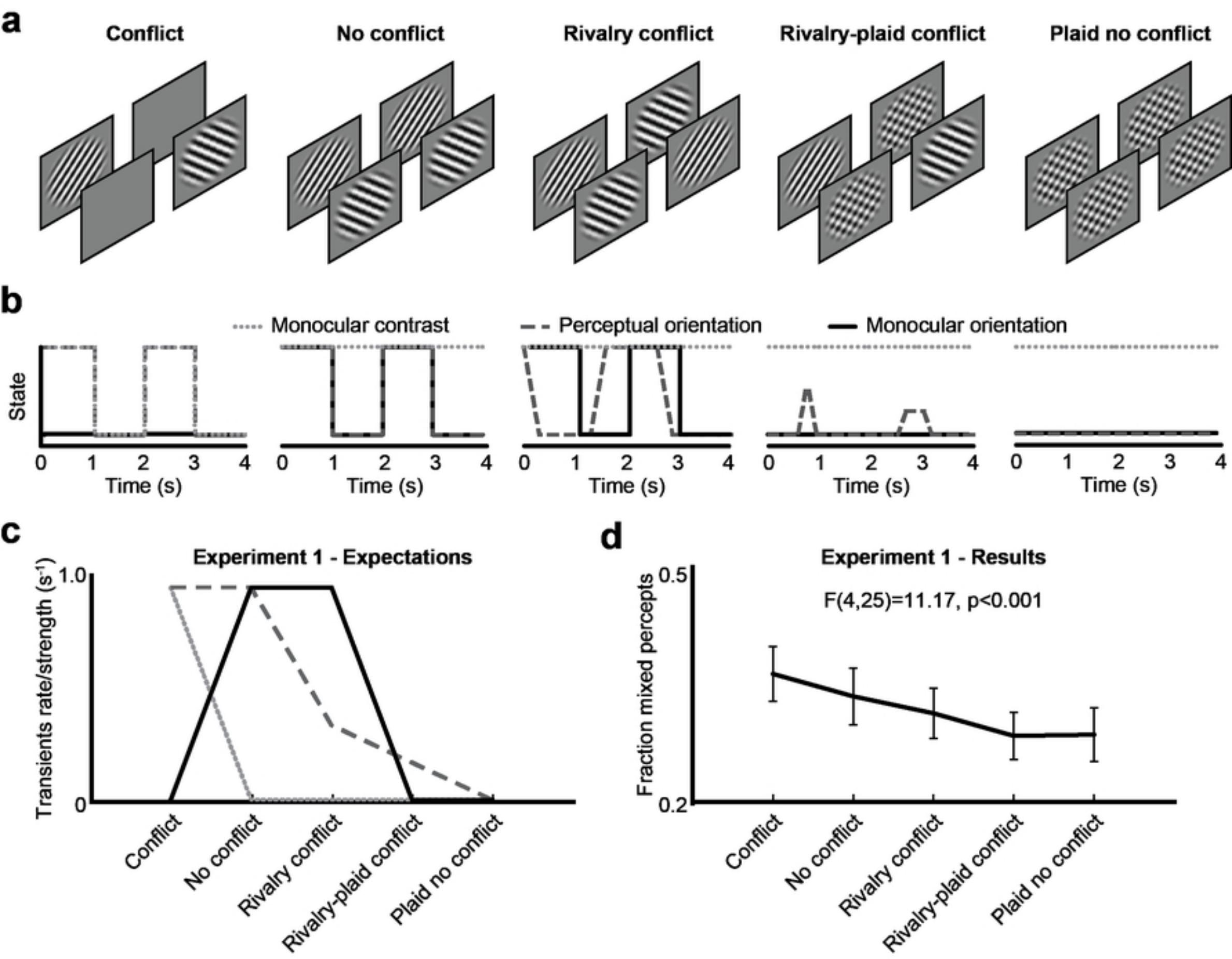


Figure 2

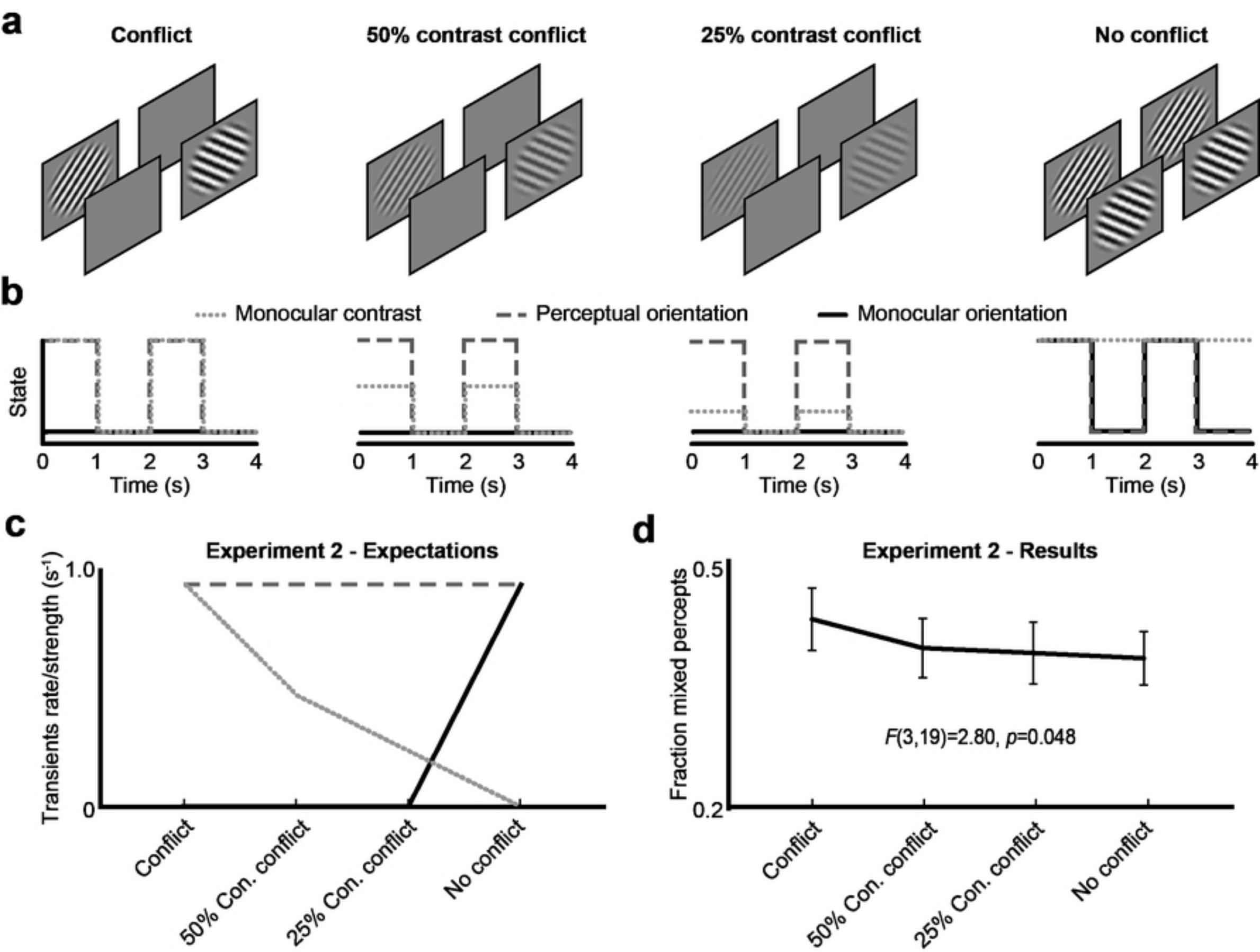
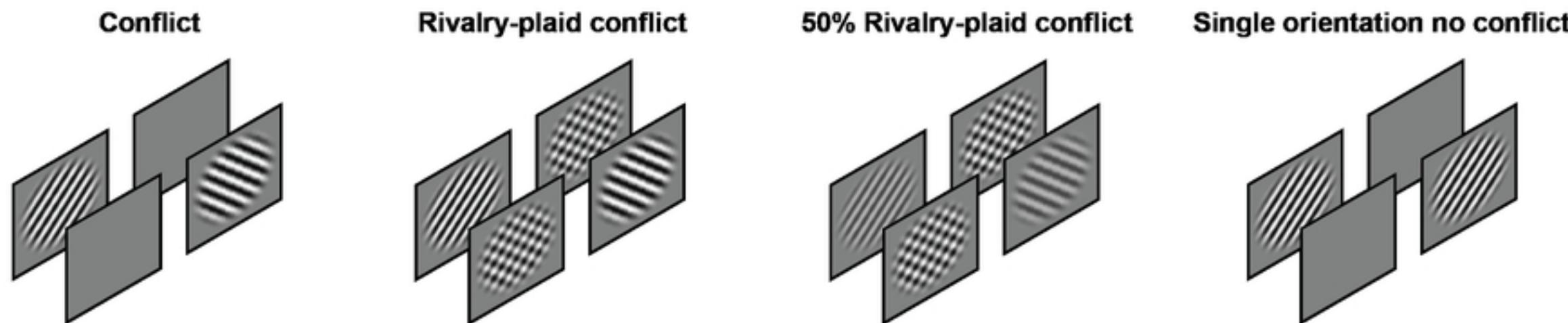
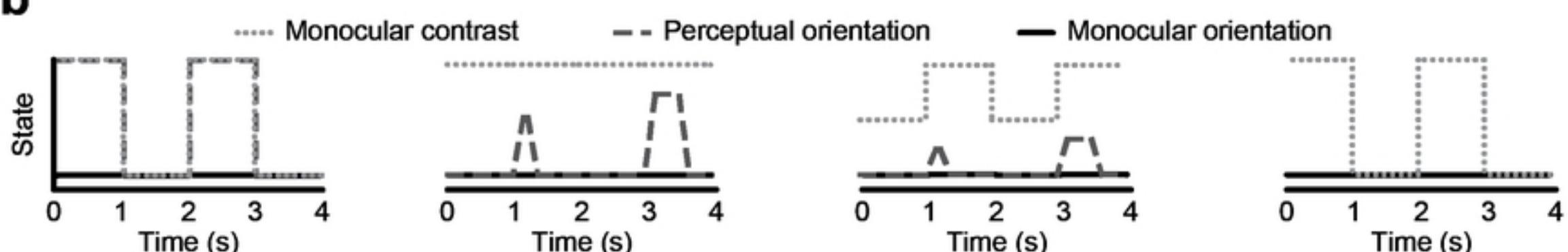
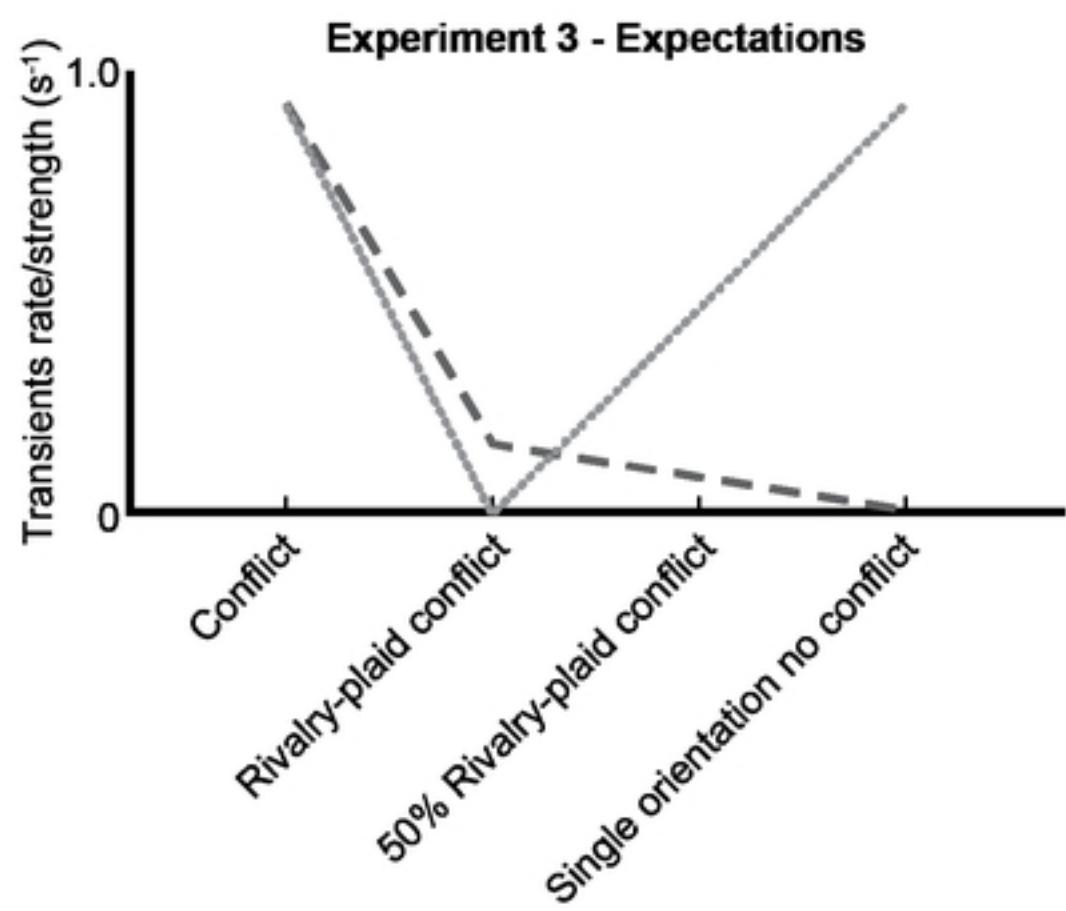
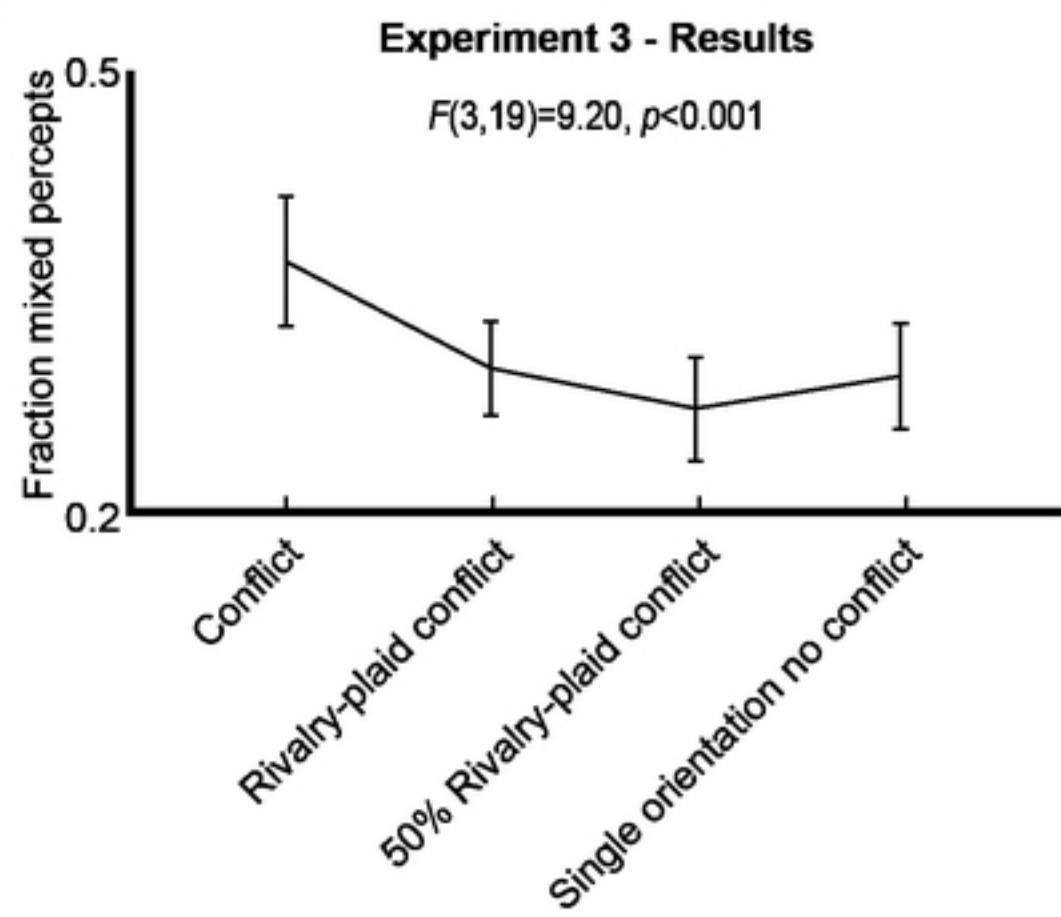


Figure 3

**a****b****c****d****Figure 4**