

1 SEPARABLE PUPILLARY SIGNATURES OF PERCEPTION AND ACTION DURING
2 PERCEPTUAL MULTISTABILITY

3
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13
14 **Abstract**

15
16 The pupil provides a rich, non-invasive measure of the neural bases of perception and cognition,
17 and has been of particular value in uncovering the role of arousal-linked neuromodulation, which
18 alters cortical processing as well as pupil size. But pupil size is subject to a multitude of
19 influences, which complicates unique interpretation. We measured pupils of observers
20 experiencing perceptual multistability -- an ever-changing subjective percept in the face of
21 unchanging but inconclusive sensory input. In separate conditions the endogenously generated
22 perceptual changes were either task-relevant or not, allowing a separation between perception-
23 related and task-related pupil signals. Perceptual changes were marked by a complex pupil
24 response that could be decomposed into two components: a dilation tied to task execution and
25 plausibly indicative of an arousal-linked noradrenaline surge, and an overlapping constriction
26 tied to the perceptual transient and plausibly a marker of altered visual cortical representation.
27 Constriction, but not dilation, amplitude systematically depended on the time interval between
28 perceptual changes, possibly providing an overt index of neural adaptation. These results show
29 that the pupil provides a simultaneous reading on interacting but dissociable neural processes
30 during perceptual multistability, and suggest that arousal-linked neuromodulation shapes action
31 but not perception in these circumstances.

32
33 **Introduction**

34
35 The brainstem's neuromodulatory systems can profoundly influence cognitive functions by
36 altering neural response properties within the cortical circuits that mediate those functions
37 (Aston-Jones & Cohen 2005; Sara & Bouret 2012; Lee & Dan 2012; Pfeffer et al. 2018). Recent
38 work has used multistable visual stimuli to examine neuromodulatory influences on visual
39 processing. Such stimuli cause perception to alternate between different interpretations of the
40 sensory data, and recent work suggests that the noradrenergic arousal system associated with the
41 brainstem's locus coeruleus impacts perception in this situation, perhaps by altering the response
42 gain of visual cortical neurons involved (Einhäuser et al 2008; Sara & Bouret 2012; Leang et al.
43 2012; Kloosterman et al. 2014; Pfeffer et al. 2018). We used a new combination of experimental
44 methods to evaluate this idea.

46 Like previous researchers we focused on pupil size changes that accompany switches between
47 alternative percepts, because pupil dilations can non-invasively convey noradrenaline release
48 (Murphy et al. 2014; Joshi et al. 2016; De Gee et al. 2017). Existing results reveal a transient
49 pupil dilation accompanying perceptual switches, suggestive of a noradrenaline surge (Einhäuser
50 et al 2008; Hupé et al. 2009; Kloosterman et al. 2015; De Hollander et al. 2018). The
51 characteristics of this dilation, including its relation to the temporal dynamics of the perceptual
52 sequence, have formed the basis for theorizing on the role of the locus coeruleus and associated
53 structures in perceptual multistability, and on the role of arousal in perception more broadly
54 (Einhäuser et al 2008; Hupé et al. 2009; Sara & Bouret 2012; Leang et al. 2012; Kloosterman et
55 al. 2015; De Hollander et al. 2018). But what complicates interpretation of the published results
56 is that perceptual switches always involved multiple neural events spaced closely in time -- some
57 related to perception and some not -- which makes it difficult to tie pupillary measures back to
58 any specific event (see Hupé et al. 2009 for a similar assessment). In particular, perceptual
59 switches in existing work were always task relevant -- observers overtly reported them or, in
60 some cases, covertly tracked them -- so that each switch included both the perceptual change and
61 further task-related processing. Of note, noradrenaline-related pupil dilations have been linked to
62 numerous cognitive factors that may be at play in such a situation: motor planning, attentional
63 reorienting, altered cognitive load, and surprise, among others (Kahneman & Beatty 1966;
64 Aston-Jones & Cohen 2005; Hupé et al. 2009; Leang et al. 2012; De Gee et al. 2014; Wang &
65 Munoz 2015). As such, it is unclear how published switch-related pupil signals map onto specific
66 perceptual and cognitive processing steps, and it is unclear whether any part of those signals is
67 tied to mechanisms that shape perception, rather than to processes that underlie task execution
68 generally.

69
70 In light of the above we evaluated switch-related pupil signals in a set of conditions that included
71 conditions where switches were irrelevant to the observer. We used binocular rivalry, a form of
72 multistability in which perception alternates between two interpretations that each correspond to
73 a stimulus shown to only one of the two eyes (Blake & Logothetis 2002). To isolate and quantify
74 distinct components that might be reflected in pupil size in association with perceptual switches,
75 we employed four conditions in a two-by-two factorial design (Figure 1A). The first factor was
76 the nature of the perceptual changes: they could either be endogenously generated in response to
77 binocularly incompatible input (*Rivalry* conditions; 'LE' and 'RE' are left and right eye,
78 respectively), or be exogenously prompted via on-screen 'replay' animations designed to
79 resemble the binocular rivalry experience (*On-screen* conditions). The second factor was task-
80 relevance: observers were asked either to manually report perceptual changes when they
81 happened (*Report* conditions) or to instead perform a task to which the perceptual changes were
82 irrelevant (*Ignore* conditions; the task was a peri-threshold detection task involving small
83 transients in both eyes' displays simultaneously -- events whose timing was uncorrelated with
84 that of the perceptual switches). The idea here was that comparisons between the *Rivalry* and
85 *On-screen* conditions would help tease apart signals linked to the mechanism of endogenous
86 perceptual switches and signals linked to perceptual changes generally (an idea copied from
87 numerous functional imaging studies; e.g. Lumer et al. 1998), whereas comparisons between the
88 *Ignore* and *Report* conditions would help distinguish signals related to perceptual changes from
89 signals related to factors such as reorienting, surprise, and report.

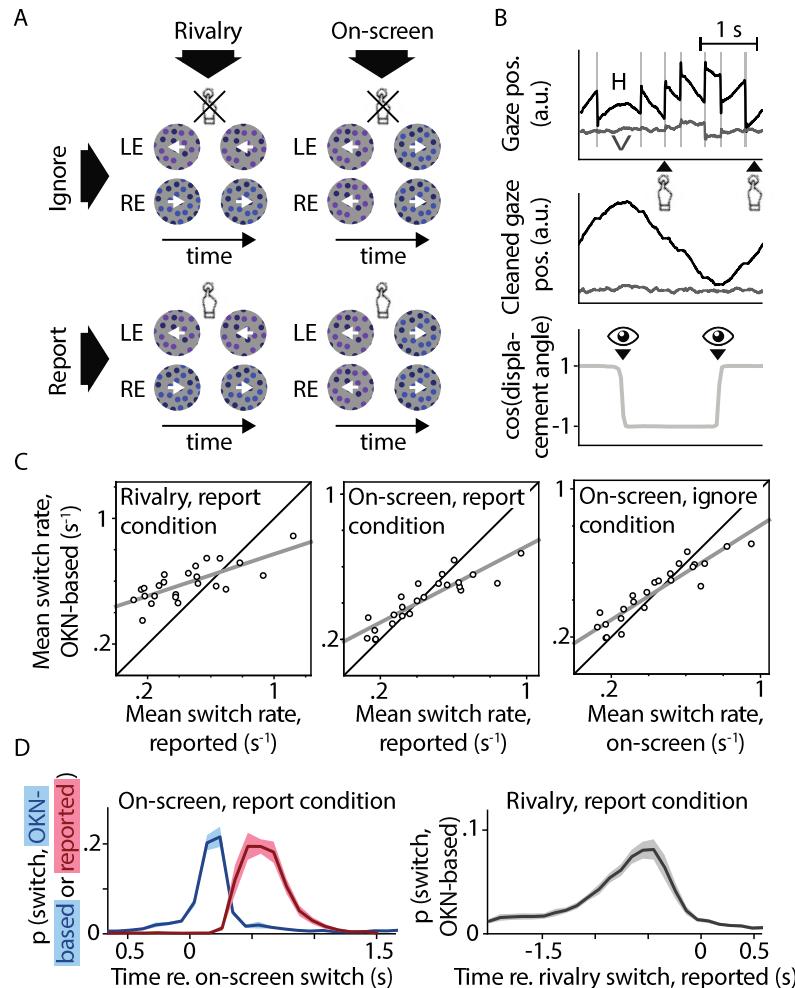
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91 To preview our main results, we found both rivalry switches and on-screen switches to be
92 accompanied by a similar pupil response, but we found this response to be markedly different
93 between the *Report* and *Ignore* conditions. The *Ignore* response consisted of a constriction tied
94 to the perceptual change itself (even though no net change in light flux was involved), whereas
95 the *Report* response was composed of this perception-related constriction component as well as
96 an overlapping dilation component linked to the behavioral report. Whereas the report-related
97 dilation is plausibly associated with noradrenaline release, the perception-related constriction is
98 not. We further found that these two response components differ in their relationship to the
99 timing of the perceptual sequence, and that it is the perception-related constriction, rather than
100 the report-related dilation, that shows a robust dependence on this timing. These results indicate
101 that pupil signals during perceptual multistability include two overlapping but separable
102 components: both a dilation that is plausibly related to arousal-linked noradrenaline release at a
103 physiological level and to task execution at a behavioral level, and a constriction that reflects
104 visual cortical processes unrelated to transient noradrenaline yet that is closely tied to perception.
105

106 **Results**

107

108 24 observers were included in our analyses. We relied on involuntary eye movements to identify
109 perceptual switch events, even in the absence of manual report. To this end the visual stimulus
110 area was filled with dots that could translate either leftward or rightward. In the *Rivalry*
111 conditions the two eyes' dots moved in opposite directions; in the *On-screen* conditions motion
112 direction physically alternated in the visual display (Figure 1A). Previous work has shown the
113 direction of reflexive pursuit eye movements (optokinetic nystagmus, or OKN) to form a reliable
114 indicator of perceived motion direction in similar situations, not just for binocularly congruent
115 motion but also during binocular rivalry (Fox et al. 1975; Leopold et al. 2001; Naber et al. 2011;
116 Frässle et al. 2014; Aleshin et al. 2019). We verified that this was also the case here (Figure 1B-
117 D). Per-observer estimates of perceptual switch rate were highly correlated (although not
118 identical; see figure caption and Methods) between our OKN-based measure and measures based
119 on either manual report or, in the *On-screen* conditions, replayed direction reversals (Figure 1C).
120 Moreover, there was a tight temporal correspondence between the moments of perceptual
121 switching as identified by the three different methods (Figure 1D), providing further confidence
122 in our OKN method's suitability. Opposite dot motions were also associated with different dot
123 colors (but not different dot luminances) to promote perceptual exclusivity during binocular
124 rivalry (i.e. to counteract perceptual mixtures of both eyes' displays; Knapen et al. 2007).
125

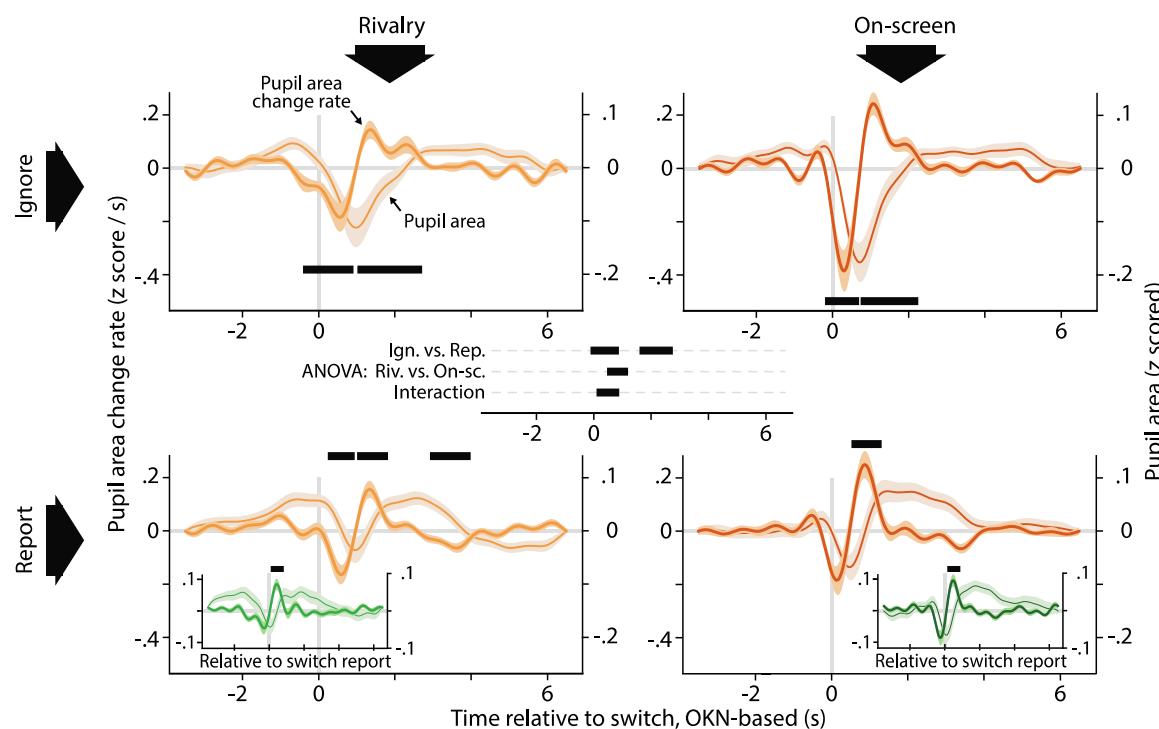


126 **Figure 1. Experimental design and behavioral validation.** A: Our 2-by-2 factorial design included both binocular
127 rivalry and on-screen replay, and both conditions where switches in perception were behaviorally relevant and ones
128 in which they were not. B: Perceptual switch moments in all conditions were identified based on reflexive eye
129 movements (OKN) in response to the moving stimulus. C: The per-observer numbers of switches identified using
130 this method correlated strongly with the numbers of switches estimated based on manual report or on-screen switch
131 events. Pearson's r values from left to right: 0.75, 0.89 and 0.92; all $p < 0.0001$. D. There was a tight correspondence
132 between the timing of perceptual switches as estimated using these three methods.

133 We used a general linear model approach to deconvolve pupil responses associated with
134 perceptual switches in each condition. To facilitate between-condition comparison we primarily
135 centered our analyses on switch events as identified using our OKN measure -- the only measure
136 available in all four conditions -- with some additional analyses using the other measures where
137 appropriate. While, in general, changes in gaze direction can be associated with changes in pupil
138 size, both real and apparent when using video-based eye trackers (Gagl et al. 2011; Wang &
139 Munoz 2015; Knapen et al. 2016; Laeng & Alnaes 2019), control analyses rule out the
140 possibility that our observations are importantly related to the association between perceptual
141 switches and changes in OKN direction in our experiment, or to eye blinks (Appendix 1-figure
142 1). Figure 2 shows pupil area (thin curves; light confidence intervals) and the rate of pupil area
143 change over time (thick curves; dark confidence intervals) during the time period surrounding

145 perceptual switch moments, averaged across observers. Statistics were performed on the latter
146 variable; a choice that follows previous work (de Gee et al. 2020) and that is consistent with the
147 notion that pupillary change (rather than size) is a more immediate marker of transient neural
148 events, which alter the input to the antagonistic iris musculature rather than altering pupil size in
149 a step-wise fashion (Reimer et al. 2016). The time axis at the center of the figure, between the
150 plots, denotes periods during which the rate of pupil change significantly differed between
151 conditions (based on an ANOVA), and black bars within each plot indicate periods of significant
152 change over time within a condition (based on one-sample t-tests). Throughout the paper all
153 effects that are marked as significant have a cluster-based $p < 0.01$ (see Methods for details).
154

155 The ANOVA results (Figure 2; center) indicate a difference in pupil response between the *Ignore*
156 conditions and the *Report* conditions during the seconds immediately following the switch event.
157 For both of the *Ignore* conditions (Figure 2; top row of plots) perceptual switches are marked by
158 a rapid drop in pupil size, followed by a rapid recovery back to near baseline. For both *Report*
159 conditions (bottom row of plots), on the other hand, the pupil response is more complex, and
160 shows both an initial constriction/re-dilation sequence and a final, more gradual constriction
161 back to near baseline. This added complexity is consistent with the fact that the *Report*
162 conditions include an additional event, the key press report, on top of the perceptual change that
163 these conditions share with the *Ignore* conditions.
164



165 **Figure 2. Pupil responses time locked to the perceptual switch. Each plot shows, for a different condition, the rate at**
166 **which pupil size changes (left y-axis; dark confidence interval; thick curve), as well as pupil size itself (right y-axis;**
167 **light confidence interval; thin curve) around the moment of the perceptual switch. Black bars within each plot show**
168 **time periods during which the rate of change differs from zero (cluster-level $p < 0.01$). The main plots (orange**
169 **curves) are based on OKN as the basis for identifying switch moments; the two insets (green curves) are based on**
170 **key presses for identifying those moments. At the center of the figure, between the plots, is a time axis that shows**
171 **the results of a repeated-measures ANOVA comparing the four conditions (Ign. = *Ignore*; Rep. = *Report*; Riv. =**
172 **Rivalry; On-sc. = *On-screen*), with black bars indicating significant differences in rate of change (cluster-level**

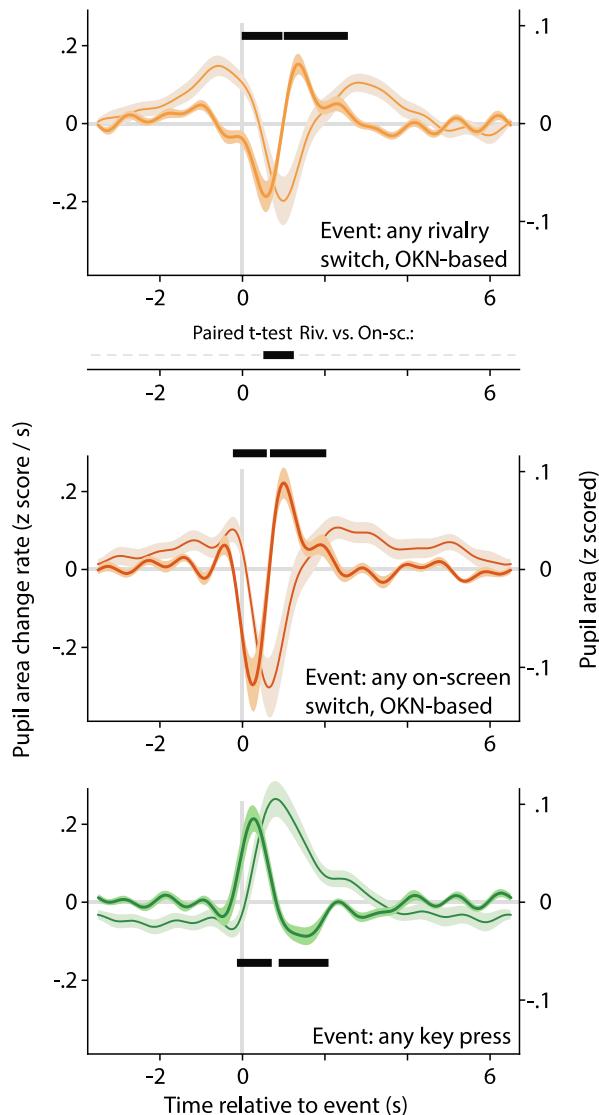
173 $p < 0.01$). All confidence intervals, both in this plot and elsewhere in the paper, show standard errors of the sample
174 mean.

175
176 The ANOVA results also indicate a, less extensive, difference in pupil response between the
177 *Rivalry* conditions and the *On-screen* conditions immediately following the switch, as well as an
178 interaction in an overlapping time period. A comparison between the curves of Figure 2 (left vs.
179 right column of plots) shows no clear qualitative difference between these two groups of
180 conditions but, instead, suggests that on-screen switches and rivalry switches are both associated
181 with a response of the same general shape, but that the *On-screen* response is more rapid and
182 pronounced.

183
184 The finding that all conditions show a similar rapid constriction and re-dilation suggests that this
185 component of the pupil response is tied to the occurrence of a (spontaneous or replayed)
186 perceptual switch: the common factor across all conditions. This suggestion is strengthened by
187 the close temporal correspondence between the onset of constriction and the moment at which
188 perception switches (the temporal reference used in Figure 2, i.e. the OKN-based estimate of the
189 switch moment, typically falls within half a second of the perceptual change; see Figure 1D).
190 The fact that only the *Report* conditions show the re-dilation going past baseline and being
191 followed by a final constriction, suggests an additional, and later, dilation associated with
192 manually reporting the perceptual switch. The delayed moment of this dilation relative to the
193 initial constriction is consistent with the fact that manual report typically follows both the
194 perceptual event and its OKN-based concomitant by up to about a second (Figure 1D). To further
195 test this interpretation of the data we re-analyzed the *Report* conditions, now using the key press
196 events as the temporal reference (bottom row of Figure 2, insets). Now the constriction falls
197 almost entirely before the reference event and is more gradual (and no longer significant),
198 whereas the start of re-dilation is temporally aligned with the reference event. This pattern of
199 results supports our interpretation, as it is consistent with a switch-linked temporary constriction
200 that precedes the key press by an amount of time that varies due to spread in response time,
201 followed by a response-linked temporary dilation. This also indicates that our OKN-centered
202 approach has two separate properties that render it particularly suitable for identifying pupil
203 signals associated with the perceptual switch itself, rather than with task execution: not only can
204 overlapping task-related pupil signals be minimized in a no-report design, the timing of the
205 relevant perceptual events can also be pinpointed more precisely than in approaches that center
206 on manual report.

207
208 To more closely examine the shapes of the individual pupil response components that appear to
209 contribute to the overall patterns shown in Figure 2, we next analyzed the data in a way designed
210 to tease apart the putative switch-related pupil constriction and report-related pupil dilation. For
211 this analysis we concatenated, for each observer, all pupil data across all four conditions into a
212 single time course, and deconvolved three pupil responses: one associated with *Rivalry* switches
213 irrespective of whether they were reported or not (i.e. including switches across both the *Report*
214 condition and the *Ignore* condition in the same regressor), one associated with *On-screen*
215 switches irrespective of whether they were reported or not, and one associated with key presses
216 irrespective of whether they reported a perceptual switch or something else. In particular, during
217 the *Ignore* conditions key presses were not in response to perceptual switches, but to subtle
218 visual changes in the peri-threshold detection task that observers performed in those conditions
219 (see Materials and Methods). For this analysis key presses of that latter type were included in the

220 same regressor as key presses in the *Report* conditions. In other words, this analysis treated the
221 pupil time course as the combined sum of both switch-related and key-related response
222 components, and their temporal independence in the *Ignore* conditions allowed those
223 components to be resolved separately in spite of their temporal association in the *Report*
224 conditions.

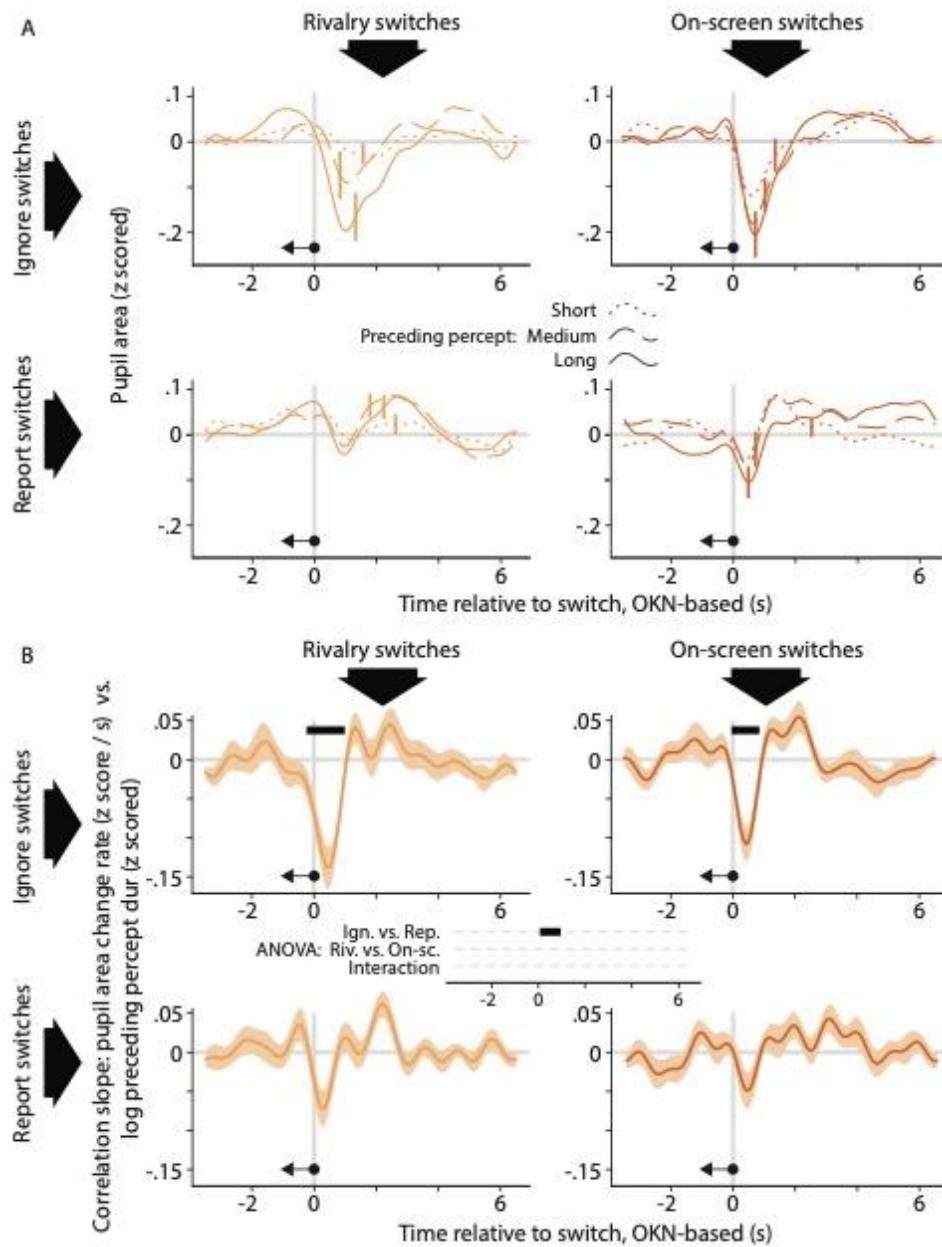


225
226 Figure 3. Alternative analysis of the data underlying Figure 2, now concatenating pupil signals across conditions,
227 and regressing key press events and (rivalry or on-screen) switch events separately. This allows the pupil response
228 associated with switches to be teased apart from the pupil response associated with key presses, even in the data
229 from the *Report* conditions where the two consistently overlap. All plotting conventions are as in Figure 2, but the
230 time axis between the top and center plot now shows the results of a paired t-test.

231
232 The results of this analysis are shown in Figure 3, using the same format as Figure 2. Both
233 rivalry switches (top plot) and on-screen switches (center plot) are marked by a rapid constriction
234 and re-dilation immediately following the switch. The response to on-screen switches is, again,
235 more rapid and pronounced, leading to a significant difference between the responses during a
236 brief time window immediately following the switch (time axis between the top and center plot).

237 Key presses, on the other hand, are accompanied by a qualitatively different (and also
238 significantly different; not shown) pupil response, characterized by a rapid dilation and then re-
239 constriction back to near baseline (bottom plot). These results are consistent with the
240 interpretation, articulated above, that the biphasic pupil responses (constriction, then dilation,
241 and then return to baseline) observed in our *Report* conditions (Figure 2, bottom row) reflect a
242 superimposition of these two separate components.
243

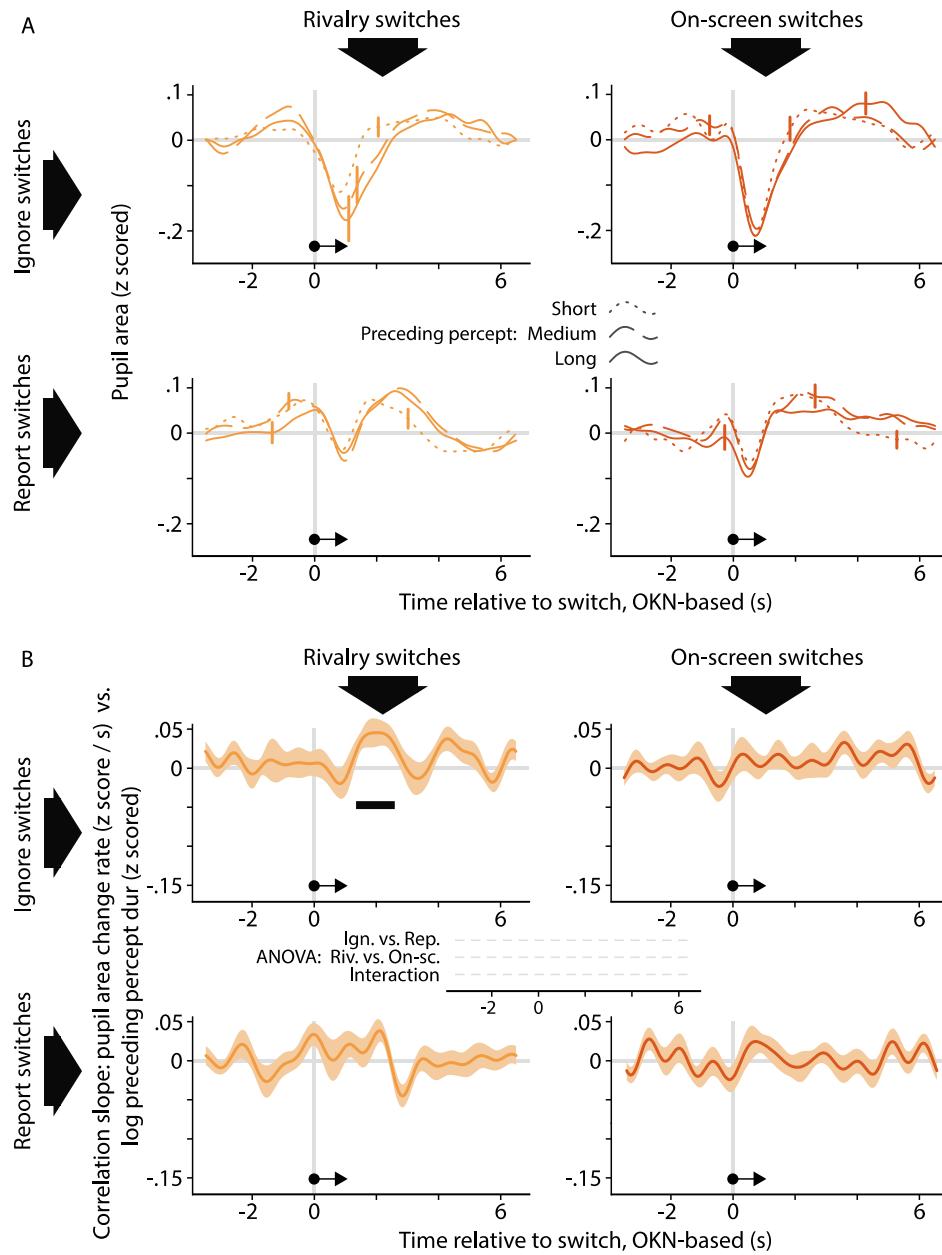
244 Previous authors have observed a biphasic pupil response for reported switches that is
245 qualitatively similar to the one we found (Einhäuser et al. 2008; Naber et al. 2011; De Hollander
246 et al. 2018; see also Einhäuser 2016). Still, published interpretations and analyses have tended to
247 focus on switch-related *dilation* (probably because the dilation is generally more pronounced,
248 with some studies reporting no constriction at all; Hupé et al. 2009; Kloosterman et al. 2015).
249 This tendency is intertwined with the literature's emphasis, discussed above, on interpretations in
250 terms of noradrenaline release from brainstem arousal systems, which would lead to dilation. A
251 further factor tied into noradrenaline-centered interpretations is an observed relation between
252 switch-related pupil responses and the temporal dynamics of the perceptual time course.
253 Specifically, using only conditions where perceptual switches were manually reported or
254 otherwise task-relevant (see Discussion), previous work has shown the net amplitude of pupil
255 dilation following a given perceptual switch to vary with the duration of the immediately
256 preceding perceptual dominance episode (Kloosterman et al. 2015; De Hollander et al. 2018), as
257 well as with the duration of the immediately following one (Einhäuser et al. 2008; De Hollander
258 et al. 2018, although see Hupé et al. 2008). The former finding fits well with the fact that
259 noradrenaline release in response to a given event depends on the degree of predictability of the
260 event, given that an earlier end to a dominance episode is less predictable than a later one
261 (Kloosterman et al. 2015; De Hollander et al. 2018; see Discussion). The latter finding, in turn, is
262 consistent with the fact that noradrenaline leads to increased neural gain and altered circuit
263 dynamics in the cortex (Aston-Jones & Cohen 2005; Gilzenrat et al. 2010; Sara & Bouret 2012),
264 which could influence the emergence of further perceptual switches (Einhäuser et al 2008; Sara
265 & Bouret 2012; Leang et al. 2012; Kloosterman et al. 2014; Pfeffer et al. 2018). In other words,
266 existing work has primarily treated switch-related pupil signals as noradrenaline-related
267 dilations, and has aimed to fit observed relationships with perceptual dynamics into this
268 framework. However, existing work has not attempted to separate individual components of the
269 switch-related pupil signal. Our above results suggest that the net dilation observed in that work
270 may well correspond to a superimposition of both a dilation and a constriction which are shifted
271 in time by the participant's reaction time for each report. Based on the available data, therefore,
272 it is unclear whether the observed association with the temporal dynamics of the perceptual cycle
273 stems from the dilation component, which would support an account in terms of noradrenaline
274 release, or whether it stems from the constriction component, which would not be consistent with
275 any existing account and would call for interpretation. Our next analyses were designed to
276 address this question.
277



278 Figure 4. The relation between the pupil response associated with a perceptual switch and the duration of the
 279 perceptual dominance duration that preceded that switch. A. Each plot shows, for a different condition, pupil size
 280 surrounding the moment of a perceptual switch, separated out into three equal-sized groups of perceptual switches
 281 on the basis of the preceding dominance duration (dotted curves: short; dashed curves: medium; solid curves: long).
 282 B. Each plot shows, for a different condition, how the rate of pupil size change correlates, per time point in the
 283 interval that surrounds perceptual switches, with the duration of the preceding dominance duration. We performed
 284 inferential statistics only on the data of panel B; not A. All plotting conventions are as in Figures 3 and 4.

285 Figures 4 and 5 focus on pupil responses separately per condition. For both A panels we grouped
 286 switch events into three separate regressors, corresponding to three quantiles of the immediately
 287 preceding (Figure 4A; symbolized by the left-pointing arrow in each plot) or subsequent (Figure
 288 5B; symbolized by the right-pointing arrow in each plot) dominance duration, from brief to long.
 289 In the former case (Figure 4A) this analysis suggests a more pronounced switch-related pupil
 290

291 constriction for switches that terminate a longer dominance episode, especially in the *Ignore*
292 conditions (top row). To quantify and statistically evaluate this impression, Figure 4B shows
293 how the rate of pupil size change varies with preceding dominance duration. Here we did not
294 separate switch events into quantiles but instead included as a covariate the (normalized)
295 durations of the perceptual dominance episodes immediately preceding the switch events. In
296 other words, we investigated whether, at any time point within our deconvolution window, per-
297 switch variability in the preceding dominance duration was correlated with per-switch variability
298 in pupil area change rate. Qualitatively all four plots show a dip shortly after the switch,
299 consistent with a stronger constriction following longer dominance episodes, but this dip is
300 significantly deeper in the *Ignore* conditions (time axis at the center between the four plots), and
301 only reaches significance in those conditions, for both *Rivalry* and *On-screen* switches.
302
303



304 **Figure 5.** The relation between the pupil response associated with a perceptual switch and the duration of the
 305 perceptual dominance duration that follows that switch. The organization of this figure is identical to that of Figure
 306 4.

307 The analyses underlying Figure 5 are the same as those underlying Figure 4, but center on the
 308 perceptual dominance episode that follows, rather than precedes, a perceptual switch. Here panel
 309 A shows only modest differences in pupil area between the three groups of perceptual switch
 310 events, now separated into quantiles of the subsequent perceptual dominance duration rather than
 311 the preceding one. Panel B is consistent with this observation. It provides some evidence that
 312 subsequent dominance duration is positively correlated with pupil area change rate around two
 313 seconds following the perceptual switch in the *Rivalry Ignore* condition, but statistical support
 314 for this is not quite compelling. Specifically, the effect is significant when assessed within that
 315 condition (top left plot), but the size of the effect does not differ between conditions (time axis at
 316 0s).

317 the center between the four plots; no effects reach our chosen alpha level of $p<0.01$, and the time
318 period in which the significant within-condition effect is observed is associated with a *Rivalry vs.*
319 *On-screen* difference with $p=0.30$ and a still weaker interaction). This lack of any between-
320 condition differences precludes strong conclusions, both because in general terms the relevance
321 of significant within-condition effects is predicated on the presence of between-condition
322 differences, and because in this specific case no meaningful effect can exist in the *On-screen*
323 conditions (because brain processes cannot influence the timing of on-screen events). Because
324 previous authors (Einhäuser et al. 2008; De Hollander et al. 2018) who reported correlations with
325 subsequent dominance duration during rivalry used somewhat different methods, we had a closer
326 look at our data using methods more similar to theirs. First, the existing work involved statistics
327 on pupil size rather than on its temporal derivative, so we repeated the ANOVA of Figure 5B
328 using the correlation with pupil area as the dependent variable, but we again found no between-
329 condition differences (the smallest cluster-level p -value, $p=0.40$, occurred around 2 seconds
330 before the switch in the *Active vs. Passive* comparison). Second, because existing work used key
331 presses as the marker of perceptual switch timing, we repeated the t-test of the *Rivalry Report*
332 condition with key presses, rather than OKN, as the index of perceptual switches (for the *Rivalry*
333 *Ignore* condition key presses are not available). The correlation between pupil size change rate
334 and subsequent duration showed no significant differences from 0, although the smallest p -value
335 ($p=0.16$) did occur for a cluster of positive correlations around 2 seconds after the reported
336 switch; a data pattern reminiscent of that shown for the *Rivalry Ignore* condition in Figure 5B. In
337 sum, although our data do not strongly argue against a relation between the pupil response and
338 subsequent dominance duration, they provide no convincing evidence in favor, either.
339

340 To summarize, our analyses provide evidence that switch-related pupil constriction, which
341 occurs in isolation in the *Ignore* conditions, depends on the duration of the preceding perceptual
342 dominance episode. Evidence that report-related dilation depends on preceding dominance
343 duration, or that either pupil response component is associated with subsequent dominance
344 duration, is not compelling in our data. A control analysis (Appendix 1-figure 2) indicates that
345 the observed relation with preceding dominance duration (Figure 4) does not reflect an artefact
346 arising from incomplete separation of overlapping pupil responses to temporally adjacent
347 perceptual switches, but that what evidence we do observe for a relation with subsequent
348 dominance duration (Figure 5) might reflect such an artefact.
349

350 Discussion

351
352 We used a combination of both no-report conditions and report conditions, involving both
353 binocular rivalry and on-screen animations, to identify and decompose the pupil response into
354 two separable components, each associated with different aspects of perceptual switches. The
355 first is a rapid pupil constriction and re-dilation time-locked to the perceptual switch, irrespective
356 of whether this switch occurs during binocular rivalry or during an on-screen animation. The
357 second is a rapid pupil dilation and re-constriction time-locked to the manual response to the
358 perceptual switch, again irrespective of the nature of the switch. We found a robust dependence
359 of the pupil response on the amount of time elapsed since the perceptual switch that immediately
360 preceded the present one, such that switch-related pupil constrictions are larger following longer
361 dominance periods, both during rivalry and during on-screen replay. We also found some
362 tentative evidence that the pupil response around two seconds following the perceptual switch is

363 related to the duration of the immediately following perceptual dominance period, but this
364 evidence does not warrant strong conclusions.

365

366 *Decomposing the pupil response to perceptual switches*

367

368 As mentioned above, the most robust finding in existing work on this topic has been of a
369 transient pupil dilation (Einhäuser et al 2008; Hupé et al. 2009; Kloosterman et al. 2015).
370 Consistent with this, when switch-related pupil responses are discussed in a broader context this
371 is invariably in relation to dilation-linked noradrenergic modulation of cortical function (Sara &
372 Bouret 2012; Laeng et al. 2012; Nassar et al. 2012). In existing pupillometry studies on
373 multistable perception the switches were always task-relevant, so we tentatively identify the
374 transient dilation in existing work with the task-related dilation in our present study. Based on
375 results from two such previous studies, we surmise that this dilation is, in part, related to the
376 motor act of reporting itself, but is also related more generally to the task-relevance of the switch
377 events. Both those previous studies included a condition where overt switch reports were
378 omitted, yet where observers did need to attend to (Hupé et al. 2009) or covertly count
379 (Kloosterman et al. 2015) the switches. In both cases, the resulting switch-related dilations were
380 substantially smaller than with overt report, yet not abolished, consistent with some role of task
381 relevance per se. In agreement with previous authors, then, we interpret our task-related dilation
382 response as an example of the pupil dilation that is generally observed in association with
383 elevated cognitive engagement, and that has been linked to increased activity of
384 neuromodulatory centers including the noradrenergic locus coeruleus (De Gee et al. 2017; Laeng
385 & Alnaes 2019; Joshi & Gold 2020).

386

387 Our *Rivalry Ignore* condition is, to our knowledge, the first to measure pupil responses to task-
388 irrelevant perceptual switches, and to show that these are associated with a pupil constriction,
389 just like switches in our *On-screen Ignore* condition, i.e. task-irrelevant on-screen switches. We
390 interpret these constrictions in the context of work showing that the pupil may constrict in
391 response to isoluminant changes in visual input, such as changes in color, spatial frequency, or
392 motion content (Barbur et al. 1992; Young et al. 1995; Conway et al. 2008; Barbur 2014). This
393 kind of constriction is similar in size, but opposite in sign, to the engagement-related dilation
394 mentioned above (about 0.1 to 1 mm in diameter; Slooter & van Norren 1980; Barbur et al.
395 1992; Young et al. 1993; Conway et al. 2008), matching our finding of similar magnitudes for
396 both our positive and our negative rapid response component. Several lines of evidence suggest a
397 cortical contribution to constrictions in response to isoluminant input transients: these
398 constrictions are virtually abolished by cortical lesions (Barbur et al. 1992; Heywood et al.
399 1998), and they are modulated by attention withdrawal and interocular suppression (Kimura et
400 al. 2014; Kaneko et al. 2019), as well as by stimulus properties that lack a specific representation
401 outside of cortex (e.g. the orientation of a viewed face; Conway et al. 2008). Indeed, the most
402 developed hypothesis as to what causes such constrictions is that the perturbation of visual
403 cortical responses that results from the visual input change, is accompanied by a temporary
404 weakening of the inhibition that cortex tonically exerts on the midbrain Edinger-Westphal
405 nucleus (Barbur et al. 1992; McDougal & Gamlan 2008; Barbur 2014). Since this nucleus drives
406 the iris sphincter muscle, reducing its inhibition would lead to a smaller pupil. Based on the
407 above, we propose that the perturbation of visual cortical activity that accompanies rivalry
408 switches (Logothetis & Schall 1989; Leopold & Logothetis 1996; Tong et al. 1998; Polonsky et

409 al. 2000), similarly, weakens cortical inhibition of the Edinger-Westphal nucleus, explaining the
410 pupil constriction we report in our rivalry conditions. This would mean that the switch-related
411 constriction identified here constitutes a new non-invasive index on the visual cortical
412 concomitants of switches in multistable perception.

413
414 Although no existing study has shown switch-related pupil constrictions in isolation, previously-
415 reported pupil response shapes do suggest a constriction as one constituent part. As mentioned
416 above, several authors have reported task-relevant switches during perceptual multistability to be
417 linked to a biphasic pupil response composed of an initial dip followed by a peak (Einhäuser et
418 al. 2008; Naber et al. 2011; De Hollander et al. 2018). This temporal order is consistent with the
419 interpretation that those authors have measured a combination of both our rapid constriction
420 (which occurs first, time-locked to the switch) and our rapid dilation (which occurs later, time-
421 locked to the report). Interestingly, reports of such a biphasic response pattern have not been
422 restricted to studies of binocular rivalry (Naber et al. 2011; De Hollander et al. 2018) but extend
423 to work on other forms of perceptual multistability (Einhäuser et al. 2008), suggesting that the
424 constriction arises more generally when perception changes. On the other hand, the most
425 prominent aspect of most published pupil response shapes is the dilation component, suggesting
426 that the constriction component elicited by our particular stimulus is larger than usual.

427
428 *Correlations with perceptual dynamics*
429

430 Existing work has resulted in a somewhat mixed picture of the way in which the durations of
431 flanking perceptual dominance durations are reflected in the switch-related pupil response.
432 Einhäuser et al. (2008), in two experiments that used multistable perception paradigms other than
433 binocular rivalry, reported that a more pronounced pupil dilation, centered around 500 ms before
434 the perceptual switch report in one condition, and around 500 ms after in the other, predicted a
435 longer subsequent dominance duration, but Hupé et al. (2008) questioned that result. De
436 Hollander et al. (2018) showed results broadly consistent with Einhäuser et al. (2008), reporting
437 that a larger pupil during binocular rivalry predicted a longer subsequent dominance duration.
438 However, this correlation was observed in a slightly different time window again: centered about
439 a second before the report. The most common interpretation of correlations with subsequent
440 dominance duration has been that a switch-related increase of cortical noradrenaline, tied to pupil
441 dilation, would stabilize the newly established perceptual interpretation, thereby delaying the
442 next perceptual switch (Einhäuser et al., 2008; Sara & Bouret 2012; see Kloosterman et al. 2014
443 for a conceptually related interpretation of different data). De Hollander et al. (2018) also
444 observed a correlation with preceding dominance duration: a smaller pupil shortly after the
445 report was linked to a longer preceding dominance period. Those authors interpreted that latter
446 result in terms of the hazard rate of the perceptual switch occurring, rather than in terms of the
447 time interval between switches as such. Specifically, given the roughly gamma-shaped
448 distribution of perceptual dominance durations during perceptual multistability (Levelt 1968;
449 Borsellino et al. 1972), the instantaneous probability of a perceptual switch monotonically
450 increases as a function of time since the previous switch. Accordingly, De Hollander et al. (2018)
451 argued that the relation with preceding dominance duration reflected the degree of surprise
452 associated with the current perceptual switch: low surprise (following long dominance periods)
453 was linked with a smaller pupil as compared to high surprise (following short dominance
454 periods). This interpretation is consistent with a more general body of work on surprise-linked

455 pupil dilations mediated by noradrenaline (e.g. Preuschoff et al. 2011), and also with the results
456 of a pupillometry study that specifically manipulated the hazard rate of on-screen switches
457 during replayed perceptual multistability (Kloosterman et al. 2015).

458
459 How do our findings on relations with flanking dominance durations compare to the existing
460 literature? Qualitatively speaking there are similarities with the existing work: similar to De
461 Hollander et al. (2018) we found a smaller pupil (in our case: a stronger pupil constriction)
462 shortly after switches that terminated longer dominance periods (Figure 4) and that would,
463 therefore, be less surprising as formalized by the hazard rate. And consistent with both Einhäuser
464 et al. (2008) and De Hollander et al. (2018) we found some anecdotal evidence that a larger pupil
465 predicts a longer subsequent dominance period (Figure 5). But there are also aspects of our data
466 that conflict with existing findings and, especially, interpretations. Our data indicate that the
467 main influence of preceding dominance duration is on the switch-related pupil constriction that
468 occurs irrespective of task relevance. This casts some doubt on interpretations centered on
469 surprise and associated noradrenaline release, notions typically related to task-relevant events
470 and to pupil dilations. A more natural interpretation of this aspect of our results is that switch-
471 related pupil constrictions may be subject to a type of adaptation, either of the underlying cortical
472 response or of a component that is closer to the iris musculature. Although we are not aware of
473 any reports of adaptation affecting similar pupil constrictions in the literature, it would explain
474 why our present pupil constrictions are less pronounced during the time period shortly after a
475 previous constriction, as the neural process that mediates constrictions would be less responsive
476 during that period.

477
478 A related remark applies to the limited evidence, in our data, that the pupil response may predict
479 the upcoming perceptual dominance duration. To the extent that this effect is real (but see
480 discussion surrounding Figure 5 and Appendix 1-figure 2), it occurs in our *Rivalry Ignore*
481 condition, in which switches were task-irrelevant and in which we did not observe any pupil
482 dilation. This is not consistent with the idea that the magnitude of, specifically, *dilation* predicts
483 upcoming percept duration, nor with the prevailing interpretation in terms of noradrenaline
484 release.

485
486 Only in the *Ignore* conditions did we observe significant correlations with preceding percept
487 duration. The data patterns observed in the *Report* conditions, where switch-related constrictions
488 and task-related dilations overlap, did qualitatively match those of the *Ignore* conditions, but
489 showed no significant correlations. One contributing factor here can be that the *Ignore* conditions
490 had more statistical power: the correlated occurrence of both switches (linked to constriction)
491 and key press reports (linked to dilation) in the *Report* conditions means that a larger amount of
492 data is required to obtain a reliable estimate of either individual response component, as
493 compared to the *Ignore* conditions in which the switches occur in isolation. An alternative
494 explanation, that both switch-related constriction and response-related dilation depend on
495 preceding percept duration yet in directions that work against each other in the combined
496 response, is not supported by a control analysis (Appendix 1-figure 3). If the explanation is,
497 indeed, to be found in statistical power, then that further underscores the value of our no-report
498 approach to studying the pupillometric correlates of switches in multistable perception.

499

500 On the balance, our present data further strengthen the notion (Kloosterman et al. 2015; De
501 Hollander et al. 2018) that the perceptual dynamics that precede a perceptual switch have an
502 impact on its pupillary signature, and add to it the finding that this impact is primarily on the
503 switch-related pupil constriction, rather than on the task-related dilation. Related, our findings
504 suggest that explanations in terms of surprise and associated noradrenaline release can, at best,
505 account for part of this impact, and we propose adaptation of the constriction mechanism as a
506 possible additional explanation. With regard to subsequent percept duration, our findings are
507 inconclusive regarding the idea (Einhäuser et al., 2008; De Hollander et al. 2018) that those can
508 be predicted from the pupil response, but they form no natural fit with the notion that this would
509 have do with switch-related noradrenaline release.

510

511 Conclusion

512

513 The application of pupillometry methods in the context of multistable perception holds promise
514 as an approach to studying perception and its neuromodulatory dependencies, both because the
515 pupil non-invasively informs about transient noradrenergic activity accompanying perceptual
516 switches, and because such activity may be reflected, on a slower timescale, in the spontaneous
517 dynamics of the perceptual cycle. We demonstrate that the inclusion of *Ignore* conditions, in
518 which switches are stripped of their cognitive significance, allows for a more incisive
519 characterization and interpretation of switch-related pupil responses. Taking this approach we
520 provide evidence that this response -- hitherto treated as a unitary signal -- is composed of two
521 overlapping but separable components, each associated with a different perceptual or cognitive
522 process. While one is a task-related dilation component that is plausibly associated with
523 noradrenergic activity stemming from brainstem arousal systems, the other is a constriction
524 component that is probably unrelated to noradrenaline, yet that has likely contributed to pupil
525 signals reported in the literature and that arguably provides a novel and easily accessible index of
526 the visual cortical response change that marks perceptual switches. As such, this work offers
527 insight into the neural processes involved in perceptual switching, as well as providing a new
528 methodological and conceptual reference point for future pupillometry work on this topic to fully
529 deliver on its promise.

530

531 Methods

532

533 *Observers*

534

535 Observers were recruited from the Michigan State University undergraduate and graduate
536 student population (age range 18-30 years). All were naive to the purposes of the investigation.
537 The study protocol was approved by the Michigan State University institutional review board,
538 and observers received financial compensation for their participation. During their first visit to
539 the lab observers received informed consent and were familiarized with the stimulus during a
540 colloquial interaction. On that occasion the experimenter verified that the observer experienced
541 perceptual alternations and that the eye tracker got a stable read of the observer's pupils. Based
542 on these criteria 26 observers were enrolled in the experiment proper. After initial data analysis
543 two observers were excluded from further analysis because they reported an excessive amount of
544 perceptual mixtures (Appendix 1-figure 4), which we deemed undesirable given our interest in

545 switches between exclusive percepts. This left 24 observers whose data are reported in the main
546 text.

547

548 *Stimulus and task*

549

550 The stimulus consisted of dots (radius 0.17 dva, density 2.7 dots/dva²) randomly placed within a
551 round aperture (radius 3.9 dva) and moving either leftward or rightward at 4.1 dva/s on a gray
552 background (34.5 cd/m²). Half of the dots of a given color were lighter than the background
553 (62.8 cd/m²) and half were darker (19.0 cd/m²). One of the colors, cyan, was created by setting
554 the screens' blue and green channels to the same luminance and turning off the red channel. The
555 other color, magenta, was created by setting the red and blue channels to the same luminance
556 while turning off the green channel.

557

558 The stimulus was surrounded by a fusion aid that consisted of a coarse random pixel array (pixel
559 side 0.72 dva) with an equal number of dark (69.1 cd/m²) and light pixels (129 cd/m²), overlaid
560 by a small black frame (side 15.5 dva; 2.9 cd/m²) and a larger white frame (side 18.6 dva; 336
561 cd/m²). The pixel array itself filled a square area (side 23.2 dva) except for a circular area (radius
562 7.7 dva) at its center. Observers viewed the stimuli on two separate computer monitors (one for
563 each eye) via a mirror stereoscope designed to be compatible with video-based eye trackers
564 (Qian & Brascamp 2017; Aleshin et al. 2019).

565

566 Each observer completed two blocks for each condition, so eight blocks in total. The blocks were
567 spread out across multiple visits to the lab, typically between two and four. The observer's eyes
568 were tracked binocularly at 1000 Hz using an Eyelink 1000 Plus video-based eye tracker (SR
569 Research, Ottawa, Canada). During each block the observer first performed a procedure in which
570 he or she visually aligned two frames shown in alternation, each on a different monitor. The
571 corresponding screen coordinates were stored to present the two eyes' stimuli at corresponding
572 visual locations during the experiment. After an eye tracker calibration the participant then
573 completed 12 trials of 60 seconds each, all for the same condition. Dot color and dot direction
574 were yoked. On half of the rivalry trials, randomly assigned, dots of a given direction and color
575 were shown to one eye; on the remaining trials they were shown to the other eye. Between trials
576 the observer was allowed to pause as needed, and he or she performed a drift correction
577 procedure before starting the next trial. If the tracker did not get a stable reading during this
578 procedure, or if gaze direction had drifted more than 6 dva since calibrating, a new calibration
579 procedure was completed before starting the next trial. The tolerance of this drift correction
580 procedure was very large (6 dva) for an experiment aimed at measuring absolute gaze direction,
581 but this approach proved to be efficient in this case, where pupil size and gaze displacement were
582 important but absolute gaze direction was not.

583

584 During the *Report* conditions observers used three keyboard keys to indicate each trial's initial
585 percept as well as any moments at which perception changed. Two of the buttons corresponded
586 to exclusive leftward or rightward motion, respectively, and the third button corresponded to
587 mixture percepts. During *Ignore* conditions observers pressed one keyboard button each time
588 they identified a so-called 'dot size probe'. These were occasions where all dots, across both eyes,
589 simultaneously shrank over the course of 250 ms and then immediately grew back to their
590 original size during another 250 ms. At the start of each block this size change was set to 20%

591 (i.e. a shrinkage down to 80% of the normal size), but it was altered during the experiment using
592 a staircase procedure: for each missed probe the size change was multiplied by 1.1, and for each
593 correct detection it was divided by 1.1. Across observers the average staircase convergence point
594 was 12.1%. The interval between consecutive probes was drawn randomly from a uniform
595 distribution between 3 s and 8 s.

596

597 During the *On-screen* conditions the same display was shown on both eyes' screens, with either
598 only cyan dots going in one direction, magenta dots going in the other direction, or a mixture of
599 the two. During these mixture periods the circular stimulus aperture was split midway into a top
600 and a bottom half, and the two halves each showed dots of a different color, and going in a
601 different direction. This is not a realistic rendering of perceptual mixtures during rivalry, which
602 do not typically involve a clean split between the two eyes' dominance regions. In previous work
603 we have attempted more realistic on-screen mimics (Knapen et al., 2011; Brascamp et al. 2018)
604 but we are not aware of ones that convincingly simulate rivalry's perceptual experience, and we
605 see no reason why such a more realistic mimic might have importantly altered our present
606 results.

607

608 During each block of the *On-screen* conditions we replayed perception as reported during the
609 observer's most recent block of the *Rivalry Report* condition, i.e. using the percept timing
610 reported there while assuming a fixed reaction time of 500 ms. This approach meant that a
611 *Rivalry Report* block had to precede any *On-screen* block for a given observer. To still minimize
612 any role of time or experience, for each observer the first four blocks included exactly one block
613 of each condition, in random order while heeding the constraint specified above, and the last four
614 blocks again included all four conditions but in reverse order.

615

616 *Sample size*

617

618 Sample size was not based on an explicit power analysis. The amount of data per observer-
619 condition was adjusted upward toward its final value on the basis of pilot experiments that
620 showed a lack of robust switch-related pupil responses within observers at smaller values yet
621 stable pupil responses for many observers at the final value. For our number of observers (24
622 whose data were included) we chose a value that was above the high end of the observer
623 numbers reported across relevant published studies, given that we wished to replicate and extend
624 upon the pupil responses reported in those studies (6 observers per experiment in Einhäuser et al
625 2008; 10 and 14 observers per experiment in Hupé et al. 2009; 22 and 19 observers per
626 experiment in Kloosterman et al. 2015; 9 observers in De Hollander et al. 2018). The number of
627 perceptual switches underlying our switch-related pupil curves averaged about 430 per condition
628 per observer (about 10,000 switches per condition in total across observers).

629

630 *Data analysis*

631

632 Percept dynamics inferred from key presses

633

634 In extracting percept sequences from key presses we ignored all key presses that repeated the
635 previous one. For the purposes of on-screen replay all transition periods were registered at their
636 manually reported duration, including so-called 'return transitions' in which perception changed

637 from one exclusive percept to a mixture and then back to the same exclusive percept again
638 (Mueller & Blake 1989). When it comes to OKN-defined switches, on the other hand, because of
639 the difficulty in accurately delineating perceptual mixture periods based on pursuit eye
640 movements (although see Aleshin et al. 2019; Qian & Brascamp 2019 for progress in that
641 direction) those were considered instantaneous and, by definition, between two different percepts
642 (see next section). Therefore, in those instances where key-defined switch timing was compared
643 to OKN-defined switch timing (either directly in Figures 1C-D, or indirectly in the insets of
644 Figure 2) we placed an instantaneous switch moment midway each key-defined mixture period
645 that separated two different percepts, and we ignored return transitions. For Figure 1D on-screen
646 switches were also treated in this way.
647

648 Percept dynamics inferred from eye movements

649

650 We inferred percept dynamics from eye movements using an approach similar to previous
651 authors (Naber et al. 2011; Frässle et al. 2014; Aleshin et al. 2019). The first analysis steps were
652 aimed at obtaining a clean gaze position signal. We first split the gaze samples into contiguous
653 sequences of 5 samples or more, thus removing all periods without signal as well as sample
654 sequences that are too short for applying our subsequent saccade detection algorithm. This
655 algorithm, from Engbert & Mergenthaler (2006), was applied to each contiguous sample
656 sequence to identify saccades on the basis of gaze displacement velocity. Here minimum saccade
657 duration was set to 6 ms (6 samples), and the velocity threshold was set to 6 standard deviations
658 (using median-based standard deviation as described in the original study). Saccades were
659 initially identified independently for each eye, after which temporally overlapping saccades from
660 the two eyes were marked as binocular, and were assigned whichever of the two eyes' saccade
661 start times was earlier, and whichever end time was later. To identify eye blinks we relied on the
662 Eyelink preprocessing software, which marks all periods of signal loss as blinks, separately for
663 each eye. Blink events were then combined across eyes in the same way as just described for
664 saccades. After saccades and blinks had been identified in this fashion we averaged gaze position
665 across the two eyes and we replaced all samples that were closer than 20 ms to a saccade or
666 closer than 50 ms to a blink. In particular, gaze positions for sample sequences that were
667 separated by such samples were collated such that any gaze displacement during those samples
668 was set to zero. These processing steps led to data like those depicted in the center plot of Figure
669 1B.
670

671

672 After the gaze position signal had been cleaned in this fashion the next processing steps were
673 aimed at identifying perceptual switch moments. For this purpose we slid a window of 750 ms
674 width over the cleaned gaze position signal in steps of 38 ms. At each step we assigned to the
675 time point at the center of the window a value that quantified the direction of gaze displacement
676 within the window. In particular, we first fit a linear curve to the vertical gaze position vs. time
677 data within the window, and another linear curve to the horizontal gaze position vs. time data.
678 The arctangent of the two slopes quantified the gaze displacement angle on the screen within that
679 time window. Because we were interested in pursuit eye movements in response to horizontally
680 moving stimuli we then computed the cosine of this angle, which ranges from -1 for due left gaze
681 displacement to +1 for due right gaze displacement. During periods without a signal (due to
682 actual eye closure or due to eye lock interruptions of a different nature) gaze displacement had
been artificially set to zero (see above). Because those periods were sometimes of non-negligible

683 duration our estimates of gaze displacement direction were sometimes unreliable near periods
684 marked as blinks. For this reason all time points that fell in a time window between 250 ms
685 before the start of a blink and 400 ms after the end of that blink were assigned the average gaze
686 displacement value computed across the 100 ms immediately before, and the 100 ms
687 immediately after that time window. These processing steps together led to data like those
688 depicted in the bottom plot of Figure 1B. On the basis of these data all time points where the
689 cosine of the gaze displacement angle was larger than 0.85 were assigned to one percept, and all
690 time points where that value was smaller than -0.85 were assigned to the other. As the final
691 analysis step perceptual switch moments were marked as all moments that lay midway two
692 adjacent time periods that had been assigned to opposite percepts.
693

694 Figures 1C and D show good correspondence between switches identified using this OKN-based
695 algorithm and both manual switch reports and on-screen switch events. Nonetheless, our
696 algorithm appears to overestimate the number of switches for slow switchers and underestimate
697 it for fast switches (Figure 1C). This pattern of results is consistent with the idea that our OKN-
698 based algorithm has a non-zero, and fixed, false alarm rate (i.e. a certain number of spurious
699 switch events is marked per unit time, irrespective of the observer's actual switch rate), as well as
700 a hit rate that is lower than 100% (i.e. a certain proportion of actual switches is not marked,
701 leading to a number of misses that increases with the observer's switch rate). While this means
702 that the algorithm is not perfect (and may be improved by incorporating some recently proposed
703 analysis choices; Aleshin et al. 2019), this does not importantly affect our conclusions as long as
704 there is a close association between switches as marked by the various methods, which there is
705 (Figure 1D).
706

707 Pupil preprocessing

708 The pupil area signal was first averaged across eyes. For each blink (identified by the Eyelink
709 software and then combined across eyes as specified above) we then replaced pupil size during
710 the interval from 50 ms before the blink to 85 ms after the blink with values that linearly
711 interpolated between the average pupil sizes during the 50-ms periods that preceded and
712 followed that interval. We observed a tendency for pupil size to slowly drift, usually downward,
713 over the course of each 60-second trial; a tendency reported previously (Knapen et al. 2016). We
714 therefore followed previous authors (Van Slooten et al. 2017) by fitting and then subtracting an
715 exponential curve to each trial's pupil size data (after interpolating blinks). Here we constrained
716 the fitted time constant to values slower than 10 s to ensure that this step captured slow drift
717 rather than transient pupil changes early in the trial. Each trial's residual was then low-pass
718 filtered using a third order Butterworth filter with a cut-off frequency of 6 Hz, and z-scored. For
719 all samples that fell between trials the pupil size was set to 0. The data were then downsampled
720 to 10 Hz and concatenated across conditions.
721

722 General linear models

723 We used a general linear model (GLM) approach to evaluate the temporal relation between
724 switch moments as identified using different methods (Figure 1D) and to evaluate pupil
725 responses associated with specific events.
726

729 Figure 1D provides estimates of the temporal relation between switch events as identified by
730 distinct methods. From the raw data it is not always clear which event from one method (e.g.
731 based on key presses) corresponds to which event from a comparison method (e.g. based on
732 OKN), for instance because one method might miss an event or mark a spurious event where the
733 other method does not, or because switch events may sometimes follow each other too closely to
734 confidently match up event pairs across methods. For this reason we did not attempt to explicitly
735 identify pairs of corresponding switch events between different methods to then compute the
736 time delay between the two. Instead we took a deconvolution approach, which does not require
737 one to explicitly identify such correspondence. For each observer, we took the list of switch
738 moments as marked using the method specified in a plot's y-axis label, and converted it to a
739 time-varying signal sampled at 10 Hz by entering a 1 at every time step that contained a switch
740 and a 0 elsewhere. We then ran a GLM deconvolution analysis that combined that time-varying
741 signal with the switch event times as marked by the method specified in the corresponding x-axis
742 label. We did this for each switch direction separately (percept A to B and vice versa) and
743 averaged the two resulting deconvolution curves for each observer. The analysis was run using
744 the FIRDeconvolution package (Knapen et al. 2016; Knapen & De Gee 2016) using a
745 deconvolution time step of 100 ms, and concatenating the data across all trials (and both blocks)
746 of a given condition.

747
748 For the pupil analyses we used a different type of GLM approach that aims to reconstruct the
749 event response using a set of basis functions (Friston et al. 1998). This approach strikes a balance
750 between deconvolution analyses and GLMs that are based on a standard response function (a
751 pupil response function in this case; Hoeks & Levelt 1993; De Gee et al. 2012; Denison et al.
752 2020). The former have a high degree of flexibility in terms of the response shapes they can
753 reconstruct, at the expense of many degrees of freedom (as many as there are time points in the
754 reconstructed response). The latter have few degrees of freedom (e.g. only a scaling parameter)
755 at the expense of flexibility. The present approach based on basis functions is intermediate: the
756 pupil response here is modeled as a weighted sum of functions from a series (e.g. a Fourier series
757 or a Taylor series), and the number of functions included determines the flexibility and degrees
758 of freedom. In our case we used the ResponseFitter class from the nideconv package (De
759 Hollander et al. 2018; De Hollander & Knapen 2018) to fit the first terms of a Fourier series to
760 the pupil signal. We fitted both an offset and the number of sines and cosines needed to capture
761 fluctuations at a frequency of 1 Hz and slower, which meant 21 terms for most regressors, for
762 which the fitted time window ran from 3.5 s before to 6.5 s after the event. For the blink
763 regressors (fitted between -0.5 and 7.5 s) and the saccade regressors (fitted between -0.5 and 4.5
764 s) it meant 17 and 11 terms, respectively. We independently performed this analysis on the
765 preprocessed pupil time series itself, and on its derivative (Figures 2 and 3 show the result of
766 both superimposed).

767
768 For the analyses of Figure 2 the regressors in our design matrix were based on the following:
769 OKN-based switches (for each condition separately), trial start events, saccades, and blinks. For
770 the *Ignore* conditions we furthermore included key presses (which were in response to dot size
771 probes) and unreported dot size probes (defined as those probes that were not followed within 2 s
772 by a key press). For the insets of Figure 2 we used key-based switches instead of OKN-based
773 switches, but did not change anything else. For the analyses of Figure 3 the regressors were
774 constructed using OKN-based switches across only the two *Rivalry* conditions combined, OKN-

775 based switches across only the two *Replay* conditions combined, key presses across all
776 conditions, trial start events, saccades and blinks. For all pupil analyses the regressors (except the
777 trial start regressors) excluded those events that occurred so close to the start or end of a trial that
778 the modeled time window would extend beyond the trial period. For the saccade regressors we
779 merged pairs of saccades (identified as described above) that were fewer than 100 ms apart
780 because of the impression, based on visual inspection of the gaze traces, that these instances
781 usually concerned single square-wave intrusion events or saccadic pulse events (Abadi & Gowen
782 2004). For the blink regressors we excluded events that the Eyelink had marked as blinks but that
783 were shorter than 130 ms or longer than 900 ms, because those were more likely to reflect signal
784 loss for reasons other than blinks (Kwon et al. 2013). For Figures 4 and 5 we used the same basic
785 design matrices but added covariates to the switch regressors. These covariates were formed by
786 the OKN-based percept durations (log transformed and z-scored) that preceded or followed the
787 switches.

788

789 Statistics

790

791 We computed cluster-level Monte Carlo *p*-values using Bullmore's cluster mass test (Bullmore
792 1999; Maris & Oostenveld 2007). Specifically, we performed conventional tests (t-tests or
793 repeated measures ANOVAs, in different cases) for each time point separately, and formed
794 clusters out of groups of adjacent time points that all had $p < 0.05$ (two-tailed) and the same sign
795 of effect. For each cluster we then computed the 'cluster mass', i.e. the sum of all time points' test
796 statistics (*t* values or *F* values, depending on the test). We then performed 1000 iterations of a
797 permutation procedure to establish the probabilities of cluster mass values at least as extreme as
798 the ones observed. For the repeated measures ANOVAs and paired t-tests each iteration involved
799 randomly assigning the observed data to conditions for each observer independently (Maris &
800 Oostenveld 2007); for one-sample t-tests each iteration involved randomly inverting or not
801 inverting the sign of the observed data for each observer independently (Nichols & Holmes
802 2002; their example 3). On each iteration we computed cluster mass values based on the
803 randomized data by applying the procedure described above and stored the most extreme of
804 those values, thus forming a permutation distribution of 1000 values. Each cluster identified in
805 the actual, non-randomized, data was then assigned a Monte Carlo *p*-value equal to the
806 proportion of the permutation distribution that was more extreme than the cluster's observed
807 mass. All clusters with a Monte Carlo *p*-value smaller than 0.01 were considered significant.

808

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810

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813

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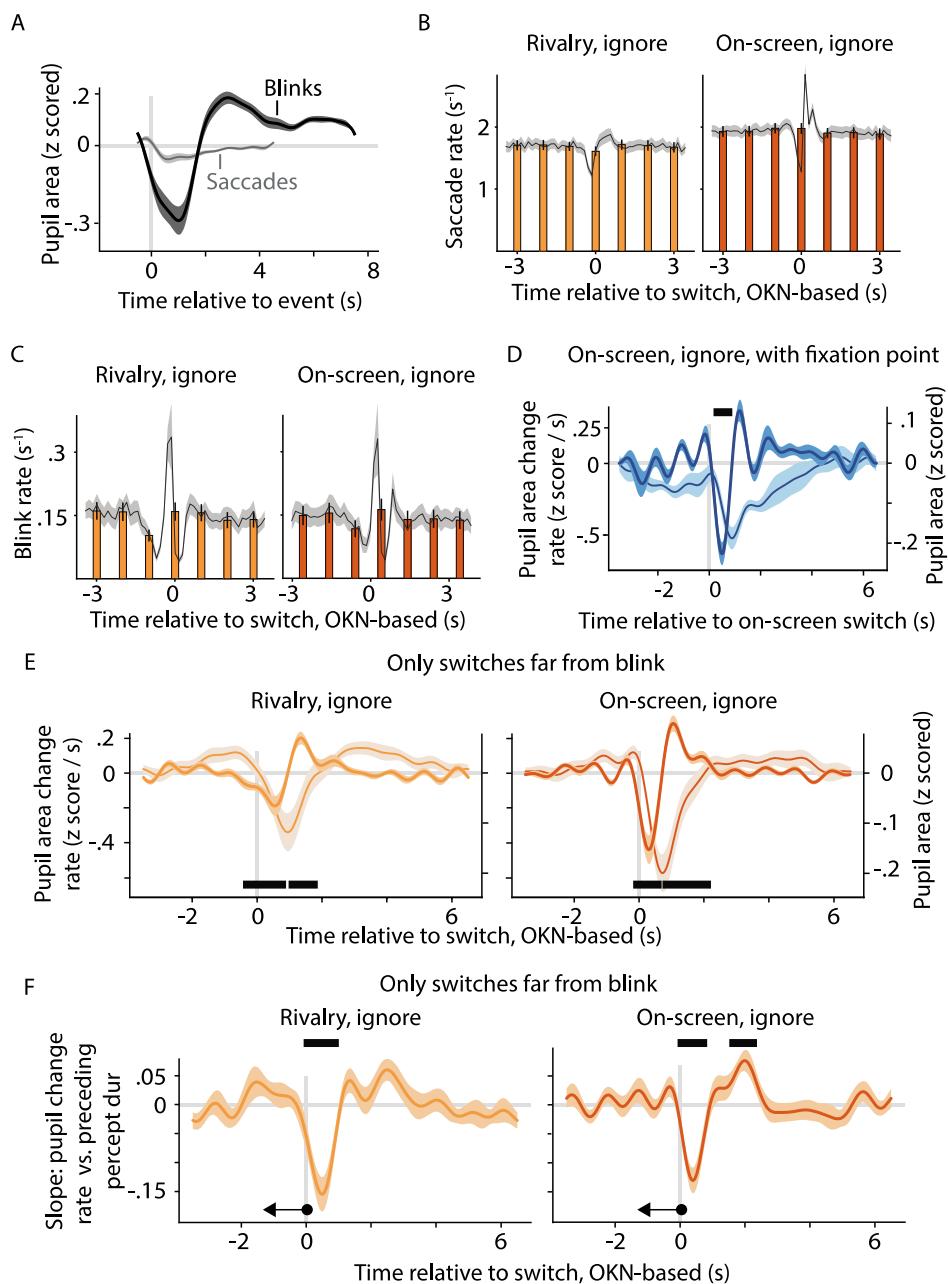
1 **Supplement**
2

3 *Artefacts from blinks and saccades*
4

5 Blinks and saccades are associated with pupillary signals of several kinds. When, as is the case
6 here, one uses a video-based eye tracker there is an apparent change in pupil size when the eyelid
7 (partly) covers the pupil during a blink, as well as when gaze angle changes (due to a saccade or
8 otherwise) and the projected size of the pupil within the camera image is altered as a result (Gagl
9 et al. 2011; Laeng & Alnaes 2019). In addition, a physiological pupil response has been observed
10 during the seconds that follow a blink or a saccade (Hupé et al. 2009; Knapen et al. 2016).
11 Unlike experimental designs that involve discrete and short trials, our design did not allow trials
12 with a blink to be discarded, and our OKN-centered approach obviously led to a large number of
13 saccades during data collection. We need to consider, therefore, how blinks and saccades may
14 have influenced our results.
15

16 Before going into control analyses and a control experiment that we performed in this context,
17 we will discuss the plausibility of an important influence of blinks and saccades given the
18 particulars of our findings and analysis approach. First, the idea of an important influence of this
19 kind on our basic finding of two switch-related pupil response components -- a constriction and a
20 slightly later dilation -- is rendered less convincing by the good match with published results. As
21 discussed in the main text, several previous studies have reported that the pupil response to task-
22 relevant switches in multistable perception, although dominated by a dilation, includes an earlier
23 constriction, as well. None of those studies employed a stimulus designed to induce OKN, and
24 one of the studies (De Hollander et al. 2018) specifically excluded switches from analysis if they
25 closely followed a blink. As such, an important role for OKN or blinks in this main result is
26 unlikely. Aside from this general consideration, our analysis approach included steps to alleviate
27 the influence of saccades and blinks. Pupil size in the period during and immediately
28 surrounding blinks was discarded and interpolated, addressing the issue of artefactual pupil
29 constriction due to eyelid closure. In addition, blink events and saccade events were both
30 included as regressors in our linear models, so the bulk of the physiological pupil response that
31 follows those events is captured by those regressors and thereby separated from the switch-
32 related responses. Exactly what proportion is captured depends on the suitability of the
33 assumptions that come with a linear model approach (e.g. the assumption of linearity), but we are
34 reassured by the good correspondence between the blink-related and saccade-related responses
35 that we estimate (Appendix 1-figure 1, panel A), and ones observed previously (Hupé et al.
36 2009; Knapen et al. 2016). Apparent pupil size changes due to altered gaze direction and, as a
37 result, projected pupil size in the video image, were not explicitly addressed by our analysis
38 steps. Given our stimulus radius of 3.9 dva, saccades confined to the stimulus area could cause
39 apparent pupil size changes of up to a few tenths of a mm (Gagl et al. 2011). That is not
40 negligible compared to the magnitude of physiological pupil size changes previously observed in
41 association with cognitive engagement (McDougal & Gamlin 2008) or isoluminant stimulus
42 changes (Barbur et al. 1992; Young et al. 1993), so an impact of this type of artifact cannot be
43 ruled out on those grounds. On the other hand, an explanation centered on such artefacts would
44 require a systematic tendency for participants to direct their gaze within a distinct eccentricity
45 range during one or two seconds following a perceptual switch as compared to other time periods
46 (i.e. during the seconds when we observed altered pupil size; main text Figures 2-5), while in

47 reality gaze angle changed continually and multiple saccades happened each second (see below).
 48 This makes it difficult to see what the specifics of an explanation in terms of this kind of artefact
 49 would be.
 50



51
 52 Appendix 1-figure 1. The role of blinks and saccades in shaping switch-related pupil responses. A. All linear models
 53 underlying the main text figures included designated regressors for blink events and saccade events. Pupil response
 54 shapes linked to those events are shown here for one of those models (these results are highly similar across the
 55 various models). B. Saccade rate during the time period around the perceptual switch in two of our conditions,
 56 assessed both at a fine time scale (black curves and gray confidence intervals) and at a coarse scale of 1 second per
 57 bin (bar charts). C. Same as B but for blink rate. D. Pupil response near the moment of on-screen switches in a
 58 variant of the *On-screen, ignore* condition in which we removed a circular region (radius: 0.72 dva) from the center
 59 of the stimulus and included a binocular fixation point in the middle, instead. As elsewhere, the thick curve and dark

60 confidence interval show pupil area change rate (left y-axis), and the thin curve and light confidence interval show
61 pupil area (right y-axis). E and F. Re-analysis of the main dataset for two conditions, now focusing exclusively on
62 switches that are at least 1.5 s removed from the closest eye blink. Both the switch-related pupil response (E) and its
63 dependence on the previous percept duration (F) are similar to the main result, obtained using switches irrespective
64 of nearby blinks (main text Figures 2 and 4). Unless otherwise stated, all conventions in this figure are the same as
65 those introduced in main text Figures 2-5.

66
67 We performed several control analyses and a control experiment to directly address the potential
68 role of saccades and blinks. First we investigated whether there was, in fact, any change in blink
69 and/or saccade frequency around the time of a perceptual switch. This analysis focused on the
70 two *Ignore* conditions; the conditions that gave rise to our most robust results. The analysis
71 reveals that saccades occurred at an average rate of just under two per second in both conditions
72 (black curves in Appendix 1-figure 1B), with a systematic change in saccade rate around the time
73 of the perceptual switch. This change -- first a drop, then a compensatory increase -- resembles
74 patterns observed in previous studies (van Dam & van Ee, 2005; Einhäuser et al. 2008). Blink
75 rate, likewise, changes around the time of a perceptual switch, in agreement with the same
76 studies, but is overall much lower (about one blink every seven seconds; black curves in
77 Appendix 1-figure 1C). The change in both saccade rate and blink rate in association with
78 perceptual switches means that saccade and blink-related pupil signals might be importantly
79 reflected in our main results, if they are not captured by their dedicated regressors in the general
80 linear model. Of note, however, for saccade rate the switch-related drop and subsequent increase
81 are both of comparable magnitude and are spaced very closely together in time. As a result
82 average saccade rate shows barely any change near the perceptual switch when assessed at a
83 coarser time scale, especially when evaluated across both conditions (orange bars in Appendix 1-
84 figure 1B, which depict saccade rate within intervals of 1 s). Given that the pupil response
85 patterns that underlie our conclusions occur in both conditions and on a coarse time scale relative
86 to the observed saccade rate fluctuation (e.g. the switch-related constriction lasts about two
87 seconds; its correlation with preceding percept duration about a second; main text Figures 2 and
88 4), it is unlikely that this rapid fluctuation can explain those response patterns. For blink rate the
89 situation is less clear based on this particular analysis, because there is a net reduction in switch
90 rate near switches, even when assessed at a coarse time scale (orange bars in Appendix 1-figure
91 1C).

92
93 To further investigate the role of saccades, and specifically OKN, in our results, we performed a
94 separate control experiment. Five observers performed a variant of our *On-screen, ignore*
95 condition, in which the inner part of the rivalry stimulus was removed and a binocular fixation
96 point was placed at the stimulus center, instead. This manipulation, as intended, led to a strong
97 reduction in eye movements, which also precluded an OKN-based approach to the identification
98 of switches. We therefore evaluated pupil size as a function of time relative to the physical, on-
99 screen, switches. In spite of the fixation point and the resulting lack of OKN, switches were still
100 associated with a pupil constriction comparable to the ones observed in our main experiment.
101 This further argues against a critical role of saccades, and specifically of OKN, in our finding of
102 a switch-related constriction.

103
104 When it comes to blinks, we re-analyzed our main dataset to further examine their role in our
105 results. Similar to De Hollander et al. (2018) we examined pupil signals surrounding only those
106 switches that are not close to any blinks: we removed from our switch regressors all switch

107 events that were within 1.5 s of a blink, and moved those events to nuisance regressors, instead.
108 This approach rules out any influence of the switch-related change in blink rate shown in
109 Appendix 1-figure 1C. Nevertheless, the results of this re-analysis closely resemble those of the
110 main analysis, with a robust switch-related constriction in both *Ignore* conditions (Appendix 1-
111 figure 1E) as well as a significant dependence on preceding percept duration (Appendix 1-figure
112 1F). This result further reduces the plausibility of an important role of blinks in our results.
113

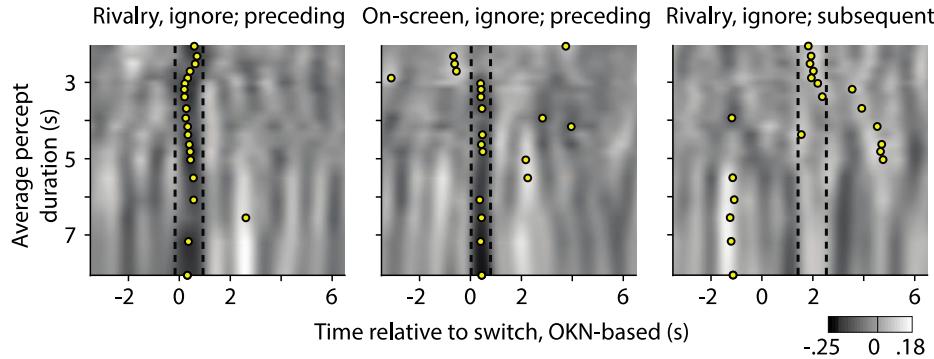
114 In sum, a critical impact of saccade and blink events on our results is unlikely when considering
115 the combination of 1) a marked consistency between key findings in our study and published
116 findings, 2) various aspects of our main analysis approach that minimize the impact of such
117 events, 3) no relevant change in saccade rate surrounding switches, 4) the results of a control
118 experiment that minimized OKN, and 5) the results of a control analysis designed to eliminate
119 any role of blinks.
120

121 *Artefacts from overlapping pupil responses*

122

123 In main text Figures 4 and 5 of the main text we show three significant correlations between the
124 switch-related pupil response and the duration of the preceding (two correlations) or subsequent
125 (one correlation) percept duration. Because the pupil response spans across a few seconds it is
126 conceivable that this type of association with flanking percept duration arises artefactually due to
127 an incomplete separation, in our analysis, of overlapping responses to consecutive perceptual
128 switches. We investigated this possibility by looking for data patterns that would be expected if
129 this explanation was correct. In particular, under this explanation we would expect correlations
130 as shown in main text Figures 4 and 5 to differ systematically between observers with different
131 average perceptual dominance durations. For instance, the observed group-level correlations with
132 percept duration might stem primarily from observers whose switches are, on average,
133 sufficiently closely spaced (by less than, say, 2 or 3 seconds) for overlap between adjacent
134 switch-related pupil responses to be substantial. In addition, one might expect an observer's
135 average percept duration to predict which exact section of the switch-related pupil response
136 appears to depend on preceding, or subsequent, percept duration: for those observers whose
137 preceding, or subsequent, switches occur relatively earlier this would be an earlier section. To
138 evaluate whether any of these expectations are reflected in our data, we performed the analysis
139 summarized in Appendix 1-figure 2. Here we examined the same curves that we previously
140 averaged across all observers to produce the mean curves of main text Figures 4B and 5B, i.e. the
141 curves that show the correlation between pupil area change rate and percept duration as a
142 function of time during the pupil response period. However, this time we did not average those
143 curves across all observers. Instead, we sorted the observers by average percept duration, and
144 moved a sliding window across these sorted observers, averaging the per-observer curves of five
145 observers at a time. In other words, we produced one average correlation curve for the five
146 fastest switchers, another average correlation curve for the second through sixth fastest
147 switchers, etcetera, down to the five slowest switchers. In the plots of Appendix 1-figure 2 the
148 gray levels along each horizontal slice can be thought of as representing one such average curve,
149 and the percept durations (averaged across groups of five observers at a time) that correspond to
150 the slices are plotted along the y-axis, with fast switchers at the top and slow switchers at the
151 bottom. Each panel corresponds to one of the three panels of Figures 4 and 5 that showed a

152 significant correlation across all observers, and the time period of this significant correlation is
153 indicated by dashed lines in the corresponding panel of Appendix 1-figure 2.
154



155 Appendix 1-figure 2. Re-analysis of the significant correlations between pupil response, and preceding (left and
156 center plot) or subsequent (right plot) dominance duration, now separated out as a function of the observer's average
157 percept duration. Gray values correspond to the correlation between pupil change rate (z-scored area per second) and
158 preceding or subsequent percept duration (z-scored); correlations also shown, but averaged across all observers, in
159 main text Figures 4 and 5. Here the correlations are averaged per groups of five observers, sorted by their average
160 percept duration along the y-axes. Dashed lines delineate the time periods within which the average across all
161 observers is significantly different from zero (periods that are marked by black bars in main text Figures 4 and 5).
162 For each group of five, a yellow disk indicates the middle of the time period at which the five-person average
163 reaches its most extreme value, after smoothing this five-person average by averaging within a sliding window as
164 wide as the interval delineated by the dashed lines.

165
166 Both effects of preceding dominance duration (Appendix 1-figure 2, left and center panel) appear
167 largely invariant with observers' average dominance durations: a vertical dark band in the
168 relevant time period extends across nearly the full range (of about 6 seconds) of average
169 dominance durations in both panels. One qualification here is that in the *On-screen, ignore*
170 condition (center panel) the effect does not seem present in those observers with the very shortest
171 dominance durations. These impressions are confirmed by identifying, for each 5-observer
172 average curve, the moment at which the curve reaches its most extreme value (here we included
173 both positive and negative extremes, within sliding windows as wide as the time window that
174 shows the across-observer significant effect that is indicated by the dashed lines). The yellow
175 dots in Appendix 1-figure 2 show these moments. For the *Rivalry, ignore* condition (left panel)
176 this extreme is found at a similar time across nearly all average percept durations. For the *On-*
177 *screen, ignore* condition (center panel, this extreme is also found at a similar time in most cases,
178 with most exceptions corresponding to the fastest switchers. Together these analyses indicate
179 that the effect of preceding dominance duration is robust in our data, and unlikely to be an
180 artifact caused by incomplete separation of overlapping pupil responses.

181
182 The right panel of Appendix 1-figure 2 shows the same, but now pertaining to the correlation
183 with subsequent dominance duration that was observed in the *Rivalry, ignore* condition (i.e.
184 corresponding to main text Figure 5B, top left plot). Here there is less consistency across average
185 dominance durations, and an impression that the effect is primarily carried by the observers who
186 have the shortest average dominance durations, of about 2 to 3.5 seconds. This might indicate a
187 role of incomplete separation of overlapping pupil responses, especially given that the significant
188 correlation with subsequent dominance duration was not observed until about 2 seconds after the

189 switch event (main text Figure 5B) -- close to the moment at which the next switch would occur,
190 on average, for the observers who seem to carry this effect.

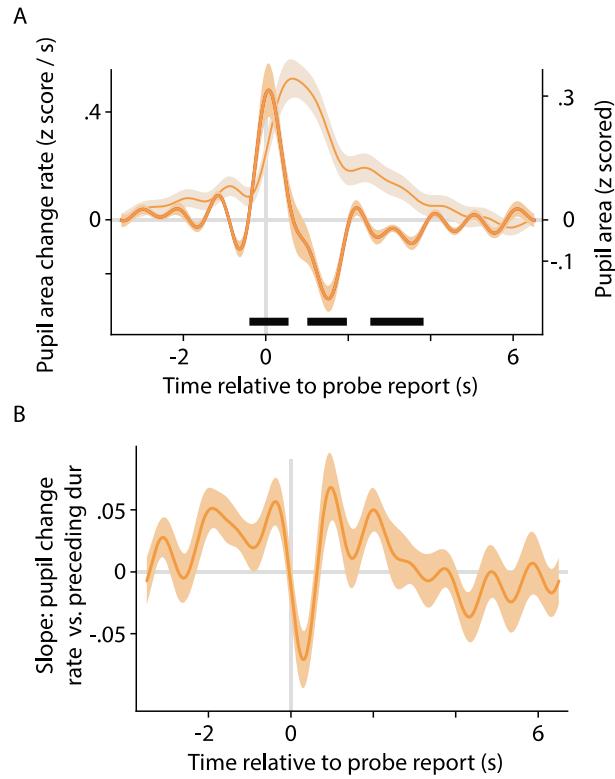
191

192 *Effect of preceding duration on response-related dilation*

193

194 The main text shows a significant correlation between preceding percept duration and pupil
195 response in the *Ignore* conditions where, arguably, the switch-related constriction is measured in
196 isolation. It does not show a significant correlation in the *Report* condition where this
197 constriction overlaps with the report-related dilation. One conceivable explanation is that the
198 report-related dilation depends on preceding percept duration in a way that counteracts the
199 dependence of the switch-related constriction. The direction of effect required for this would be
200 one in which report-related dilations are larger following longer percept durations. That direction
201 of effect would not be consistent with existing literature which, if anything, suggests that
202 dilations might be larger following *shorter* percept durations, possibly related to the fact that
203 switches that terminate shorter dominance periods are more surprising (Kloosterman et al. 2015;
204 De Hollander et al. 2018). Based on our design it is difficult to obtain a clean estimate of the
205 relation between preceding duration and the dilation that accompanies the switch report, because
206 this dilation always overlaps with the switch-related constriction which, as shown, itself depends
207 on preceding percept duration. Our design does, however, allow this type of estimate for the
208 dilation response that accompanies the report of a so-called dot size probe. In the *Ignore*
209 conditions observers reported these transient stimulus changes, which occurred randomly and
210 independently of perceptual switches (drawn from a uniform distribution between 3 and 8 s).
211 Appendix 1-figure 3A shows that these reports are associated with a pronounced dilation that
212 starts shortly before the key press, in agreement with numerous reports of transient dilations
213 associated with task execution (e.g. Richer & Beatty 1987; Hupé et al. 2009; Gilzenrat et al.
214 2010), and also with main text Figure 3C. Appendix 1-figure 3B shows how the amplitude of this
215 dilation relates to the duration that separates this probe report from the previous one. The panel
216 shows no significant correlation, although a brief period immediately after the key press is
217 marked by a non-significant negative correlation. The direction of this effect means that the
218 report-related dilation is numerically larger following briefer intervals. Although not significant,
219 this trend is consistent with existing observations (Kloosterman et al. 2015; De Hollander et al.
220 2018) and also with interpretations in terms of surprise: when drawing from a uniform
221 distribution the instantaneous probability of a new event (given that it has not happened yet)
222 increases monotonically with time passed since the previous event. The trend is opposite,
223 however, to what would be needed to support the idea that, in our *Report* conditions, the switch-
224 related constriction component and the response-related dilation component cancel each other
225 out in terms of dependence on preceding percept duration.

226

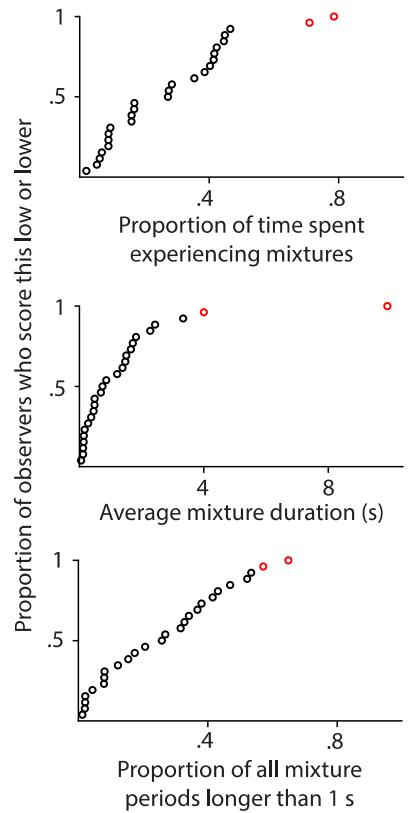


227 Appendix 1-figure 3. Pupil response associated with key presses in response to dot size probes in the *Ignore*
228 conditions (both conditions combined). A. Pupil change rate (left y-axis; thick curve and dark confidence interval)
229 and pupil size (right y-axis; thin curve and light confidence interval). B. Correlation between pupil change rate (z-
230 scored area per second) and the amount of time passed since the previous key press (z-scored). All plotting
231 conventions are the same as those introduced in main text Figures 2-5.

232
233 *Perceptual mixtures*
234

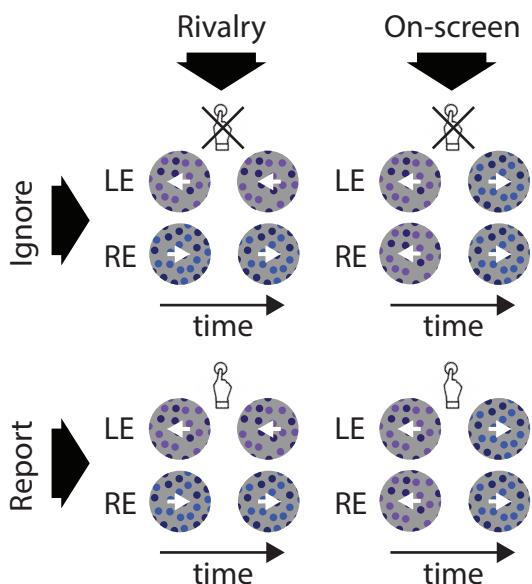
235 In the *Report* conditions observers could indicate experiencing either of the two exclusive
236 percepts, or a mixture made up of parts of the two monocular displays perceived at the same
237 time. Although there is no single clear criterion as to what counts as 'too much' mixture
238 perception for our purposes, it is clear that observers who experience more mixtures are less
239 suitable, as our study focuses on perceptual switches between the two exclusive percepts. We
240 quantified mixture perception in three different ways and decided to discard the data of two
241 participants who consistently scored the highest of all participants on each of the three measures.
242 The three panels of Appendix 1-figure 4 illustrate the three approaches, with each dot marking
243 one participant and the two red dots in each panel marking the two discarded participants. The
244 top panel shows the proportion of viewing time spent experiencing a mixture percept (as based
245 on key press reports); a standard measure of mixture perception. The two participants marked in
246 red are outliers on this scale, and are the only observers who reported experiencing a mixture
247 more than half of the time. But one could argue that the validity of our pupil analyses is
248 dependent, not so much on what proportion of time is occupied by mixtures, but on how long
249 mixtures last while transitioning from one exclusive percept to the other. As long as such
250 transition durations are brief the pupil responses we quantify can reasonably be interpreted as
251 associated with perceptual switches. The center panel, therefore, shows the average duration of
252 mixture periods for all observers. Again, the same two observers score the highest. Finally, one

253 could argue that the average mixture duration is not critical -- an observer might experience a
254 small number of excessively long mixture periods that pull up this average -- as long as there is a
255 sufficient number of brief transitions that contribute heavily to our switch-related pupil
256 estimates. The bottom plot, therefore, shows for each observer the proportion of all mixture
257 periods that last longer than 1 second. Again, the same two participants score highest: they are
258 among only four observer for whom over half of the mixture periods last longer than a second.
259 Because those two participants scored highest on all three measures, and also because the order
260 of the next-highest scoring participants was inconsistent across the three measures, we decided to
261 base our main analyses on the data from all observers except those two.
262

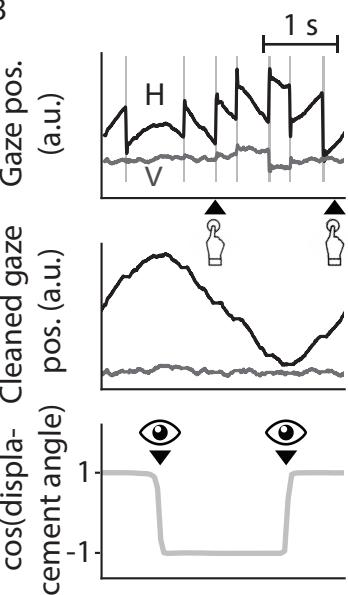


263 Appendix 1-figure 4. Perceptual mixtures: percepts that feature parts of both eyes' images. Each plot uses a different
264 measure to quantify the reported prevalence of perceptual mixtures for individual observers. Each disk corresponds
265 to one observer. Data from the two observers that are indicated in red here were not included in the analyses for any
266 of the other figures in this paper, because those observers scored high on all three indices of the prevalence of
267 perceptual mixtures.

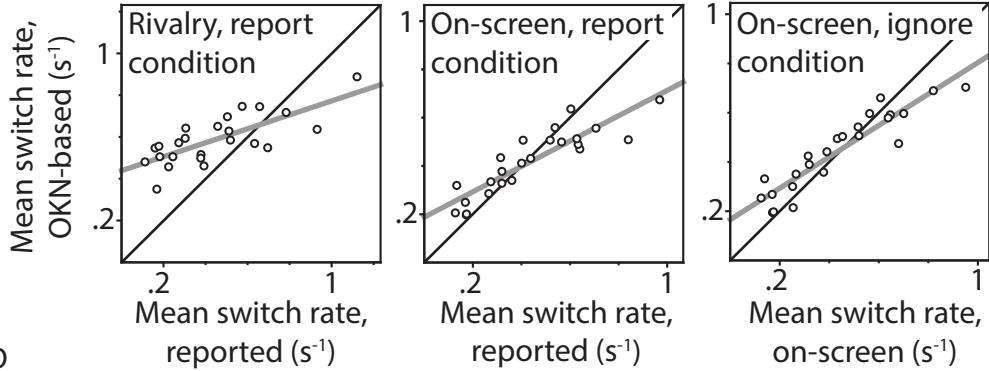
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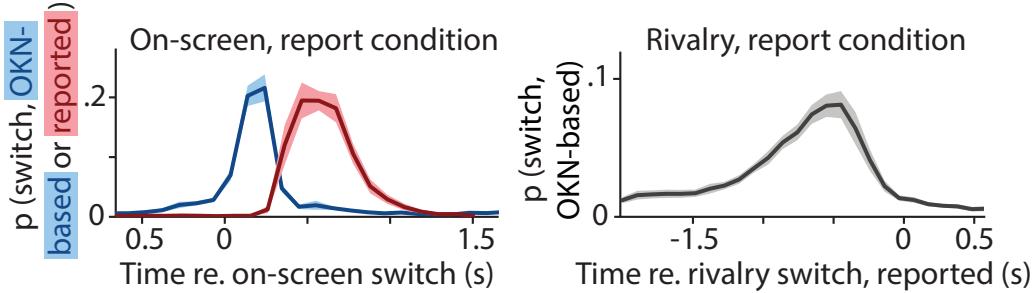
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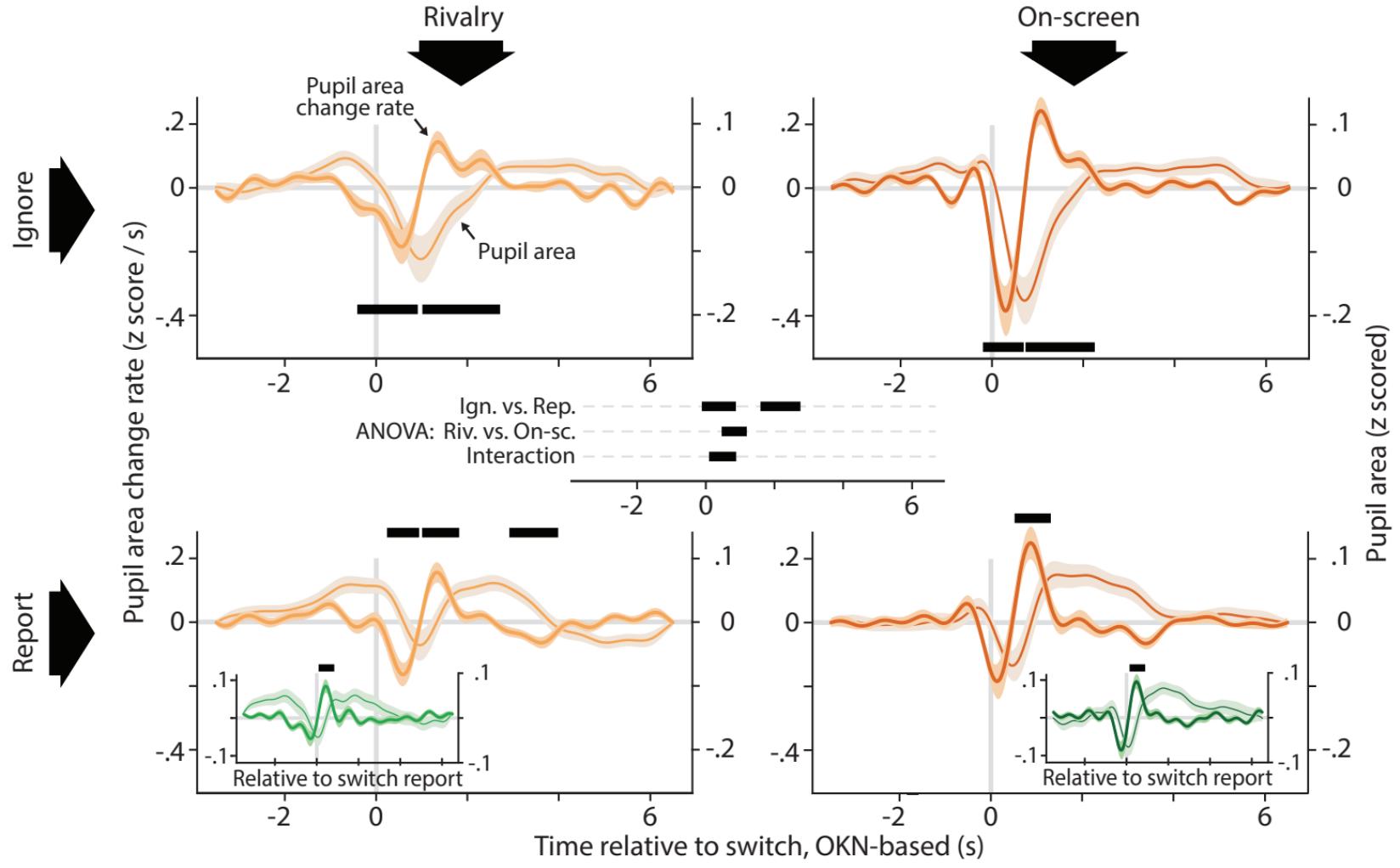


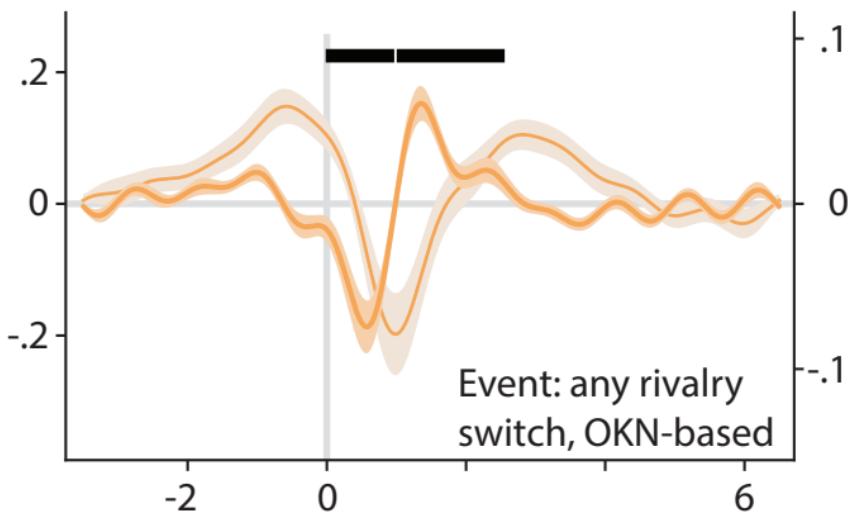
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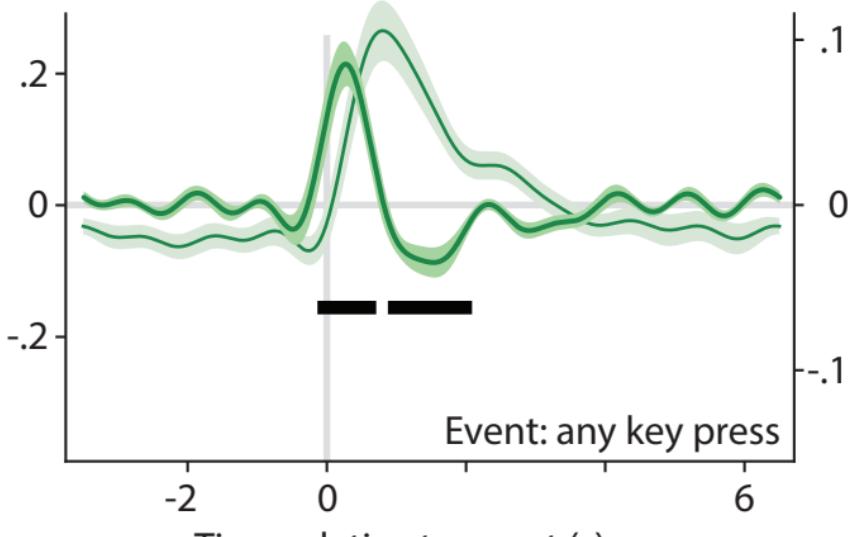
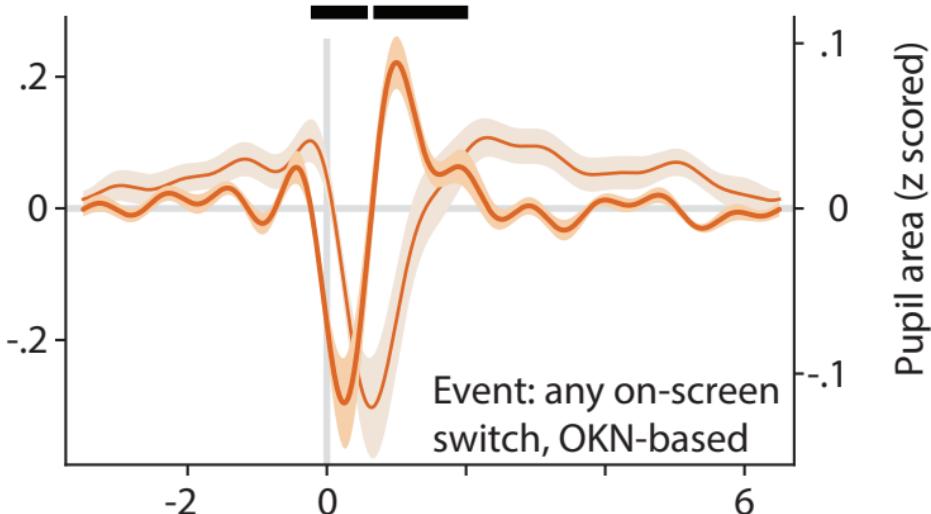
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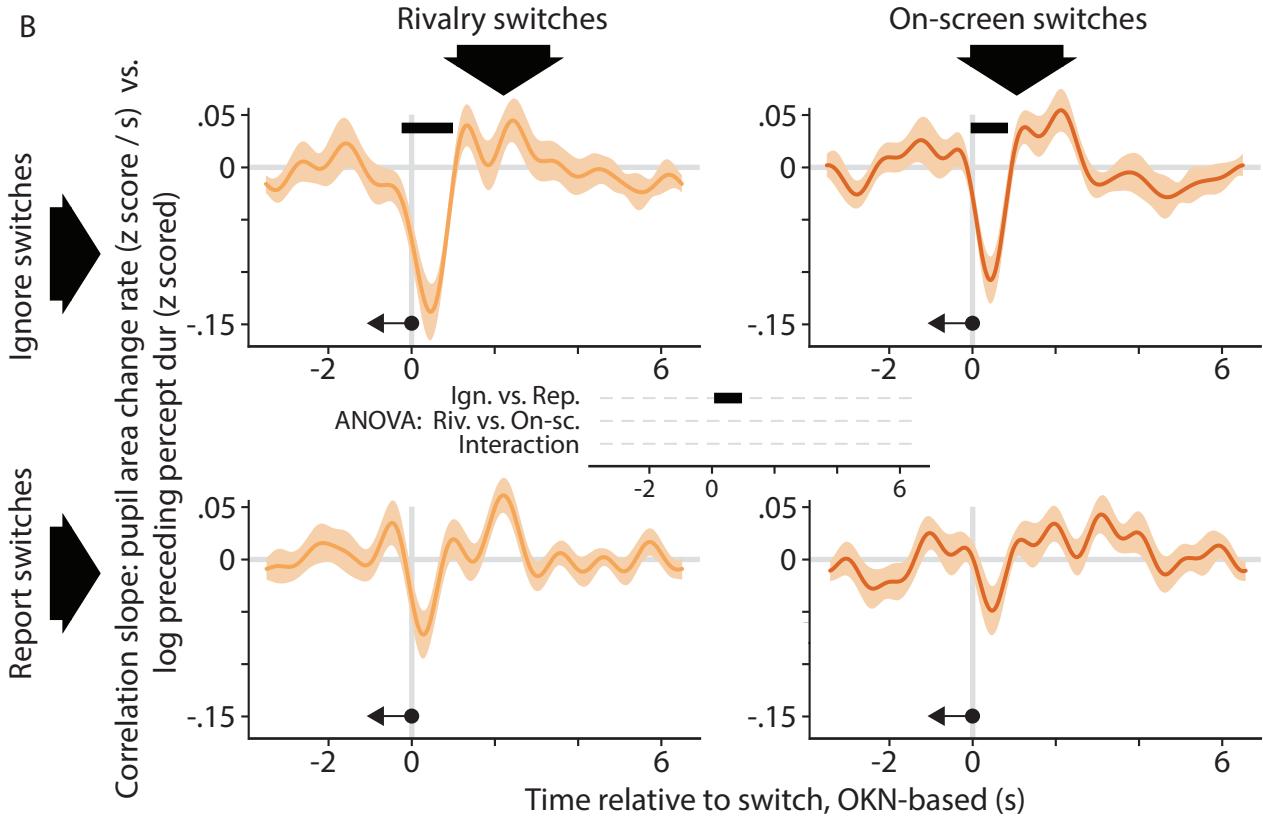
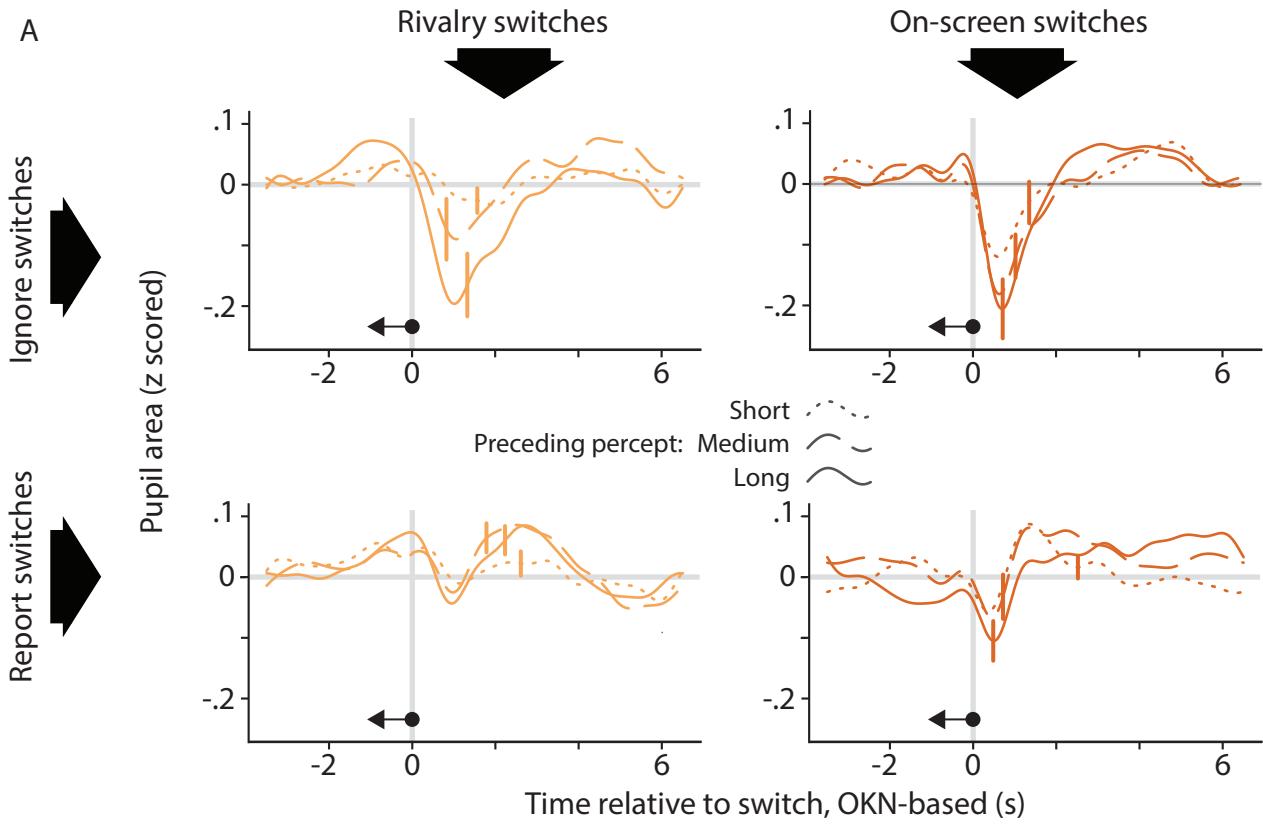


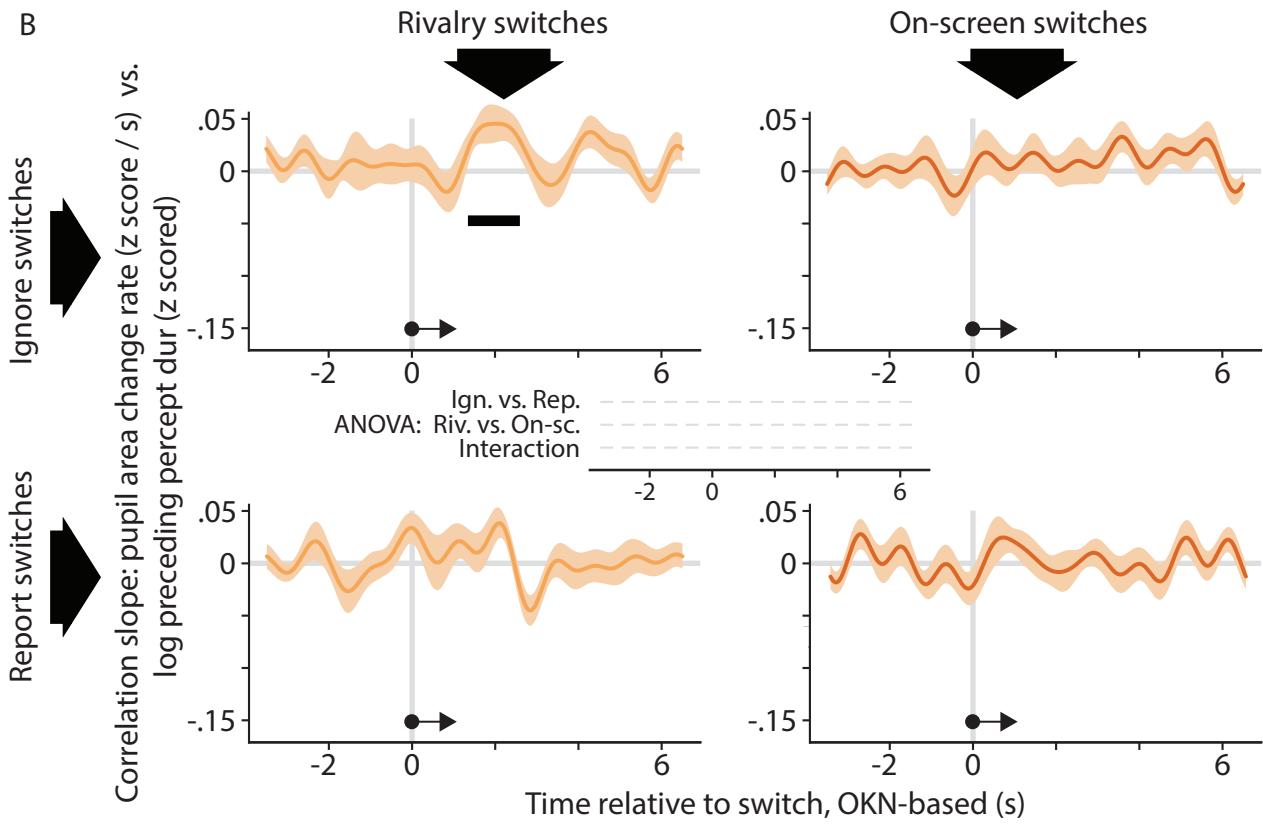
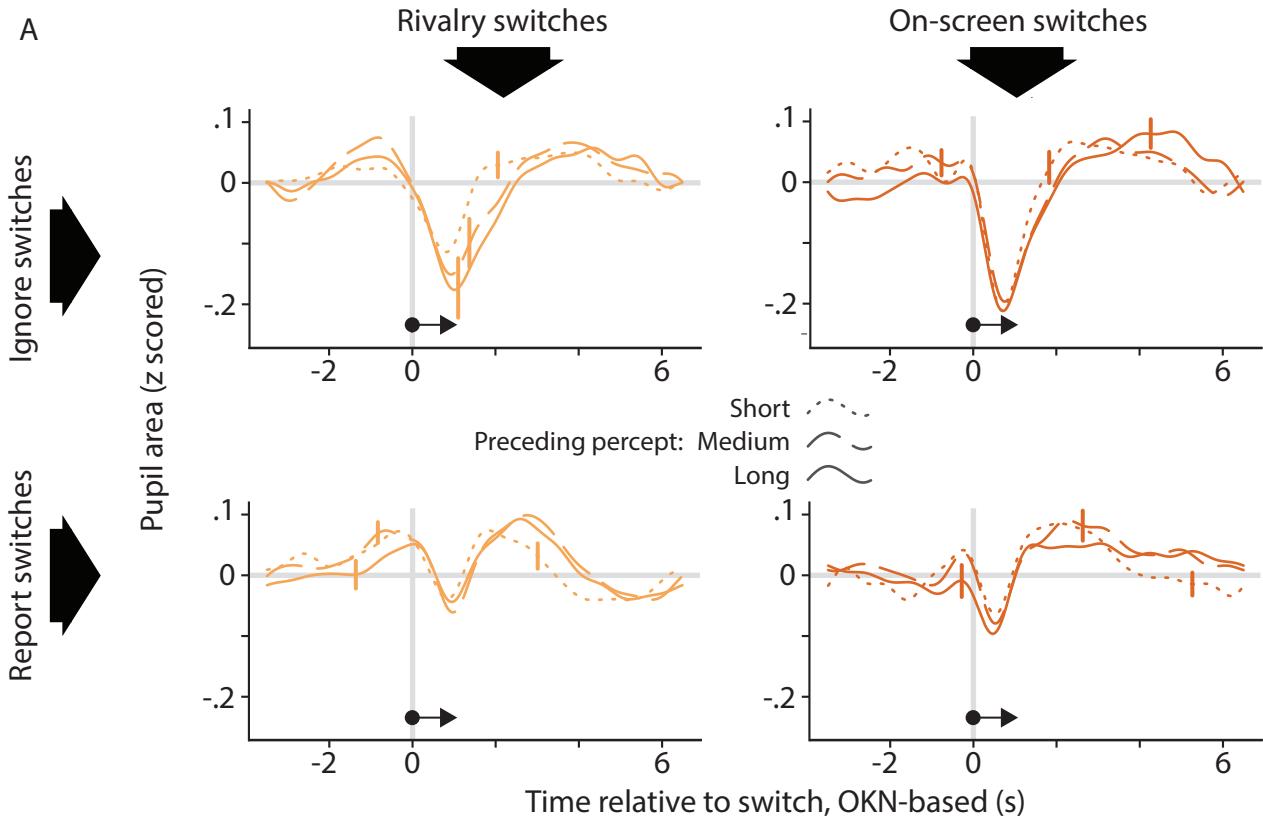


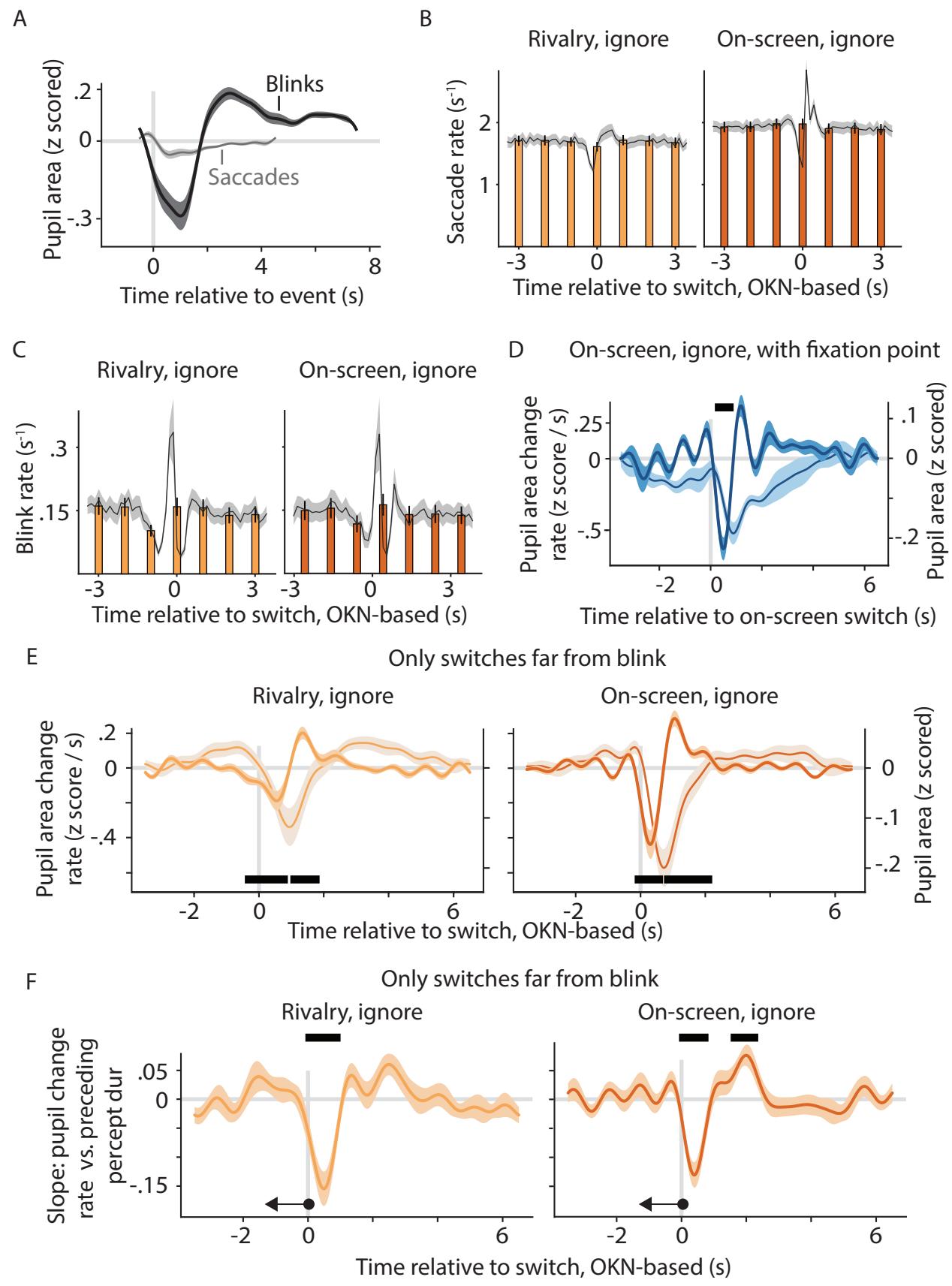
Paired t-test Riv. vs. On-sc.:



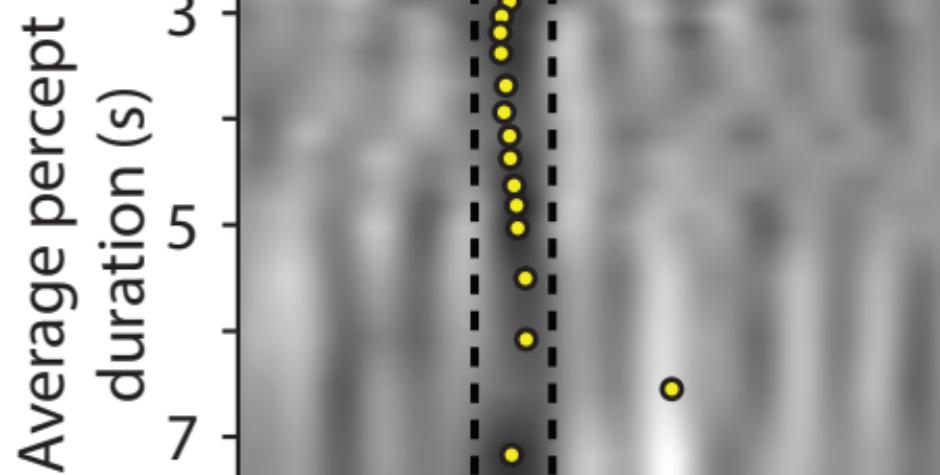
Time relative to event (s)



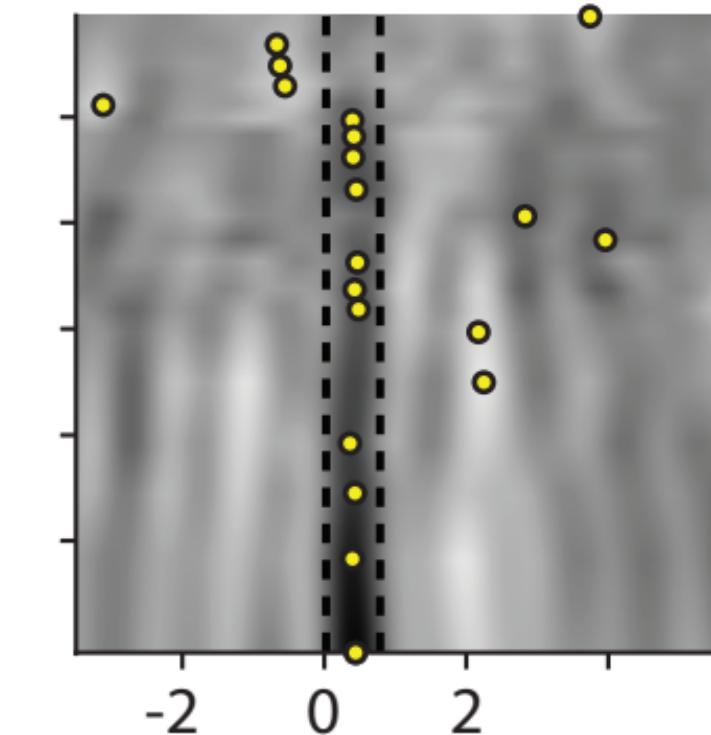




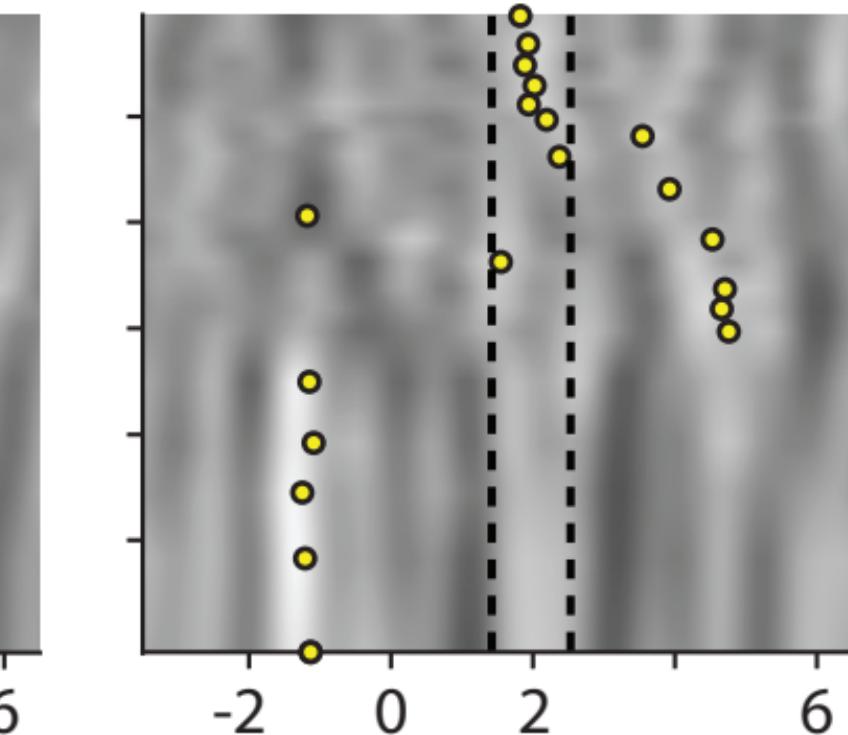
Rivalry, ignore; preceding



On-screen, ignore; preceding



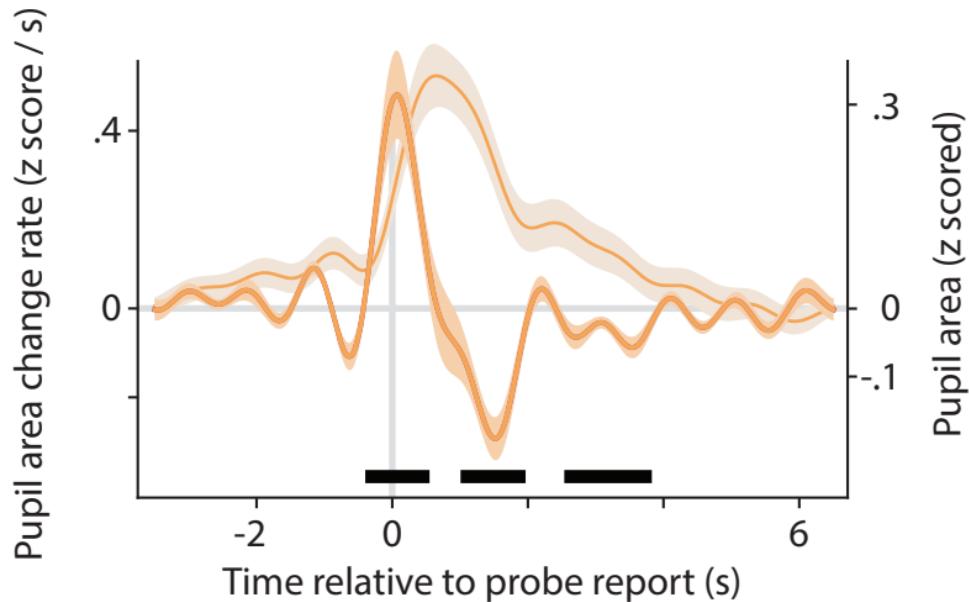
Rivalry, ignore; subsequent



Time relative to switch, OKN-based (s)

-.25 0 .18

A



B

