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Neuroplasticity in older adults revealed by temporary occlusion of one eye

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1 **Cortex – Research Report**

2

3 **Title**

4 Neuroplasticity in older adults revealed by temporary occlusion of one eye

5

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## 28 **Declarations of interest**

29 None

30

## 31 **Author contributions**

32 **Bao N Nguyen:** Methodology, Software, Validation, Formal Analysis, Investigation, Data

33 Curation, Writing – Original Draft, Writing – Review and Editing, Visualization, Project

34 Administration **Menaka Malavita:** Validation, Investigation, Data Curation, Writing – Review

35 and Editing **Olivia L Carter:** Conceptualization, Methodology, Resources, Writing – Review

36 and Editing, Supervision, Funding Acquisition **Allison M McKendrick:** Conceptualization,

37 Methodology, Software, Resources, Writing – Original Draft, Writing – Review and Editing,

38 Visualization, Supervision, Funding Acquisition

39

## 40 **Highlights**

41 1. Temporarily depriving one eye of visual experience reveals adult

42 neuroplasticity

43 2. Two hours of monocular deprivation alters ocular dominance in healthy older

44 adults

45 3. Neuroplasticity of visual cortex is preserved and possibly strengthened in

46 healthy older adults

47

48

49 **Abstract**

50       Occluding one eye for several hours alters visual experience. Specifically, occluding one  
51 eye shifts the balance of ocular dominance to favour the recently deprived eye, which can  
52 be measured using binocular rivalry. This ocular dominance shift demonstrates homeostatic  
53 neuroplasticity within the visual system and has been explored in detail in younger adults.  
54 Here we measure whether the strength and general features of neuroplasticity revealed by  
55 monocular patching are maintained in older adults. Thirty younger (18-35 years) and 30  
56 older adults (60-81 years) participated. Binocular rivalry features were measured before and  
57 after 2 hours of occlusion. Post-patching, perceptual dominance of the non-patched eye  
58 decreased ( $p < 0.001$ ) in both age groups. The effect of occlusion on all features of binocular  
59 rivalry did not significantly differ between groups. The older visual system maintains the  
60 ability to rapidly adjust to changes in perceptual experience induced by eye occlusion. This  
61 preservation of neuroplasticity suggests that visual training methods designed to improve  
62 visual performance based on eye occlusion should maintain effectiveness into older age.

63

64 **Keywords (max 5 words)**

65 Short-term monocular deprivation, ocular dominance, neuroplasticity, visual cortex, ageing

66

67 **Funding**

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69 and OLC (DP180102596).

70

## 71        **1. Introduction**

72        There has been considerable recent interest in the ability of short-term monocular  
73        deprivation to alter visual experience in adults, as a means of exploring neuroplasticity  
74        within the adult visual system (Baldwin & Hess, 2018; Lunghi, Burr, & Morrone, 2011;  
75        Lunghi, Burr, & Morrone, 2013; Lunghi & Sale, 2015; Zhou, Clavagnier, & Hess, 2013). The  
76        general, and highly replicated, observation is that when ocular dominance is measured  
77        before and after short-term monocular deprivation (by patching one eye), there is a shift in  
78        ocular dominance to favour the recently deprived eye. Ocular dominance describes the  
79        preference of input from one eye over the other. Many prior experiments have used the  
80        following approach: occlude one eye with a patch for a duration of around two hours, then  
81        measure the temporary shift in ocular dominance after patch removal. The shift in ocular  
82        dominance is maximal immediately post-patch removal but has been shown to last for  
83        several hours (Lunghi et al., 2011; Lunghi et al., 2013). The most common method used in  
84        these patching experiments to determine the balance in dominance between the two eyes  
85        is binocular rivalry. Binocular rivalry involves presenting the two eyes with different but  
86        similarly salient stimuli, which then compete for perceptual dominance. The result is regular  
87        switching between the perceptual dominance and suppression of the competing stimuli.  
88        After temporary occlusion, the stimulus presented to the recently patched eye dominates  
89        perception, with the strength of this effect used as an index of short-term homeostatic  
90        neuroplasticity (Zhou, Baker, Simard, Saint-Amour, & Hess, 2015; Zhou et al., 2013).

91        Physiologically, prior evidence from magnetic resonance spectroscopy (MRS) suggests  
92        that temporary occlusion decreases resting state GABA concentration in visual cortex, with  
93        the amount of GABA reduction being correlated with the magnitude of effect of deprivation

94 on the rivalry task (Lunghi, Emir, Morrone, & Bridge, 2015). Cholinergic mechanisms have  
95 also been implicated, with a recent study demonstrating that the ingestion of donepezil (a  
96 cholinesterase inhibitor) reduces the magnitude and duration of the ocular dominance shift  
97 following temporary occlusion (Sheynin, Chamoun, et al., 2019). Consequently, short-term  
98 plasticity might be phenomenologically altered in individuals with conditions that impact on  
99 the regulation of either cholinergic or GABA-ergic systems. We propose that one such  
100 situation is healthy human aging. Indeed, the presence or absence of visual system  
101 neuroplasticity in older adults has potentially important implications for the ability to adapt  
102 to changes in visual status with age and disease, and may influence the choice of future  
103 clinical approaches designed to enhance visual performance through training.

104 The precise visual neural circuitry underlying the effects of temporary occlusion on eye  
105 dominance is still being uncovered (for example see: Bai, Dong, He, & Bao, 2017; Baldwin &  
106 Hess, 2018; Binda et al., 2018; Ramamurthy & Blaser, 2018; Wang, Yao, He, Zhou, & Hess,  
107 2017). It is generally accepted that patching influences inter-ocular contrast gain control  
108 mechanisms (Zhou et al., 2015; Zhou et al., 2013) such that localised changes in the balance  
109 between activation and inhibition allow up/down regulation of selected neural signals. The  
110 resulting effect is reduced inhibition of the signal from the deprived eye after the patch is  
111 removed. To date, all reports investigating this phenomenon have tested younger adults.  
112 However, other visual processes that are reliant on contrast gain control mechanisms can be  
113 markedly altered in the older visual system. Examples include: differences in contrast  
114 adaptation properties to chromatic stimuli (Elliott, Werner, & Webster, 2012), differences in  
115 contrast gain (Elliott & Werner, 2010), and strengthening of perceptual spatial surround  
116 effects involving contrast judgements (for review see: McKendrick, Chan, & Nguyen, 2018).  
117 The balance of evidence from this broad range of visual perceptual studies suggests a

118 strengthening of contrast gain control mechanisms in the aging visual system. Further  
119 evidence for this proposition comes from neurophysiological study of aged cat primary  
120 visual cortex that demonstrates significantly stronger contrast adaptation in some visual  
121 cortical cells relative to those found than in younger animals (Hua, Li, Tang, Wang, & Chang,  
122 2009). Taken together, these findings suggest that the effects of temporary occlusion of one  
123 eye might actually be strengthened in older adults.

124 An additional physiological factor that suggests that older adults might have an altered  
125 neuroplastic experience post-occlusion arises from the study of GABA concentrations in  
126 visual cortex (Pitchaimuthu et al., 2017). Previous study of temporary monocular occlusion  
127 in younger adults implicated visual cortical modulation of GABA levels as key to the strength  
128 of neuroplastic effects demonstrated within individuals (Lunghi et al., 2015). While GABA-  
129 ergic inhibition within visual cortex in older adults is often assumed to be reduced based on  
130 inferences from single-cell neurophysiology in senescent primates (Leventhal, Wang, Pu,  
131 Zhou, & Ma, 2003), direct evidence for reduced GABA-ergic inhibition in humans is lacking.  
132 Indeed, a recent human MRS study actually revealed elevated GABA concentrations in visual  
133 cortex in older adults (Pitchaimuthu et al., 2017). Of further relevance was the observation  
134 that increased GABA levels correlated with slower binocular rivalry (Pitchaimuthu et al.,  
135 2017), consistent with the idea that rivalry switch rate is dependent, at least in part, on  
136 levels of cortical inhibitory neurotransmitter. While it is not immediately apparent how this  
137 cross-sectional observation may relate to the ability for resting state GABA levels to change  
138 under conditions of monocular deprivation, the presence of dysregulation of the GABA-ergic  
139 system in older adults adds further support to the possibility of increased perceptual biasing  
140 in the response to temporary occlusion.

141 Here we explore whether the strength and general features of neuroplasticity revealed  
142 by two hours of monocular patching is maintained in older adults. Specifically, we  
143 investigated binocular rivalry outcome measures that provide insight into the balance  
144 between excitation and inhibition in visual cortex. Mutual inhibition is considered critical for  
145 the alternation between two exclusive-dominance percepts (Blake, 1989; Blake &  
146 Logothetis, 2002; Klink, Brascamp, Blake, & van Wezel, 2010; Said & Heeger, 2013; Tong,  
147 Meng, & Blake, 2006), while pharmacological agonism of specific GABA-ergic inhibitory  
148 receptors has recently been linked to the prominence of mixed percept (Mentch, Spiegel,  
149 Ricciardi, & Robertson, 2019). Furthermore, the initial period of dominance before the first  
150 binocular rivalry switch (or 'onset rivalry'), which has previously been unexplored in the  
151 context of short-term monocular deprivation paradigms, is also considered to depend  
152 critically on inhibition (akin to other forms of visual suppression or masking, see review by  
153 Stanley, Forte, Cavanagh, & Carter, 2011). We show that the older visual system maintains  
154 the neuroplastic ability to respond to short term changes in visual experience. The  
155 preservation of neuroplasticity suggests that visual training methods designed to improve  
156 visual performance based on eye occlusion (Lunghi, Sframeli, et al., 2019; Sauvan et al.,  
157 2019) should maintain effectiveness into older age.

158

## 159 **2. Material and methods**

160 The study was approved by the University of Melbourne Human Research Ethics  
161 Committee (#1851069) according to a protocol consistent with the Declaration of Helsinki.  
162 We report how we determined our sample size, all data exclusions, all inclusion/exclusion

163 criteria, whether inclusion/exclusion criteria were established prior to data analysis, all  
164 manipulations, and all measures in the study below.

### 165 2.1. *Participants*

166 We performed a power analysis based on the effect size (0.73) of patching on ocular  
167 dominance reported by previous work (Lunghi & Sale, 2015) and a two-tailed difference  
168 between matched pairs in G\*Power (Faul, Erdfelder, Lang, & Buchner, 2007). Twenty-seven  
169 participants would be required in each group to achieve a power of 0.95 at a significance  
170 level of 0.05. Accordingly, thirty younger (aged 18-35 years; mean age, 25 years) and 30  
171 older adults (aged 60-81 years; mean age, 68 years) were recruited via advertisements  
172 within the University, on community noticeboards and from a database of previous research  
173 participants. Written consent was obtained from participants prior to testing and  
174 participants received a \$20 gift voucher to contribute to any out-of-pocket travel expenses.

175 The single testing session was 4 hours duration including a vision and ocular health  
176 screening. The following inclusion/exclusion criteria were established prior to data analysis:  
177 All participants had distance best corrected visual acuity equal or better than 6/7.5 in each  
178 eye with corrective lenses of less than  $\pm 5$  D sphere and less than 2 D astigmatism. Ocular  
179 health was screened using slit lamp biomicroscopy and ophthalmoscopy to ensure absence  
180 of ocular pathology. All participants had a cataract grading of less than 1.5 according to the  
181 Lens Opacities Classification System III (LOCS III) (Chylack et al., 1993).

### 182 2.2. *Experimental procedure*

183 Figure 1 is a schematic of the experimental procedure, including a depiction of the  
184 binocular rivalry test stimuli and procedure. Participants were trained on the binocular

185 rivalry task and completed at least one practice run before commencing the actual trials.

186 Binocular rivalry was measured at baseline prior to two hours of monocular deprivation by

187 patching, followed by post-patching binocular rivalry tests at 0, 3, 6, 9, 12, 15, 30, 45, 60 and

188 90 minutes after patch removal. To investigate the effect of short-term monocular

189 deprivation, we compared baseline rivalry data (sum of 3-4 baseline trials) to the data

190 collated in the period 0-9 minutes immediately after patching (sum of 3 trials, one trial each

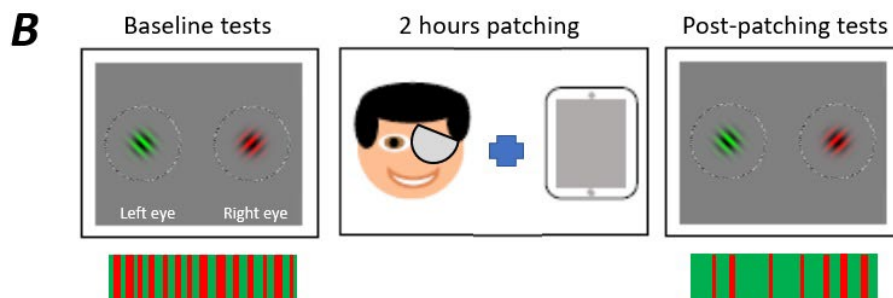
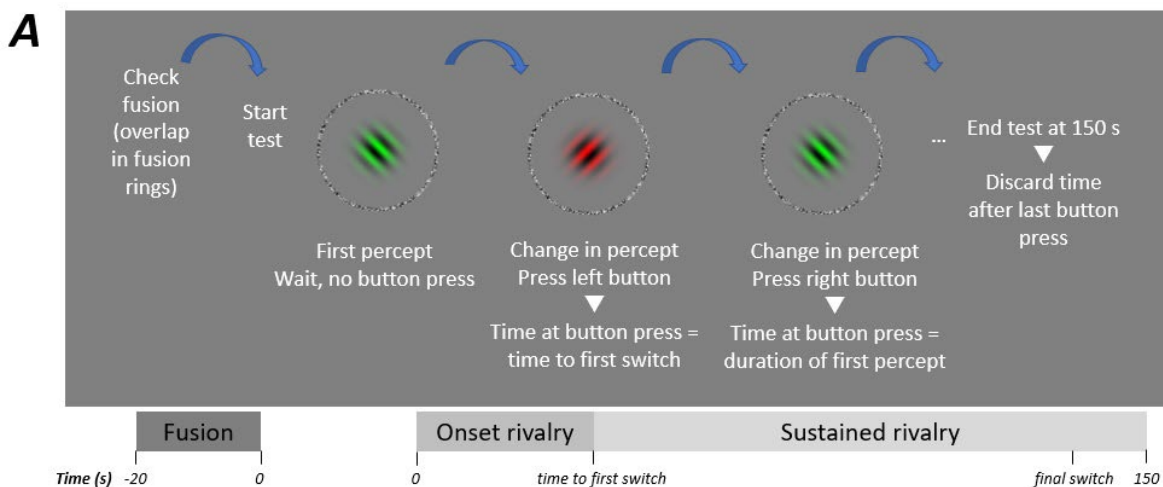
191 at 0, 3 and 6 minutes) and 9-18 minutes after patching (sum of 3 trials, one trial each at 9,

192 12 and 15 minutes). We also collected data at later timepoints (one trial each at 30, 45, 60

193 and 90 minutes) to demonstrate the longevity of the effect of temporary occlusion.

194 Between each trial, participants were given a short (~20 s) break.

195



196

197 **Figure 1 (colour print). Schematic of the visual perceptual testing.** (A) Schematic of a single  
198 binocular rivalry trial. The trial started when the participant confirmed fusion. The trial ran  
199 for 150 seconds. Time to first switch was taken as the measure of onset rivalry. During the  
200 subsequent period of sustained rivalry, percept duration for red, green, and mixed percepts  
201 was recorded. The time after the last button press was discarded for analysis. (B) Schematic  
202 of the test session. Baseline binocular rivalry tests were conducted, followed by two hours of  
203 monocular deprivation with a translucent patch over the dominant eye and normal visual  
204 tasks (including watching a movie and/or computer work). After patch removal, binocular  
205 rivalry was tested at 0, 3, 6, 9, 12, 15, 30, 45, 60 and 90 minutes (one trial at each  
206 timepoint). Under each panel, we include an idealised example of perceptual switches  
207 between the dominant and non-dominant exclusive percepts (red stimulus seen by right eye,  
208 green stimulus seen by left eye) that typically occur randomly at baseline. After patching, the  
209 deprived eye (in this case, left eye patched) is typically reported to become more dominant  
210 (more green percepts).

211

### 212 2.3. Binocular rivalry

213 The visual stimuli for the binocular rivalry task were presented using software  
214 ([https://melbourne.figshare.com/articles/software/\\_/14368988](https://melbourne.figshare.com/articles/software/_/14368988)) written in PsychoPy Version 3.0  
215 and presented on an LCD monitor (BenQ ZOWIE XL2430-B, Taoyuan City, Taiwan) with a  
216 refresh rate of 100 Hz and a screen resolution of 1920 x 1080 pixels. The stimuli were  
217 dichoptically presented using a stereoscope (ScreenScope, Stereo Aids, Albany, Australia)  
218 and the response was collected via mouse press. Participants were seated comfortably at a

219 chinrest and wore the appropriate refractive correction for the working distance (60 cm). All  
220 participants were naïve to the experimental purpose.

221 A schematic of a single binocular rivalry trial (150 second duration) is shown in Figure 1.  
222 A red and green circularly windowed sinusoidal grating pattern (diameter=2°, spatial  
223 frequency= 4 cyc/deg), oriented at 45° and 135°, were presented to the left and right eyes,  
224 respectively. The stimuli presented to each eye remained consistent throughout the  
225 experiment. Two surrounding circles of 12° diameter (width = 0.3°) constructed of random  
226 black and white dots with zero disparity were present throughout testing to aid fusion. At  
227 the beginning of each trial, a central vertical line (left, length = 0.5°) and a central horizontal  
228 line (right, length= 0.5°) were used to indicate the target location and ensure that the  
229 participant could see a binocularly fused fixation cross. The binocular rivalry trial started as  
230 soon as the participant indicated fusion, at which point the fixation cross disappeared but  
231 the fusion circles remained throughout the trial. Participants were instructed not to press a  
232 button until the first switch in percept (time to first switch). Participants then indicated  
233 subsequent changes in percept by clicking a mouse button (right button if the percept was  
234 predominantly red or left button if the percept was predominantly green). Otherwise, if the  
235 percept was a combination of red and green (either piecemeal or superimposed) where  
236 neither red nor green dominated, participants were instructed to press the middle button to  
237 indicate mixed percept. Duration of each percept (time between switches) was recorded.

238

#### 239 2.4. *Monocular deprivation*

240 The dominant eye was determined using a clinical test of sighting dominance (i.e. which  
241 eye dominated when a distant target was viewed binocularly) and was occluded for two

242 hours. Two layers of translucent adhesive tape (3M Transpore surgical tape, Maplewood,  
243 Minnesota, USA) was fixed to a Halberg trial lens clip over a participant's own spectacles, or  
244 attached to a customised eye patch (BSN Medical Leukofix transparent tape, Mulgrave,  
245 Victoria, Australia) if the participant did not wear spectacles. The translucent tape degraded  
246 form perception but allowed light to reach the retina (approximately 30% light attenuation).  
247 Participants were advised to sit quietly during the two hours of patching and were free to  
248 perform normal activities in standard room lighting such as working on a computer,  
249 watching a movie on an iPad and having food and beverages, with the exception of caffeine  
250 intake, which was avoided due to cholinergic alteration of perceptual eye dominance  
251 plasticity (Sheynin, Chamoun, et al., 2019) and the potential for caffeine to increase brain  
252 acetylcholine levels (Carter, O'Connor, Carter, & Ungerstedt, 1995; Corradetti, Pedata,  
253 Pepeu, & Vannucchi, 1986).

254

## 255 2.5. *Data analysis*

256 Our outcome measures of interest are presented herein in the sequential order by  
257 which binocular rivalry characteristics are extracted, starting with time to first switch (as a  
258 measure of onset rivalry), sustained rivalry switch rate (ratio of the number of perceptual  
259 switches to total sustained rivalry time), and proportion of total sustained rivalry time spent  
260 in the dominant eye, non-dominant eye and mixed percepts. Time to first switch and time  
261 after final switch (Figure 1A) were deducted from 150 seconds (length of trial) to obtain  
262 total sustained rivalry time. Although we recorded all percept durations for each of the  
263 dominant eye, non-dominant eye and mixed percepts, binocular rivalry percept duration  
264 distributions are typically a gamma distribution (Levelt, 1967) hence calculating median

265 percept duration is a limited descriptor of the data. Nevertheless, we present median  
266 percept duration data in Supplementary Material A for comparison to other published  
267 reports. Our analysis concentrates on the timepoints immediately after patch removal (0-9  
268 minutes), and on the final measured timepoint (90 minutes post patch removal). Data for all  
269 timepoints is provided in Supplementary Material A.

270 Statistical tests were predominantly conducted in SPSS version 25.0 (IBM, Armonk, NY,  
271 USA). Data were tested for normality using a Kolmogorov-Smirnov test (see Supplementary  
272 Material A). Between-group comparisons of normally distributed data (switch rate,  
273 proportion of time spent in deprived and non-deprived eye percepts) were conducted using  
274 independent student t-tests (paired and unpaired, where appropriate) and repeated  
275 measures analysis of variance (RM-ANOVA). A Huynh-Feldt correction was applied for data  
276 that did not satisfy Mauchly's test of sphericity. For non-normally distributed data (time to  
277 first switch, proportion of time spent in mixed percept), between-group comparisons were  
278 conducted using Mann-Whitney rank sum tests, paired non-parametric Wilcoxon signed  
279 rank tests to compare across two timepoints within groups, and Friedman non-parametric  
280 tests to compare across several timepoints within groups. A  $p$  value of 0.05 was set as the  
281 criterion for statistical significance. Effect sizes (eta-squared, or partial eta-squared values)  
282 and Bayes factors are provided. Bayes factors were determined using JASP (JASP Team,  
283 2020). In addition, in order to demonstrate the effect of deprivation, we normalised the  
284 binocular rivalry outcome measures to each individual's baseline and compared these  
285 normalised values between the groups.

286

287

289 No part of the study procedures nor study analysis were preregistered prior to the research  
290 being conducted.

### 291 3. Results

#### 292 3.1. Onset of rivalry at baseline and after temporary occlusion

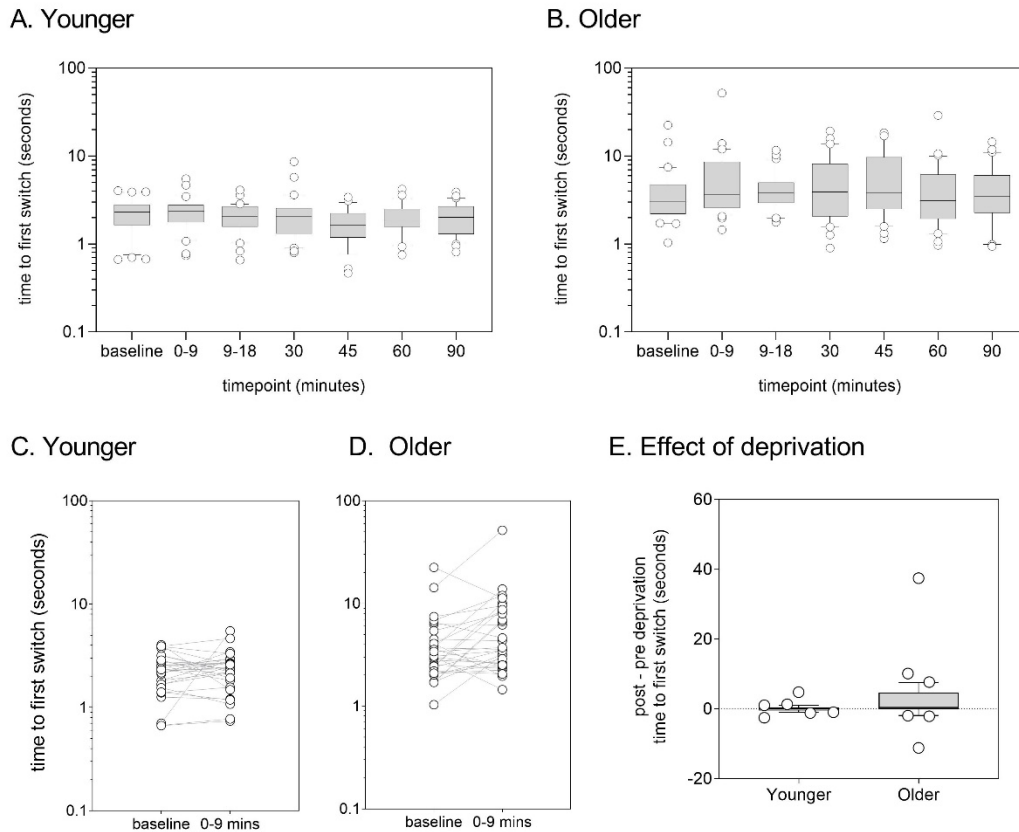
293 Figure 2 shows the time to first switch (i.e. onset of rivalry) in the younger and older  
294 groups at baseline and after temporary occlusion. At baseline, time to first switch was  
295 delayed in the older group by, on average, ~750ms relative to the younger group (median  $\pm$   
296 IQR: younger  $2.30 \pm 1.16$  seconds, older  $3.06 \pm 2.56$  seconds; Mann-Whitney rank sum test:  
297  $p=0.003$ ,  $\eta^2 = 0.15$ ). It is worth noting that this difference between age-groups is  
298 substantively larger than predicted by age-related differences in choice-reaction times  
299 which are slowed by approximately 20ms per decade (Woods, Wyma, Yund, Herron, &  
300 Reed, 2015). Immediately after occlusion (i.e. comparing baseline to 0-9 minutes  
301 immediately after patching), time to first switch increased in the older group (Figure 2D;  
302 Wilcoxon paired signed rank test:  $p=0.032$ , partial  $\eta^2 = 0.15$ ) but not in the younger group  
303 (Figure 2C; Wilcoxon paired signed rank test:  $p=0.77$ , partial  $\eta^2 = 0.003$ ). This age-related  
304 delay in time to first switch remained at the 90 min timepoint (Figure 2B; Wilcoxon paired  
305 signed rank test:  $p=0.079$ , partial  $\eta^2 = 0.10$ ), suggesting a prolonged effect of short-term  
306 monocular deprivation in older adults.

307 To directly compare the effect of deprivation on onset rivalry between groups, we  
308 normalised the time to first switch at 0-9 minutes after patch removal to baseline for each  
309 individual. A larger positive value on the y-axis (Figure 2E) indicates a delayed time to first  
310 switch after deprivation relative to baseline. Although some older adults show a substantial

311 delay in time to first switch immediately after patching (see outliers in Figure 2E), there was  
312 no between-group difference in normalised time to first switch at 0-9 minutes (Mann-  
313 Whitney rank sum test,  $p=0.08$ ,  $\eta^2 = 0.052$ ). Bayes factor analysis suggested anecdotal  
314 evidence for the null hypothesis ( $BF_{01} = 1.20$ ).

315 We also investigated the nature of the immediate percept after patch removal (i.e.  
316 whether from the deprived or non-deprived eye). At the first timepoint after deprivation,  
317 older adults showed relatively more deprived eye percepts (63% dominant/deprived eye,  
318 37% non-dominant eye) than the younger group (30% dominant/deprived eye, 70% non-  
319 dominant eye; chi-square test of proportions:  $\chi^2=6.70$ ,  $p=0.010$ ). This was not the case at  
320 baseline, where the proportion of dominant and non-dominant percepts at onset was the  
321 same for both younger and older groups (47% dominant eye, 53% non-dominant eye).

322



323

324 **Figure 2. Onset of rivalry (time to first switch).** Time to first switch is shown at all timepoints

325 for the (A) younger adults and (B) older adults. Before-after plots show the paired

326 comparisons between baseline vs 0-9 minutes only for the (C) younger adults and (D) older

327 adults. (E) Effect of deprivation (difference between time to first switch measured before and

328 after monocular deprivation), at 0-9 minutes immediately after patch removal. A higher

329 positive value on the y-axis indicates a relatively delayed time to first switch after

330 deprivation compared to baseline. Boxes depict the median, 25<sup>th</sup> and 75<sup>th</sup> percentiles, with

331 the whiskers showing the 10<sup>th</sup> and 90<sup>th</sup> percentiles. All outliers are shown as individual

332 symbols.

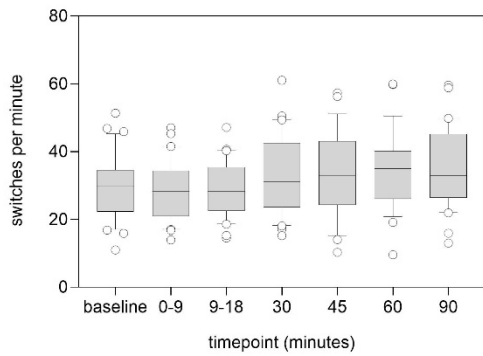
333

334 3.2 Sustained rivalry switch rate at baseline and after temporary occlusion

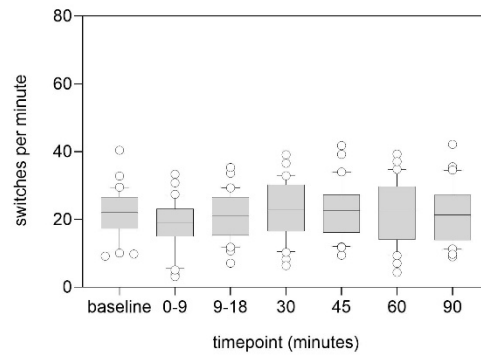
335 At baseline, older adults showed slower sustained rivalry switching compared to  
336 younger adults ( $t_{58}=3.73$ ,  $p<0.001$ ,  $\eta^2 = 0.19$ ), consistent with previous reports (Abuleil,  
337 McCulloch, & Thompson, 2019; Pitchaimuthu et al., 2017). The age-related difference in  
338 switch rate was also present after patching (Figure 3; RM-ANOVA main effect of group:  
339  $F(1,58)=18.9$ ,  $p<0.001$ , partial  $\eta^2 = 0.25$ ). Both groups showed a similar reduction in switch  
340 rate 0-9 mins immediately after temporary occlusion (RM-ANOVA main effect of patching:  
341  $F(1,58)=13.6$ ,  $p=0.001$ , partial  $\eta^2 = 0.19$ ; group x patching interaction:  $F(1,58)=1.70$ ,  $p=0.20$ ,  
342 partial  $\eta^2 = 0.03$ ), suggesting no age-related difference in the effect of short-term monocular  
343 deprivation on switch rate. This result is further supported by directly comparing the switch  
344 rate normalised to baseline (Figure 3E; Mann-Whitney rank sum test,  $p=0.10$ ,  $\eta^2 = 0.046$ ). A  
345 larger positive value on the y-axis (Figure 3E) indicates slower sustained rivalry switch rate  
346 after deprivation relative to baseline. The Bayes factor for the data in Figure 3E was 1.24  
347 ( $BF_{01}$ ), providing anecdotal support for the null hypothesis (that the effect of deprivation on  
348 switch rate is equivalent between groups).

349 To consider the longevity of the effect of patching on switch rate, we compared data  
350 from 0-9 mins to 90 mins post-patching. Both groups showed an increase in switch rate at  
351 90 mins post-patching (RM-ANOVA main effect of time post-patching:  $F(1,58)=35.7$ ,  
352  $p<0.001$ , partial  $\eta^2 = 0.38$ ; group x time post-patching interaction:  $F(1,58)=3.79$ ,  $p=0.056$ ,  
353 partial  $\eta^2 = 0.06$ ), suggesting a recovery in the number of switches over time in younger and  
354 older adults.

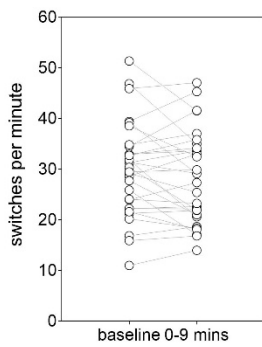
A. Younger



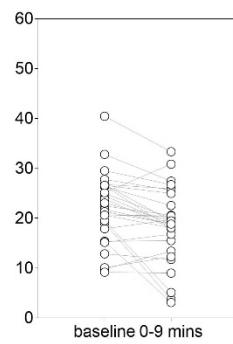
B. Older



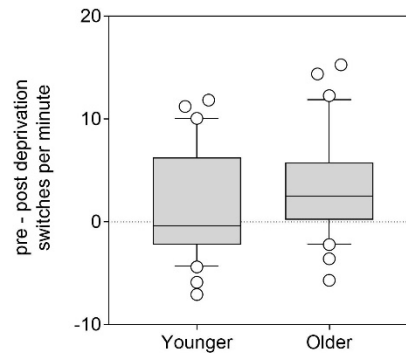
C. Younger



D. Older



E. Effect of deprivation



355

356 **Figure 3. Sustained rivalry switch rate (switches per minute).** Switch rate is shown at all  
 357 timepoints for the (A) younger adults and (B) older adults. Before-after plots show the paired  
 358 comparisons between baseline vs 0-9 minutes only for the (C) younger adults and (D) older  
 359 adults. (E) Effect of deprivation (difference between switch rate measured before and after  
 360 monocular deprivation), at 0-9 minutes immediately after patch removal. A higher positive  
 361 value on the y-axis indicates a relatively slower switch rate after deprivation compared to  
 362 baseline. Boxes depict the median, 25<sup>th</sup> and 75<sup>th</sup> percentiles, with the whiskers showing the  
 363 10<sup>th</sup> and 90<sup>th</sup> percentiles. All outliers are shown as individual symbols.

364

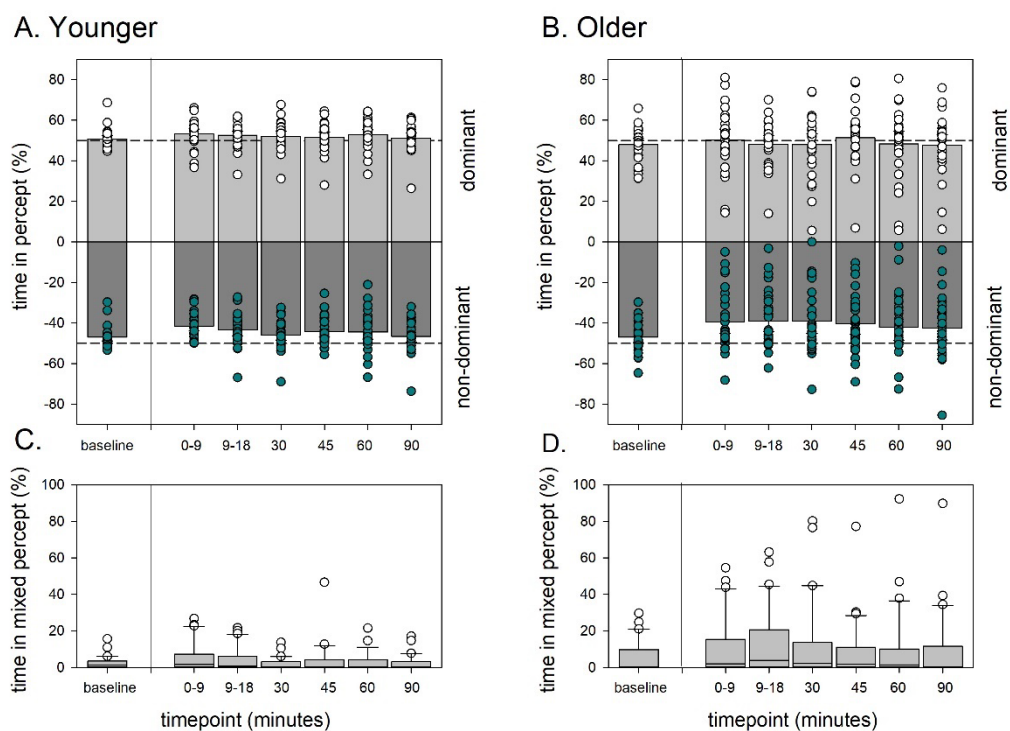
365 **3.3. Time spent in exclusive dominance and mixed percepts after temporary occlusion**

366 Figure 4 summarises the percentage of time spent in the deprived (or dominant) eye,  
367 non-deprived (or non-dominant) eye and mixed percepts before and after patching. Time  
368 spent in the dominant eye percept tended to increase in the 0-9 mins after the patch was  
369 removed (white symbols in Figures 4A and 4B; RM-ANOVA main effect of patching:  
370  $F(1,58)=3.71$ ,  $p=0.059$ , partial  $\eta^2 = 0.06$ ). However, there was no group difference (RM-  
371 ANOVA main effect of group:  $F(1,58)=2.00$ ,  $p=0.16$ , partial  $\eta^2 = 0.03$ ; group x patching  
372 interaction:  $F(1,58)=0.002$ ,  $p=0.97$ , partial  $\eta^2 < 0.001$ ), indicating that both older and  
373 younger adults showed similar effects of short-term monocular deprivation on the  
374 dominant eye percept. In both groups, the dominant eye percept returned to baseline  
375 dominance at 90 mins post-patching (RM-ANOVA main effect of time post-patching:  
376  $F(1,58)=4.53$ ,  $p=0.038$ , partial  $\eta^2 = 0.07$ ; group x time post-patching interaction:  
377  $F(1,58)=0.10$ ,  $p=0.75$ , partial  $\eta^2 = 0.002$ ).

378 On the other hand, time spent in the non-dominant eye percept decreased immediately  
379 following patching (green symbols in Figures 4A and 4B; main effect of patching:  
380  $F(1,58)=29.6$ ,  $p<0.001$ , partial  $\eta^2 = 0.34$ ) in both groups (main effect of group:  $F(1,58)=0.21$ ,  
381  $p=0.65$ , partial  $\eta^2 = 0.004$ ; group x patching interaction:  $F(1,58)=0.64$ ,  $p=0.43$ , partial  $\eta^2 =$   
382  $0.01$ ). At 90 mins post-patching, the time spent seeing the non-dominant eye percept  
383 increased in both groups (RM-ANOVA main effect of time post-patching:  $F(1,58)=7.99$ ,  
384  $p=0.006$ , partial  $\eta^2 = 0.12$ ; group x time post-patching interaction:  $F(1,58)=0.53$ ,  $p=0.47$ ,  
385 partial  $\eta^2 = 0.009$ ). Overall, our results are consistent with a shift in ocular dominance  
386 towards the dominant eye after short-term monocular deprivation, in both younger and  
387 older groups, which did not persist at 90 minutes after the patch was removed.

388 A possible interpretation of our ocular dominance data is that the increase in time spent  
 389 in the dominant eye percept compensated entirely for the reduction in time spent in the  
 390 non-dominant eye percept following patching. However, this interpretation does not  
 391 consider the time spent in mixed percept. Ageing did not affect baseline levels of mixed  
 392 percept (Mann-Whitney rank sum test,  $p=0.96$ ,  $\eta^2 < 0.001$ ). Patching significantly increased  
 393 the time spent in mixed percept in younger adults (Figure 4C; Wilcoxon paired signed rank  
 394 test:  $p=0.007$ , partial  $\eta^2 = 0.24$ ), which returned to baseline levels at 90 mins after patch  
 395 removal (Wilcoxon paired signed rank test:  $p=0.022$ , partial  $\eta^2 = 0.18$ ). The same increase  
 396 was seen in mixed percept after short-term monocular deprivation in the older adults  
 397 (Figure 4D; Wilcoxon paired signed rank test:  $p=0.044$ , partial  $\eta^2 = 0.13$ ). However, the effect  
 398 did not return to baseline and rather persisted at 90 minutes post-patching (Wilcoxon  
 399 paired signed rank test:  $p=0.66$ , partial  $\eta^2 = 0.007$ ) in the older adults.

400



401

402 **Figure 4 (colour print). Time spent in each percept (%) at baseline and after short-term**  
403 **monocular deprivation (0-9, 9-18, 30, 45, 60, 90 minutes after patch removal) in the**  
404 **younger and older groups. (A) Time spent seeing the dominant and non-dominant eye**  
405 **percept for the younger group (n=30). The bars indicate the group mean, and the symbols**  
406 **represent individual results. Horizontal dashed lines at 50% demonstrate that at baseline,**  
407 **the average % time spent in the dominant eye percept is just above 50%, and the average %**  
408 **time spent in the non-dominant eye percept is below 50%. (B) Time spent seeing the**  
409 **dominant and non-dominant eye percept for the older group (n=30). (C) and (D) show**  
410 **boxplots of the time spent in mixed percept for the younger and older groups, respectively.**  
411 **Boxes depict the median, 25<sup>th</sup> and 75<sup>th</sup> percentiles, with the whiskers showing the 10<sup>th</sup> and**  
412 **90<sup>th</sup> percentiles. All outliers are shown as individual symbols.**

413

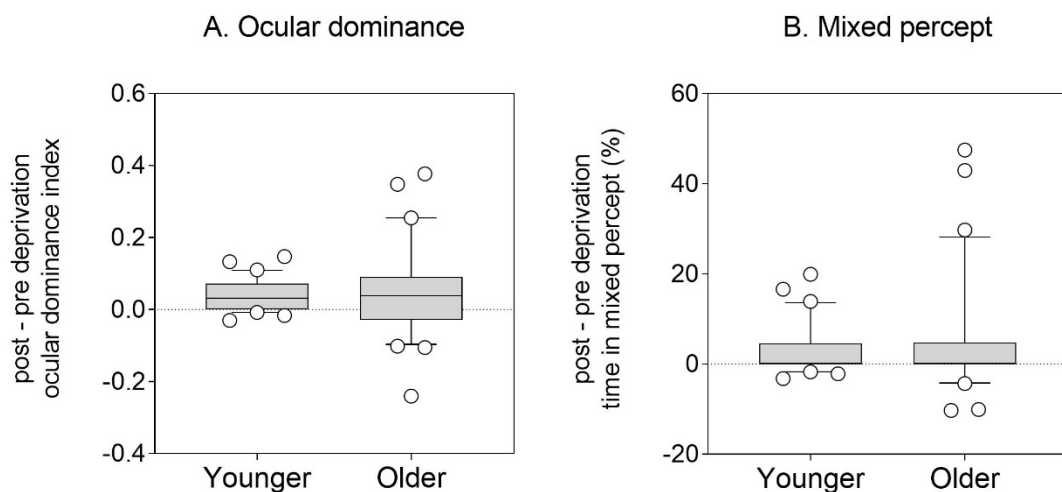
414 To compare the effect of monocular deprivation on exclusive dominance percepts  
415 between groups, we first calculated an index of ocular dominance (Equation 1) as per  
416 previous work (Lunghi, Daniele, et al., 2019), and subtracted the pre-deprivation ocular  
417 dominance index from the post-deprivation ocular dominance index. In equation 1, T refers  
418 to time, spent in the deprived (Dep) and non-deprived (NonDep) eyes.

419 
$$\frac{T_{Dep}}{T_{Dep}+T_{NonDep}} \quad \text{(Equation 1)}$$

420 Complete dominance of the deprived eye is indicated by an ocular dominance index of 1;  
421 therefore, a smaller difference in ocular dominance on the y-axis (Figure 5A) implies a  
422 weaker effect of deprivation. At 0-9 minutes immediately after patch removal, although  
423 both groups showed a consistent bias towards the deprived (or dominant) eye percept,

424 there was no difference between older and younger adults in the strength of the effect of  
 425 deprivation on ocular dominance (Figure 5A; Mann-Whitney rank sum test,  $p=0.84$ ,  $\eta^2 <$   
 426  $0.001$ ). The Bayes factor for this analysis is 3.55 ( $BF_{01}$ ) suggesting moderate evidence for the  
 427 null hypothesis. Similarly, when comparing the proportion of mixed percept before and  
 428 after deprivation between groups, older and younger adults did not differ in the effect of  
 429 deprivation at 0-9 minutes (Figure 5B; Mann-Whitney rank sum test,  $p=0.95$ ,  $\eta^2 < 0.001$ ,  $BF_{01}$   
 430  $= 3.66$ ). At 90 minutes post-deprivation (Figures 5C and 5D), neither ocular dominance  
 431 (Mann-Whitney rank sum test,  $p=0.32$ ,  $\eta^2 = 0.017$ ,  $BF_{01} = 2.10$ ) nor mixed percept (Mann-  
 432 Whitney rank sum test,  $p=0.13$ ,  $\eta^2 = 0.038$ ,  $BF_{01} = 1.69$ ) showed significant group differences  
 433 when normalised to baseline. Thus we find no evidence for a difference in neuroplasticity  
 434 effects on exclusive dominance and mixed percepts with ageing.

435



436

437 **Figure 5. Effect of deprivation (difference between outcomes measured before and after**  
 438 **monocular deprivation) on ocular dominance and mixed percept. Immediate effect of**  
 439 **deprivation at 0-9 minutes on (A) ocular dominance index, calculated as per Equation 1**

440 *based on proportion of total time spent in the deprived (or dominant) and non-deprived (or*  
441 *non-dominant) eye percepts, and on (B) proportion of total time spent in mixed percept.*  
442 *Boxes depict the median, 25<sup>th</sup> and 75<sup>th</sup> percentiles, with the whiskers showing the 10<sup>th</sup> and*  
443 *90<sup>th</sup> percentiles. All outliers are shown as individual symbols. Smaller values on the y-axis*  
444 *indicate a weaker effect of deprivation.*

445

#### 446 **4. Discussion**

447 Our data demonstrates that the older adult visual system is still highly capable of short-  
448 term neuroplastic regulation of visual experience. The ability of a short period (2 hours) of  
449 monocular translucent occlusion to alter binocular rivalry dynamics is similar in older and  
450 younger adults, despite age-related differences in rivalry characteristics in the absence of  
451 occlusion (i.e. slower rivalry switching and longer time to the first switch in older adults).

452 Based on previous literature suggesting a strengthening of some forms of contrast gain  
453 regulation effects in older adults (Elliott & Werner, 2010; Elliott et al., 2012; McKendrick et  
454 al., 2018), we hypothesised that the effects of short-term deprivation might be  
455 strengthened in older adults. Our data did not provide evidence in support of this outcome.  
456 Specifically, the standard metric of homeostatic neuroplasticity (ocular dominance index,  
457 Figure 5A) was not different between groups. Interpretation of the Bayes factor suggests  
458 moderate evidence in support of the null hypothesis in this case. However, it is worth noting  
459 that we observed substantial inter-individual differences in the effect of occlusion,  
460 particularly in the older adult group.

461 Further work is required to explore the likely mechanisms underpinning inter-individual  
462 differences in various aspects of binocular rivalry, however, there is recent data that

463 points to interesting relationships between mechanisms underpinning different types of  
464 inhibitory phenomena in human vision. Of particular relevance is a recent observation  
465 that interindividual differences in tilt illusion strength (an alternate measure of inhibition  
466 within the visual system) partially predicts the magnitude of effect of occlusion on ocular  
467 dominance in younger adults, such that a stronger tilt illusion predicts a stronger effect of  
468 occlusion (Steinwurz, Animal, Cicchini, Morrone, & Binda, 2020). We have previously  
469 shown that the tilt illusion strength is, on average, elevated in older adults (Nguyen &  
470 McKendrick, 2016). However substantial interindividual differences in performance existed  
471 in that dataset also. One interpretation of the finding of Steinwurz et al (2020), is  
472 that older adults with stronger tilt illusion strength, which is associated with stronger visual  
473 cortical inhibition (Seymour, Stein, Clifford & Sterzer 2018), should be predicted to have  
474 slower binocular rivalry switch rates, and in turn, a stronger effect of occlusion on the ocular  
475 dominance index. Clearly we do not have data on the strength of the tilt illusion in our  
476 participants. However, we did check whether there was any evidence in our data for a  
477 relationship between baseline rivalry switch rate and the effect of occlusion on ocular  
478 dominance. There was not (Kendall's tau = 0.054,  $p=0.54$ ,  $BF_{01} = 4.9$ ). We also considered  
479 whether ocular dominance plasticity is related to the proportion of mixed percept at  
480 baseline (Kendall's tau = -0.03,  $p = 0.74$ ,  $BF_{01} = 5.6$ ). Consequently, in our dataset, we did not  
481 find evidence to support a relationship between baseline features of rivalry and the strength  
482 of the effect of occlusion.

483 At the time of experimental design, we were primarily interested in the measurement of  
484 exclusive visual percepts (entirely red or entirely green) because the majority of previous  
485 literature exploring the effects of short-term monocular deprivation on binocular rivalry  
486 dynamics has concentrated on the analysis of exclusive percepts. We did ask participants to

487 report the presence of mixed percept (a mix of red and green) but did not explore in detail  
488 the specific phenomenology of the mixed percept experience. Mixed percepts can have  
489 varied forms but are typically either superimposed versions of the two component gratings  
490 or piecemeal representations. It has recently been reported that short-term monocular  
491 occlusion results in an increase in mixed percept, and specifically, an increase of  
492 superimposition (Sheynin, Proulx, & Hess, 2019); although an increase of mixed percept  
493 post occlusion is not universal (Steinwurz et al., 2020). Consistent with the general findings  
494 of Sheynin et al (2019), our Figure 4 shows a trend for a decrease in the time spent in the  
495 non-dominant eye post-patching with some reallocation of that time to mixed percept. This  
496 effect occurred in both younger and older adults. While the mechanisms underlying mixed  
497 percept are a matter of considerable debate, a recent study has shown that the  
498 pharmacological modulation of GABA receptors in humans can increase the predominance  
499 of exclusive perceptual dominance relative to mixed percept (Mentch et al., 2019). Our  
500 study clearly cannot contribute to further informing knowledge of the mechanisms  
501 underpinning mixed percept, with the exception of suggesting that the regulation of these is  
502 not markedly affected by the normal aging process, at least for the age groups tested  
503 herein.

504 On average, our deprivation effects on ocular dominance are smaller than reported  
505 previously in younger adults (Lunghi, Daniele, et al., 2019, Binda & Lunghi 2017, Steinwurz  
506 et al., 2020). In our main results, we chose to present ocular dominance in terms of the total  
507 time spent in the deprived (or dominant) and non-deprived (or non-dominant) eye percept  
508 (see Equation 1 from Lunghi et al., 2019) to make use of all data collected across the  
509 binocular rivalry runs, instead of taking a single estimate of central tendency (i.e. mean or  
510 median percept duration). Subtracting the pre-deprivation ocular dominance index from the

511 post-deprivation ocular dominance index (Figure 5A), we found approximately half the  
512 effect of deprivation as reported previously in normal-weighted adults (Lunghi et al., 2019).  
513 To directly compare the magnitude of the effect of patching with other previous work, we  
514 have also calculated a ‘deprivation index’ (Equation 2) based on mean percept duration,  
515 using the same method as in Binda and Lunghi (2017):

516 
$$\frac{\text{deprived eye}_{pre}}{\text{deprived eye}_{post}} \times \frac{\text{nondeprived eye}_{post}}{\text{nondeprived eye}_{pre}} \quad (\text{Equation 2})$$

517

518 An index of 1 indicates no change in ocular dominance after deprivation, an index of < 1  
519 indicates increased dominance of the deprived eye, and an index of > 1 indicates increased  
520 dominance of the non-deprived eye. The mean deprivation effect in our study was smaller  
521 (mean ± standard deviation: younger 0.9 ± 0.1, older 0.9 ± 0.5) than that reported by Binda  
522 and Lunghi (2017) of 0.7 (± 0.3). There are numerous differences in experimental design that  
523 might contribute to the difference in strength of deprivation. These include methodological  
524 differences in the binocular rivalry paradigm such as the use of shutter goggles in the study  
525 of Binda and Lunghi (2017), continuous button pressing (here we asked participants to press  
526 a button only when a switch in percept was observed) and duration of test run; and the  
527 choice of dominant eye being through sighting dominance (as was the case here) or  
528 assessed from the baseline binocular rivalry data. It is also worth noting that the study of  
529 Binda and Lunghi (2017) only assessed 10 individuals and that some significant variance in  
530 the effect of deprivation was noted within that group.

531 Temporary occlusion is a potent method for demonstrating short-term visual system  
532 neuroplasticity, but in addition to being an experimental method, may have some direct  
533 utility in improving visual performance. There has been intense interest in this effect in the

534 context of treatments for sight improvement in amblyopia (Lunghi, Sframeli, et al., 2019;  
535 Sauvan et al., 2019). Amblyopia is a developmental disorder resulting in reduced visual  
536 acuity in one eye, and typically occurs due to strabismus, anisometropia or deprivation (for  
537 example due to congenital cataract), early in life. Approximately 1-5% of people have  
538 amblyopia (Webber & Wood, 2005), which carries significant risk of further visual  
539 impairment in older age, if the residual eye with better vision is damaged due to common  
540 age-related eye disease. Traditionally, therapies for amblyopia are considered effective in  
541 childhood, but more recently have been shown to maintain effectiveness into adulthood  
542 (Astle, Webb, & McGraw, 2011; Li et al., 2013; Simonsz-Toth, Joosse, & Besch, 2019). Such  
543 treatments typically involve varying the regulation of input from the two eyes to the  
544 binocular percept. Recent studies have begun to explore whether short-term occlusion of  
545 the amblyopic eye (which is counter to traditional therapies that occlude the “good” eye in  
546 order to make the amblyopic eye work) can be used to upregulate the visual system to  
547 respond to input from the amblyopic eye after patch removal (Lunghi, Sframeli, et al., 2019;  
548 Sauvan et al., 2019). Our findings suggest that these effects should be maintained in older  
549 age. Future studies are required to determine whether occlusion driven neuroplastic  
550 responses can be exploited to improve perceptual training in older adults, not only for  
551 amblyopia, but to perhaps improve perceptual retraining post visual loss due to age-related  
552 eye disease.

553

## 554 **5. Conclusions**

555 The older brain is able to rapidly adjust to changes in perceptual experience induced by  
556 temporary eye occlusion similarly to that observed previously in younger adults. We find no

557 evidence for a reduction in this ability. Previous studies have shown that visual perceptual  
558 learning methods are often equally as effective in older as in younger adults (DeLoss,  
559 Watanabe, & Andersen, 2015; McKendrick & Battista, 2013). Our data provides additional  
560 evidence for the ability of the older brain to dynamically respond to local visual experience  
561 and demonstrates that visual plasticity is maintained throughout the lifespan.

562

## 563 **6. Appendices**

564 Supplementary Material A contains all individual data for a) age, b) percentage time spent in  
565 dominant percept, non-dominant percept and mixed percept; c) switches per minute; d)  
566 time to first switch; e) median percept duration for dominant eye, non-dominant eye and  
567 mixed percept.

568

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