



**QUEEN'S
UNIVERSITY
BELFAST**

The duration compression effect is mediated by adaptation of both retinotopic and spatiotopic mechanisms

Latimer, K., & Curran, W. (2016). The duration compression effect is mediated by adaptation of both retinotopic and spatiotopic mechanisms. *Vision Research*, 122, 60-65. <https://doi.org/10.1016/j.visres.2016.01.010>

Published in:
Vision Research

Document Version:
Peer reviewed version

Queen's University Belfast - Research Portal:
[Link to publication record in Queen's University Belfast Research Portal](#)

Publisher rights

© 2016 Elsevier Ltd. This manuscript version is made available under the CC-BY-NC-ND 4.0 license <http://creativecommons.org/licenses/by-nc-nd/4.0/> which permits distribution and reproduction for non-commercial purposes, provided the author and source are cited.

General rights

Copyright for the publications made accessible via the Queen's University Belfast Research Portal is retained by the author(s) and / or other copyright owners and it is a condition of accessing these publications that users recognise and abide by the legal requirements associated with these rights.

Take down policy

The Research Portal is Queen's institutional repository that provides access to Queen's research output. Every effort has been made to ensure that content in the Research Portal does not infringe any person's rights, or applicable UK laws. If you discover content in the Research Portal that you believe breaches copyright or violates any law, please contact openaccess@qub.ac.uk.

Open Access

This research has been made openly available by Queen's academics and its Open Research team. We would love to hear how access to this research benefits you. – Share your feedback with us: <http://go.qub.ac.uk/oa-feedback>

The duration compression effect is mediated by adaptation of both retinotopic and
spatiotopic mechanisms

Kevin Latimer and William Curran

School of Psychology, Queen's University Belfast

Corresponding author: klatimer01@qub.ac.uk

Word count: 5,293

1 **Abstract**

2 The duration compression effect is a phenomenon in which prior adaptation to a spatially
3 circumscribed dynamic stimulus results in the duration of subsequent subsecond stimuli
4 presented in the adapted region being underestimated. There is disagreement over the
5 frame of reference within which the duration compression phenomenon occurs. One view
6 holds that the effect is driven by retinotopic-tuned mechanisms located at early stages of
7 visual processing, and an alternate position is that the mechanisms are spatiotopic and
8 occur at later stages of visual processing (MT+). We addressed the retinotopic-spatiotopic
9 question by using adapting stimuli – drifting plaids - that are known to activate global-motion
10 mechanisms in area MT. If spatiotopic mechanisms contribute to the duration compression
11 effect, drifting plaid adaptors should be well suited to revealing them. Following adaptation
12 participants were tasked with estimating the duration of a 600ms random dot stimulus,
13 whose direction was identical to the pattern direction of the adapting plaid, presented at
14 either the same retinotopic or the same spatiotopic location as the adaptor. Our results
15 reveal significant duration compression in both conditions, pointing to the involvement of
16 both retinotopic-tuned and spatiotopic-tuned mechanisms in the duration compression effect.

17 **Key words: Time perception, adaptation, motion processing**

18

19

20 **1. Introduction**

21 The ability to accurately perceive and time subsecond durations is critical for a number of
22 everyday tasks including understanding and producing speech, and executing complex
23 motor actions such as intercepting targets and avoiding collisions (Mauk & Buonomano,
24 2004; Zarco et al., 2009). There is a growing body of evidence suggesting that encoding of
25 subsecond durations is carried out by distributed modality-specific mechanisms (Buonomano
26 & Karmarkar, 2002; Grondin, 2010; Karmarkar & Buonomano, 2007). Evidence for the

27 existence of timing mechanisms within the visual modality has been provided by a number of
28 studies which have shown that duration judgments of subsecond visual stimuli can be
29 distorted following prior visual adaptation. Johnston, Arnold and Nishida (2006) reported
30 that prior adaptation to a 20Hz oscillating sine wave pattern resulted in the duration of a
31 subsequent subsecond (600ms) 10Hz test pattern presented in the same location being
32 underestimated. However no such effect was found when the adaptor oscillated at 5Hz. A
33 similar pattern of results was observed when the grating stimuli were replaced with Gaussian
34 patches, whose brightness changed sinusoidally, thus demonstrating that the underlying
35 mechanisms are temporal frequency tuned. Johnston et al. (2006) also provided evidence
36 to suggest that the duration compression effect is orientation-independent, by showing that
37 the effect persists when the adaptor is rotated 90° relative to the test stimulus. Given that
38 area V1 is the earliest visual area to exhibit orientation selectivity (Hubel & Wiesel, 1968), it
39 has been suggested that direction-independent duration compression points to the
40 involvement of pre-striate timing mechanisms (Bruno, Ng & Johnston, 2013).

41

42 Since Johnston et al.'s initial study a number of similar adaptation paradigms have been
43 employed in an attempt to determine where in the visual pathway the mechanisms
44 underlying the duration compression effect reside. Some of these studies have provided
45 more evidence in favour of pre-cortical timing mechanisms. For instance Ayhan et al. (2009)
46 demonstrated that even very narrow (0.75° x 1°) adaptors can induce duration compression
47 and that the effect is tightly tuned to the spatial location of the adaptor. These findings would
48 suggest that visual neurons with small receptive fields, typically found at early pre-cortical
49 locations, are involved in timing subsecond stimuli. A duration compression effect has also
50 been induced with flickering adaptors whose flicker was set to above the flicker fusion
51 threshold (Johnston et al., 2008). Pre-cortical regions have been shown to respond to
52 higher temporal frequencies than cortical areas (Hawken, Shapley & Grosf, 1996). The
53 finding that duration compression is induced with an adaptor whose temporal frequency is

54 above the flicker fusion threshold, but low enough to stimulate LGN cells, provides further
55 support for the involvement of pre-cortical timing mechanisms.

56

57 Despite the compelling evidence that adaptation-induced duration compression is driven by
58 pre-cortical mechanisms, cortical mechanisms also appear to contribute to the effect. For
59 example, a number of studies have shown the duration compression effect to be direction
60 contingent. Curran and Benton (2012) were the first to demonstrate this direction-contingent
61 effect using unidirectional random dot kinematograms (RDK). In their study participants
62 adapted to an RDK drifting upwards at a speed of 3°s^{-1} before judging the duration of a
63 600ms test RDK presented in the same location as the adaptor, and which drifted in either
64 the same direction or in the opposite direction to the adaptor. Whilst robust duration
65 compression was observed when the adaptor and test stimuli drifted in the same direction,
66 there was no evidence of a duration distortion when they drifted in opposite directions. The
67 direction-contingent nature of this effect implies the involvement of cortical timing
68 mechanisms, as cortical area V1 is the earliest point in the visual pathway to contain
69 direction-selective neurons (Hubel & Wiesel, 1968).

70

71 In contrast to Curran and Benton's (2012) findings, Marinovic and Arnold (2012) found no
72 evidence to suggest that the duration compression effect is direction contingent. In their
73 study participants adapted to six white dots (each with diameter 0.88°) arranged in a circular
74 pattern rotating at high speed (410°s^{-1}), then estimated the duration of a short-lasting (300-
75 500ms) single white dot (speed = $205.2^{\circ}\text{s}^{-1}$) presented within the adapted area. Duration
76 compression was observed irrespective of the test dot's direction of rotation. The observed
77 direction-independent duration compression was at odds with the direction-contingent effect
78 reported by Curran & Benton. However, the absence of a direction-contingent effect in
79 Marinovic & Arnold's study is likely to be a consequence of the high speed stimuli used.

80 Indeed a recent study by Bruno, Ng and Johnston (2013) suggests that direction-contingent
81 duration compression occurs with low speed, but not high speed, stimuli. Bruno et al.
82 adapted participants to sinusoidal gratings drifting at a range of temporal frequencies (3Hz,
83 8Hz, 13Hz & 18Hz) before judging the duration of a 600ms test grating drifting at the same
84 temporal frequency and drifting in either the same or opposite direction as the adaptor.
85 Duration compression was found to be direction-contingent when 3Hz stimuli were used;
86 however when the higher temporal frequency stimuli were used the effect was observed
87 irrespective of test stimulus drift direction. Bruno et al. take this to be evidence that
88 adaption-induced duration compression is driven by both pre-cortical, direction-independent
89 mechanisms and cortical, direction-contingent mechanisms. They suggest that the cortical
90 mechanisms are likely to reside early in the cortex at area V1.

91

92 Attempts are ongoing to determine where the mechanisms underlying duration compression
93 are located in the visual system. Related to these attempts is the debate regarding the
94 frame of reference within which the phenomenon takes place. This debate was sparked by
95 Burr, Tozzi and Morrone (2007), who carried out a study to determine whether or not the
96 duration compression effect reported by Johnston et al. was governed by retinotopic-tuned
97 or spatiotopic-tuned mechanisms. In their study they adapted participants to an oscillating
98 grating before asking them to judge the duration of a subsequent 600ms test grating
99 stimulus presented under one of three conditions. In the 'full adaptation' condition
100 participants maintained their fixation at the same location following adaptation; the test
101 grating was presented in the same location as the adaptor, and thus had the same retinal
102 and spatial coordinates as the adaptor. In the other two conditions the participants
103 performed a saccade to a new fixation point following the adaptation period, which allowed
104 the effects of retinotopic and spatiotopic adaptation to be examined separately. In the
105 spatiotopic condition the test stimulus was presented in the same spatial location on the
106 screen as the adaptor, whilst in the retinotopic condition the test stimulus was placed in the

107 same location as the adaptor relative to the fixation point. Duration compression was
108 observed in all three conditions when the physical speeds of the test and comparison stimuli
109 were matched; however, when their speeds were matched perceptually duration
110 compression only occurred in the full and spatiotopic conditions. It was concluded that the
111 duration compression observed in the retinotopic condition reflected a change in the
112 perceived speed of the test stimulus as a result of adaptation, and that the neural
113 mechanisms underlying the duration compression effect must operate in a spatiotopic frame
114 of reference. Visual area MT+ has been suggested as a candidate area for the location of
115 these timing mechanisms (Morrone, Cicchini & Burr, 2010), as past evidence has linked this
116 area to subsecond timing (Janssen & Shadlen, 2005; Leon & Shadlen, 2003) and it is the
117 earliest visual area in which spatiotopic encoding has been shown to occur (Goosens et al.,
118 2006).

119

120 This proposal that the mechanisms underlying the duration compression effect are
121 spatiotopic-tuned is disputed by Bruno, Ayhan and Johnston (2010). Using similar methods
122 to Burr et al.'s study they reported a duration compression effect which only occurred in the
123 'full' and 'retinotopic' conditions, with no evidence found to support spatiotopic duration
124 compression. This finding suggests that the underlying timing mechanisms operate in a
125 retinotopic frame of reference, a finding which also implies that the mechanisms are likely to
126 be situated early in the visual pathway. The contrasting results reported by Bruno et al. and
127 Burr et al. have proven difficult to reconcile, however there were some methodological
128 differences between the two studies which may account for this. For instance Bruno et al.
129 matched only the physical speeds of their test and comparison stimuli. Under such
130 conditions Burr et al. reported a significant duration distortion in both the retinotopic and
131 spatiotopic conditions. However, whilst this methodological difference might offer an
132 explanation for Bruno et al.'s reported retinotopic effect it doesn't explain the study's lack of
133 a spatiotopic effect. Differences in presentation order may also offer some insight into the

134 contrasting results. Burr et al. always presented their test stimulus before the comparison in
135 their experiment, whilst Bruno et al. randomised their presentation order. Bruno et al. have
136 speculated that order effects might therefore partly explain the spatiotopic duration
137 compression observed in Burr et al.'s study. This is because the magnitude of the second of
138 a pair of stimuli tends to be overestimated for a number of different characteristics, including
139 duration (Lapid, Ulrich & Rammsayer, 2008; Nachmias, 2006). However Burr et al. (2011)
140 have dismissed this notion, pointing out that their data were calculated as the difference
141 between the adapted and unadapted conditions, thus cancelling out any potential temporal
142 order effects.

143

144 Latimer, Curran & Benton (2014) attempted to address the retinotopic-spatiotopic debate;
145 however, instead of using oscillating gratings, they used slow-speed (3°s^{-1}) unidirectional
146 RDK's identical to those used by Curran and Benton (2012). Under these conditions a
147 significant duration compression effect was observed in both the full and retinotopic
148 conditions, but not in the spatiotopic condition. However, the duration compression in the full
149 adaptation condition was significantly larger than that observed in the retinotopic condition,
150 suggesting a possible contribution to the effect from spatiotopic mechanisms. Additionally,
151 despite the lack of a significant spatiotopic effect in their study, the results hinted at the
152 possible involvement of spatiotopic mechanisms as 3 out of the 7 participants showed
153 evidence of a weak, but significant duration compression in the spatiotopic condition. These
154 two findings seem to suggest that retinotopic adaptation alone may not fully explain the
155 duration compression effect and leaves the door open for a possible spatiotopic influence.

156

157 The contrasting results of previous research addressing the retinotopic-spatiotopic question
158 may be a consequence of using adaptor and test stimuli that are not well suited to
159 uncovering spatiotopic mechanisms. The present study attempts to overcome this by using

160 an adaptor-test stimulus combination suited to the task. Our choice of stimuli was based on
161 an experiment reported by Curran and Benton (2012). In their experiment participants
162 adapted to a plaid stimulus comprising two superimposed drifting sinusoidal gratings (1 cycle
163 deg^{-1}), whose orientations differed by 40° ($\pm 20^\circ$ off vertical) such that their drift directions
164 were $\pm 70^\circ$ either side of vertically upwards at a speed of 1.03°s^{-1} . Participants perceived the
165 stimulus as a uni-directional drifting plaid moving upwards at a speed of 3°s^{-1} . Following
166 adaptation to the plaid, participants underestimated the duration of a subsequently
167 presented upwards drifting RDK. However when a transparent moving dot pattern, whose
168 two motion directions matched the plaid's component directions, was used as the adaptor
169 there was no subsequent duration compression observed. Given that drifting plaids are
170 known to selectively stimulate MT neurons tuned to the plaid's global motion direction
171 (Movshon et al., 1985) Curran and Benton concluded that it is likely cortical timing
172 mechanisms exist at or beyond area MT. Since MT direction-sensitive neurons respond to
173 plaid global motion, and area MT+ is the earliest known point in the motion pathway where
174 spatiotopic encoding occurs (Goosens et al., 2006), we reasoned that if spatiotopic
175 mechanisms contribute to the duration compression effect then the stimuli used by Curran
176 and Benton would be well suited to revealing them.

177

178 We ran a modified version of our previous study (Latimer, Curran & Benton, 2014).
179 Whereas Latimer et al. used drifting RDKs as adaptor and test stimuli, the current
180 experiment used a drifting plaid stimulus as the adaptor and the test stimulus was an RDK
181 drifting in the same direction as the adaptor's pattern motion. Following adaptation
182 participants judged the duration of a drifting RDK presented in either the same retinotopic or
183 spatiotopic location (or both in the full condition) as the adaptor. The drift directions of the
184 plaid's components were $\pm 70^\circ$ either side of vertically upwards. Previous research (Bruno et
185 al., 2013) has shown duration compression to be direction tuned when slow moving stimuli
186 (3Hz) are used, with the effect's magnitude rapidly reducing with increased adaptor-test

187 direction difference, and is abolished for adaptor-test direction differences of between 45°
188 and 90°. Thus, while the plaid adaptor in our experiment induces adaptation in both local
189 and global motion mechanisms, the large difference (70°) between each component
190 direction and test stimulus direction ensures that any observed duration compression must
191 be the result of global motion adaptation.

192

193 As with our previous study a significant duration compression was observed in the full and
194 retinotopic conditions. However, this time around we also found compelling evidence for the
195 involvement of spatiotopic mechanisms in the duration compression effect.

196

197

198 **2. Methods**

199 **2.1. Participants**

200 Seven participants (2 authors, 5 naïve) completed the experiment. All participants had
201 normal or corrected-to-normal vision. The experiment was conducted in accordance with the
202 Code of Ethics of the World Medical Association (Declaration of Helsinki), and informed
203 consent was obtained from each participant.

204

205 **2.2. Apparatus**

206 All stimuli were presented on a Mitsubishi Diamond Pro 2070^{SB} monitor driven by a
207 Cambridge Research Systems Visage at a frame rate of 120 Hz. The viewing distance was
208 71cm.

209

210 **2.3. Stimuli**

211 The adaptor was an upwards drifting plaid stimulus and was constructed by superimposing
212 two drifting sinusoidal gratings (1 cycle deg⁻¹, Michelson contrast = 0.6) whose orientations
213 differed by 40° (±20° off vertical). The drift directions of the plaid components were ±70° to
214 either side of vertically upwards at a speed of 1.03°s⁻¹, resulting in an upwards pattern speed
215 of 3°s⁻¹. The test and comparison stimuli were both unidirectional, mixed-polarity, translating
216 RDKs (dot diameter = 1.8 arcmin; dot density = 12.9 dots/deg²) set against a mean
217 luminance background (28.5 cd/m²). Each stimulus was presented within a circular aperture
218 (diameter 6.3°).

219

220 **2.4. Procedure**

221 Participants initially adapted to a plaid drifting upwards at a speed of 3°s⁻¹ for 30s whilst
222 fixating on a black 'x' to its lower left (see Figure 1). Following adaptation the fixation marker
223 either remained in the same location (full adaptation condition) or was re-plotted 7.6° to the
224 right and participants made a saccade to it (retinotopic and spatiotopic conditions).
225 Participants were then presented with the test and comparison RDK stimuli, with
226 presentation order being randomised from trial to trial, and were required to judge which one
227 had the longer duration. Subsequent duration judgment trials were preceded with a 5s 'top
228 up' adaptor, thus ensuring that the adaptive state was maintained. In the full adaptation
229 condition the test and comparison stimuli were presented above and to the right and below
230 and to the right of fixation, respectively; thus the test stimulus was presented in the same
231 retinal and spatial location as the adaptor and the comparison was presented outside of the
232 adapted region. In the retinotopic condition participants performed a saccade after
233 adaptation and the test stimulus was presented above and to the right of the fixation's new
234 location, at the same retinal coordinates as the adaptor, and the comparison stimulus was
235 presented below and to the right of the new fixation. In the spatiotopic condition participants
236 again performed a saccade after adaptation, but this time the test stimulus was presented at
237 the same physical location on the screen as the adaptor, above and to the left of the

238 fixation's new location, and the comparison was presented below and to the left of the new
239 fixation. The test and comparison stimuli were always presented in the same hemifield, thus
240 controlling for previously reported biases in duration estimation of stimuli presented in
241 different hemifields (Vicario et al., 2008).

242

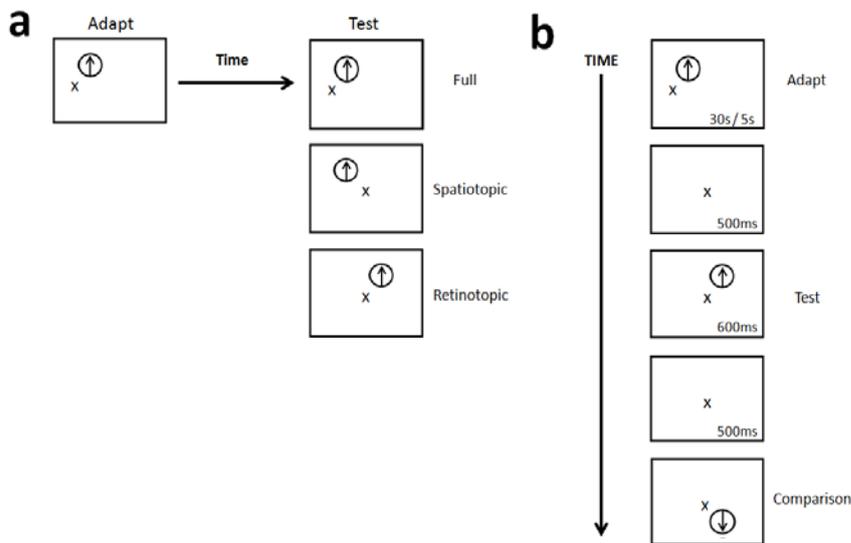
243 In all three conditions the test stimulus was an RDK drifting upwards at a speed of 3°s^{-1} and
244 the comparison stimulus was an RDK which drifted downwards. Comparison stimulus speed
245 was set to match each participant's perceived speed of the test stimulus; thus controlling for
246 adaptation-induced speed distortions (Thompson, 1981), and taking into account previous
247 reports that perceived speed influences apparent duration (Brown, 1995; Kanai et al., 2006;
248 Kaneko & Murakami, 2009). The perceived speed measurements were gathered in an initial
249 preliminary experiment which was identical to the duration experiment, with the exception
250 that the test and comparison stimuli were presented for the same duration (600ms),
251 comparison speed varied from trial to trial, and participants judged whether the comparison
252 stimulus was moving faster or slower than the test stimulus. Mean perceived speed of the
253 test stimulus following adaptation was $2.69^{\circ}\text{s}^{-1}$ (range: 2.14 – 3.13) for the full adaptation
254 condition, $2.73^{\circ}\text{s}^{-1}$ (range: 2.16 - 3.24) for the retinotopic condition, and $2.78^{\circ}\text{s}^{-1}$ (range: 2.3 –
255 3.17) for the spatiotopic condition.

256

257 In the main duration experiment test stimulus duration was fixed at 600ms, while comparison
258 stimulus duration was varied from trial to trial. Comparison stimulus duration was chosen by
259 an adaptive method of constants procedure (Watt & Andrews, 1981) thus optimising the
260 estimation of the 'point of subjective equality' (PSE), i.e. the duration at which the
261 comparison stimulus was judged to match that of the test stimulus. Each PSE was
262 generated from 64 duration judgments with 4 PSEs generated per viewing condition, such

263 that each participant's duration estimate for each condition was generated based on a total
264 of 256 trials.

265



266

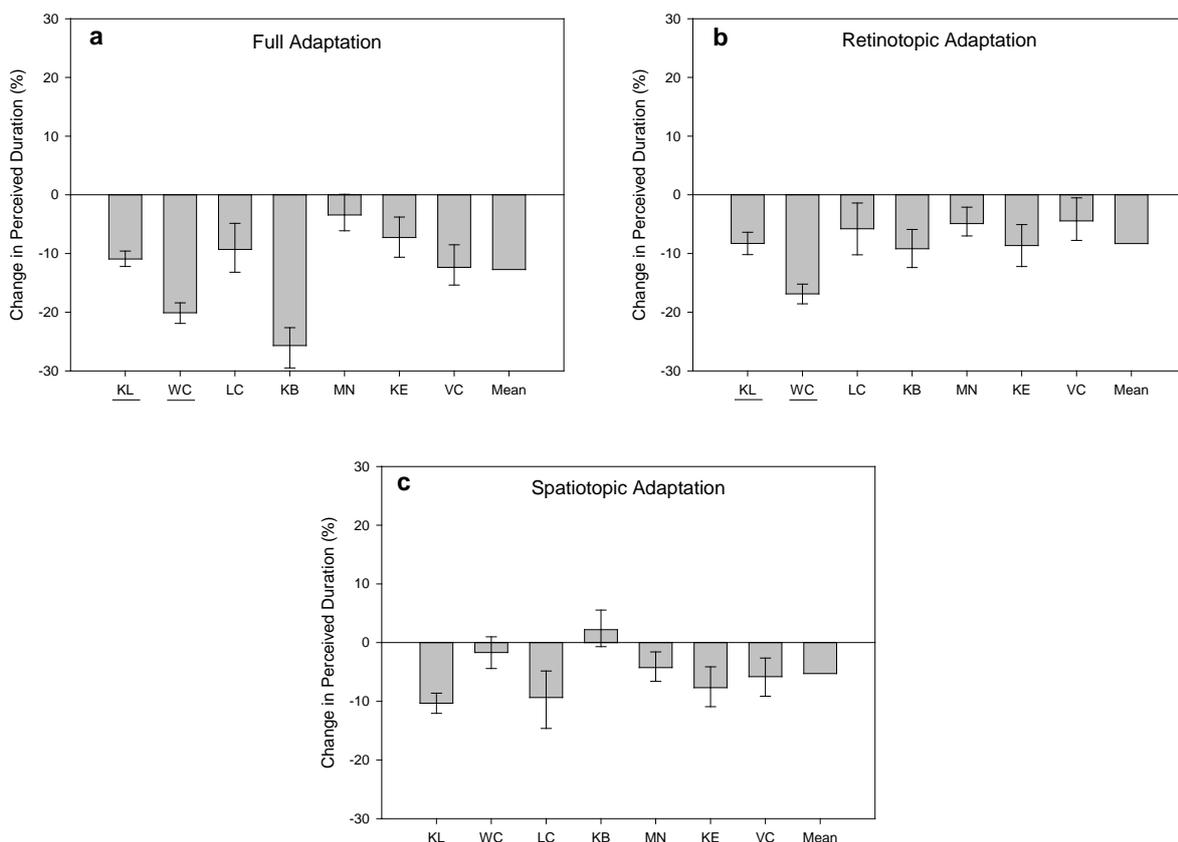
267 **Figure 1.** (a) The locations of the adaptor and test stimuli for each condition. The location of the
268 fixation is represented by an 'x'. During adaptation the plaid adaptor was centred 4.2° to the right and
269 3.5° above fixation. Following adaptation the fixation either remained in the same location (full
270 adaptation condition) or moved 7.6° to the right. In the 'full adaptation' condition the RDK test
271 stimulus had the same spatiotopic and retinotopic coordinates as the adapting stimulus. In the
272 spatiotopic condition the test stimulus was centred on the same screen coordinates as the adaptor
273 (3.4° to the left and 3.5° above fixation). In the retinotopic condition the test stimulus was presented
274 at the same retinal location as the adaptor (centred 4.2° to the right and 3.5° above fixation). The
275 RDK comparison stimulus (not shown) was aligned vertically with the test stimulus (3.5° below
276 fixation) in all three conditions. The plaid adaptor stimulus comprised two superimposed sinusoidal
277 gratings (1 cycle deg⁻¹) drifting 70° either side of vertical upwards, resulting in the perception of an
278 upwards drifting plaid. (b) Experimental timeline showing the retinotopic condition.

279

280 3. Results

281 Figure 2a-c plots change in perceived duration of the test stimulus for each viewing condition
 282 (full, retinotopic and spatiotopic). A series of t-tests were conducted using Holm-Bonferroni
 283 adjusted alpha levels (Holm, 1979). One-tailed t-test analyses revealed significant duration
 284 compression in all three conditions: full ($t(6) = 4.390$, $p = 0.013$), retinotopic ($t(6) = 5.206$, $p =$
 285 0.006), spatiotopic ($t(6) = 3.339$, $p = 0.04$). Two-tailed t-test analyses showed no significant
 286 differences between the full and spatiotopic conditions ($t(6) = 1.933$, $p = 0.303$), between the
 287 retinotopic and spatiotopic conditions ($t(6) = 1.781$, $p = 0.25$), and between the full and
 288 retinotopic conditions ($t(6) = 1.882$, $p = 0.218$). Our results seem to suggest a role for both
 289 retinotopic and spatiotopic mechanisms in the duration compression effect.

290



291

292 **Figure 2.** Percentage change in perceived duration of the test stimulus relative to its actual (600ms)
 293 duration in (a) the full adaptation condition, (b) the retinotopic condition, and (c) the spatiotopic
 294 condition. Negative values indicate duration compression. There was significant duration
 295 compression in all three conditions. 95% confidence intervals were generated by parametric

296 bootstrapping (10,000 iterations, percentile method; Wichmann & Hill, 2001). Underlined initials
297 indicate the two authors.

298

299 These results suggest a) that the duration compression effect is mediated by the adaptation of timing
300 mechanisms at the global motion processing level, and b) the existence of retinotopic and spatiotopic
301 timing mechanisms at this level. It is possible that timing mechanisms also exist at the local
302 processing level; indeed, as pointed out in the Introduction, there is ample evidence for this. We ran
303 an additional experiment to test whether adapting to the plaid also results in duration compression
304 induced by local motion adaptation. The experiment was a repeat of the full adaptation condition of
305 Experiment 1; but this time the test stimulus comprised a drifting sinewave grating with the same
306 frequency, contrast, orientation and speed as one of the plaid components. However, we found no
307 evidence of duration distortion with this adapt-test stimulus combination (mean duration = 616ms; $t(4)$
308 = 1.69; $p = 0.167$); which suggests that drifting plaid adaptors do not induce duration distortion at the
309 local processing level.

310

311 **4. Discussion**

312 Our experiment was designed to further address the ongoing debate regarding the frame of
313 reference – retinotopic or spatiotopic – in which the mechanisms underlying adaptation-
314 induced duration compression operate. Previous research of this question has failed to
315 reach a consensus, with one camp proposing that the effect is mediated by retinotopic
316 mechanisms early in the visual pathway (Bruno et al., 2010) and another positing that it is
317 mediated by spatiotopic mechanisms located at higher visual cortical areas (Burr et al.,
318 2007; 2011). Although the methodologies used by both groups were not identical, it is
319 unlikely that their disparate results can be explained by such methodological differences. An
320 alternative explanation for their conflicting results is that adaptor-test stimulus combinations
321 used were not well suited for revealing spatiotopic mechanisms.

322

323 In a previous paper (Latimer et al., 2014) we provided compelling evidence that the duration
324 compression effect is primarily retinotopic. However our results had shown that the amount
325 of duration compression that occurred following 'full' adaptation was significantly greater
326 than the duration compression observed in the retinotopic condition. This finding, coupled
327 with the evidence that a small number of our participants (3 out of 7) showed a significant
328 duration compression in the spatiotopic viewing condition, hinted at a possible role for
329 spatiotopic mechanisms in adaptation-induced duration compression. To address this
330 possibility the current experiment used drifting plaid adaptor and RDK test stimuli, which
331 have been used previously to demonstrate that global motion mechanisms are implicated in
332 the duration compression effect (Curran & Benton, 2012); as such this stimulus combination
333 is well suited to uncovering a spatiotopic component (if it exists) of the duration compression
334 effect.

335

336 The results of our experiment reveal significant duration compression in all three of our
337 viewing conditions (full, retinotopic and spatiotopic). This suggests the duration compression
338 effect may be underpinned by both retinotopic and spatiotopic timing mechanisms. Using
339 oscillating gratings Burr et al. (2007) have previously demonstrated retinotopic and
340 spatiotopic duration compression occurring when test and comparison stimulus speeds were
341 matched physically; when comparison stimulus speed was matched to the test stimulus's
342 perceived speed there was no evidence of retinotopic duration compression, yet spatiotopic
343 duration compression persisted. Burr et al. attributed the retinotopic compression in the
344 former scenario to the fact that adaptation can reduce the apparent speed of a subsequent
345 stimulus (Thompson, 1981), and the apparent speed of a stimulus can influence its
346 perceived duration (Kanai et al., 2006). In our experiment comparison stimulus speed was
347 matched to the test stimulus's perceived speed across all test conditions. To our knowledge,
348 our experiment is the first demonstration of both retinotopic and spatiotopic duration
349 compression occurring whilst controlling for distortions in perceived speed.

350

351 In our experiment we used an adaptor-test stimulus combination (plaid and RDKs) to target
352 global motion mechanisms. Area MT, which is associated with global motion processing,
353 has been shown to exhibit some degree of retinotopic mapping (Gattass & Gross, 1981; van
354 Essen, Maunsell & Bixby, 1981), and area MT+ is known to encode spatiotopic mapping
355 (d'Avossa et al., 2007; Goosens et al., 2006). Our observation of both retinotopic and
356 spatiotopic duration compression point to the existence of visual timing mechanisms at the
357 global motion processing level and suggest that the observed retinotopic and spatiotopic
358 effects may be driven by adaptation of MT and MT+ mechanisms, respectively. Indeed a
359 number of previous studies have already implicated these areas as playing a role in
360 subsecond duration timing (Janssen & Shadlen, 2005; Leon & Shadlen, 2003; Bueti,
361 Bahrami & Walsh, 2008; Burr et al., 2007; Curran & Benton, 2012). This evidence for
362 cortical timing mechanisms in area MT/MT+, alongside previous reports of pre-cortical timing
363 mechanisms (Johnson et al., 2006, 2008; Ayhan et al., 2009, Bruno et al., 2013), adds
364 further evidence to the suggestion that subsecond timing mechanisms are distributed
365 throughout the visual pathway (Curran & Benton, 2012).

366

367 To conclude, our previous paper (Latimer et al., 2014) argued that the duration compression
368 phenomenon is primarily mediated by adaptation of retinotopic-tuned mechanisms.
369 However, by using an adaptor-test stimulus combination suited to uncovering adaptation
370 effects at the level of global motion processing, the current experiment extends our previous
371 findings by demonstrating that both retinotopic-tuned and spatiotopic-tuned mechanisms
372 contribute to the effect. While our data do not provide an explanation as to how duration of
373 brief visual events is encoded, they demonstrate that the duration encoding of brief visual
374 events is mediated by both retinotopic-tuned and spatiotopic-tuned mechanisms, with the
375 former pointing to the involvement of area MT and the latter pointing to the involvement of
376 area MT+ in duration encoding.

377

378

379 **Acknowledgments:** We thank the reviewers for their helpful comments; and Victoria Carson
380 and Kathryn Elkin, who assisted in gathering data as part of their final year project.

References

- Ayhan, I., Bruno, A., Nishida, S. & Johnston, A. (2009). The spatial tuning of adaptation-based time compression. *Journal of Vision*, *9*(11), 1-12 (article no. 2).
- Brown, S. W. (1995). Time, change and motion: The effects of stimulus movement on temporal perception. *Perception and Psychophysics*, *57*, 105-116.
- Bruno, A., Ayhan, I. & Johnston, A. (2010). Retinotopic adaptation-based visual duration compression. *Journal of Vision*, *10*(10), 1-18.
- Bruno, A., Ng, E. & Johnston, A. (2013). Motion-direction specificity for adaptation-induced duration compression depends on temporal frequency. *Journal of Vision*, *13*(12), 1-11 (article no. 19).
- Bueti, D., Bahrami, B. & Walsh, V. (2008). Sensory and association cortex in time perception. *Journal of Cognitive Neuroscience*, *20*(6), 1054-1062.
- Buonomano, D. V. & Karmarkar, U. R. (2002). How do we tell time? *The Neuroscientist*, *8*, 42-51.
- Burr, D. C., Cicchini, M., Arrighi, R. & Morrone, M. C. (2011). Spatiotopic selectivity of adaptation-based compression of event duration. *Journal of Vision*, *11*(2), 1-9.
- Burr, D., Tozzi, A. & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience*, *10*, 423-425.
- Curran, W., & Benton, C. P. (2012). The many directions of time. *Cognition*, *122*, 252-257.
- d'Avossa, G., Tosetti, M., Crespi, S., Biagi, L., Burr, D. C. & Morrone, M. C. (2007). Spatiotopic selectivity of BOLD responses to visual motion in human area MT. *Nature Neuroscience*, *10*(2), 249-255.
- Gattass, R. & Gross, C. G. (1981). Visual topography of striate projection zone (MT) in posterior superior temporal sulcus of the Macaque. *Journal of Neurophysiology*, *46*, 621-638.

- Goosens, J., Dukelow, S. P., Menon, R. S., Vilis, T. & van den Berg. A. V. (2006). Representation of head-centric flow in the human motion complex. *The Journal of Neuroscience*, 26, 5616-5627.
- Grondin, S. (2010). Timing and time perception: A review of recent behavioural and neuroscience findings and theoretical directions. *Attention, Perception and Psychophysics*, 72, 561-582.
- Hawken, M. J., Shapley, R. M. & Gross, D. H. (1996). Temporal-frequency selectivity in monkey visual cortex. *Visual Neuroscience*, 13(3), 477-492.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 6(2), 65-70.
- Hubel, D. H. & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215-243.
- Janssen, P. & Shadlen, M. N. (2005). A representation of the hazard rate of elapsed time in macaque area LIP. *Nature Neuroscience*, 8(2), 234-241.
- Johnston, A., Arnold, D. H. & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, 16, 472-479.
- Johnston, A., Bruno, A. Watanabe, J., Quansah, B., Patel, N., Dakin, S. & Nishida, S. (2008). Visually based temporal distortion in dyslexia. *Vision Research*, 48(17), 1852-1858.
- Kanai, R., Paffen, C. L. E., Hogendoorn, H. & Verstraten, F. A. J. (2006). Time dilation in dynamic visual display. *Journal of Vision*, 6, 1421-1430.
- Kaneko, S. & Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision*, 9(7), 1-12 (article no. 14).
- Karmarkar, U. R. & Buonomano, D. V. (2007). Timing in the absence of clocks: Encoding time in neural network states. *Neuron*, 53, 427-438.

Lapid, E., Ulrich, R. & Rammsayer, T. (2008). On estimating the difference limen in duration discrimination tasks: A comparison of the 2AFC and the reminder task. *Perception and Psychophysics*, 70, 291-305.

Latimer, K., Curran, W. & Benton, C. P. (2014). Direction-contingent duration compression is primarily retinotopic. *Vision Research*, 105, 47-52.

Leon, M. L. & Shadlen, M. N. (2003). Representation of time by neurons in the posterior parietal cortex of the macaque. *Neuron*, 38, 317-327.

Marinovic, W. & Arnold, D. (2012). Separable temporal metrics for time perception and anticipatory actions. *Proceedings of the Royal Society B*, 279, 854-859.

Mauk, M. D., & Buonomano, D. V. (2007). The neural basis of temporal processing. *Annual Review of Neuroscience*, 27, 307-330.

Morrone, M. C., Cicchini, M. & Burr, D. C. (2010). Spatial maps for time and motion. *Experimental Brain Research*, 206, 121-128.

Movshon, J. A., Adelson, E. H., Gizzi, M. S. & Newsome, W. T. (1985). The analysis of moving visual patterns. In C. Chagas, R. Gattass & C. Gross (Eds.). *Pattern recognition mechanisms. Pontificiae Academiae Scientiarum Scripta Varia* (Vol. 54, pp. 117-151). Rome: Vatican Press.

Nachmias, J. (2006). The role of virtual standards in visual discrimination. *Vision Research*, 46, 2456-2464.

Thompson, P. (1981). Velocity after-effects: The effects of adaptation to moving stimuli on the perception of subsequently seen moving stimuli. *Vision Research*, 21, 337-345.

van Essen, D. C., Maunsell, J. H. R. & Bixby, J. L. (1981). The middle temporal visual area in the macaque: Myeloarchitecture, connections, functional properties and topographic organization. *Journal of Comparative Neurology*, 199, 293-326.

- Vicario, C. M., Pecoraro, P., Turriziani, P., Koch, G., Caltagirone, C. & Oliveri, M. (2008). Relativistic compression and expansion of experiential time in the left and right space. *PLoS ONE*, 3, e1716.
- Watt, R. J. & Andrews, D. P. (1981). Adaptive probit estimation of psychometric functions. *Current Psychological Review*, 1, 205-214.
- Wichmann, F. A. & Hill, N. J. (2001). The psychometric function: II. Bootstrap-based confidence intervals and sampling. *Perception and Psychophysics*, 63, 1314-1329.
- Zarco, W., Merchant, H., Prado, L. & Mendez, J. C. (2009). Subsecond timing in primates: Comparison of interval production between human subjects and rhesus monkeys. *Journal of Neurophysiology*, 102, 3191-3202.