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

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Abstract

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

Key words: Time perception, adaptation, motion processing

1. Introduction

The ability to accurately perceive and time subsecond durations is critical for a number of everyday tasks including understanding and producing speech, and executing complex motor actions such as intercepting targets and avoiding collisions (Mauk & Buonomano, 2004; Zarco et al., 2009). There is a growing body of evidence suggesting that encoding of subsecond durations is carried out by distributed modality-specific mechanisms (Buonomano & Karmarkar, 2002; Grondin, 2010; Karmarkar & Buonomano, 2007). Evidence for the existence of timing mechanisms within the visual modality has been provided by a number of studies which have shown that duration judgments of subsecond visual stimuli can be distorted following prior visual adaptation. Johnston, Arnold and Nishida (2006) reported that prior adaptation to a 20Hz oscillating sine wave pattern resulted in the duration of a subsequent subsecond (600ms) 10Hz test pattern presented in the same location being underestimated. However no such effect was found when the adaptor oscillated at 5Hz. A similar pattern of results was observed when the grating stimuli were replaced with Gaussian patches, whose brightness changed sinusoidally, thus demonstrating that the underlying mechanisms are temporal frequency tuned. Johnston et al. (2006) also provided evidence to suggest that the duration compression effect is orientation-independent, by showing that the effect persists when the adaptor is rotated 90° relative to the test stimulus. Given that area V1 is the earliest visual area to exhibit orientation selectivity (Hubel & Wiesel, 1968), it has been suggested that direction-independent duration compression points to the involvement of pre-striate timing mechanisms (Bruno, Ng & Johnston, 2013).

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

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

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

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

Attempts are ongoing to determine where the mechanisms underlying duration compression are located in the visual system. Related to these attempts is the debate regarding the frame of reference within which the phenomenon takes place. This debate was sparked by Burr, Tozzi and Morrone (2007), who carried out a study to determine whether or not the duration compression effect reported by Johnston et al. was governed by retinotopic-tuned or spatiotopic-tuned mechanisms. In their study they adapted participants to an oscillating grating before asking them to judge the duration of a subsequent 600ms test grating stimulus presented under one of three conditions. In the ‘full adaptation’ condition participants maintained their fixation at the same location following adaptation; the test grating was presented in the same location as the adaptor, and thus had the same retinal and spatial coordinates as the adaptor. In the other two conditions the participants performed a saccade to a new fixation point following the adaptation period, which allowed the effects of retinotopic and spatiotopic adaptation to be examined separately. In the spatiotopic condition the test stimulus was presented in the same spatial location on the screen as the adaptor, whilst in the retinotopic condition the test stimulus was placed in the same location as the adaptor relative to the fixation point. Duration compression was observed in all three conditions when the physical speeds of the test and comparison stimuli were matched; however, when their speeds were matched perceptually duration compression only occurred in the full and spatiotopic conditions. It was concluded that the duration compression observed in the retinotopic condition reflected a change in the perceived speed of the test stimulus as a result of adaptation, and that the neural mechanisms underlying the duration compression effect must operate in a spatiotopic frame of reference. Visual area MT+ has been suggested as a candidate area for the location of these timing mechanisms (Morrone, Cicchini & Burr, 2010), as past evidence has linked this area to subsecond timing (Janssen & Shadlen, 2005; Leon & Shadlen, 2003) and it is the earliest visual area in which spatiotopic encoding has been shown to occur (Goosens et al., 2006).

This proposal that the mechanisms underlying the duration compression effect are spatiotopic-tuned is disputed by Bruno, Ayhan and Johnston (2010). Using similar methods to Burr et al.'s study they reported a duration compression effect which only occurred in the 'full' and 'retinotopic' conditions, with no evidence found to support spatiotopic duration compression. This finding suggests that the underlying timing mechanisms operate in a retinotopic frame of reference, a finding which also implies that the mechanisms are likely to be situated early in the visual pathway. The contrasting results reported by Bruno et al. and Burr et al. have proven difficult to reconcile, however there were some methodological differences between the two studies which may account for this. For instance Bruno et al. matched only the physical speeds of their test and comparison stimuli. Under such conditions Burr et al. reported a significant duration distortion in both the retinotopic and spatiotopic conditions. However, whilst this methodological difference might offer an explanation for Bruno et al.'s reported retinotopic effect it doesn't explain the study's lack of a spatiotopic effect. Differences in presentation order may also offer some insight into the contrasting results. Burr et al. always presented their test stimulus before the comparison in their experiment, whilst Bruno et al. randomised their presentation order. Bruno et al. have speculated that order effects might therefore partly explain the spatiotopic duration compression observed in Burr et al.'s study. This is because the magnitude of the second of a pair of stimuli tends to be overestimated for a number of different characteristics, including duration (Lapid, Ulrich & Rammsayer, 2008; Nachmias, 2006). However Burr et al. (2011) have dismissed this notion, pointing out that their data were calculated as the difference between the adapted and unadapted conditions, thus cancelling out any potential temporal order effects.

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

The contrasting results of previous research addressing the retinotopic-spatiotopic question may be a consequence of using adaptor and test stimuli that are not well suited to uncovering spatiotopic mechanisms. The present study attempts to overcome this by using an adaptor-test stimulus combination suited to the task. Our choice of stimuli was based on an experiment reported by Curran and Benton (2012). In their experiment participants adapted to a plaid stimulus comprising two superimposed drifting sinusoidal gratings (1 cycle deg^{-1}), whose orientations differed by 40° (±20° off vertical) such that their drift directions were ±70° either side of vertically upwards at a speed of 1.03°s^{-1}. Participants perceived the stimulus as a uni-directional drifting plaid moving upwards at a speed of 3°s^{-1}. Following adaptation to the plaid, participants underestimated the duration of a subsequently presented upwards drifting RDK. However when a transparent moving dot pattern, whose two motion directions matched the plaid's component directions, was used as the adaptor there was no subsequent duration compression observed. Given that drifting plaids are known to selectively stimulate MT neurons tuned to the plaid's global motion direction (Movshon et al., 1985) Curran and Benton concluded that it is likely cortical timing mechanisms exist at or beyond area MT. Since MT direction-sensitive neurons respond to plaid global motion, and area MT+ is the earliest known point in the motion pathway where spatiotopic encoding occurs (Goosens et al., 2006), we reasoned that if spatiotopic mechanisms contribute to the duration compression effect then the stimuli used by Curran and Benton would be well suited to revealing them.

We ran a modified version of our previous study (Latimer, Curran & Benton, 2014). Whereas Latimer et al. used drifting RDKs as adaptor and test stimuli, the current experiment used a drifting plaid stimulus as the adaptor and the test stimulus was an RDK drifting in the same direction as the adaptor's pattern motion. Following adaptation participants judged the duration of a drifting RDK presented in either the same retinotopic or spatiotopic location (or both in the full condition) as the adaptor. The drift directions of the plaid's components were ±70° either side of vertically upwards. Previous research (Bruno et al., 2013) has shown duration compression to be direction tuned when slow moving stimuli (3Hz) are used, with the effect's magnitude rapidly reducing with increased adaptor-test direction difference, and is abolished for adaptor-test direction differences of between 45° and 90°. Thus, while the plaid adaptor in our experiment induces adaptation in both local and global motion mechanisms, the large difference (70°) between each component direction and test stimulus direction ensures that any observed duration compression must be the result of global motion adaptation.

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

2. Methods

2.1. Participants

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

2.2. Apparatus

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

2.3. Stimuli

The adaptor was an upwards drifting plaid stimulus and was constructed by superimposing two drifting sinusoidal gratings (1 cycle deg^{-1}, Michelson contrast = 0.6) whose orientations differed by 40° (±20° off vertical). The drift directions of the plaid components were ±70° to either side of vertically upwards at a speed of 1.03°s^{-1}, resulting in an upwards pattern speed of 3°s^{-1}. The test and comparison stimuli were both unidirectional, mixed-polarity, translating RDKs (dot diameter = 1.8 arcmin; dot density = 12.9 dots/deg^{2}) set against a mean luminance background (28.5 cd/m^{2}). Each stimulus was presented within a circular aperture (diameter 6.3°).

2.4. Procedure

Participants initially adapted to a plaid drifting upwards at a speed of 3°s^{-1} for 30s whilst fixating on a black 'x' to its lower left (see Figure 1). Following adaptation the fixation marker either remained in the same location (full adaptation condition) or was re-plotted 7.6° to the right and participants made a saccade to it (retinotopic and spatiotopic conditions). Participants were then presented with the test and comparison RDK stimuli, with presentation order being randomised from trial to trial, and were required to judge which one had the longer duration. Subsequent duration judgment trials were preceded with a 5s 'top up' adaptor, thus ensuring that the adaptive state was maintained. In the full adaptation condition the test and comparison stimuli were presented above and to the right and below and to the right of fixation, respectively; thus the test stimulus was presented in the same retinal and spatial location as the adaptor and the comparison was presented outside of the adapted region. In the retinotopic condition participants performed a saccade after adaptation and the test stimulus was presented above and to the right of the fixation's new location, at the same retinal coordinates as the adaptor, and the comparison stimulus was presented below and to the right of the new fixation. In the spatiotopic condition participants again performed a saccade after adaptation, but this time the test stimulus was presented at the same physical location on the screen as the adaptor, above and to the left of the fixation's new location, and the comparison was presented below and to the left of the new fixation. The test and comparison stimuli were always presented in the same hemifield, thus controlling for previously reported biases in duration estimation of stimuli presented in different hemifields (Vicario et al., 2008).

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

In the main duration experiment test stimulus duration was fixed at 600ms, while comparison stimulus duration was varied from trial to trial. Comparison stimulus duration was chosen by an adaptive method of constants procedure (Watt & Andrews, 1981) thus optimising the estimation of the 'point of subjective equality' (PSE), i.e. the duration at which the comparison stimulus was judged to match that of the test stimulus. Each PSE was generated from 64 duration judgments with 4 PSEs generated per viewing condition, such that each participant's duration estimate for each condition was generated based on a total of 256 trials.

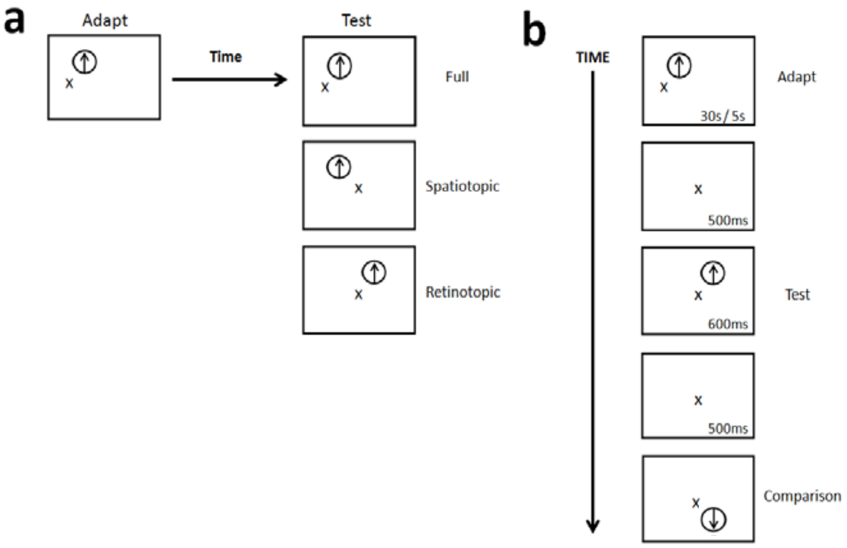

Figure 1. (a) The locations of the adaptor and test stimuli for each condition. The location of the fixation is represented by an 'x'. During adaptation the plaid adaptor was centred 4.2° to the right and 3.5° above fixation. Following adaptation the fixation either remained in the same location (full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

3. Results

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

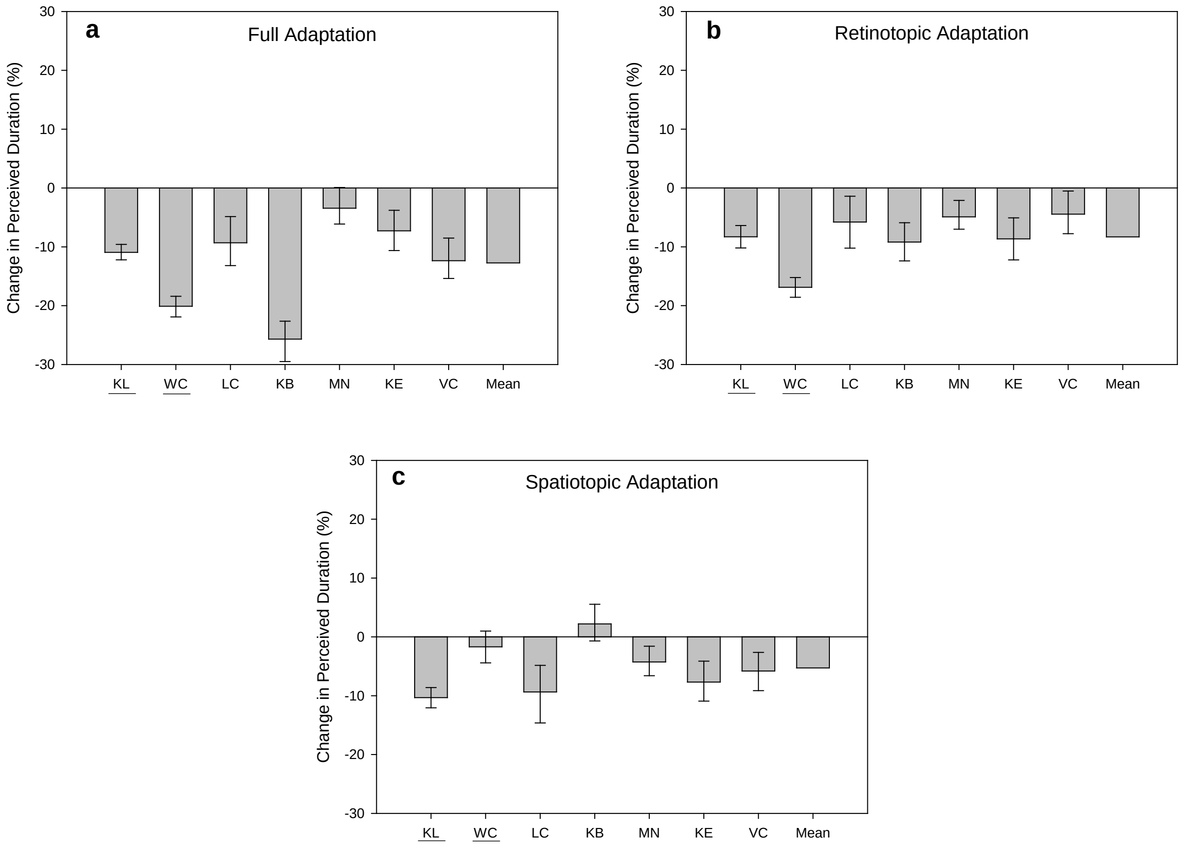

Figure 2. Percentage change in perceived duration of the test stimulus relative to its actual (600ms) duration in (a) the full adaptation condition, (b) the retinotopic condition, and (c) the spatiotopic condition. Negative values indicate duration compression. There was significant duration compression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

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

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

4. Discussion

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

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

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

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

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

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