Adapting to time: Duration channels do not mediate human time perception

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Accurately encoding the duration and temporal order of events is essential for survival and important to everyday activities, from holding conversations to driving in fast-flowing traffic. Although there is a growing body of evidence that the timing of brief events (<1 s) is encoded by modality-specific mechanisms, it is not clear how such mechanisms register event duration. One approach gaining traction is a channel-based model; this envisages narrowly-tuned, overlapping timing mechanisms that respond preferentially to different durations. The channel-based model predicts that adapting to a given event duration will result in overestimating and underestimating the duration of longer and shorter events, respectively. We tested the model by having observers judge the duration of a brief (600 ms) visual test stimulus following adaptation to longer (860 ms) and shorter (340 ms) stimulus durations. The channel-based model predicts perceived duration compression of the test stimulus in the former condition and perceived duration expansion in the latter condition. Duration compression occurred in both conditions, suggesting that the channel-based model does not adequately account for perceived duration of visual events.

Introduction

Time perception underpins our interactions with the external world, ranging from events occurring on the scale of milliseconds (e.g., processing temporal information in speech) to circadian rhythms occurring on the scale of hours and days (e.g., appetite cycles). The encoding of brief temporal events (<1 s) is the most sophisticated and least well understood area of time perception (Buonomano & Karmarkar, 2002; Mauk & Buonomano, 2004); yet many important sensory processes, such as visual motion perception and speech processing, occur within this range, as does the fine motor coordination that top athletes rely on to perform competitively. There is evidence that the timing of brief events is encoded by modality-specific processes (Buonomano & Karmarkar, 2002; Grondin, 2010; Heron et al., 2012), with the duration of, for example, visual or auditory events being encoded within the pertinent sensory pathway. However, the nature of these timing mechanisms is unclear. One view is encapsulated in the intrinsic model approach (Ivry & Schlerf, 2008), in which an event’s apparent duration is an emergent property of the neural processing circuitry and does not require a specialized timing mechanism. An alternative view is that event duration is encoded by mechanisms dedicated to extracting time. The most influential example of the dedicated mechanisms approach is the pacemaker-accumulator model (Creelman, 1962; Treisman, 1963), in which a pacemaker emits pulses that are accumulated by a counter, and perceived duration is determined by the number of pulses counted. An alternative dedicated model, which is
currently gaining traction, proposes that event duration is encoded by a set of processors differentially tuned to duration (Ivry, 1996). This “channel-based” approach to duration perception envisages neural units with overlapping duration tuning properties, with each unit displaying selective responsivity to a narrow range of durations centered on its preferred duration. From this perspective perceived duration is determined by comparing relative activation across the population of duration-tuned neurons. The channel-based model is supported by recent fMRI data pointing to the existence of duration-tuned neurons in human inferior parietal lobule (Hayashi, et al., 2015). If multiple, narrowly-tuned and overlapping duration channels do exist, such a channel-based model would predict that selective adaptation of neural units tuned to an intermediate duration should result in a repulsive shift in the perceived duration of relatively shorter and longer events, with perceived duration of the former being underestimated and the latter being overestimated. This logic follows from the spatial vision literature, where, for example, it is thought that channels tuned to narrow bandwidths of spatial frequency underlie the contrast sensitivity function (Campbell & Robson, 1968).

Support for a channel-based model of duration perception has been reported by Heron et al. (2012), who had participants judge the duration of a test stimulus (visual or auditory) following adaptation to either longer or shorter presentations of the same stimulus. As predicted by the channel-based model, observers showed perceived duration expansion for test stimuli presented longer than the adapter, but perceived duration compression when test stimulus presentation was briefer than the adapter. Their data point to the existence of narrowly tuned duration channels, with bandwidths up to 1.5 octaves. Duration compression effects have also been reported for dynamic, moving stimuli when the adapter has a longer duration than the test stimulus (Ayhan, Bruno, Nishida, & Johnston, 2009; Bruno, Ayhan, & Johnston, 2010; Bruno, Ng, & Johnston, 2013; Burr, Tozzi, & Morrone, 2007; Curran & Benton, 2012; Johnston, Arnold, & Nishida, 2006; Latimer, Curran, & Benton, 2014). On the face of it, these results appear to be consistent with those of Heron et al. (2012); however, the compression effects reported were induced using adapter durations at least three octaves greater than the test. The test duration in those experiments was 600 ms, which is close to one of the test durations used by Heron et al. (2012: 640 ms). Based on Heron et al.’s data (2012), we would expect no duration compression for adapter-test duration differences of three octaves. Yet robust duration compression was induced using adapter durations at least three octaves greater than the test. This discrepancy is likely a consequence of methodological differences; whereas participants in Heron et al.’s (2012) experiments adapted to duration, participants in the aforementioned dynamic stimulus experiments did not adapt to duration per se—instead, they adapted to motion or flicker stimuli.

The current experiments test the crucial hypothesis that a channels-based model (as envisaged by Heron et al., 2012) predicts both duration compression and duration expansion, depending on the conditions measured. We find that, counter to this prediction, only compression occurs, regardless of whether the adapting stimulus’s duration is longer or shorter than the test stimulus. Furthermore the effect is shown to be direction contingent; that is, it occurs when adapter and test stimuli move in the same direction but not when they move in opposite directions. The direction-contingent nature of duration compression is consistent with previous reports (Bruno et al., 2013; Curran & Benton, 2012), and is difficult to explain in terms of duration channels since observers adapted to the same duration in each condition. To test whether the observed duration compression is specific to dynamic visual stimuli, we repeated the experiment using static stimuli. Again, regardless of adapter duration, adaptation results in perceived duration compression of the test stimulus. In a third experiment we explored whether the different outcomes to Heron et al.’s (2012) and our experiments could be explained by a key methodological difference—we had used an intramodal design in which both test and comparison stimuli were presented to the adapted modality, while Heron et al. used a cross-modal design which presented comparison stimuli to the adapted modality and test stimuli to an unadapted modality. To address this question we repeated Experiment 2 only this time, like Heron et al. (2012), presented comparison stimuli to the adapted modality and test stimuli to the unadapted modality. While data from one participant were consistent with a channels based model, four of the five other participants perceived duration compression only and the fifth perceived duration expansion only. Crucially, the direction of duration distortion for all but one of the participants was the same regardless of whether the adapting duration was longer or shorter than the test duration. Taken together, the results of our experiments challenge the view that the temporal encoding of brief visual events is mediated by duration-tuned channels.

Material and methods

Stimuli

Stimuli in Experiment 1 were random dot kinematograms, with equal numbers of black and white
dots, presented within a circular aperture (6.3° diameter). Adapter and test stimuli were centered 5° left of fixation, and comparison stimuli were centered 5° right of fixation. The viewing distances (Belfast lab 71 cm; Bristol lab 67 cm) ensured stimuli subtended the same visual angle on both experimental set-ups. Stimuli were presented on a Sony GDM-F500R monitor (Belfast) and a Sony CPD-500 monitor (Bristol), driven by a Cambridge Research Systems VSG 2/5 graphics board (Cambridge Research Systems, Rochester, Kent, UK) at a frame rate of 120 Hz.

Procedure

Observers adapted to a random dot pattern centered 5° left of fixation and drifting upwards at a constant speed (3° s⁻¹). Using similar methodology to Heron et al. (2012), the adapting stimulus was presented for a brief (340 ms or 860 ms) duration, with each adapter instantiation being preceded by a variable interval (500–1000 ms) until the cumulative adapting duration was complete (Figure 1). The adapter was presented 88 times (cumulative duration of 29.9 s) in the 340 ms condition and 35 times in the 860 ms condition during the initial adaptation phase. In a third (continuous) adaptation condition the adapter was presented continuously for 30 s. An auditory tone signaled the end of each adaptation phase.

Following the initial adaptation phase, observers judged the duration of a 600 ms upward- or downward-moving test pattern presented in the adapted region and moving at the same speed as the adapting pattern. Observers judged whether a comparison pattern of variable duration, centered 5° right of fixation and moving in the opposite direction to the test pattern, was of longer or shorter duration than the test pattern. Comparison stimulus speed was matched to observers’ perceived speed of the test stimulus, controlling for adaptation-induced speed distortions (Thompson, 1981) and taking into account that perceived speed influences apparent duration (Kaneko & Murakami, 2009). The perceived speed measurements were gathered in an initial preliminary experiment that was identical to the duration experiment, with the exception that the test and comparison stimuli were presented for the same duration (600 ms), comparison speed varied from trial to trial, and participants judged whether the comparison stimulus was moving faster or slower than the test stimulus.

In the main experiments, adaptation was maintained by preceding each subsequent test-comparison pair with a 5.1 s (15 × 340 ms epochs, 6 × 860 ms epochs, and continuous) presentation of the adapting stimulus. Presentation order of test and comparison stimuli was randomized on each trial, thus controlling for possible temporal order effects on duration perception (Lapid, Ulrich, & Rammsayer, 2008; Nachmias, 2006). Comparison stimulus duration was chosen on each trial by an adaptive method of constants procedure (Watt & Andrews, 1981) and was selected to optimize the estimation of the “point of subjective equality” (PSE), that is when comparison stimulus duration appeared to equal that of the test stimulus (see example psychometric functions, Figure 2a). Each observer generated four PSEs per condition, with each PSE being derived from a block of 64 trials; thus the continuous, 860 ms and 340 ms conditions each comprised a total of 256 trials in both the speed-matching and duration-matching experiments.

Results

Figure 2b plots change in perceived duration of a 600-ms test stimulus following adaptation to continuous motion (dark green bars), a train of 860-ms motion epochs (dark yellow bars) and a sequence of 340-ms motion epochs (dark red bars). Negative and positive values indicate duration compression and expansion, respectively. Repeated-measures ANOVA reveals no significant difference in perceived duration between the conditions, F(2, 8) = 0.018, p = 0.98; using Holm–Bonferroni adjusted alpha levels (Holm, 1979), additional two-tailed t-test analyses reveal significant duration compression in each adaptation condition [continuous: t(4) = 6.126, p = 0.008, dL = 2.72; 860 ms: t(4) = 6.204, p = 0.009, dL = 3.25; 340 ms: t(4) = 5.121, p = 0.007, dL = 2.27]. Of course one must be cautious in using t tests with small sample sizes, since large sample sizes would be required to control for the possibility that there is considerable individual variation in the context of time perception. Whilst the duration compression observed in the 860-ms condition is consistent with a channel-based model, such a model predicts duration expansion in the 340 ms condition. When test and adapter stimuli moved in opposite directions in the 340 ms condition (Figure 2c), no significant duration distortion was found, t(4) = 0.345, p = 0.748, dL = 0.15, a finding which replicates previous results (Curran & Benton, 2012). This direction-contingent duration compression is also problematic for a purely channel-based model, as observers adapted to the same duration in the “same” and “opposite directions” conditions. Given the scalar property of time perception, and the bandwidth of duration channels described by Heron et al. (2012), the choice of 860 ms for the longer-adapter condition may be considered inappropriate. Heron et al.’s (2012) data suggest that a 1200 ms to 1500 ms adapter would be more appropriate for inducing duration compression of
a 640-ms test stimulus; consequently a 860-ms adapter used by that group could lead to results inconsistent with those we found. As noted above, the duration compression magnitude in the continuous condition is not significantly different from that found in the 340 ms and 860 ms conditions, despite the fact that participants were not adapted to duration per se in the continuous condition. This similarity in duration distortion magnitude, in conjunction with the direction-contingent nature of the effect, questions the existence of duration channels in the visual modality.

The results of Experiment 1, in which both the 840 ms and 360 ms adapters induced duration compression, do not fit with the notion that perceived duration of subsecond visual events is mediated by differentially tuned duration channels, and stand in stark contrast to the findings of Heron et al. (2012). It is, of course, possible that the repelling effect of the shorter duration adapter may be active but is overshadowed by a much stronger duration compression effect. This would mean that adapting to the shorter stimulus would produce less compression than the longer adapter; however the absence of a significant difference between the two conditions suggests that this explanation does not hold.

We note that Heron et al. (2012) used static adapter and test visual stimuli, whereas we used dynamic motion stimuli. It is feasible that the duration of static, but not dynamic, visual stimuli is encoded through the activity of multiple duration channels. We tested this possibility in Experiment 2 by repeating the 340 ms and 860 ms conditions of Experiment 1, but this time using static random dot adapter and test stimuli. Using Holm–Bonferroni adjusted alpha levels the results (Figure 2d) again reveal significant perceived duration compression of the 600-ms test stimulus, regardless of whether the adapter had a longer or shorter duration [860 ms: $t(3) = 8.081, p = 0.012, dz = 4.04$; 340 ms: $t(3) = 3.604, p = 0.03, dz = 1.8$].

While it is difficult to reconcile our results with those of Heron et al. (2012), we note that our experiments employed intramodal duration judgments, whereas Heron et al. (2012) used cross-modal judgments by comparing perceived duration of a visual test stimulus with that of an auditory stimulus (and vice versa). We ran a third experiment to test whether the different outcomes in Heron et al.’s (2012) and our experiments could be explained by this methodological difference.
Experiment 3: Duration compression persists with cross-modal testing

The adapter conditions were identical to Experiment 2; however, in this experiment we used a cross-modal duration judgment task similar to that used by Heron et al. (2012). Following adaptation participants were presented with a 600-ms burst of auditory white noise followed by a static random dot comparison stimulus presented in the adapted field. The fixation point was a black spot (diameter of 8 pixels) surrounded by a white annulus (band width of 3 pixels), and its mean luminance was equal to the display mean luminance (Bristol: 42.5 cd/m²; Belfast: 57.52 cd/m²). The end of each adaptation phase was signalled by inverting the contrast of the fixation spot. Stimuli were generated in Matlab using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997), and were presented on an Iiyama MA20 3DT monitor (Belfast) and Iiyami Vision Master Pro 513 monitor (Bristol) at a frame rate of 120 Hz. The comparison stimulus duration varied from
trial to trial and participants judged which of the two stimuli’s duration was longer. As in previous experiments, participants generated four psychometric functions from blocks of 64 trials for each condition. As well as testing participants in the 860 ms and 360 ms adapter conditions, we also tested them in a “no-adaptation” baseline condition. This was motivated by previous reports that identical-duration auditory and visual stimuli are not perceived as having the same duration (Wearden, Todd, & Jones, 2006). The baseline condition showed that the visual stimulus was either of substantially shorter duration (CB: 539 ms; LB: 570 ms; KL: 578 ms) or longer duration (WC: 666 ms; AR: 733 ms; JD: 735 ms) than the 600 ms auditory stimulus when the two stimuli were perceived to be of equal duration. Any subsequent adaptation-induced duration distortions were calculated relative to each participant’s baseline measure. Bootstrap populations were propagated through the various averaging and differencing operations to derive the bootstrapped confidence limits (Benton, Jennings, & Chatting, 2006).

Figure 3 contains the data from the cross-modal experiment, and shows the difference between the comparison stimulus duration and each participant’s baseline measure when the former’s duration was perceptually matched to the auditory test stimulus. The first thing to note is that, because the comparison stimulus was presented to the adapted modality, positive values denote adaptation-induced duration compression and negative values reflect duration expansion. One participant’s (JD) results are consistent with the predictions of a channel-based model of duration perception with prior adaptation to 860 ms and 340 ms resulting in duration compression and expansion, respectively. However, four of the six participants show the same pattern of response as in the previous experiments; i.e., prior duration adaptation results in duration compression regardless of whether the adapting durations are shorter or longer than that of the test stimulus. One participant (AR) shows the opposite pattern of results—duration expansion for both conditions. What is also noteworthy about these data is that, with the exception of JD, both duration—adaptation conditions result in duration distortion in the same direction relative to their baseline measures. Again, this is inconsistent with duration being encoded by multiple, narrow-bandwidth and overlapping duration channels. As in Experiment 1, we considered the possibility that the repelling effect of the shorter duration adapter may be active but is overshadowed by a much stronger duration compression effect. However, if this were the case, participant AR’s data should have shown stronger duration expansion in the 340 ms condition than in the 860 ms condition. Nonetheless, we explored this explanation by treating AR as an outlier and testing whether the remaining five participants differed significantly in their responses across the two conditions. Two tailed t test analysis failed to find a
significant difference between the 340 ms and 860 ms conditions, $t(8) = 1.905; p = 0.093; d_z = 0.85$.

**Discussion**

Research by Heron et al. (2012) has provided evidence for the existence of multiple duration channels with narrow, overlapping duration tuning functions, in both the auditory and visual modalities. In their experiments adaptation to a subsecond duration stimulus resulted in perceived duration distortion of a subsequent stimulus presented to the adapted modality, and this distortion was repellent; in other words, observers perceived duration expansion of test stimuli presented longer than the adapter, but perceived duration compression when test stimulus presentation was briefer than the adapter. The duration distortion effect peaked at adapt-test duration differences of approximately 0.8–1.5 octaves. Previous research had reported duration compression of a 600 ms dynamic visual stimulus following adaptation to 5 s, continuously presented dynamic stimulus in the same retinal location (Johnston, Arnold, & Nishida, 2006; Bruno et al., 2010; Bruno et al., 2013; Burr et al., 2007; Curran & Benton, 2012; Ayhan, Bruno, Nishida, & Johnston, 2009; Latimer, Curran, & Benton, 2014). As pointed out in the Introduction, while this appears at first sight to be consistent with a channels-based model proposed by Heron et al. (2012), the duration compression would not have been predicted by their model because of the large duration difference between the adapter and test stimuli (up to three octaves). Furthermore, participants in these experiments did not adapt to duration per se and, consequently, it is unlikely that any putative duration channels would have undergone adaptation. Nevertheless, duration compression was found.

The current series of experiments tested the claim by Heron et al. (2012) that the duration encoding of brief visual events is mediated by multiple duration channels with narrow, overlapping duration tuning functions. Participants in Experiment 1 adapted to a train of unidirectional random dot patterns whose duration was set to either 340 ms or 860 ms, then judged the duration of a 600-ms test stimulus positioned at the adapted location. In the additional, “continuous” condition the adapter was presented continuously for 5 s (after initial 30-s adaptation) during each adaptation phase. All three adaptation conditions resulted in significant perceived duration compression of the 600-ms test stimulus. While the observed duration compression in the 860-ms condition appears consistent with a channels-based model of timing, duration compression in the 340-ms condition is opposite to what would be predicted by such a model. Also of concern to a channels-based model of timing is our finding that the “continuous” adaptation condition, in which participants did not adapt to duration per se, induced similar duration compression as the 860 ms and 340 ms conditions. Finally the direction-contingent nature of the observed duration compression also poses a problem for a channel-based model, since observers adapted to identical duration in the “same direction” and “opposite directions” conditions. This latter finding is consistent with previous reports of direction-contingent duration compression (Bruno et al., 2013; Curran & Benton, 2012) following adaptation to slow-speed stimuli; however, there is evidence that the duration compression effect is direction independent when high-speed adapters are used (Bruno et al., 2013; Johnston et al., 2006; Marinovic & Arnold, 2012).

There were a number of key differences between the methodology of Experiment 1 and that used by Heron et al. (2012). For instance, in contrast to the static visual stimuli used by Heron et al. (2012), our stimuli were dynamic; and Heron et al. used a cross-modal comparison task to measure perceived duration distortion, while we used an intramodal comparison task. Experiments 2 and 3 were performed to control for the possibility that the differing results could be explained by these differences in methodologies. In Experiment 2 participants adapted to, and were tested with, static random dot patterns. Just as in Experiment 1, adaptation resulted in perceived duration compression for both adapter durations. This demonstrates that the contrasting results between Experiment 1 and Heron et al.’s (2012) experiments cannot be explained by appealing to the static stimuli versus dynamic stimuli distinction. In Experiment 3 we again used static adapters, but this time used a cross-modal comparison task. This resulted in perceived duration compression for four of the six participants, with duration compression occurring for both adapter durations (340 ms and 860 ms). Furthermore, for all but one participant the 340 ms and 860 ms adapters induced duration distortion in the same direction. Thus, despite controlling for these two methodological differences between Experiment 1 and the experiments of Heron et al. (2012), we were unable to replicate their bidirectional duration distortion effects. Our inability to extend Heron et al.’s (2012) results to different conditions does not question their particular finding; however, it does question the generality of their findings and their conclusions.

As outlined, above, a problem facing a channels-based model of timing is that the duration compression effect is direction contingent; the effect occurs when adapter and test stimuli drift in the same direction, but is abolished when they move in opposite directions. This is problematic for a channels-based model simply
because participants adapted to the same duration in both conditions. This direction-contingent nature of the effect, however, may be an important factor in revealing how brief visual event duration is encoded. This and previous similar reports (Bruno et al., 2013; Curran & Benton, 2012) of direction-contingent duration compression point to the involvement of cortical visual timing mechanisms, because direction selectivity in motion-sensitive neurons is first expressed in the visual cortex (Hubel & Wiesel, 1968). One potential explanation for the effect being direction contingent comes from the motion adaptation literature. The responsiveness of direction-sensitive neurons is known to be suppressed following repeated presentation of their preferred motion direction, while the responsiveness of neurons tuned to the opposite direction is either not suppressed or even enhanced (Kohn, 2007). It may be the case that the presence of duration compression when the adapter and test drift in the same direction is partly driven by this reduced neuronal responsiveness; likewise the absence of duration distortion when adapter and test move in opposite directions may be a reflection of motion-sensitive neurons tuned to the test direction being unaffected by prior adaptation. Indeed, recent studies have reported a correlation between perceived duration and stimulus-specific neural response magnitude in the visual (Sadeghi, Pariyadath, Apte, Eagleman, & Cook, 2011) and auditory domains (Kononowicz & van Rijn, 2014).

Given the relatively broad tuning functions of direction-sensitive neurons (Snowden, Treue, & Andersen, 1992), if suppressed neural responsiveness does underpin the direction dependent nature of duration compression, then we would expect the effect’s magnitude to gradually drop down to zero with increasing adapter-test direction difference. There is limited evidence to support the view that the effect is direction tuned; Bruno et al. (2013) report that the effect’s magnitude drops off with increasing adapter-test direction differences up to 90°, at which point the effect is abolished. However, while the effect was found to be direction tuned for low adapter and test speeds there was no evidence of direction tuning when high-speed stimuli were used. Research by Schindel, Rowlands, & Arnold (2011) also poses some problems for the “neuronal suppression” interpretation of our data. As these researchers point out, if apparent duration is driven by neural response magnitude then perceived duration might be expected to scale with stimulus intensity. Instead, they found that when a low-intensity “oddball” was inserted into a train of higher intensity standard stimuli participants reported duration expansion of the oddball stimulus.

An alternative explanation for duration compression being direction contingent may be found in Tse et al.’s (2004) work on the subjective expansion of time. These authors propose a modification to the pacemaker-accumulator model of timing, and propose that the apparent duration expansion of an “oddball” stimulus is a consequence of the engagement of attention by, and subsequent increased information processing of, an unexpected event. In other words, the appearance of an “oddball” results in more stimulus-specific information being processed per unit of objective time, which, in turn, results in fewer “ticks” of the pacemaker being missed by the accumulator. From this perspective the test stimuli in the “opposite direction” condition of our Experiment 1 would be viewed as an “oddball” stimulus, and its engagement of additional attention could lead to the duration compression effect being nulled by duration expansion. At first sight this explanation does seem to explain the absence of duration compression when adapter and test stimuli drift in opposite directions. However, because it was presented at a different spatial location than the adapter stimuli, one might also expect the comparison stimulus to act as an “oddball” and undergo a similar amount of duration expansion to the test stimulus; in which case apparent duration compression of the test relative to the comparison should persist. Thus we feel that this attention-based suggestion is not an adequate explanation of our results.

To conclude, we ran a series of experiments to test whether the duration encoding of brief visual events is mediated by multiple, narrowly tuned and overlapping duration channels as proposed by Heron et al. (2012). We failed to find evidence supporting this stance, regardless of the type of stimuli used (dynamic or static) and the mode of comparison (intramodal or cross-modal). It is not obvious why our data and those of Heron et al. (2012) result in opposing outcomes. All we can state with certainty is that support for duration channels is not a general result—an observation that clearly argues against duration channels as the general mechanism for duration perception.

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