

Duration expansion at low luminance levels

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Duration distortions have been shown to occur at the time of saccades and following high temporal frequency or contrast adaptation. Under all these conditions, changes in the temporal tuning of M neurons also occur, suggesting that there might be a link between the two phenomena. In order to explore this relationship further, we measured the apparent duration of visual stimuli in the dark, where the temporal impulse response has been reported to lengthen. We first measured a progressive shift and reduction of the occurrence of an apparent motion reversal as we decreased the luminance level, indicating a lengthening of the temporal impulse response. We then measured perceived duration at these luminance levels (0.75, 3, and 50 cd/m²) after matching for apparent contrast and temporal frequency. While perceived temporal frequency did not substantially differ across luminance levels, duration appeared expanded at the lowest luminance level relative to the highest by approximately 60 ms. Thus, we have shown that reduced luminance is associated with both a lengthening of the temporal impulse response and a duration expansion, linking the two and providing further evidence for a relationship between changes in the neuronal tuning in the early stages of the visual system and time perception.

Keywords: temporal vision, light/dark adaptation, low vision

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Introduction

Our ability to process time information related to a sensory stimulus has been thought to rely on different mechanisms at different temporal scales. While we have some knowledge about the mechanisms operating at the shortest (microseconds) and the longest (circadian rhythms) time scales, the mechanisms underlying timing in the millisecond and second ranges remain mysterious (Buonomano & Karmarkar, 2002; Mauk & Buonomano, 2004).

In this article, we will focus on visual durations in the millisecond range. Temporal processing within this range is often referred to as perceptual timing. In the last few years, an increasing number of studies have reported apparent duration distortions for visual intervals that fall within this range. The duration of an interval displayed immediately before a saccadic eye movement appears compressed relative to an interval presented well before a saccade (Morrone, Ross, & Burr, 2005). Duration compression for an interval containing 10-Hz visual flicker or drifting

motion has been reported after high (20 Hz) but not low (5 Hz) temporal frequency adaptation (Ayhan, Bruno, Nishida, & Johnston, 2009; Bruno, Ayhan, & Johnston, 2010; Burr, Tozzi, & Morrone, 2007; Johnston, Arnold, & Nishida, 2006; Johnston et al., 2008). Finally, an apparent duration compression has also been found for a 50% contrast interval preceded by a 90% contrast inducer relative to when it is preceded by a 10% contrast inducer (Bruno & Johnston, 2010).

A possible common factor in these time distortion effects is the changes in the temporal tuning of M neurons that occur under all these different circumstances. The temporal impulse response (which describes the temporal response of a cell to brief pulses of contrast) provides us with an estimate of the shape of the temporal tuning function and it has the advantage that it can also be measured psychophysically. The temporal impulse response has been reported to sharpen at the time of the execution of a saccadic eye movement (Burr & Morrone, 1996) for luminance- but not for chromaticity-modulated stimuli. In addition, there is some neurophysiological evidence pointing to a shortening of the temporal impulse response after high temporal

frequency adaptation (Clifford, Ibbotson, & Langley, 1997; Ibbotson, 2005; Ibbotson, Clifford, & Mark, 1998). Finally, contrast gain control mechanisms have been shown to shorten the temporal impulse response in M cells but not in P cells in primates (Benardete & Kaplan, 1999).

Reducing luminance provides a simple way to manipulate the temporal response of the eye. In fact, the temporal impulse response lengthens (by around 30%) and neural latencies increase at low light level (Kelly, 1961; Peterson, Ohzawa, & Freeman, 2001; Takeuchi & De Valois, 1997, 2009). If there is a link between changes in the shape of the temporal impulse response and distortions of apparent visual duration, we should expect to find biases in perceived timing when we measure duration at low relative to high luminance levels. However, to properly relate changes in temporal tuning and duration, we need to measure both effects in the same experiment. In this study, we first measured variation in the temporal impulse response psychophysically (using an apparent motion reversal paradigm) and then the perceived duration of visual stimuli under different illumination levels (0.75, 3, and 50 cd/m²). We observed a lengthening of the temporal impulse response when we decreased the average luminance and a corresponding expansion of the apparent duration of flickering Gaussian blobs and drifting gratings. Changes in apparent temporal frequency have previously been reported for reduced illumination conditions (Hammett, Champion, Thompson, & Morland, 2007; Vaziri-Pashkam & Cavanagh, 2008). We therefore also measured perceived temporal frequency to allow us to equate the apparent stimulus' modulation across luminance levels, controlling for any effect of apparent temporal frequency on duration. Finally, we showed that changes in apparent onset relative to apparent offset of the visual stimuli could not explain the observed effects on duration.

General methods

Observers

Five observers participated in the study, two authors and three naive subjects. All participants had normal or corrected-to-normal visual acuity.

Apparatus

Observers sat in a darkened room in front of a 19-inch Clinton Monoray monitor, with a refresh rate of 150 Hz, driven by a VISAGE visual stimulus generator (Cambridge Research Systems). The resolution of the monitor was 800 × 600 pixels. The monitor subtended 40 × 30 degrees of visual angle at a viewing distance of 57 cm. The auditory

stimuli were generated by a TDT Basic Psychoacoustic Workstation (Tucker-Davis Technologies) and delivered binaurally by Sennheiser HD 265 linear headphones.

Procedure

All the experiments were composed of an adaptation phase followed by a test phase. In the adaptation phase, subjects were blindfolded and they were required to sit in the dark for 25 min. The room was darkened and light-shielded, with no other source of illumination present. Neutral density filters were applied to the monitor surface to obtain three different stimulus average luminances: 0.75, 3, and 50 cd/m² (measured with a UDT S370 Optometer). At the end of this phase, a loud and prolonged (around 10 s) sound signaled the end of the adaptation phase. Subjects were instructed to take off their blindfold and position their head comfortably on the provided chin rest. They then started the test phase of the experiment by pressing a button on the keyboard in front of them. The test phase always began with the lowest luminance level (0.75 cd/m²). Subjects were required to run no more than three experimental sessions (each of them lasting approximately 10 min) before moving to the next luminance level. In between sessions with different luminance levels, subjects were given about a minute to adapt to the new luminance level. The visual stimuli were displayed within a 5° × 5° rectangular window that was centered 10° either above or below the center of the monitor in different sessions. Only the stimulus window was illuminated; the remainder of the screen was dark (less than 0.01 cd/m²). Subjects viewed the stimuli binocularly and were required to maintain the gaze on a central fixation spot. In the test phase, subjects were required, in different sessions, to judge the direction of motion (Experiment 1), the temporal frequency (Experiment 2), the duration (Experiments 3 and 4), or the onset or offset (Experiment 5) of the visual stimuli.

Motion reversal occurs progressively later at low luminance levels

The temporal impulse response function has been estimated from summation data for the detection of two pulses, as a function of pulse separation (Ikeda, 1965, 1986) or from flicker-sensitivity curves using the Fourier transform (Swanson, Uneno, Smith, & Pokorny, 1987). However, there is evidence for up to three temporal mechanisms (Hess & Snowden, 1992), which undermines these techniques. Fortunately, Johnston and Clifford (1995) showed that visual temporal filters have a single

underlying temporal scale. Motion reversal induced by a mean luminance interstimulus interval (ISI; Braddick, 1980) provides a quick and effective way to measure the scale of temporal processing. The introduction of a blank gray interval between two spatially displaced frames can generate a reversal of apparent direction (Pantle & Turano, 1992). This phenomenon has been explained by the presence of an underlying motion mechanism with a biphasic impulse response (Shioiri & Cavanagh, 1990). The reversal point occurs at a particular ISI, which has been shown by modeling (Johnston & Clifford, 1995) to be related to the scale of the temporal impulse response.

In Experiment 1, we used the variant developed by Takeuchi et al., who successfully demonstrated shifts in the motion reversal point at low luminance levels (Takeuchi & De Valois, 1997, 2009; Takeuchi, De Valois, & Motoyoshi, 2001). A grating displaced by a quarter of a cycle with an interposed gray ISI appears to move in one direction for long intervals but in the opposite for shorter ISIs. A shift toward a short-ISI reversal point would indicate a shortening, while a shift toward a long-ISI reversal point would indicate a lengthening of the impulse response functions. We asked subjects to judge the motion direction for a range of different ISIs and for three average luminance levels (0.75, 3, and 50 cd/m^2).

Methods

In Experiment 1, after dark adapting for 25 min, observers had to fixate the center of the monitor and were required to perform a motion direction judgment. The stimuli (Figure 1A) were composed of eight frames, each

containing a vertically oriented sinusoidal grating (spatial frequency: 1 cycle/deg) displayed within a square window (size: $5^\circ \times 5^\circ$, position: centered 10° above or below the center of the monitor in blocked trials), that were sequentially displayed, separated by a blank interval (average luminance) of variable duration across trials (range: 0–600 ms). The phase step size between successive frames was $\pi/2$ (90 deg) to the left or right and each frame stayed on for 120 ms. Subjects had to report the direction of apparent motion (right or left) by pressing a button on a computer keyboard. The Michelson contrast of the stimuli was previously determined in a direction discrimination task to equate stimulus visibility across average luminance levels (0.75, 3, and 50 cd/m^2). For the direction discrimination task, no blank interval was displayed between the stimulus frames and the contrast was varied on a trial-by-trial basis using the QUEST algorithm (Watson & Pelli, 1983). Once the 75% contrast threshold was determined for each luminance level and for each subject individually, we multiplied the thresholds by twelve for the motion reversal task.

Results

Figure 2 describes the mean results of the apparent motion reversal task. For each subject and for each mean luminance level, we first determined the 75% contrast thresholds in a direction discrimination task. As expected, the stimulus visibility, as revealed by contrast threshold measurements, increased progressively with the average luminance level (data not shown). In particular, when the average luminance was approximately 0.75 cd/m^2 , the

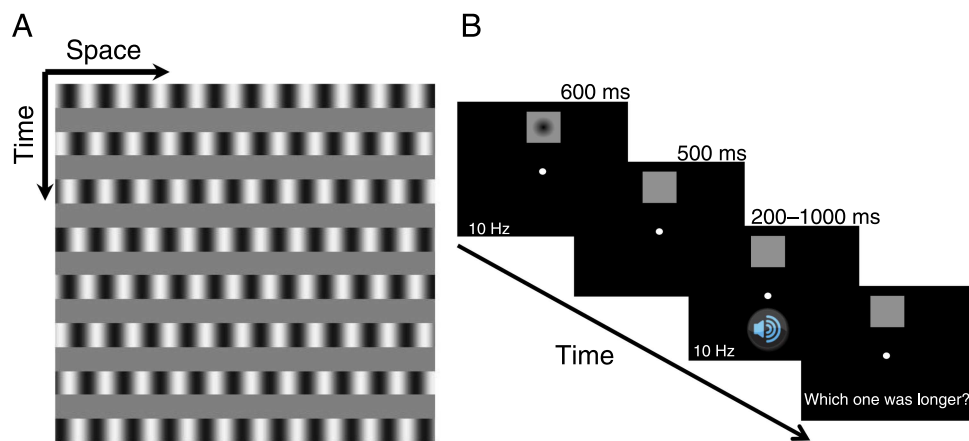


Figure 1. Schematic representations of the stimuli and the task. (A) Space–time representation of the stimulus used in the motion reversal task (Experiment 1). Eight intervals, each containing a sinusoidal grating modulated in luminance with a $\pi/2$ (90 deg) phase shift between successive intervals, were sequentially displayed, interleaved with blank (average luminance) intervals of variable duration across trials (see Methods section for a more detailed description). (B) Schematic representation of the duration task (Experiment 3). Subjects were asked to judge the relative duration of a visual and an auditory stimulus. They had to keep fixation on the middle of the screen while two stimuli (the standard, fixed duration, and the comparison, with variable duration across trials) were sequentially presented. Presentation order and the type (visual or auditory) of standard and comparison stimuli were randomized on a trial-by-trial basis. At the end of each trial, subjects had to report which stimulus appeared to stay on for longer by pressing a button.

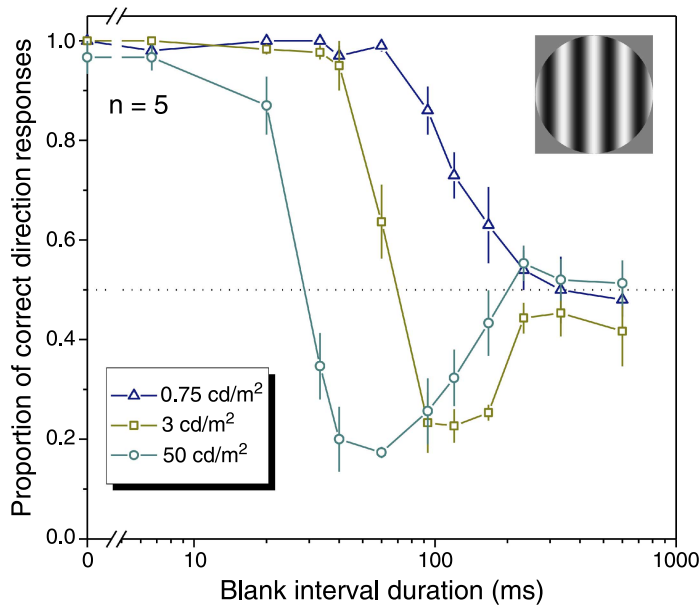


Figure 2. Effect of luminance modulation on apparent motion direction. Proportions of correct motion direction responses (averaged across five subjects) for Experiment 1 are plotted as a function of the duration of the blank intervals for three average luminance levels. The dotted line represents chance level. Error bars indicate ± 1 SEM.

75% Michelson contrast threshold (averaged across five subjects) was 2.95% (standard error: ± 0.29), whereas when it was around 3 or 50 cd/m^2 , it was 0.48% ($SE: \pm 0.07$) and 0.31% ($SE: \pm 0.05$), respectively.

For each luminance level, we multiplied the individual contrast threshold values by twelve to measure the occurrence of motion reversal as a function of the blank interval duration (Figure 2). Confirming previous results (Takeuchi & De Valois, 2009), we observed that for brief blank interval durations (<20 ms), subjects reliably perceived the correct direction of apparent motion regardless of the average luminance. However, a substantial difference between luminance levels emerges for longer durations. At the highest luminance levels we used (50 cd/m^2), subjects experienced an illusory reversal of the apparent motion direction for blank interval durations in the range of ~30–150 ms, whereas performance was at chance for longer durations. The pattern of results for the intermediate luminance level (3 cd/m^2) was similar but shifted toward longer blank interval durations. More specifically, the apparent motion reversal occurred in the range of ~100–250 ms. Conversely, for the lowest luminance level we used (0.75 cd/m^2), subjects reliably perceived the correct direction of motion for blank interval durations up to approximately 100 ms. Then, their performance decreased to reach chance level for blank intervals longer than 200 ms, but, more importantly, no motion reversal was observed. Johnston and Clifford (1995) showed that three temporal filters were required to model the reversal.

The lack of reversal at low luminance, alongside an intact perception of motion direction, suggests that only two temporal filters (one low-pass and one band-pass) remain active.

Apparent temporal frequency changes at different luminance levels

When we reduce retinal illumination by introducing neutral density filters into the optical path, the apparent speed (Hammett et al., 2007; Vaziri-Pashkam & Cavanagh, 2008) or temporal frequency (Peterson et al., 2001) of a stimulus may change. To measure this, in Experiment 2, we asked subjects to compare the apparent flicker rate of a dynamic Gaussian blob to a fluttering sound at different luminance levels. Armed with this information, we can then compensate for any differences due to changes in apparent temporal frequency by standardizing the perceived temporal frequency of the visual stimulus at the test luminance levels.

Methods

In the test phase, following the dark adaptation of Experiment 2, subjects were required to judge the relative temporal frequency of two stimuli (one visual and the other auditory) presented sequentially. The visual stimuli were Gaussian blobs (window size: $5^\circ \times 5^\circ$ of visual angle, standard deviation = 0.5° , spatial position: centered 10° above or below the center of the monitor in blocked trials) that flickered (counterphase flicker) at the same rate (10 Hz) in all the trials. The auditory stimuli were amplitude-modulated 3-kHz tones (generated by a TDT Basic Psychoacoustic Workstation, Tucker-Davis Technologies, and delivered binaurally by Sennheiser HD 265 linear headphones at 80 dB with a sample frequency of 24,420 Hz). We varied the temporal frequency of the sinusoidal amplitude modulation across trials (range of 2–18 Hz) while asking subjects to report which stimulus had the faster modulation rate in order to generate a psychometric function. We decided to keep the temporal frequency of the visual stimulus constant and vary the modulation frequency of the auditory stimulus to avoid differences in visibility at different temporal frequencies. The two test stimuli had the same duration (600 ms). After the dark adaptation phase, subjects were required to fixate the center of the monitor, while the two stimuli were displayed sequentially, separated by a 500-ms blank interval with no sound. The presentation order of the stimuli was randomized on a trial-by-trial basis. At the end of each trial, subjects were required to indicate whether the stimulus that had been modulated at the higher rate had

been displayed first or second (regardless of whether it was visual or auditory) by pressing a button on a computer keyboard. We chose this procedure to avoid subjects focusing their attention more on one modality than another. The 50% point (Point of Subjective Equality, PSE) on the psychometric function (fitted with a cumulative Gaussian) provided a measure of the perceived temporal frequency of the visual stimulus required to match the frequency of the auditory stimulus. The PSIGNIFIT toolbox version 2.5.6 for MATLAB (which implements the maximum likelihood method described by Wichmann & Hill, 2001, see <http://bootstrap-software.org/psignifit/>) was used to compare the collapsed psychometric functions for the different luminance conditions in this and the following experiments. The statistical significance of the difference in PSE between different conditions was determined by the lack of overlap between the 95% confidence intervals (reported in the text and in the figures).

The Michelson contrast of the Gaussian blobs was previously determined using a detection threshold task, in which subjects were presented with a sequence of two 600-ms intervals, separated by a brief beep, one of them containing a 10-Hz flickering Gaussian blob with variable contrast and the other a blank page (average luminance). The presentation order of the two intervals was randomized on a trial-by-trial basis. Contrast was varied across trials using the Quest algorithm (Watson & Pelli, 1983) in order to determine a 75% contrast threshold. Subjects were required to report whether the flickering stimulus was displayed first or second. The contrast thresholds were determined individually and for each luminance level in separate sessions. We multiplied the contrast threshold value by five for the temporal frequency task.

Results

Figure 3 shows the main results of the temporal frequency task. For each subject and for each luminance level, we first obtained a 75% contrast threshold (data not shown). When the average luminance was 0.75 cd/m², the mean threshold (averaged across four subjects) was 16.93% (standard Error = ±1.74), whereas for 3 and 50 cd/m², it was 4.92% ($SE = \pm 0.53$) and 2.69% Michelson contrast ($SE = \pm 0.35$), respectively. We then multiplied the individual thresholds by five to obtain the values we used in the temporal frequency task.

In Figure 3, we plotted the average subjects' performance (psychometric functions collapsed over four subjects) for correctly indicating the visual stimulus as flickering at the higher rate as a function of the difference between the visual and auditory temporal frequencies. Zero indicates trials in which they both had the same temporal frequency (10 Hz), whereas positive and negative values indicate that the visual stimulus had a higher or lower temporal frequency than the auditory stimulus, respectively. We first note that the 50% points of all three

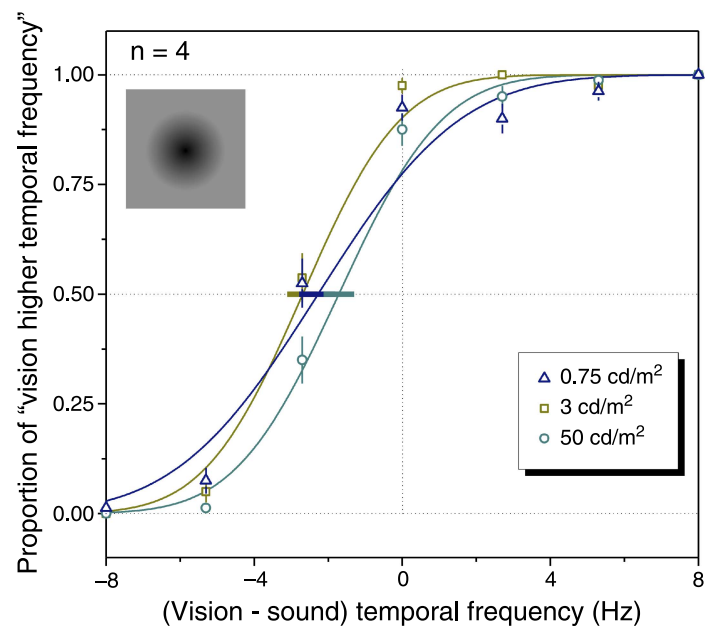


Figure 3. Effect of luminance modulation on the perceived temporal frequency of flickering Gaussian blobs. Average psychometric functions (collapsed over four subjects) for three luminance levels describing the results of Experiment 2. The proportion of trials in which the visual stimulus (flickering Gaussian blob) was judged to have a higher temporal frequency than the sound (amplitude-modulated tone) is plotted as a function of the difference between visual and auditory temporal frequencies. Thick horizontal bars indicate the 95% confidence intervals of the PSEs for each luminance level. Error bars indicate ± 1 SEM.

psychometric functions (one for each luminance level) lie to the left of the zero line. This indicates a common tendency across the luminance levels to perceive the visual stimulus as being modulated at a higher rate than the auditory stimulus and the shift in apparent temporal frequency is approximately 2.5 Hz. However, we do not observe a significant difference in the visual temporal frequency matches across average luminance levels as indicated by the 95% confidence intervals for the PSEs (0.75 cd/m²: PSE = -2.28 Hz, $P_{0.025} = -2.78$ Hz, $P_{0.975} = -1.81$ Hz; 3 cd/m²: PSE = -2.68 Hz, $P_{0.025} = -3.11$ Hz, $P_{0.975} = -2.31$ Hz; 50 cd/m²: PSE = -1.71 Hz, $P_{0.025} = -2.12$ Hz, $P_{0.975} = -1.3$ Hz).

Perceived duration expansion at low luminance levels

The possibility of interocular transfer of dark adaptation (Auerbach & Peachey, 1984; Lansford & Baker, 1969; Makous, Teller, & Boothe, 1976) prevented us from using a direct comparison between a low luminance visual stimulus presented to one eye and a high luminance visual

stimulus presented to the other eye. Therefore, we measured the effect of luminance on perceived duration by asking subjects to compare the duration of a visual stimulus (flickering Gaussian blob in Experiment 3 and drifting luminance-modulated grating in Experiment 4) with that of an auditory stimulus (amplitude-modulated tone in Experiment 3 and pure tone in Experiment 4). Stimulus visibility and apparent temporal frequency for each mean luminance level was equated for each subject. We should expect an overestimation of the duration of an auditory stimulus relative to a visual one (Goldstone & Lhamon, 1974; Walker & Scott, 1981; Wearden, Edwards, Fakhri, & Percival, 1998). However, we are interested in the comparison between luminance levels, regardless of the absolute differences in apparent duration between auditory and visual stimuli within each level.

Methods

In the test phase following the dark adaptation of Experiments 3 and 4, subjects were required to judge the relative duration of two sequentially displayed stimuli (one visual and the other auditory). The experimental procedure was similar to that followed for Experiment 2 (see Figure 1B for a schematic representation of the duration task). The visual stimuli were flickering Gaussian blobs (window size: $5^\circ \times 5^\circ$ of visual angle, standard deviation = 0.5° , spatial position: centered 10° above or below the center of the monitor in blocked trials) for Experiment 3 or drifting sinusoidal gratings modulated in luminance (spatial frequency = 1 cycle/deg, same window size and spatial position as the Gaussian blobs) for Experiment 4. The auditory stimuli were amplitude-modulated tones (same as in Experiment 2) for Experiment 3 or pure tones for Experiment 4. The temporal frequency of the amplitude modulation for the tones was 10 Hz, whereas for the Gaussian blobs we used the temporal frequency estimates obtained individually in Experiment 2 in order to equate for apparent temporal frequency across luminance levels. The temporal frequency of the drifting gratings was 10 Hz. The individual contrast values for the Gaussian blobs were set at 5 times the detection threshold task as measured in Experiment 2, whereas, for the drifting gratings, we multiplied the thresholds obtained in the direction discrimination task in Experiment 1 by 20. After the adaptation phase, subjects were required to fixate the center of the screen while the two test stimuli were presented sequentially, separated by a 500-ms blank interval with no sound. One of the stimuli (the standard) had fixed duration across trials (600 ms), whereas the other (the comparison) had variable duration (range of 200–1000 ms) in order to determine a psychometric function. Within the same session, we interleaved trials in which the visual stimulus was the standard with trials in which it was the comparison. Subjects were instructed to pay attention to

the relative duration of the two intervals (regardless of whether they contained a visual or an auditory stimulus) and report which interval appeared to stay on for longer. The 50% point on the psychometric function (the psychometric data from each condition were fitted with a cumulative Gaussian) provided a measure of the perceived duration of the comparison required to match the duration of the standard.

Results

Figure 4 describes the main results of Experiment 3, in which subjects were required to judge the duration of a flickering Gaussian blob relative to that of an amplitude-modulated tone. The temporal frequency of the visual stimulus was adjusted individually using the estimates obtained in Experiment 2, while the auditory stimulus was modulated at 10 Hz. The paradigm and procedure used (schematically described in Figure 1B) were the same as for Experiment 2. The only difference was that the comparison stimulus varied in duration and not in temporal frequency across trials. We used the same contrast values

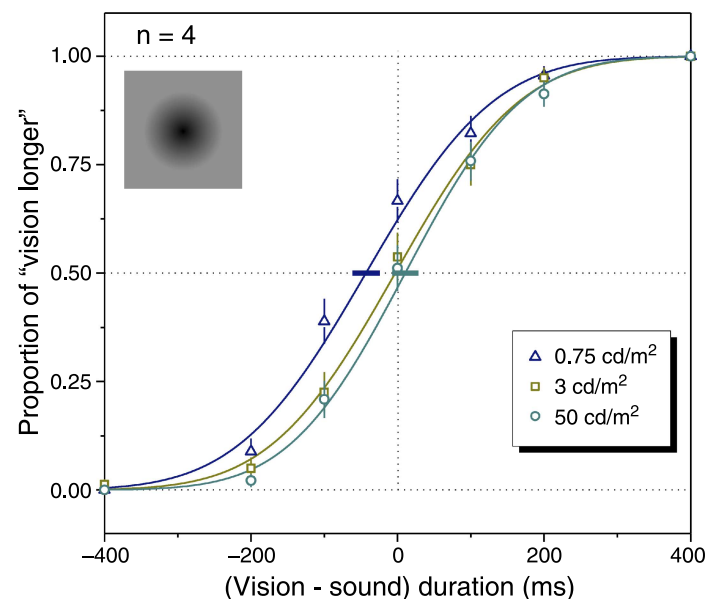


Figure 4. Effect of luminance modulation on the perceived duration of flickering Gaussian blobs. Average psychometric functions (collapsed over four subjects) for three luminance levels describing the results of Experiment 3. The proportion of trials in which the visual stimulus (flickering Gaussian blob) was judged to have a longer duration than the sound (amplitude-modulated tone) is plotted as a function of the difference between visual and auditory duration. Thick horizontal bars indicate the 95% confidence intervals of the PSEs for the lowest (navy bar) and highest (dark cyan bar) luminance levels. The bar describing the 95% confidence interval for the intermediate luminance level was omitted for ease of representation. Error bars indicate ± 1 SEM.

determined for Experiment 2 to equate stimulus visibility across average luminance levels.

The proportion of the visual stimulus judged as longer than the auditory one is plotted as a function of the difference in duration between the two stimuli, with zero indicating trials in which they had the same duration and positive and negative values indicating the visual stimulus to be longer and briefer, respectively. Average psychometric functions (collapsed over four subjects) for the three mean luminance levels used are plotted. First, it is noticeable that the PSEs for an average luminance level of 50 cd/m² (PSE = 10.57 ms, $P_{0.025} = -7.46$ ms, $P_{0.975} = 28.85$ ms) and for 3 cd/m² (PSE = -3.4596 ms, $P_{0.025} = -24.07$ ms, $P_{0.975} = 15.42$ ms) do not substantially differ from zero, indicating that subjects were not biased in perceiving the relative duration of vision and sound. The classic finding that sounds seem to last longer than lights (Goldstone & Lhamon, 1974; Walker & Scott, 1981; Wearden et al., 1998) has been challenged recently (Aaen-Stockdale, Hotchkiss, Heron, & Whitaker, 2011) by showing that the advantage of the auditory modality disappears for mid to low spatial frequencies. However, when the average luminance was very low (0.75 cd/m²),

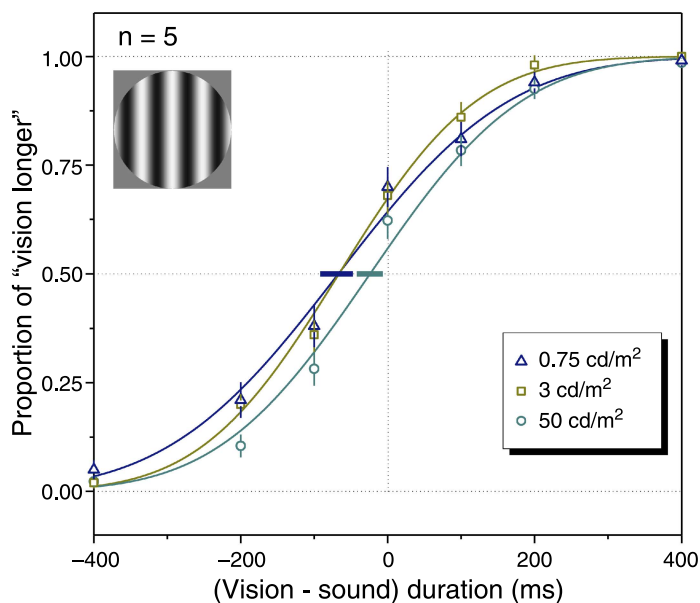


Figure 5. Effect of luminance modulation on the perceived duration of drifting gratings. Average psychometric functions (collapsed over five subjects) for three luminance levels describing the results of Experiment 4. The proportion of trials in which the visual stimulus (drifting grating) was judged to have a longer duration than the sound (pure tone) is plotted as a function of the difference between visual and auditory duration. Thick horizontal bars indicate the 95% confidence intervals of the PSEs for the lowest (navy bar) and highest (dark cyan bar) luminance levels. The bar describing the 95% confidence interval for the intermediate luminance level was omitted for ease of representation. Error bars indicate ± 1 SEM.

the flickering Gaussian blobs were perceived as longer in duration than the amplitude-modulated sounds (PSE = -42.98 ms, $P_{0.025} = -61.86$ ms, $P_{0.975} = -24.07$ ms), and also, the PSE differed significantly from that obtained for the highest luminance level (50 cd/m²), indicating an expansion of apparent duration at low relative to high illumination.

Figure 5 illustrates the results of Experiment 5, in which subjects were again asked to judge duration as described in Figure 1B, but this time between a sinusoidal grating drifting at 10 Hz and a pure tone. Since the spatial configuration of the gratings was identical to that used for Experiment 1, we used the same contrast thresholds to equate for stimulus visibility across luminance levels. As in Experiment 4, the visual stimuli appeared to last longer at the lowest (0.75 cd/m²: PSE = -67.4 ms, $P_{0.025} = -91.9$ ms, $P_{0.975} = -47.12$ ms) relative to the highest (50 cd/m²: PSE = -24.33 ms, $P_{0.025} = -42.13$ ms, $P_{0.975} = -6.64$ ms) luminance level. In this case, for all the luminance levels, including the intermediate one (3 cd/m²: PSE = -66.50 ms, $P_{0.025} = -86.13$ ms, $P_{0.975} = -86.13$ ms), the PSEs differed significantly from zero, indicating a general tendency to see the visual stimulus as longer than the auditory one.

Changes in offset relative to onset at different luminance levels

By equating apparent temporal frequency and stimulus visibility across luminance levels in Experiments 2 and 3, we showed that the duration expansion we found at low luminance levels can be dissociated from changes in perceived flickering rate or contrast. However, it is still possible that luminance-related changes in apparent onset or offset of the visual stimulus (Wilson, 1983) might be responsible for the observed duration effect. In order to distinguish pure duration effects from onset–offset latency effects, in Experiment 5, we measured the apparent time of onset and offset of the visual interval relative to an auditory stimulus using temporal order judgments as described in Johnston et al. (2006).

Methods

In Experiment 5, we asked subjects to judge the onset or the offset of a visual stimulus relative to the onset of a brief auditory stimulus. The visual stimuli were the same sinusoidal gratings drifting at 10 Hz used in Experiment 4, whereas the auditory stimuli were 30-ms pure tones generated by a TDT Basic Psychoacoustic Workstation, Tucker-Davis Technologies, and delivered binaurally by Sennheiser HD 265 linear headphones at 80 dB. After the dark adaptation phase, subjects were asked to compare the

time of onset (or offset, in separate sessions) of the visual stimulus with the time of onset of the auditory stimulus and reported which occurred first. The delay of the auditory stimulus relative to the visual stimulus was varied across trials (range: -400 to $+400$) to generate a psychometric function and the 50% point provided a measure of the apparent time of onset (or offset) of the visual stimuli.

Results

Figure 6 describes the main results of Experiment 5, in which subjects were required to judge the onset of an auditory stimulus relative to the onset (or the offset) of a visual stimulus at three different average luminance levels. The mean psychometric functions (collapsed over five subjects) are plotted for onset and offset and for each luminance level separately. The proportion of trials in which the onset of the auditory stimulus was judged to occur after the onset (or offset) of the visual stimulus is reported as a function of the delay between the two. A PSE equal to zero would indicate that the onset (or offset) of the visual stimulus was perceived veridically relative to the onset of the sound, whereas negative and positive values indicate that the onset (or the offset) of the visual stimulus was perceived to occur earlier or later, respectively, than the onset of the sound. For all three mean luminance

levels, the psychometric functions describing the onset conditions are almost indistinguishable (overlapping 95% confidence intervals of the 50% point) from those that describe the offset conditions. This means that even when the PSEs differ from zero (as for 0.75 cd/m^2), the same bias affects both onset and offset, arguably leaving the total apparent duration of the interval unaffected. In other words, the distortions in apparent duration we found in Experiments 3 and 4 (Figures 4 and 5) do not seem to be due to changes in apparent onset relative to offset.

Discussion

We investigated the role of average luminance on the apparent duration of visual intervals that fall within the millisecond range. We found that:

- reducing retinal illumination caused the apparent motion reversal induced by interposing a blank interval between two stimulus frames to occur at longer interstimulus intervals confirming previous observations (Takeuchi & De Valois, 1997, 2009; Takeuchi et al., 2001).

- for the lowest luminance level used in this study (0.75 cd/m^2), no motion reversal occurred for any of the blank interval durations.

- a general tendency to judge the temporal frequency of a 10-Hz flickering Gaussian blob as higher than that of an

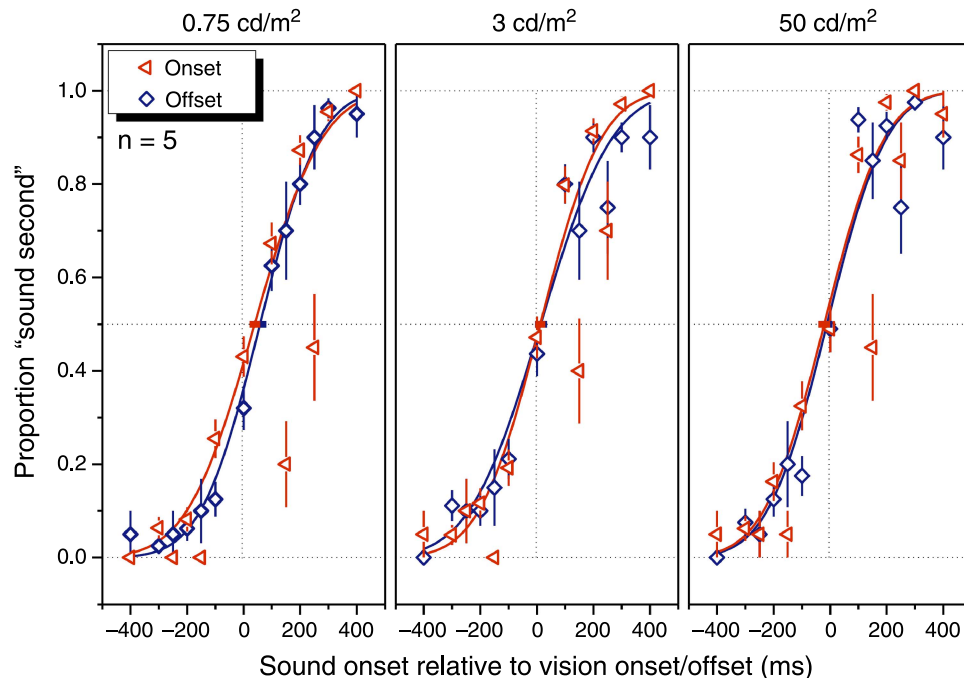


Figure 6. Effect of luminance modulation on the perceived onset and offset of drifting gratings. Average psychometric functions (collapsed over five subjects) for three luminance levels describing the results of Experiment 5. The proportion of trials in which the onset of the auditory stimulus (30-ms pure tone) was judged to occur later than the onset (red symbols and curve) or the offset (blue symbols and curve) of the visual stimulus (drifting grating) is plotted as a function of the onset time of the sound relative to the onset or offset sound of the visual stimulus. Thick horizontal bars indicate the 95% confidence intervals of the PSEs for the onset (red bar) and offset (blue bar) conditions. Error bars indicate $\pm 1 \text{ SEM}$.

amplitude-modulated tone was observed, but no substantial difference in the pattern of results emerged between the three mean luminance levels.

—after equating for stimulus apparent temporal frequency and visibility across average luminance levels, the duration of a 600-ms visual interval containing a flickering Gaussian blob was judged to be longer at low illumination (0.75 cd/m^2) than at high illumination (50 cd/m^2) by approximately 50 ms, when compared with an amplitude-modulated tone.

—approximately the same difference in duration between high and low illumination was observed when the visual stimuli were drifting gratings and the auditory stimuli were pure tones.

—no substantial change emerged in the apparent temporal interval between onset and offset of a drifting grating, as judged by temporal order relative to the onset of a brief auditory stimulus at different luminance levels.

Changes in the apparent direction of motion induced by interleaving stimulus intervals containing spatially uniform fields with luminance equal to the average stimulus luminance in the motion sequence have been attributed to the interaction between induced pattern generated by temporal filtering and the stimulus sequence (Shioiri & Cavanagh, 1990; Stromeyer & Martini, 2003). One way of understanding this effect is to consider the space–time image in Figure 1A convolved with a biphasic temporal impulse response. When two stimulus frames are sufficiently close together in time, the filtering operation induces contrast in the blank frames, which results in space–time orientated contrast in the direction of reversed motion (Shioiri & Cavanagh, 1990; Stromeyer et al., 2000; Stromeyer & Martini, 2003). Motion can be calculated from the ratio of a band-pass and low-pass temporal filter (with appropriate spatial filters) or from two band-pass filters representing second and first temporal derivatives (Johnston and Clifford, 1995). Since temporal filters can be cascaded, the operation of a band-pass plus low-pass motion mechanism following a biphasic (first derivative) filter is equivalent to that of a second derivative–first derivative motion mechanism. The loss of reversal at low luminance can be interpreted as a loss in sensitivity of a first and second derivative motion mechanism relative to a zero-order and first derivative motion mechanism (Johnston and Clifford, 1995). Therefore, the changes in the proportion of correct direction responses of Experiment 1 (plotted in Figure 2) for different luminance levels mirror the changes in the shape and relative sensitivities of the underlying temporal impulse responses. At high mean luminance (50 cd/m^2), the motion reversal first occurs for a blank interval duration of around 30 ms. When we shifted the luminance to 3 cd/m^2 , a motion reversal still occurred but for longer durations (starting from around 75 ms), indicating a lengthening of the underlying temporal impulse response functions (i.e., since the wider filter will match the wider gap). However, at the lowest luminance level (0.75 cd/m^2), no motion reversal is

observable and the subjects' performance dropped to chance level at long durations ($>200 \text{ ms}$), indicating a further lengthening of the underlying temporal impulse responses and a reduction in sensitivity of the band-pass filter tuned to higher temporal frequencies.

Johnston et al. (2006) proposed a link between changes in the shape of the temporal tuning of magnocellular neurons and duration distortions. In their paper, they showed a local duration compression following a purely visual adaptation to flicker or motion. They reported that the effect was limited to high temporal frequencies and it was orientation-independent, leading them to suggest that the adaptation occurred at an early site in the magnocellular pathway. This initial observation was further supported by finding that adaptation to a cortically invisible flicker still causes duration compression in normal, but not in dyslexics (Johnston et al., 2008), for whom a magnocellular impairment has been proposed (Lovegrove, Martin, & Slaghuis, 1986; Lovegrove, Bowling, Badcock, & Blackwood, 1980; Lovegrove, Garzia, & Nicholson, 1990; Stein & Walsh, 1997) and that the spatial specificity of the effect is very narrow (Ayhan et al., 2009). We found that adaptation-induced duration compression occurs in a retinocentric frame of reference (Bruno et al., 2010), but spatiotopic effects have also been reported (Burr et al., 2007, see also Burr, Cicchini, Arrighi, & Morrone, 2011; Johnston, Bruno, & Ayhan, 2011 for further discussion). Duration compression has also been reported for visual intervals displayed perisaccadically (Morrone et al., 2005), when the magnocellular system is thought to be suppressed (Burr, Morrone, & Ross, 1994). The involvement of the magnocellular pathway has also been posited for the effects of stimulus eccentricity (Aedo-Jury & Pins, 2010) and of the visibility of transient signals (Terao, Watanabe, Yagi, & Nishida, 2008) on apparent duration.

Neurophysiological recordings of the nucleus of the optic tract of the wallaby show a shortening of the temporal impulse response after high temporal frequency adaptation (Clifford et al., 1997; Ibbotson, 2005; Ibbotson et al., 1998). The temporal impulse response has also been shown to sharpen during saccades for luminance-modulated but not for isoluminant stimuli (Burr & Morrone, 1996). In their paper, Burr and Morrone (1996) discuss the possibility that this shortening might be linked to contrast gain control mechanisms (Mante, Bonin, & Carandini, 2008; Shapley & Victor, 1978) that operate in M cells but not in P cells. In fact, it was shown that contrast gain control mechanisms cause a sharpening of the temporal impulse response that is specific to magnocellular neurons (Benardete & Kaplan, 1999; Kaplan & Benardete, 2001). Stromeyer and Martini (2003) showed psychophysically that increasing stimulus contrast sharpens the impulse response function. Bruno and Johnston (2010) have recently shown that the contrast context of a stimulus influences its apparent duration. In particular, the duration of an interval containing a 50% luminance contrast stimulus appears compressed when it follows a 90%

contrast inducer relative to when it follows a 10% contrast inducer. The effect disappears with isoluminant chromaticity-modulated stimuli as it does after temporal frequency adaptation (Ayhan, Bruno, Nishida, & Johnston, 2011).

The parvocellular contribution to visual sensitivity when the retinal illumination is reduced has been debated in the literature. We know from primate physiology that the magnocellular retinogeniculate pathway receives a much stronger rod input than the parvocellular pathway (Purpura, Kaplan, & Shapley, 1988; Sun, Pokorný, & Smith, 2001), suggesting its predominant role at mesopic and scotopic light levels. Sensitivity to both coherent (Grossman & Blake, 1999) and biological (Billino, Bremmer, & Gegenfurtner, 2008) motion, which requires the magnocellular pathway, has been shown to survive significant reductions in retinal illumination. However, visual acuity under scotopic illumination is higher than predicted by just the magnocellular contribution (Lennie & Fairchild, 1994).

There is evidence that both M and P cells become less sensitive to high temporal frequencies at low luminance. Purpura, Tranchina, Kaplan, and Shapley (1990), recording from single ganglion cells in the monkey retina, found a comparable increase for M and P cells in the time to peak of the temporal impulse response as the illumination was decreased. Lee, Pokorný, Smith, Martin, and Valberg (1990), in a similar study, investigated the population response of groups of phasic (magnocellular) and tonic (parvocellular) cells to luminance modulation at different illumination levels (ranging from 2 to 2000 Td). They reported a similar change in temporal tuning of phasic and tonic cells with reduction in luminance. The change in perceived duration at low luminance level (~50-ms duration expansion) is more modest than the changes induced by high temporal frequency adaptation (>100 ms) even though the changes in temporal tuning as shown in the motion reversal task are substantial. Therefore, it is likely that the temporal impulse response of both M and P cells broaden at low luminance, but the change is greater for M cells.

In this paper, we showed that, just as a shortening of the temporal impulse response seems to result in a reduction in perceived duration, a lengthening of the impulse response function induced by reduced illumination (Kelly, 1961; Peterson et al., 2001; Takeuchi & De Valois, 1997, 2009) results in a duration expansion. We have recently proposed a model that could provide a link between these two phenomena (Johnston, 2010). This model can also offer an account of the changes in apparent duration with changes in luminance. In this model, unlike the traditional stopwatch model for time perception (Creelman, 1962; Treisman, 1963; Treisman, Faulkner, Naish, & Brogan, 1990), the content of an interval is fundamental to the determination of its duration. As in the stopwatch model, the final duration estimate is provided by counting the number of ticks stored in an accumulator, but the generation of the ticks depends on a “predict and compare” strategy. The system predicts what the content of a visual

interval will look like in the future (for example, 100 ms ahead). This prediction is continuously compared with the present appearance of the stimulus. When the input stimulus matches the prediction, the system knows that 100 ms has passed, it generates a tick and resets the prediction. In this clock model, timing is intimately related to perceptual processing and sensory calibration. To predict forward in time, we require a temporal derivative in order to construct a Taylor series expansion of the time series of image brightness at a point. A temporal first derivative operator has a biphasic impulse response, as do transient magnocellular neurons, whereas parvocellular neurons are temporally low-pass. Magnocellular neurons are more prone to adaptation than parvocellular neurons and contrast adaptation has two effects: a reduction in sensitivity and a shift in temporal tuning that causes a phase advance in their response (Benardete & Kaplan, 1999; Kaplan & Benardete, 2001). The phase advance (which occurs after high temporal frequency adaptation and contrast adaptation and during saccades) shifts the prediction forward in time. The consequence is that the match between the prediction (carried by the magnocellular system) and the current input (carried by the parvocellular system, which is unaffected by contrast or high temporal frequency adaptation) is delayed and the content-dependent clock ticks later. Consequently, there are fewer ticks in the accumulator and apparent duration is reduced. When retinal illumination is reduced, we assume that the peak of the temporal impulse response occurs later in M cells (phase delay), shifting the prediction backward in time and that this luminance-induced phase shift is greater in M cells than in P cells. This process would accelerate the match between the prediction and the current input, causing a higher number of ticks to be stored in the accumulator, therefore producing duration expansion. The comparison may not be possible until early stages of cortical processing when magnocellular and parvocellular signals combine (Sincich & Horton, 2005).

The effect we found on duration appeared to be dissociable from the effect of apparent temporal frequency or onset/offset, confirming previous observations (Ayhan et al., 2009, 2011; Bruno et al., 2010; Bruno & Johnston, 2010; Johnston et al., 2006, 2008). Unlike Hammett et al. (2007) and Vaziri-Pashkam and Cavanagh (2008), who both reported a speed overestimation at low luminance, we did not observe a substantial difference in the apparent temporal frequency across luminance levels. One of the reasons might be that both the stimuli and the setup we used were very different. They used sinusoidal gratings and they displayed both the standard and the comparison stimuli simultaneously, while we asked subjects to compare the relative modulation rate of an amplitude-modulated tone and a flickering Gaussian blob that were sequentially presented. Moreover, Vaziri-Pashkam and Cavanagh reported a significant speed overestimation only for stimuli that differed in luminance for at least $2.4 \log_{10}$ units. In our experiment, the difference between the

highest (50 cd/m²) and lowest (0.75 cd/m²) luminance levels is only 1.8 log₁₀ units.

In conclusion, we showed that the subjective experience of the passing of time in the millisecond range is dilated in the dark. We attribute this effect to changes in the temporal tuning of magnocellular neurons that would affect the accuracy of a “predict and compare” mechanism in determining the duration of a visual interval.

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