

The effect of space on subjective time is mediated by apparent velocity

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In contrast to the intuitive and traditional assumption of a centralized and universal neural clock, many recent studies have provided evidence against this idea. Here, we investigated whether subjective duration is estimated by a mechanism that tracks the trajectory of a moving object. Such a mechanism would integrate over the velocity and the spatial distance the object traveled to derive its duration. We exposed observers to a moving object that covered either a small or large spatial distance. We found that subjective duration decreased after this exposure when intervals were tested that were defined by stimuli covering a large, but not by stimuli covering a small, spatial distance. We compared the effects of our velocity exposure to previously used adaptation to a drifting grating and found a dependence of spatial distance only for velocity exposure. The finding that temporal estimations decrease after exposure to fast-moving stimuli selectively at large distances suggests that subjective duration is derived from measurements of velocity and space.

Introduction

The flow of time appears natural to us despite the fact that we are not equipped with an organ sensing time. Humans are well able to discriminate the duration of temporal intervals with Weber fractions between 5% and 20% for intervals between 150 and 1,500 ms (Mauk & Buonomano, 2004). An intuitive explanation of the capability to discriminate time consists in a neural clock model (Treisman, 1963). While such models were the first that have been proposed in the time perception literature, they are not entirely consistent with experimental findings and are unlikely to be precise in the subsecond range (Buhusi & Meck, 2005). From a biological perspective, the idea of a module dedicated to tell time that is separate from stimulus processing seems implausible. Temporal

estimations alone are not sufficient to guarantee survival but rather precise timing of actions in response to moving objects or enemies. However, these processes work without involving a dedicated neural clock. We therefore wondered whether the subjective duration of visual stimuli is derived from mechanisms detecting external motion. Duration estimates could be easily constructed from these signals by simply integrating the speed and the distance an object traveled. A prime example for the assumed role of speed and spatial distance in temporal estimations is the Kappa effect: When two visual stimuli are flashed successively, observers judge the interflash interval longer, the further apart the stimuli are presented (Cohen, Hansel, & Sylvester, 1953; Cohen, Hansel, & Sylvester, 1955; Price-Williams, 1954; Suto, 1952). Early on, a model was constructed to formalize the intuitive idea of a constant velocity between the first and the second interval marker (Collyer, 1977). In the model, apparent interval duration was interpreted as the weighted average of the physical time and the assumed time given as the ratio of spatial distance and velocity. A more recent model suggested that the brain implements Bayesian inference by consulting a slow motion prior (Goldreich, 2007; Chen, Zhang, & Kording, 2016). Perceived motion and time are linked: Motion adaptation compresses apparent duration (Fornaciai, Arrighi, & Burr, 2016) selectively for matching durations between adapter and probe stimulus (Bruno, Ng, & Johnston, 2013; Latimer, Curran, & Benton, 2014). Consistent with this explanation of the Kappa effect, direct evidence for the involvement of areas computing stimulus velocity in duration judgments comes from studies that reported how velocity adapters reduce subjective duration: Curran and Benton (2012) adapted observers to a random dot plaid pattern, which selectively activate middle temporal (MT) neurons (Movshon, Adelson, Gizzi, & Newsome, 1985). They found duration compression only if the

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motion direction of adapter and test stimuli matched. Beattie, Curran, Benton, Harris, and Hibbard (2017) moved on to show that adapting global speed mechanisms induced reductions in subjective duration. Other evidence for temporal processing in higher areas is provided by investigations into the reference frame of the duration compression effect. While a controversy arose whether duration adaptation occurs in a spatiotopic or a retinotopic reference frame (Burr, Tozzi, & Morrone, 2007; Bruno, Ayhan, & Johnston, 2010; Burr, Cicchini, Arrighi, & Morrone, 2011; Latimer & Curran, 2016), the most recent study found that it contains both, a retinotopic and a spatiotopic component (Latimer & Curran, 2016). A candidate area suggested to establish spatiotopic coding is MT (Latimer & Curran, 2016).

Evidence showing that a motion mechanism might provide temporal estimates comes from studies demonstrating influences of speed and space on time. Many studies have demonstrated that either speed (Kaneko & Murakami, 2009; Tomassini, Gori, Burr, Sandini, & Morrone, 2011; Bruno, Ayhan, & Johnston, 2015; Gorea & Kim, 2015; Yamamoto & Miura, 2016) or spatial extent (Mo & Michalski, 1972; Thomas & Cantor, 1976; Xuan, Zhang, He, & Chen, 2007; Ono & Kitazawa, 2009; Rammsayer & Verner, 2014; Kanai, Dalmaijer, Sherman, Kawakita, & Paffen, 2017) influence duration estimations.

In this study we sought to investigate whether the interactions between object speed and object size with apparent duration are a signature of a motion mechanism that tells time by detecting and integrating velocity and spatial distance. We first determined the strength of the Kappa effect for four probe interval durations and four spatial distances. In the Kappa effect, time is overestimated as a function of distance. It is commonly assumed that the brain imputes a velocity between the two flashed interval markers. Since there is no physical motion occurring, the brain might rely on prior knowledge derived from environment statistics about average object speed (Stocker & Simoncelli, 2006). To manipulate the internal prior about object speed, we exposed participants to a bunch of trials with either a slow- or a fast-moving object. If speed is used in calculating time, the exposure to slow or fast motion should affect temporal duration estimates.

We also wanted to know how far our results relate to findings from studies that used adaptation to a drifting grating to strongly modulate temporal estimates (Johnston, Arnold, & Nishida, 2006). We found that our velocity stimulus decreased subjective duration in dependence on the spatial extent of the visually defined interval. Adaptation to a drifting grating, however, compressed interval duration irrespective of the spatial distance that the object covered. The results of our experiments demonstrate that estimates of visually defined duration take into account velocity and spatial

distance, indicating that temporal estimations involve motion processing areas.

Experiment 1: Measuring the magnitude of the Kappa effect

Participants

Fourteen subjects (four male, 10 female; age: $M = 26.8$; $SD = 6.3$) participated in Experiment 1. Due to technical reasons, the data from three subjects could not be recorded for all four temporal intervals: Two participants had to be removed completely from analysis because their temporal discrimination data did not allow to estimate a psychometric function. One participant only completed the 700 ms and the 1,000 ms interval sessions because she did not reappear to test the remaining sessions. In all experiments, participants had normal or corrected-to-normal vision and gave their written informed consent. They were paid for their participation.

Apparatus

Stimuli were presented on a 17-in. cathode ray tube color monitor (actual viewing diagonal: 15.9 in., FlexScan T57S, MA-1790, EIZO Corporation, Japan; refresh rate: 120 Hz, resolution: 800×600 pixels). The distance between participants' eyes and the screen was 85 cm, corresponding to a $16^\circ \times 22^\circ$ field of view.

Procedure

A fixation point (black, radius: 0.25°) was displayed on a gray background, on the vertical meridian, 2.5° above the screen center (see Figure 1a). Participants were required to keep their gaze directed at the fixation point throughout the entire session. A clock stimulus consisting of a circle (black, radius: 5° , line width: 0.5°) with a blue hand ($3.9^\circ \times 0.75^\circ$) was displayed 7.5° below screen center for the entire duration of the experiment. In the first trial, the hand was shown in the 12 o'clock position. After 1,000 ms, the probe interval was presented. This interval was defined by a red square ($1.5^\circ \times 1.5^\circ$) that was flashed for one frame on the left side of the screen and a second red square shown for one frame at the same eccentricity in the right side of the screen. The presentation of the squares marked one of four possible horizontal spatial distances (2.5° , 6.65° , 10.8° , or 15°) and one of four possible interval durations (100 ms, 400 ms, 700 ms, or 1,000 ms). After 1,000 ms, the hand of the clock rotated clockwise to provide a temporal comparison for the probe interval. The clock moved constantly with an angular velocity of $26.95^\circ/\text{s}$ and the rotation duration was one of seven equidistant and equiprobable durations, depending on the duration of the probe interval (for 100 ms probe: 33–183 ms, 400 ms

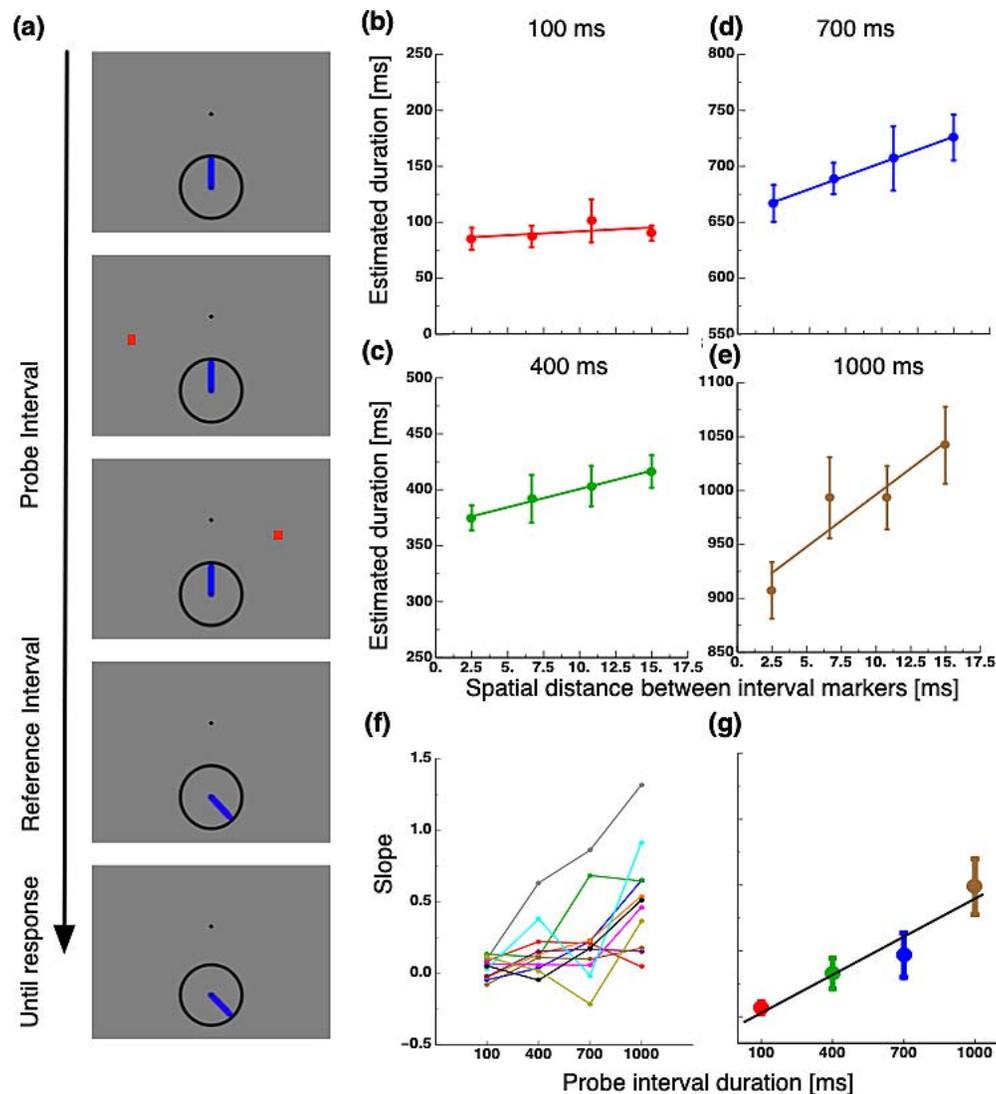


Figure 1. (a) Arrangement of the stimuli of Experiment 1. A clock stimulus and a fixation point were visible throughout the whole block. First, two interval markers, i.e., red squares, were flashed successively on the left and right side of the screen center. The temporal interval between the flashes defined the probe interval duration. After presentation of the probe interval, the clock hand rotated clockwise. Participants had to compare the duration of the probe interval against the duration that the clock hand had moved. (b–e) Temporal estimations of the probe interval as a function of spatial distance between the interval markers for the four probe interval durations. Data are fitted by linear functions. Errors bars represent *SEM*. (f) Single-subject slopes. Different colors represent different observers. (g) Slopes of the linear fits for each probe interval duration.

probe: 250–550 ms, 700 ms probe: 550–850 ms, 1,000 ms probe: 550–1,450 ms). The participants were instructed to indicate whether the interval defined by the presentation of the squares appeared shorter or longer than the duration the hand moved. They responded by pressing the left (shorter) or the right (longer) arrow button on the keyboard. Each participant completed 16 blocks of 70 trials. Probe intervals were presented blockwise with interval duration and spatial distance counterbalanced across observers. Experiment 1 was measured in two separate testing sessions of 1 hour each.

For analysis in Experiment 1 and all other experiments, we estimated psychometric functions by aver-

aging the 10 responses for each of the seven reference durations within each observer and fitted a cumulative gaussian function to these data using Mathematica (Version 10.1, Wolfram Research, Inc., Champaign, IL, 2015). Points of subjective duration equality were chosen from each observer and then used for the calculation of average data and for statistical analysis. The dependence of duration estimations on spatial distance was estimated within each observer by fitting a linear regression line to the points of subjective duration equality. The slope parameter was chosen as an index of the Kappa effect. We then compared for each of the four temporal intervals the slope values

against zero using a paired t test, including a Bonferroni correction for multiple comparisons.

Results

We measured the Kappa effect for four temporal and four spatial intervals. We implemented a setup in which both, the test and the comparison interval were presented visually (see Figure 1a). Figure 1b shows average estimated durations for a 100 ms interval for which the interval markers were presented at spatial distances between 2.5° and 15° . On average, observers judged the interval nearly veridically irrespective of the spatial distance the markers covered. For the 400 ms interval however, a slight influence of spatial distance on perceived duration can be seen (see Figure 1c). At the shortest spatial distance of 2.5° the interval duration was underestimated, whereas at the longest spatial distance (15°) it was slightly overestimated. This trend occurred similarly for the 700 ms interval. For the 1,000 ms interval, we found a very strong dependence of spatial distance on estimated duration. To estimate the dependence of perceived time on spatial distance with inference statistics we determined for each participant a linear regression. We used the slope parameter from each single subject fit to compare them statistically. Single subject slopes are shown in Figure 1f. The slopes scaled with the duration of the test interval. For each of the four interval durations we calculated one-sample t tests, comparing the single subject slopes against zero [100 ms: $t(10) = 1.62$, $p = 0.14$, $d = 0.49$; 400 ms: $t(10) = 2.82$, $p = 0.018$, $d = 0.85$, 700 ms: $t(11) = 2.79$, $p = 0.017$, $d = 0.80$, 1,000 ms: $t(11) = 4.68$, $p < 0.001$, $d = 1.35$]. Only the p -value of slopes that derived from the 1,000 ms lay below the alpha level after Bonferroni correction (0.013). Figure 1g shows average slopes. The Kappa effect grew linearly as a function of interval duration ($-0.03 + 0.0005x$), illustrating the scalar properties of duration perception. Variability increases as a function of interval duration (Wearden & Lejeune, 2008), thus longer durations are highly susceptible for the influence of spatial distance.

Experiment 1 aimed to test the appropriate interval duration to obtain a significant Kappa effect. We found that an interval duration of at least 1,000 ms is necessary to find a dependence of space on time. We next sought to find whether prior exposure to a certain velocity would modify temporal estimations.

Experiment 2: Spatially selective changes in perceived duration after velocity exposure

Participants

In Experiment 2, 14 participants (five male, nine female; age: $M = 25.4$, $SD = 5.0$) were tested in the small distance condition and 15 participants (seven

male, eight female; age: $M = 25.0$, $SD = 4.4$) were tested in the high distance condition.

Procedure

In Experiment 2 we tested whether and how prolonged velocity exposure would modify apparent duration. Experiment 2 contained two trial kinds: Exposure and test trials. A session started with 20 exposure trials. After these, five test trials and five top-up exposure trials alternated until the end of the experiment. In total, 155 trials were presented. Each trial began with the presentation of a fixation point (green / black, radius: 0.25°) in the center of the screen ($0^\circ \times 0^\circ$). Beneath the fixation point (7.5° below the screen center), the clock stimulus was displayed throughout the whole session. The color of the fixation point signaled the participants to which trial kind was upcoming: A green fixation point indicated an exposure trial and a back fixation point a test trial.

In exposure trials, after 1,000 ms a red square ($1.5^\circ \times 1.5^\circ$) moved at the height of the fixation point either with fast ($0.045^\circ/\text{ms}$) or slow velocity ($0.015^\circ/\text{ms}$). In the condition, testing a spatial distance of 2.5° , the dot moved from $-1.25^\circ \times 2.5^\circ$ to $1.25^\circ \times 2.5^\circ$, and in the condition testing a spatial distance of 15° , it moved from $-7.5^\circ \times 2.5^\circ$ to $7.5^\circ \times 2.5^\circ$ (see Figure 2a). The moving rectangle was repeatedly shown for a total duration of 1,000 ms.

In test trials, a red square ($1.5^\circ \times 1.5^\circ$) was flashed after 1,000 ms in the left side of the screen for one frame, followed by a flashed square on the right side 1,000 ms later. The eccentricities of the test stimuli corresponded to the start and the end positions of the adapter stimuli. Another 1,000 ms later, the hand of the clock rotated clockwise for 547 ms to 1,444 ms (seven equiprobable and equidistant steps, each presented 10 times). The participants were instructed to indicate if the interval between the appearance of the squares was shorter or longer than the duration the hand had moved. They responded by pressing the left (shorter) or the right (longer) arrow button on the keyboard.

We compared the average estimations of the 1,000 ms intervals (for 2.5° and 15° distances) of the exposure condition from Experiment 2 with the estimates of the 1,000 ms intervals (for 2.5° and 15° distances) from Experiment 1. As in Experiment 1, there was no velocity exposure before the interval durations had to be judged. These results served as a baseline measure.

Results

We used a rectangle that moved across the visual field either with a fast or with the same velocity as the test interval. We tested two spatial interval distances: 2.5° and 15° . For both intervals, exposure stimuli

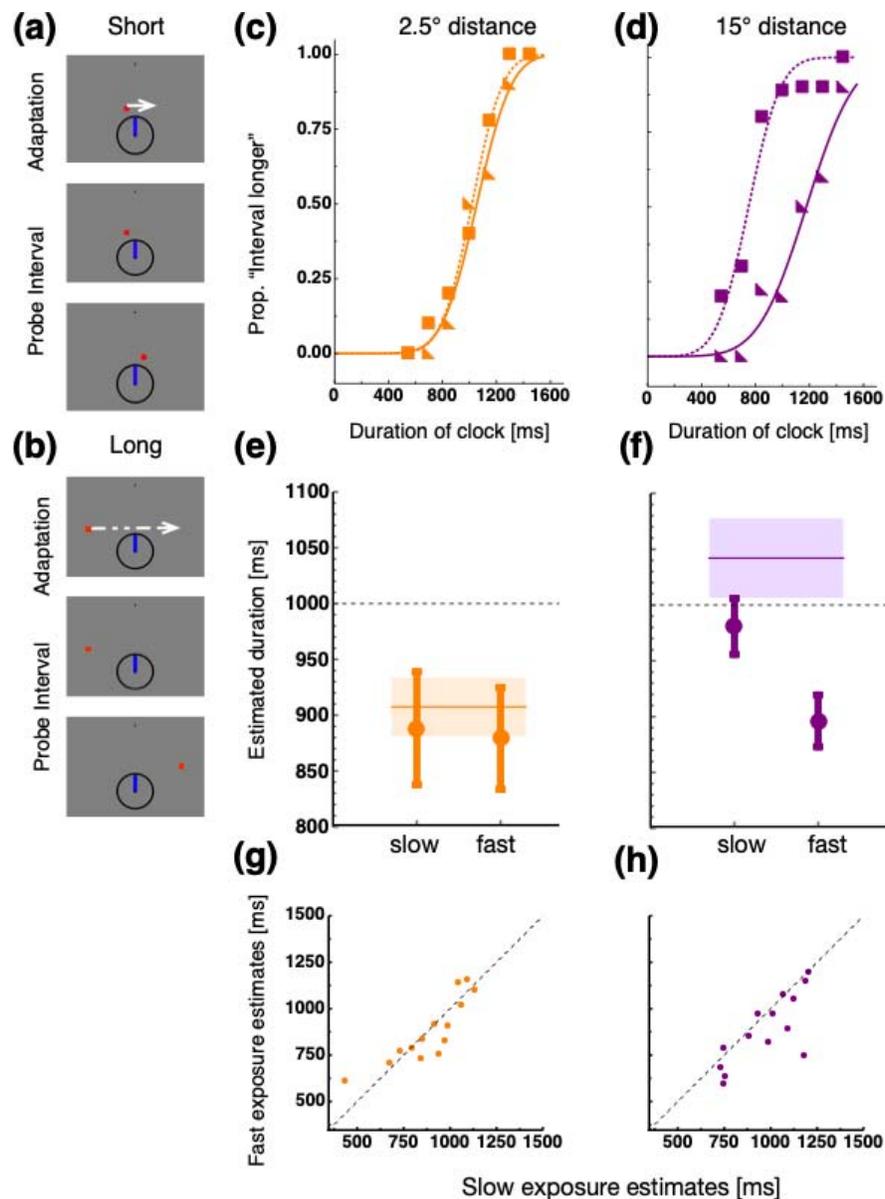


Figure 2. (a) Arrangement of the stimuli for adaptation and test trials. A clock stimulus and a fixation point were visible throughout the whole block. In adaptation trials, a red square moved fast or slowly from 3.8° left to 3.8° right at the height of the fixation point. In test trials, two interval markers, i.e., red squares, were flashed successively on the left and right side of the screen center. After presentation of the probe interval, the clock hand rotated clockwise. (b) Arrangement of the stimuli within the long condition of Experiment 2. (c) Psychometric functions for adaptation to a stimulus moving with slow (triangle objects and thick fits lines) or fast (rectangle objects and dotted lines) velocity at a short distance. (d) Psychometric functions for adaptation to a stimulus moving at a long distance. Same conventions as in (c). (e) Average duration estimations for probe intervals after adaptation to a slow or fast moving stimulus for probe interval markers presented at a short spatial distance. Errors bars represent *SEM*. The colored, thick line indicates the mean estimated time without previous adaptation (see Experiment 1) with the corresponding *SEM* (shaded colored area). The back, dotted line indicates the physical probe interval duration. (f) Average duration estimations for probe intervals after adaptation to a slow- or fast-moving stimulus for probe interval markers presented at a long spatial distance. Same conventions as in (E). (g–h) Single-subject data after exposure to slow- and fast-moving rectangles. The dashed line shows the identity line.

covered the same spatial distance as the stimulus in the test interval. Figure 2c shows an example psychometric function for temporal estimations of intervals presented at a short distance. In this condition the psychometric functions are almost identical. However, when intervals

were presented at a long distance, duration judgements were clearly reduced (see Figure 2d). We tested probe intervals with a spatial distance of 2.5° after velocity exposure (see Figure 2e). Average probe interval durations were indistinguishable from the mean base-

line performance (data taken from results shown in Figure 1e). Figure 2f shows average duration estimations for intervals covering 15° , shown after stimuli moving with the same velocity as the test interval, and for those moving faster. The average baseline estimation of a 1,000 ms interval tested without exposure (data taken from results shown in Figure 1e) is shown as an orange thick line (shadings indicate standard error of the mean or *SEM*). One can see that the presentation of both exposure velocities reduced apparent temporal duration. However, exposure to a fast adapter decreased the perceived duration significantly stronger than the adapter moving with the same velocity as the probe interval. For statistical analysis we subtracted the baseline values from the duration estimates obtained after exposure to the moving rectangle. A 2×2 repeated-measures analysis of variance (ANOVA) with the within-subject factor velocity (slow, fast) and the between-subject factor condition (short, long) confirmed that the velocity exposure changed the apparent probe interval duration, $F(1, 27) = 4.40$, $p = 0.045$, $\eta^2 = 0.140$. A significant interaction effect between velocity and condition was found, $F(1, 27) = 4.66$, $p = 0.040$, $\eta^2 = 0.147$, indicating that exposure selectively affected intervals with long spatial distances. The between-subject factor condition was not significant, $F(1, 27) = 1.38$, $p = 0.250$, $\eta^2 = 0.049$.

Studies have demonstrated that speed estimates likely rely on a slow motion prior (Stocker & Simoncelli, 2006). We elevated this prior to faster speeds by repeatedly presenting a fast moving rectangle. Experiment 2 demonstrated that prolonged exposure to a fast moving rectangle reduces apparent duration. However, it did so only if the moving rectangle traveled a larger distance. This is consistent with the finding from Experiment 1 that showed that large distances led to an overestimation of duration. If space and speed are integrated to retrieve time, larger distances will lead to longer durations in case velocity is kept constant. However, by changing the prior velocity expectation that an object needs to travel a 15° distance, temporal estimations are reduced. The most probable reason for this reduction is that velocity and space are integrated to retrieve time. In this view, larger distances can be reached quicker, thus taking less time. We next wondered how far our results were comparable to modulations of temporal estimate by adaptation to a drifting grating.

Experiment 3: Comparison of velocity exposure and adaptation to a drifting grating

Participants

In Experiment 3, three conditions were measured. In condition 1, 13 participants (five male, eight female;

age: $M = 23.54$, $SD = 4.52$), in condition 2, 11 different participants (one male, 10 female; age: $M = 27.18$, $SD = 5.76$), and in condition 3, 11 different participants (three male, eight female; age: $M = 25.73$, $SD = 4.4$) were measured.

Procedure

Experiment 3 consisted of three conditions. In condition 1, we tested duration estimations for a grating of varying sizes. In condition 2, we tested how exposure to either a drifting grating or a moving rectangle would affect duration estimation for a drifting grating of two different sizes. In condition 3, we tested how exposure to a drifting grating would affect temporal estimates of intervals defined by flashed rectangles.

The procedure of condition 1 was identical to Experiment 1, except that the probe interval in Experiment 3 was defined by the presentation duration of a drifting grating. The grating was presented 1,000 ms after trial start and consisted of a sinusoid (spatial frequency: 1 c° , temporal frequency: 10 Hz, rightward direction). The size of the grating was systematically varied across blocks, consistent with the spatial distances of the probe intervals presented in Experiment 1 (width: 2.5° , 6.65° , 10.8° , or 15° ; height: always 1.5°).

In condition 2, exposure blocks were identical to those in Experiment 2, except that the velocity stimulus was either a drifting grating (spatial frequency: 1 c° , temporal frequency: 20 Hz, direction alternating after 0.5 s) or a moving rectangle (velocity: $0.045^\circ/\text{ms}$). Exposure blocks were tested for small ($2.5^\circ \times 1.5^\circ$) and large ($15^\circ \times 1.5^\circ$) test gratings. The spatial extent of adapter and test gratings were always matched, likewise the spatial distance the rectangle moved and the extent of grating were identical. We took the data from the 2.5° and the 15° gratings from condition 1 as baseline. In condition 3, we measured baseline and exposure blocks for intervals defined by flashed markers. The procedure for measuring baseline blocks in that condition were identical to those of Experiment 1, except that at probe interval start and again at interval end, both the rectangle on the left and the one on the right were flashed simultaneously. The rectangles either spanned a distance of 2.5° or 15° . In exposure blocks, a drifting grating was presented. The exposure grating was identical to that in condition 2 and again its size always matched the spatial distance that the interval markers spanned.

Results

We tested temporal duration estimations for a drifting sine grating and found a clear dependence of

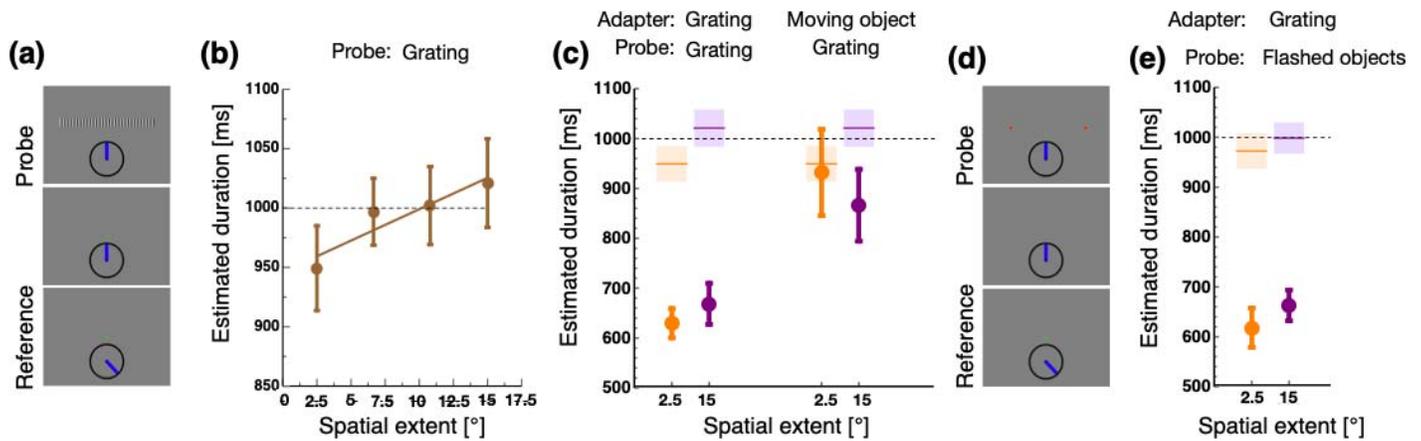


Figure 3. (a) Arrangement of the stimuli for duration estimations of a grating in Experiment 3. (b) Average duration estimations as a functions of the spatial extent of a grating stimulus. Errors bars represent SEM. The black, dotted line indicates the physical probe interval duration. (c) Average duration estimations of a small (orange) or a large (purple) grating stimulus after adaptation to a drifting grating or a moving object. Errors bars represent SEM. The colored, thick line indicates the mean estimated time without previous adaptation (see Experiment 1) with the corresponding SEM. (shaded colored area). The black, dotted line indicates the physical probe interval duration. (e) Arrangement of the stimuli for duration estimations of a grating after adaptation in Experiment 3. (f) Average duration estimations of a small (orange) or a large (purple) interval defined by simultaneously flashed interval markers after adaptation to a drifting grating. Errors bars represent SEM. The colored, thick line indicates the mean estimated time without previous adaptation (see Experiment 1) with the corresponding SEM. (shaded colored area). The black, dotted line indicates the physical probe interval duration.

subjective duration on spatial extent as in the Kappa effect. A one-way ANOVA confirmed a significant dependence of temporal estimations on space, $F(3, 36) = 3.787$, $p = 0.02$, $\eta^2 = 0.240$. We also compared the influence of spatial extent of the gratings on temporal estimations against the corresponding Kappa effect (data measured in Experiment 1). A two-way ANOVA with the within-subject factor spatial extent (four distances) and the between-subjects factor condition (Kappa effect / drifting grating) only revealed a significant main effect for the factor spatial extent, $F(3, 69) = 13.728$, $p < 0.001$, $\eta^2 = 0.374$. The absence of a significant main effect for condition, $F(1, 23) = 1.239$, $p < 0.302$, $\eta^2 = 0.051$, and the absence of a significant interaction effect, $F(3, 69) = 0.023$, $p < 0.881$, $\eta^2 = 0.001$, indicate that the Kappa effect and the effect of spatial extent on perceived duration were statistically indistinguishable. Since similarity of effect does not entail causality, we used exposure to a fast velocity to check whether temporal estimations for both, our Kappa stimulus and drifting gratings would be processed by related mechanisms. We used two stimuli: first, the moving rectangle and second, gratings that drifted with a temporal frequency of 20 Hz. In their seminal study Johnston et al. (2006) found a strong reduction in apparent duration after adaptation to drifting gratings. They suggested that this adaptation affects temporal channels at early precortical levels. We therefore expected that both exposure stimuli we used would decrease temporal estimates but only the moving

rectangle would selectively annul the overestimation for large distances. Figure 3c shows temporal estimations for gratings of two different sizes (2.5° / 15°) after adaptation to a grating drifting at 20 Hz and after adaptation to a moving rectangle tested in condition 2. One can see that both stimuli decreased subjective duration. However, the two stimuli changed apparent duration in very different ways. We calculated a two-way ANOVA with the between-subjects factor stimulus (grating / moving object) and the within-subject factor test grating size (small / large). The drifting grating produced significantly stronger adaptation than the moving rectangle, $F(1, 20) = 12.12$, $p = 0.002$, $\eta^2 = 0.377$. However, only the moving rectangle selectively modified subjective durations for large gratings as indicated by a significant interaction effect, $F(1, 20) = 4.59$, $p = 0.045$, $\eta^2 = 0.187$. No significant main effect for the factor grating size was found, $F(1, 20) = 0.166$, $p = 0.688$, $\eta^2 = 0.008$.

We then compared the effect of a moving rectangle on the duration estimations for a drifting grating (see Figure 3c) against the effect of a moving rectangle on the duration estimations for the flashed interval markers that we measured in Experiment 2 (see Figure 2f). We subtracted the corresponding baseline conditions from the temporal estimates. For the drifting grating we used as baseline values the data obtained in condition 1 of Experiment 1 (see Figure 3b). For the flashed interval markers we used as baseline the data from Experiment 1 (see Figure 1e). A two-way

ANOVA with the within-subject factor spatial extent (short / long) and the between-subjects factor probe stimulus (flashed markers / drifting grating) revealed a significant main effect for the factor spatial extent, $F(1, 23) = 11.519$, $p = 0.002$, $\eta^2 = 0.334$, but no significant main effect for the factor probe stimulus, $F(1, 23) = 0.001$, $p < 0.989$, $\eta^2 = 0.001$, nor an interaction effect, $F(1, 23) = 0.303$, $p < 0.587$, $\eta^2 = 0.013$). The effect of the moving rectangle on temporal estimations for flashed markers or for gratings was therefore statistically indistinguishable.

The standard Kappa stimulus consists of a stimulus being flashed successively at two different locations (Suto, 1952; Cohen et al., 1953; Price-Williams, 1954; Cohen et al., 1955), thereby having a direction in the stimulus presentation. The drifting gratings reversed direction and therefore, on average, had zero motion direction. We wanted to know whether the Kappa effect could be observed even for a zero motion direction. To this end, we flashed two rectangles simultaneously (see Figure 3d), being separated by a certain spatial distance (2.5° or 15°). After 1,000 ms, both rectangles were flashed again and participants had to estimate the apparent duration of the temporal interval, marked by the two flashes. Figure 3e shows average duration estimations for probe intervals with a spatial distance of 2.5° (shown in orange) and of 15° (shown in purple). Data points with bright colors show results from sessions including exposure to a grating and colored, thick lines indicate the mean estimated durations without previous exposure (data from Experiment 1) with the corresponding *SEM* (shaded colored area). The grating adaptation led to a very strong temporal underestimation also for this Kappa-like stimulus. A two-way repeated-measures ANOVA with the within-subject factors condition (baseline / exposure) and spatial distance (small / large) revealed a significant main effect for the factor condition, $F(1, 10) = 297.05$, $p > 0.001$, $\eta^2 = 0.967$, and for the factor spatial distance, $F(1, 10) = 12.222$, $p = 0.006$, $\eta^2 = 0.550$. The interaction effect was not significant, $F(1, 10) = 0.95$, $p = 0.353$, $\eta^2 = 0.086$. A post-hoc *t* test revealed that larger spatial distances led to a temporal overestimation even after adaptation to a drifting grating, paired *t* test, $t(10) = 2.57$, $p = 0.028$, $d = 0.774$.

Experiment 3 demonstrated that temporal duration estimates for extended objects show a dependence on space very comparable to the Kappa effect, which is tested by isolated flashed markers. A drifting grating adapter produced a strong decrease of apparent duration irrespective of the spatial extent of the test grating. The moving rectangle stimulus, however, decreased the subjective durations only of large but not of small gratings.

Discussion

In this study we aimed to investigate the idea that the effect of space on subjective time is mediated by apparent velocity. We first tested which probe interval duration would yield a strong Kappa effect, i.e., an overestimation of duration when interval markers cover a large distance. In Experiment 1, we found that there was no Kappa effect for short intervals (100 ms). The Kappa effect grew with longer interval durations. For the following experiments we used the interval duration that produced the strongest Kappa effect (1,000 ms). As the Kappa effect is a demonstration of the influence of space on subjective time, we next sought to find evidence for an influence of speed on time. Speed estimates might be retrieved by consulting an internal prior about average object velocities (Stocker & Simoncelli, 2006). In Experiment 2, we manipulated this prior by repeatedly presenting a moving rectangle. Prolonged exposure to this stimulus produced an interval underestimation only if interval markers covered a large distance. We suggest that elevating the prior to higher speeds levels out the overestimation of duration for interval markers at large distances (i.e., the Kappa effect). Put differently, if the brain experiences for several times that objects move fast, it updates its prior and assumes that even long distances can be covered in a short amount of time. Consequently, temporal intervals will be estimated as shorter in duration if the brain imputes velocity to estimate time.

In Experiment 3, we compared our exposure to fast motion against adaptation to a shifting grating, which has been used in previous studies (Johnston et al., 2006). We found that grating adaptation leads to a strong duration underestimation, regardless of the size of the grating. Exposure to the moving rectangle, however, selectively modulated duration estimations for large gratings. In the choice of our motion exposure we aimed to present a stimulus that is inherently connected to space by traveling a certain distance. We assumed that this explicit linkage might be necessary to update the speed prior. This linkage might explain why only exposure to the moving rectangle but not grating adaptation selectively modulated duration estimations for large gratings. The same difference in the stimuli might also explain why the modulation of duration estimations was much stronger after grating adaptation. While a moving rectangle stimulates neighboring motion detectors consecutively, a drifting grating stimulates simultaneously all detectors that are covered by the size of the grating. Thus, the global motion adaptation will be stronger for grating adaptation than for the moving rectangle. It might also have been the case that grating adaptation leads to a ceiling effect and

therefore is too strong to reveal a dependence on spatial distance.

Experiment 3 also showed that intervals defined by spatially extended objects are generally overestimated, irrespective of whether interval markers are presented in succession or simultaneously or whether intervals are defined by extended objects. The latter finding is consistent with studies reporting time overestimation for larger objects (Mo & Michalski, 1972; Thomas & Cantor, 1976; Xuan et al., 2007; Ono & Kitazawa, 2009; Rammsayer & Verner, 2014; Kanai et al., 2017). This result suggests that temporal duration is generally retrieved by integrating space and speed, not only when interval markers are flashed but also for stationary objects with on- and offsets.

Bayesian modeling studies have successfully explained the Kappa effect as arising from a slow motion prior (Goldreich, 2007; Chen et al., 2016). Including slow motion priors into computational models yielded successful predictions and explanations of illusions and biases in human motion (Weiss, Simoncelli, & Adelson, 2002) and in visual speed perception (Stocker & Simoncelli, 2006). Consulting learned environmental statistics that include higher probabilities for objects moving with a slow velocity naturally lead to an overestimation for the duration of temporal intervals that are spatially more extended. This account has so far been proposed only to explain the Kappa effect. However, we show that it might be a general mechanism for visual duration estimation that can illuminate why temporal estimates are biased by parameters that seem irrelevant for duration estimations. Since the influences of spatial extent (Mo & Michalski, 1972; Thomas & Cantor, 1976; Xuan et al., 2007; Ono & Kitazawa, 2009; Rammsayer & Verner, 2014; Kanai et al., 2017) and of velocity (Kaneko & Murakami, 2009; Tomassini et al., 2011; Bruno et al., 2015; Gorea & Kim, 2015; Yamamoto & Miura, 2016) on temporal estimates are well documented, one must answer the question why the brain should undertake the apparent extra effort of taking these signals into account.

Spatiotemporal energy models assume that velocity is encoded by comparing two motion energy measures and electrophysiology demonstrated that such a computation might take place in area MT (Priebe, Cassanello, & Lisberger, 2003). Although motion and position estimates are considered to be separate in classical motion models (Burr & Thompson, 2011), the motion induced position shift (Whitney, 2002) demonstrated a linkage. After adaptation to motion, a flashed bar appears to be shifted in the direction of motion. The object-tracking model (Kwon, Tadin, & Knill, 2015) offers a unifying account of visual motion and position perception, suggesting that both are inherently linked. It has not yet been established at which stage motion and spatial

signals are integrated. One of us has used functional magnetic resonance imaging to show that area MT supports spatial stimulus localization (Bonkhoff, Zimmermann, & Fink, 2017). If area MT indeed has access to both signals, it is a likely candidate to estimate interval duration based on velocity since first, neurons are tuned to the direction and speed of a moving object (Dubner & Zeki, 1971; Maunsell & van Essen, 1983) and second, velocity adaptation changes their speed-tuning (Price & Born, 2013). Retrieving duration by determining spatial distance given a certain velocity is computationally convenient as only two existing signals have to be combined.

This approach of estimating time is applicable only if stimuli are suited to activate motion detectors. However, estimation of temporal intervals is possible also for isoluminant color changes (Morrone, Ross, & Burr, 2005). Thus, our suggested mechanism to measure time can be only one among others. An elegant solution to retrieve time has been suggested by Mauk and Buonomano: They could demonstrate that signals to tell time are implicitly embedded in neural activation (Mauk & Buonomano, 2004). This account avoids a dedicated clock-like mechanism to estimate time that has been suggested early on (Treisman, 1963). We conclude that the effects of spatial distance on subjective time are mediated by apparent velocity.

Keywords: duration, velocity adaptation, Kappa effect

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References

Beattie, L., Curran, W., Benton, C. P., Harris, J. M., & Hibbard, P. B. (2017). Perceived duration of brief

- visual events is mediated by timing mechanisms at the global stages of visual processing. *Royal Society Open Science*, 4(3), 160928.
- Bonkhoff, A. K., Zimmermann, E., & Fink, G. R. (2017). Veridical stimulus localization is linked to human area V5/MT+ activity. *NeuroImage*, 156, 377–387. <https://doi.org/10.1016/j.neuroimage.2017.05.010>.
- Bruno, A., Ayhan, I., & Johnston, A. (2010). Retinotopic adaptation-based visual duration compression. *Journal of Vision*, 10(10):30, 1–18, <https://doi.org/10.1167/10.10.30>. [PubMed] [Article]
- Bruno, A., Ayhan, I., & Johnston, A. (2015). Changes in apparent duration follow shifts in perceptual timing. *Journal of Vision*, 15(6):2, 1–18, <https://doi.org/10.1167/15.6.2>. [PubMed] [Article]
- Bruno, A., Ng, E., & Johnston, A. (2013). Motion-direction specificity for adaptation-induced duration compression depends on temporal frequency. *Journal of Vision*, 13(12):19, 1–11, <https://doi.org/10.1167/13.12.19>. [PubMed] [Article]
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? Functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, 10, 755–765.
- Burr, D. C., Cicchini, M., Arrighi, R., & Morrone, M. C. (2011). Spatiotopic selectivity of adaptation-based compression of event duration. *Journal of Vision*, 11(2):21, 1–9, <https://doi.org/10.1167/11.2.21>. [PubMed] [Article]
- Burr, D., & Thompson, P. (2011). Motion psychophysics: 1985–2010. *Vision Research*, 13, 1431–1456, <https://doi.org/10.1016/j.visres.2011.02.008>.
- Burr, D., Tozzi, A., & Morrone, M. C. (2007). Neural mechanisms for timing visual events are spatially selective in real-world coordinates. *Nature Neuroscience*, 10, 423–425.
- Chen, Y., Zhang, B., & Kording, K. P. (2016). Speed constancy or only slowness: What drives the Kappa effect. *PLoS One*, 11(4), e0154013, <https://doi.org/10.1371/journal.pone.0154013>.
- Cohen, J., Hansel, C. E., & Sylvester, J. D. (1953). A new phenomenon in time judgment. *Nature*, 4385, 901, <https://doi.org/10.1038/172901a0>.
- Cohen, J., Hansel, C. E. M., & Sylvester, J. D. (1955). Interdependence in judgments of space, time and movement. *Acta Psychologica*, 11, 360–372, [https://doi.org/10.1016/S0001-6918\(55\)80098-4](https://doi.org/10.1016/S0001-6918(55)80098-4).
- Collyer, C. E. (1977). Discrimination of spatial and temporal intervals defined by three light flashes: Effects of spacing on temporal judgments and of timing on spatial judgments. *Perception & Psychophysics*, 4, 357–364.
- Curran, W., & Benton, C. P. (2012). The many directions of time. *Cognition*, 122, 252–257.
- Dubner, R., & Zeki, S. M. (1971). Response properties and receptive fields of cells in an anatomically defined region of the superior temporal sulcus in the monkey. *Brain Research*, 35, 528–532.
- Fornaciai, M., Arrighi, R., & Burr, D. C. (2016). Adaptation-induced compression of event time occurs only for translational motion. *Scientific Reports*, 6, 23341, <https://doi.org/10.1038/srep23341>.
- Goldreich, D. (2007). A Bayesian perceptual model replicates the cutaneous rabbit and other tactile spatiotemporal illusions. *PLoS One*, 2(3), e333.
- Gorea, A., & Kim, J. (2015). Time dilates more with apparent than with physical speed. *Journal of Vision*, 15(1):7, 1–11, <https://doi.org/10.1167/15.1.7>. [PubMed] [Article]
- Johnston, A., Arnold, D. H., & Nishida, S. (2006). Spatially localized distortions of event time. *Current Biology*, 16, 472–479.
- Kanai, R., Dalmaijer, E. S., Sherman, M. T., Kawakita, G., & Paffen, C. L. E. (2017). Larger stimuli require longer processing time for perception. *Perception*, 46(5), 605–623.
- Kaneko, S., & Murakami, I. (2009). Perceived duration of visual motion increases with speed. *Journal of Vision*, 9(7):14, 1–12, <https://doi.org/10.1167/9.7.14>. [PubMed] [Article]
- Kwon, O. S., Tadin, D., & Knill, D. C. (2015). Unifying account of visual motion and position perception. *Proceedings of the National Academy of Sciences, USA*, 112(26), 8142–8147, <https://doi.org/10.1073/pnas.1500361112>.
- Latimer, K., & Curran, W. (2016). The duration compression effect is mediated by adaptation of both retinotopic and spatiotopic mechanisms. *Vision Research*, 122, 60–65.
- Latimer, K., Curran, W., & Benton, C. P. (2014). Direction-contingent duration compression is primarily retinotopic. *Vision Research*, 105, 47–52.
- Mauk, M. D., & Buonomano, D. V. (2004). The neural basis of temporal processing. *Annual Review of Neuroscience*, 27, 307–340.
- Maunsell, J. H., & Van Essen, D. C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *Journal of Neurophysiology*, 5, 1127–1147.
- Mo, S. S., & Michalski, V. A. (1972). Judgement of temporal duration of area as a function of stimulus configuration. *Psychonomic Science*, 27, 97–98.

- Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience*, *8*(7), 950–954.
- Movshon, J. A., Adelson, E. H., Gizzi, M. S., & Newsome, W. T. (1985). The analysis of moving visual patterns. In C. Chagas, R. Gattass, & C. Gross (Eds.), *Pattern recognition mechanisms. Pontificiae Academiae Scientiarum Scripta Varia* (Vol. 54, pp. 117–151). Rome: Vatican Press.
- Ono, F., & Kitazawa, S. (2009). The effect of marker size on the perception of an empty interval. *Psychonomic Bulletin & Review*, *16*(1), 182–189.
- Price, N. S., & Born, R. T. (2013). Adaptation to speed in macaque middle temporal and medial superior temporal areas. *Journal of Neuroscience*, *10*, 4359–4368.
- Price-Williams, D. R. (1954). The kappa effect. *Nature*, *173*(4399), 363–364.
- Priebe, N. J., Cassanello, C. R., & Lisberger, S. G. (2003). The neural representation of speed in macaque area MT/V5. *Journal of Neuroscience*, *23*(13): 5650–5661.
- Rammsayer, T. H., & Verner, M. (2014). The effect of nontemporal stimulus size on perceived duration as assessed by the method of reproduction. *Journal of Vision*, *14*(5):17, 1–10, <https://doi.org/10.1167/14.5.17>. [PubMed] [Article]
- Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience*, *4*, 578–585.
- Suto, Y. (1952). The effect of space on time estimation (S-effect) in tactual space. *Japanese Journal of Psychology*, *22*, 45–57.
- Thomas, E. A. C., & Cantor, N. E. (1976). Simultaneous time and size perception. *Perception & Psychophysics*, *19*, 353–360.
- Tomassini, A., Gori, M., Burr, D., Sandini, G., & Morrone, M. C. (2011). Perceived duration of visual and tactile stimuli depends on perceived speed. *Frontiers in Integrative Neuroscience*, *5*, 51.
- Treisman, M. (1963). Temporal discrimination and the indifference interval: Implications for a model of the ‘internal clock’. *Psychological Monographs*, *77*, 1–31.
- Wearden, J. H., & Lejeune, H. (2008). Scalar properties in human timing: Conformity and violations. *Quarterly Journal of Experimental Psychology*, *61*(4): 569–587.
- Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, *6*, 598–604.
- Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Science*, *6*(5), 211–216.
- Xuan, B., Zhang, D., He, S., & Chen, X. (2007). Larger stimuli are judged to last longer. *Journal of Vision*, *7*(10):2, 1–5, <https://doi.org/10.1167/7.10.2>. [PubMed] [Article]
- Yamamoto, K., & Miura, K. (2016). Effect of motion coherence on time perception relates to perceived speed. *Vision Research*, *123*, 56–62.