



Compression of time during smooth pursuit eye movements

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ABSTRACT

Humans have a clear sense for the passage of time, but while implicit motor timing is quite accurate, explicit timing is prone to distortions particularly during action (Wenke & Haggard, 2009) and saccadic eye movements (Morrone, Ross, & Burr, 2005). Here, we investigated whether perceived duration is also affected by the execution of smooth pursuit eye movements, showing a compression of apparent duration similar to that observed during saccades. To this end, we presented two brief bars that marked intervals between 100 and 300 ms and asked subjects to judge their duration during fixation and pursuit. We found a compression of perceived duration for bars modulated in luminance contrast of about 32% and for bars modulated in chromatic contrast of 14% during pursuit compared to fixation. Interestingly, Weber ratios were similar for fixation and pursuit, if they are expressed as ratio between JND and perceived duration. This compression was constant for pursuit speeds from 7 to 14 deg/s and did not occur for intervals marked by auditory events. These results argue for a modality-specific component in the processing of temporal information.

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1. Introduction

Although we have no direct sensor for the passage of time, like for light or sound intensity, humans are able to judge time at different scales from milliseconds up to hours. The perception of time has been extensively studied in the last few years and discussed in a large number of recent reviews (Bhattacharjee, 2006; Buhusi & Meck, 2005; Buonomano & Karmarkar, 2002; Eagleman, 2008; Grondin, 2008, 2010; Ivry & Schlerf, 2008; Ivry & Spencer, 2004; Lewis & Miall, 2003b; Mauk & Buonomano, 2004; Meck, Penney, & Pouthas, 2008; Nobre, Correa, & Coull, 2007; Walsh, 2003). Despite this large amount of research, the brain's mechanism to estimate time is still unknown (for reviews see Buhusi & Meck, 2005; Mauk & Buonomano, 2004). There is converging evidence that the perception of time is affected by basic stimulus features (for a review see Eagleman, 2008), like predictability (Pariyadath & Eagleman, 2007, 2008), size (Xuan, Zhang, He, & Chen, 2007), visibility (Terao, Watanabe, Yagi, & Nishida, 2008) and temporal frequency (Kanai, Paffen, Hogendoorn, & Verstraten, 2006), speed (Kaneko & Murakami, 2009) or motion direction (Ono & Kitazawa, 2010). This large number of distortions suggests that the estimation of time is not mediated by a separate neuronal system but is rather deeply integrated within the sensory system. This is also supported by the fact that the perception of time can be locally al-

tered by visual adaptation (Burr, Tozzi, & Morrone, 2007; Johnston, Arnold, & Nishida, 2006), further suggesting the existence of several independent clocks instead of one single centralized clock. Perceived time is also distorted by spatial attention (Cicchini & Morrone, 2009; Mattes & Ulrich, 1998; Yeshurun & Marom, 2008) and by the execution of saccadic eye movements (Morrone, Ross, & Burr, 2005).

Saccades are used to shift the gaze to a new location in the visual field and cause a fast motion of the retinal image. It has been shown that these jerk-like movements induce spatial (Ross, Morrone, & Burr, 1997) as well as temporal distortions (Morrone et al., 2005). Humans shift gaze also by performing smooth pursuit eye movements that track moving objects of interest keeping their image on the fovea. These pursuit eye movements are much slower than saccades and can be executed for an extended period of time. Traditionally, pursuit has been regarded as dynamic fixation. However, behavioral (Robinson, Gordon, & Gordon, 1986; Schwartz & Lisberger, 1994) and neurophysiological studies (Newsome, Wurtz, & Komatsu, 1988) showed that pursuit is a system in its own, distinct from fixation (for a review see Ilg, 1997). In addition, psychological studies (Bedell & Lott, 1996; Schütz, Braun, Kerzel, & Gegenfurtner, 2008; Tong, Stevenson, & Bedell, 2008) showed that perception is actively altered during pursuit. Given the susceptibility of timing to distortions and the known perceptual changes during pursuit, it is likely that also time perception is affected by the execution of smooth pursuit. Hence, we compared perceived duration of intervals marked by visual events during fixation and pursuit.

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2. Methods

2.1. Subjects

Twenty-three subjects in total participated in the experiments, among them the authors ACS & MCM. We had to exclude the data of four subjects, because they had difficulties to do the timing task, leading to exceptionally large variability during pursuit as well as during fixation.

2.2. Experimental design

Subjects had to judge which of two intervals had been shorter in duration. The duration of the first interval (test) was varied according to two staircase procedures, while the duration of the second interval (standard) was kept constant at a fixed duration. Two 1-up 1-down staircase procedures were presented interleaved and had starting values above and below the standard interval. We tested three different standard intervals: 100, 200 and 300 ms. In pursuit trials, the test interval was presented during fixation and the standard interval during steady-state pursuit. In fixation trials, both intervals were presented during fixation (Fig. 1). Fixation and pursuit conditions were collected in separate blocks. If not otherwise stated, the pursuit target moved horizontally towards the screen center at a speed of 10 deg/s. In order to undermine the effects of temporal expectations, we randomized the onset of each interval in a 250 ms range.

2.3. Experimental procedure

Both in fixation and in pursuit trials, the test interval started between 750 and 1000 ms after trial onset (Fig. 1). In fixation trials, the standard interval started 1750–2250 ms after the offset of the test interval. A fixation trial ended 750–1000 ms after the offset of the standard interval. In pursuit trials, the pursuit target started to move 1000–1250 ms after the offset of the test interval. The standard interval started 750–1000 ms after the motion onset of the pursuit target. Like fixation trials, pursuit trials ended 750–1000 ms after the offset of the standard interval. Please note

that the temporal distance between the test and the standard interval was the same in both fixation and pursuit trials.

2.4. Equipment Gießen

Stimuli were displayed on a 21 in CRT monitor (ELO Touchsystems, Fremont, CA) driven by a Nvidia Quadro NVS 285 graphics board with a refresh rate of 100 Hz non-interlaced. At a viewing distance of 47 cm, the active screen area subtended 45 deg of visual angle in the horizontal direction, and 36 deg vertical. With a spatial resolution of 1280 × 1024 pixels, this resulted in 28 pixels/deg. The luminance of gray and black pixels amounted to 32 cd/m² and 16 cd/m², respectively, resulting in a Michelson contrast of 33%. Eye movements were recorded at 250 Hz with an Eye-link II. Saccades were detected using the EyeLink saccade parser. Subjects had to press the 1 and 2 key on the number block of a standard keyboard to indicate which interval was shorter. The direction of pursuit was randomized for each trial.

2.5. Equipment Pisa

Stimuli were displayed on a 21 in CRT monitor (SONY Trinitron), driven by a VSG 2.5 with a refresh rate of 120 Hz non-interlaced. At a viewing distance of 55 cm, the active screen area subtended 37.5 deg in the horizontal direction, and 28.7 deg vertical on the subject's retina. With a spatial resolution of 1056 × 792 pixels, this resulted in 28 pixels/deg. The luminance of gray and black pixels amounted to 9 cd/m² and 0.05 cd/m² respectively, resulting in a Michelson contrast of 99%. Eye movements were recorded at 240 Hz with an ASL 504 remote eye tracker. Saccades were detected using a velocity cut-off criterion of 31 deg/s. Subjects had to press the button of a VSG response box up (first interval shorter) or down (second interval shorter). The direction of pursuit alternated every trial. There were no systematic differences in the data collected in Gießen or in Pisa.

2.6. Visual stimuli

To mark the time interval, we flashed black horizontal bars at the top or the bottom of the gray screen for one refresh cycle of

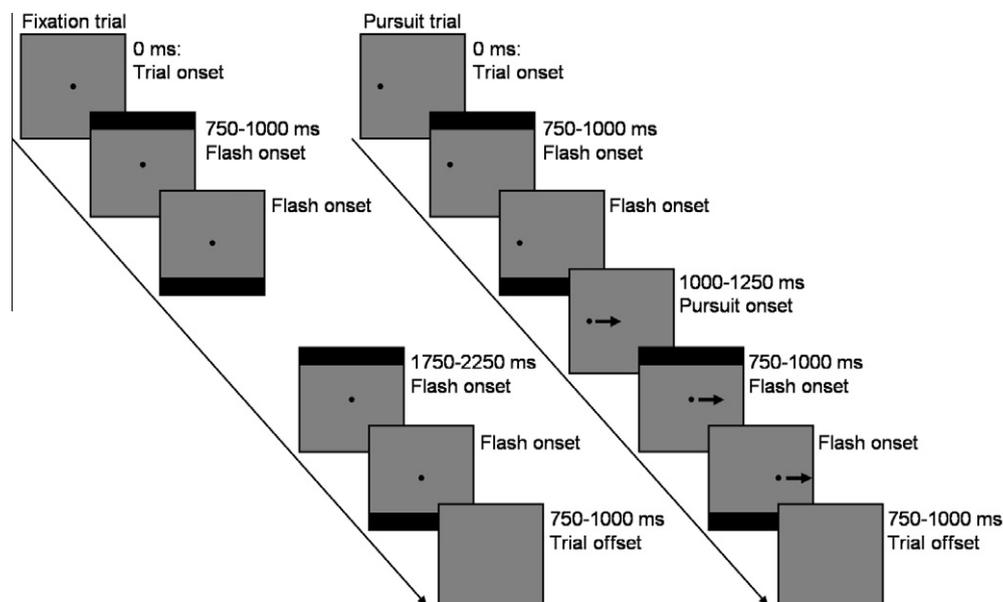


Fig. 1. Experimental procedure for the time discrimination task for fixation and pursuit trials. The first time interval (test), marked by brief horizontal peripheral bars, was presented during fixation and the second (standard) during pursuit or fixation. Numbers denote the minimal and maximal temporal separation to the previous event. At the end of each trial, subjects had to judge which interval had been shorter.

the monitor. The two bars of one interval were never presented at the same position, and the position of the first bar was randomized. The bars were 3 deg high and covered the whole screen width. We used these stimuli to reduce the perception of flicker or apparent motion, which could interfere with the time judgments. The fixation and pursuit targets were black circles of 0.3 deg diameter.

2.7. Main experiment

The experiment as described above was performed for all three standard durations by four subjects in Pisa and seven subjects in Gießen. Four additional subjects performed the experiment only for a standard duration of 200 ms in Gießen.

2.8. Control experiment with varying pursuit speed

Here, we measured the PSE for a standard interval of 200 ms during two additional pursuit speeds: 7 deg/s and 14 deg/s. The different speed conditions were measured in separate blocks. Nine subjects performed this experiment in Gießen.

2.9. Control experiment with equiluminant bars

In this experiment, we presented green bars in front of a red background. The matching intensities of the green and red phosphors were individually determined by peripheral flicker photometry (Pisa) or were modulated along the *L–M* axis of the DKL (Derrington, Krauskopf, & Lennie, 1984) color space (Gießen). The CIE chromaticity coordinates (*x* and *y*) were 0.234 and 0.380 for green and 0.381 and 0.307 for red. As the maximum color contrast along the *L–M* axis of the DKL color space is limited, we increased the height of the bars to 7 deg for the Gießen setup. Four subjects performed the experiment for all three standard durations in Pisa, and nine subjects performed the experiment only for a 200 ms standard duration in Gießen.

2.10. Control experiment with auditory stimuli

To measure auditory time interval judgments, we presented brief noise bursts of 11 ms duration via head phones. Like for visual targets, subjects had to judge the separation between two clicks. We tested only one standard interval of 200 ms. Two subjects performed the experiment in Pisa.

2.11. Control experiment with position change

To study the effect of retinal position error on perceived duration, the pursuit target made a step in two-thirds of the trials. The step was either 1.6 deg against pursuit direction or 0.8 deg in pursuit direction, in one-third of trials each. We chose an asymmetric step size, because pursuit gain is typically slightly below unity, so that the eye lags the pursuit target under normal conditions. The step change occurred in a time interval of 250 ms before to 250 ms after the onset of the standard interval. We tested only one standard interval of 200 ms. Eight subjects performed the experiment in Gießen.

2.12. Control experiment with speed change

Here, we investigated the influence of retinal velocity error on perceived duration. To induce velocity errors, the target accelerated to 14 deg/s or decelerated to 7 deg/s in one-third of trials each. The speed change occurred in a time interval of 250 ms before to 250 ms after the onset of the standard interval. We tested only one standard interval of 200 ms. Seven subjects performed the experiment in Gießen.

2.13. Control experiment with speed change and parafoveal bars

Here, we investigated the influence of spatial attention on the perceived duration. The experiment was identical to the speed change experiment, except that we presented thin bars of 1 deg height at an eccentricity of 1 deg, in order to move the bars closer to the focus of spatial attention. Four subjects performed the experiment in Pisa and seven in Gießen.

2.14. Data analysis

We used the *psignifit* toolbox (Wichmann & Hill, 2001) to fit a cumulative Gaussian function to the data and analyzed the point of subjective equality (PSE) and the standard deviation (SD) of the fitted functions. For pursuit analysis, we calculated the retinal position and velocity error as well as the catch-up saccade frequency and size in a time interval from 100 ms before until 100 ms after the standard interval.

3. Results

3.1. Luminance stimuli

In the first experiment ($N = 11$), we measured the perceived temporal separation of luminance-defined flashes in the periphery (Fig. 2a and b). The average PSEs were reduced during pursuit to 75.0 ms (SD 15.8), 141.9 ms (SD 24.4) and 233.6 ms (SD 31.4), compared with the standard intervals of 100, 200 and 300 ms. During fixation, these values were much closer to the standard intervals: 85.6 ms (SD 16.9), 188.5 ms (SD 22.9) and 291.9 ms (SD 46.2). This led to average fixation – pursuit differences of 10.6 ms, 46.6 ms and 58.3 ms. To test these differences statistically, we computed a repeated-measures ANOVA with the factors standard duration and eye movement condition. The main effect of standard duration was significant ($F(2, 20) = 200.440$, $P < 0.001$) as well as the main effect of eye movement condition ($F(1, 10) = 26.721$, $P = 0.001$). The interaction between standard duration and eye movement condition was also significant ($F(2, 20) = 11.740$, $P = 0.002$). This indicates that the compression magnitude changed with the standard intervals. Indeed, we were able to fit the data with a linear regression with a slope of 0.78 ($P = 0.002$, intercept = 0, $P = 0.826$), indicating that the compression magnitude is proportional to the standard interval. Although there was a significant compression of time during pursuit, it is important to note that there was great inter-individual variability with some subjects never showing a compression effect at all. This suggests that there might have been idiosyncratic differences either in the way to measure time or in the way to pursue the target (see Section 4).

We also analyzed the SD of the fitted Gaussian functions, as a measure of judgment precision (Fig. 2a and c). On average, the SDs were lower during pursuit (42.2, 92.9 and 113.5 ms) than during fixation (66.7, 118.14 and 153.2 ms). However, the Weber fractions (i.e. ratio between SD and PSE) were similar for pursuit (0.60, 0.64 and 0.50%) and fixation (0.80, 0.64 and 0.53%). To estimate the average Weber fractions for pursuit and fixation independently, we calculated a linear regression between the PSE and the SD for the three standard intervals. This is justified, because Weber fractions should be constant at least for interval durations longer than 200 ms (Mauk & Buonomano, 2004). We obtained a slope of 0.50 ($P = 0.028$) for pursuit and 0.52 ($P = 0.020$) for fixation. This means that the precision during pursuit was proportional to the perceived temporal separation, but not to the physical separation. In general, these Weber fractions are rather large, which might be due to the presentation order

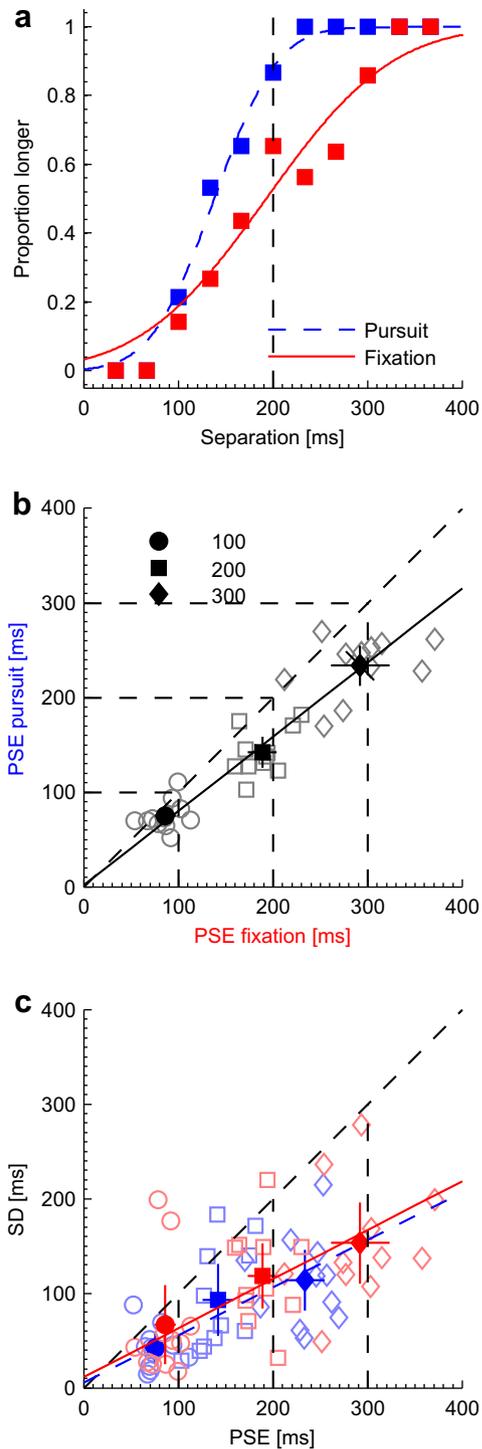


Fig. 2. Experiment using intervals marked by luminance bars. (a) Example of a psychometric function of one observer for a standard interval of 200 ms. (b) PSEs during fixation and pursuit for three standard intervals. The dashed black diagonal marks equal PSEs for fixation and pursuit. The solid black line is obtained by linear regression. (c) SD over PSE for fixation and pursuit. The dashed black diagonal marks Weber ratios of 1. The solid red and dashed blue lines are linear regressions for the fixation and pursuit data, respectively. (a–c) Blue indicates data for pursuit and red for fixation. The dashed vertical and horizontal lines mark the standard intervals. (b and c) Open symbols show individual subject data; filled symbols the mean across subjects; the error bars 95% confidence intervals.

test first, standard second. It has been shown that such an order leads to less precise judgments than the order standard first and test second (Grondin & McAuley, 2009; Nachmias, 2006).

3.2. The influence of catch-up saccades

Smooth pursuit is frequently interrupted by catch-up saccades, because the pursuit gain is typically slightly smaller than unity. As it is known that saccades distort the perception of time (Morrone et al., 2005), the measured effects might be caused by these catch-up saccades. We reanalyzed the whole data excluding trials in which saccades occurred in a time interval of 100 ms before the interval onset to 100 ms after interval offset. Using this criterion, we excluded 35.6% (SD 24.3) trials in pursuit conditions and 14.0% (SD 13.9) trials in fixation conditions. Despite this large quantity of data, we did not find any systematic changes in the average PSE (Fig. 3a and b). During pursuit, the average PSE differences between all trials and trials without saccades amounted to -0.2 ms (SD 3.2), 3.1 ms (SD 12.1) and 0.9 ms (SD 19.9) for the three standard intervals. During fixation, these differences were 0.3 ms (SD 4.9), 0.5 ms (SD 7.3) and 5.7 ms (SD 14.8).

To test whether these small differences were statistically significant, we computed a repeated-measures ANOVA with the factors standard interval, eye movement condition and saccade exclusion. The main effects of standard interval ($F(2, 20) = 194.077$, $P < 0.001$) as well as of eye movement condition ($F(1, 10) = 23.370$, $P = 0.001$) were significant. The interaction between standard interval and eye movement condition was also significant ($F(2, 20) = 9.514$, $P = 0.005$). Neither the saccade main effect ($F(1, 10) = 0.706$, $P = 0.421$) nor any of the interactions involving the saccade factor were significant. Hence, the occurrence of saccades in single trials did not influence the average PSE.

The average amplitude of the catch-up saccades was very small and equal to 1.37 deg (SD 0.53). Given that most of the saccade effects scale with saccade amplitude (Mitrani, Yakimoff, & Mateeff, 1970; Ridder & Tomlinson, 1997; Stevenson, Volkman, Kelly, & Riggs, 1986; Van Wetter & Van Opstal, 2008), we would not expect a large compression due to the catch-up saccades.

3.3. The influence of pursuit direction

It has been suggested that there is a mental time line which associates past and short intervals with left space and future and long intervals with right space (see Oliveri, Koch, & Caltagirone, 2009 for a review). For instance, perceived duration is reduced for stimuli presented on the left and increased for stimuli on the right (Vicario et al., 2008). As we started with a peripheral fixation in pursuit trials, the test interval was located either on the left or on the right side of gaze. The standard interval however was presented when the eyes had moved approximately to the center of the screen, hence it was visible on both sides of gaze. This position difference between test and standard interval should lead to larger PSEs for leftward trials than for rightward trials. On the other hand, leftward optokinetic stimulation reduces and rightward optokinetic stimulation increases perceived duration (Vicario, Caltagirone, & Oliveri, 2007). This should lead to smaller PSEs for leftward trials than for rightward trials. To test whether either of these directional asymmetries was present in our data, we computed the PSE separately for left- and right-ward pursuit (Fig. 3c).

The average PSEs for rightward trials were 78.6 ms (SD 13.5), 148.2 ms (SD 25.0) and 223.3 ms (SD 29.9). For leftward trials, these values amounted to 72.4 ms (SD 24.2), 141.3 ms (SD 34.4) and 247.0 ms (SD 39.4). This leads to right-left difference of 6.2, 6.8 and -23.7 ms. To test these effects statistically, we computed a repeated-measures ANOVA with the factors standard interval and pursuit direction. The main effect of standard interval was significant ($F(2, 20) = 238.263$, $P < 0.001$) but not the main effect of pursuit direction ($F(1, 10) = 0.435$, $P = 0.525$). This indicates that the pursuit direction did not influence perceived duration across all standard intervals. However, the two-way interaction was

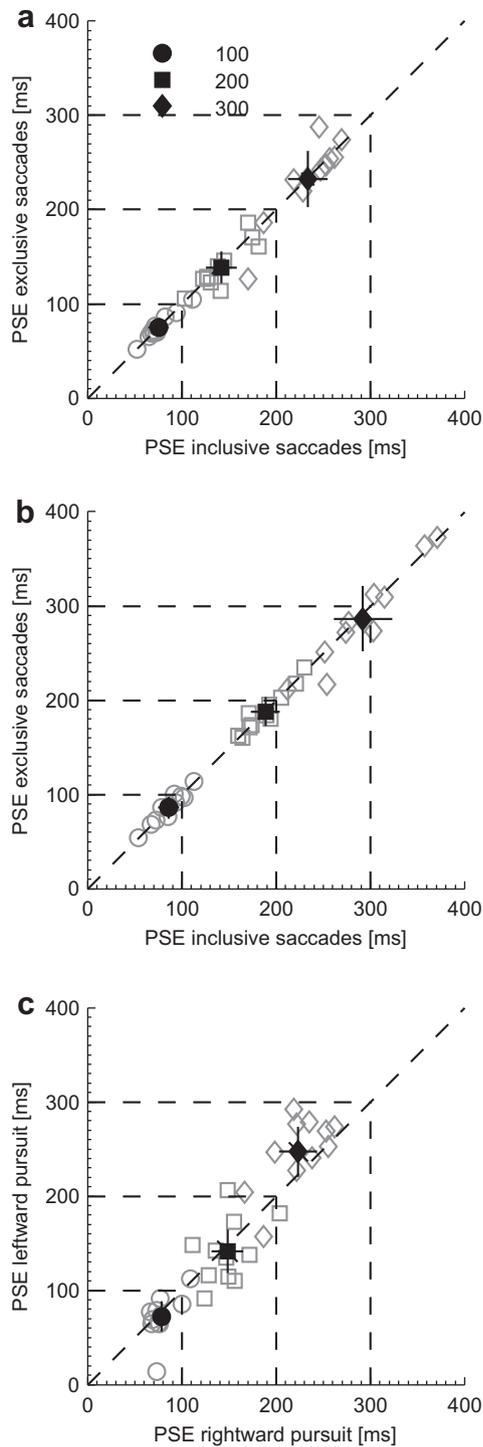


Fig. 3. Influence of catch-up saccades (a and b) and pursuit direction (c) on time compression. The different symbols denote different standard intervals. Open gray symbols show individual subject data; the filled black symbols the mean across subjects; the error bars the 95% confidence interval. The dashed vertical and horizontal lines indicate the standard intervals and the diagonal marks points with equal PSEs. (a and b) PSEs excluding saccade trials are plotted over PSEs including saccade trials. (a) Pursuit data. (b) Fixation data. (c) PSEs for leftward pursuit are plotted over PSEs for rightward pursuit.

significant ($F(2, 20) = 4.604$, $P = 0.043$), indicating that the influence of pursuit direction varied with the standard interval. There was no significant difference for the 100 ms ($t(10) = 1.03$, $P = 0.33$) and the 200 ms interval ($t(10) = 0.68$, $P = 0.51$). However, for 300 ms there was a significant difference between the pursuit directions ($t(10) = 2.60$, $P = 0.03$). To conclude, we found only a

significant effect of pursuit direction for the 300 ms interval: here the PSE was higher for leftward than for rightward direction. This is consistent with the finding that stimuli presented on the left side are perceived as shorter (Vicario et al., 2008).

3.4. The influence of pursuit speed

Similar to saccades, the perceptual effects of smooth pursuit scale with the pursuit speed (Schütz, Braun, & Gegenfurtner, 2009a; Schütz et al., 2008). To test whether the compression of time also depends on pursuit speed, we varied the pursuit speed in three steps at 7, 10 and 14 deg/s and measured the PSE for a standard interval of 200 ms ($N = 9$). The average PSE amounted to 143.8 ms (SD 25.8), 156.0 ms (SD 24.1) and 151.4 ms (SD 19.8) for 7, 10 and 14 deg/s, respectively (Fig. 4).

To test this statistically, we computed a one-way repeated-measures ANOVA. There was no significant main effect for pursuit speed ($F(2, 16) = 1.453$, $P = 0.265$). Although the pursuit speed did not influence the PSE, the SD was affected by the pursuit speed: the average SD was 105.8 ms (SD 62.7), 62.0 ms (SD 24.8) and 58.3 ms (SD 23.0) for 7, 10 and 14 deg/s, respectively. A repeated-measures ANOVA resulted in an almost significant main effect for pursuit speed ($F(2, 16) = 4.656$, $P = 0.052$). Hence, there was a negative relation between the pursuit speed and the precision, although the PSE did not vary with pursuit speed.

The absence of a difference in PSE between the speed conditions indicates that the pursuit speed itself does not influence the compression of time. We analyzed the retinal position and velocity error as well as the average catch-up saccade frequency and size to investigate whether the temporal compression was related to any of these eye movement parameters. The average position error was -0.1 (SD 0.2), 0.0 (SD 0.2) and -0.7 deg (SD 0.2) for 7, 10 and 14 deg/s, respectively. The average velocity error was -0.6 (SD 0.8), -0.4 (SD 0.5) and -0.9 deg/s (SD 1.0) for 7, 10 and 14 deg/s, respectively. The catch-up saccade frequency was 27.2 (SD 21.0), 16.0 (SD 12.2) and 27.2% (SD 17.7) for 7, 10 and 14 deg/s, respectively. The average catch-up saccade size was 0.6 (SD 0.4), 0.7 (SD 0.2) and 1.2 deg (SD 0.4) for 7, 10 and 14 deg/s, respectively. Hence, retinal errors and catch-up saccades tended to be larger in the 14 deg/s condition, while the catch-up saccade frequency was higher in the 7 and 14 deg/s condition. This indicates that the temporal compression is not related to these eye movement parameters, because we did not find any systematic difference between the PSEs in the different speed conditions. However, the eye movement parameters differed only to a small amount, which might explain why we did not find any influence.

3.5. Color stimuli

In a further experiment ($N = 4$), we measured the perceived separation between equiluminant bars (Fig. 5a and b). Similar to the first experiment, the PSEs during pursuit were reduced to 71.7 ms (SD 9.3), 144.1 ms (SD 32.3) and 256.7 ms (SD 32.5), compared with the standard durations of 100, 200 and 300 ms. During fixation, these values were much closer to the standard durations: 98.3 ms (SD 16.1), 182.2 ms (SD 42.8) and 298.7 ms (SD 28.7). The resulting fixation – pursuit differences were 26.5 ms, 38.1 ms and 42.0 ms. Like for the luminance experiment, we computed a repeated-measures ANOVA with the factors standard duration and eye movement condition. The main effect of standard duration was significant ($F(2, 6) = 111.480$, $P < 0.001$) as well as the main effect of eye movement condition ($F(1, 3) = 16.981$, $P = 0.026$). The interaction between standard duration and eye movement condition was not significant ($F(2, 6) = 0.494$, $P = 0.541$), probably due to the use of only four subjects. Interestingly, the slope of a linear regression was significantly different from unity, but with a value

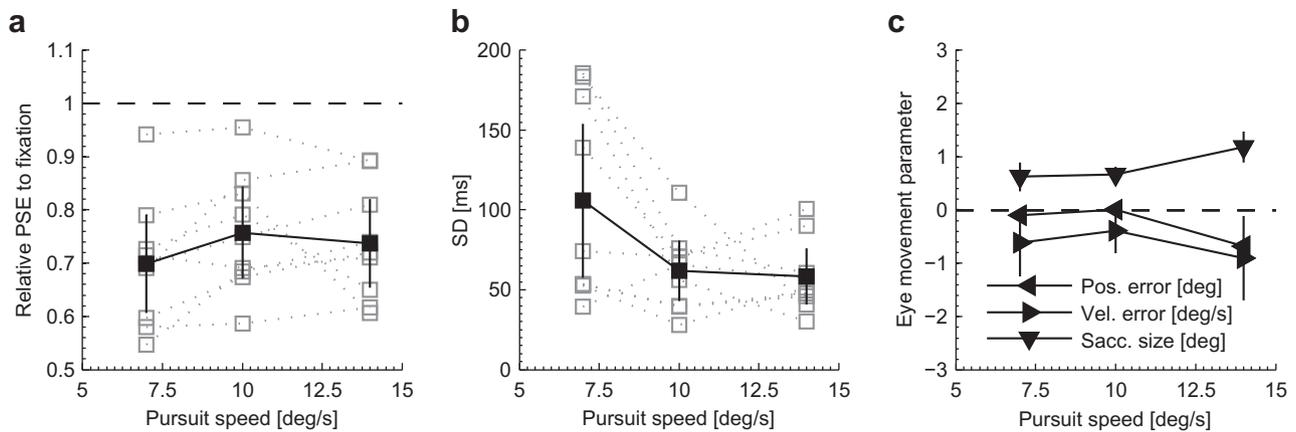


Fig. 4. Influence of pursuit speed on time compression. Open gray symbols show individual subject data; the filled black symbols the mean across subjects; the error bars are the 95% confidence interval. (a) PSE relative to fixation as function of pursuit speed. The horizontal dashed line indicates values with a PSE equal to fixation. (b) SD as function of pursuit speed. (c) Eye movement parameters. Retinal position error is indicated by left-pointing triangles, retinal velocity error by right-pointing triangles and catch-up saccade size by downward-pointing triangles.

of 0.86 ($P = 0.003$; intercept = -0.01 , $P = 0.496$) slightly closer than that observed for luminance.

For the SD (Fig. 5a and c), the picture was very similar to the luminance results. On average, the SDs were lower during pursuit (19.5, 65.1 and 141.4 ms) than during fixation (58.9, 106.6 and 155.4 ms). However, expressed as Weber fractions (i.e. fraction of the SD and the PSE), the values were similar for pursuit (0.28, 0.47 and 0.53) and fixation (0.59, 0.61 and 0.51). To estimate the Weber fractions for pursuit and fixation independently, we calculated a linear regression between the PSE and the SD. We obtained a slope of 0.57 ($P = 0.017$) for pursuit and 0.52 ($P = 0.005$) for fixation. This means that the precision during pursuit was proportional to the perceived separation, but not the actual separation.

In order to compare the effects of luminance and color more in detail, we collected a larger sample of subjects ($N = 9$) with a standard duration of 200 ms (Fig. 6). Consistent with the higher regression slope in the luminance experiment, also in this additional data set the average time compression was smaller for color (34.1 ms) than for luminance (62.4 ms). However, the PSE for color and luminance was highly correlated during pursuit ($\rho = 0.70$, $P = 0.04$) but not during fixation ($\rho = -0.14$, $P = 0.72$). This suggests that the fixation values were more affected by measurement variability than by inter-individual differences, while the pursuit compression seemed to reflect an individual property shared between the luminance and color mechanisms.

3.6. Auditory stimuli

In order to investigate whether the temporal compression is a visual effect or a modality unspecific effect (Fig. 7), we measured the perceived separation of two auditory clicks ($N = 2$). The individual PSEs during pursuit were very close to the standard of 200 ms (180 and 198 ms) as well as the PSEs during fixation (196 and 187 ms). Hence, there was practically no compression for auditory events, indicating that the compression is specific for the visual modality. Although there was no effect on the PSEs, the SDs were different between fixation and pursuit: for fixation, SDs were rather low (31.2 and 8.8 ms), which lead to Weber fractions that were much lower (0.16 and 0.05) than for the visual events. This is in line with previous reports of higher precision for auditory than for visual duration judgments (Grondin, Meilleur-Wells, Ouellette, & Macar, 1998; Rousseau, Poirier, & Lemyre, 1983). During pursuit, these SDs were higher than during fixation (84.1 and 49.0 ms), which resulted in higher Weber fractions (0.42 and 0.27). Hence, we found that pursuit reduces the precision of auditory timing

judgments but leaves the perceived duration unaffected. In contrast to fixation, where auditory timing judgments were more precise than visual, during pursuit the precision was similar for vision and audition. Hence, there is no auditory benefit during pursuit.

3.7. The influence of retinal position error

The experiment with different pursuit speeds did not show any systematic dependency of perceived duration on eye movement parameters like retinal velocity or position error. However, the natural variability of position and velocity errors was limited in that experiment, for which reason we performed further experiments to artificially modulate these errors. In order to measure the contribution of retinal position errors to the temporal compression effect (Fig. 8a–c), we added a position change to the pursuit trajectory ($N = 8$). The pursuit target stepped either 0.8 deg forward or 1.6 deg backward each in one-third of the trials. To evaluate the manipulation, we averaged the position error during the presentation of the standard interval: it amounted to -0.31 deg (SD 0.09) in the no-step condition, -0.60 deg (SD 0.32) in the forward condition and 0.59 (SD 0.12) in the backward condition. As a position error is typically compensated by catch-up saccades, we also calculated the average saccade frequency and amplitude. The saccade frequency was 5.7% (SD 3.1) in the no-step condition, 20.8% (SD 6.7) in the forward condition and 11.5% (SD 4.6) in the backward condition. The average catch-up saccade amplitude was 0.99 deg (SD 0.71) in the no-step condition, 1.26 deg (SD 0.34) in the forward condition and -0.17 deg (SD 0.7) in the backward condition.

The average PSEs were 173.2 ms (SD 43.4) in the no-step condition, 105.1 ms (SD 19.1) in the forward condition and 119.4 ms (SD 29.0) in the backward condition. This indicates that the compression of perceived duration was stronger in conditions with larger position error, irrespective of its direction. To test the decline of the PSE with larger position error statistically, we computed a one-way repeated-measures ANOVA. The main effect of position step was significant ($F(2, 14) = 22.684$, $P < 0.001$).

The average SDs were not affected by the position step. They amounted to 72.0 ms (SD 25.8) in the no-step condition, 62.9 ms (SD 43.5) in the forward condition and 55.9 ms (SD 23.0) in the backward condition. An ANOVA showed no significant main effect of position change ($F(2, 14) = 0.546$, $P = 0.507$).

In sum, we found a stronger temporal compression for conditions with a position step of the pursuit target, irrespective of the step's direction. As both the catch-up saccade frequency and amplitude were lower for backward steps than for forward steps,

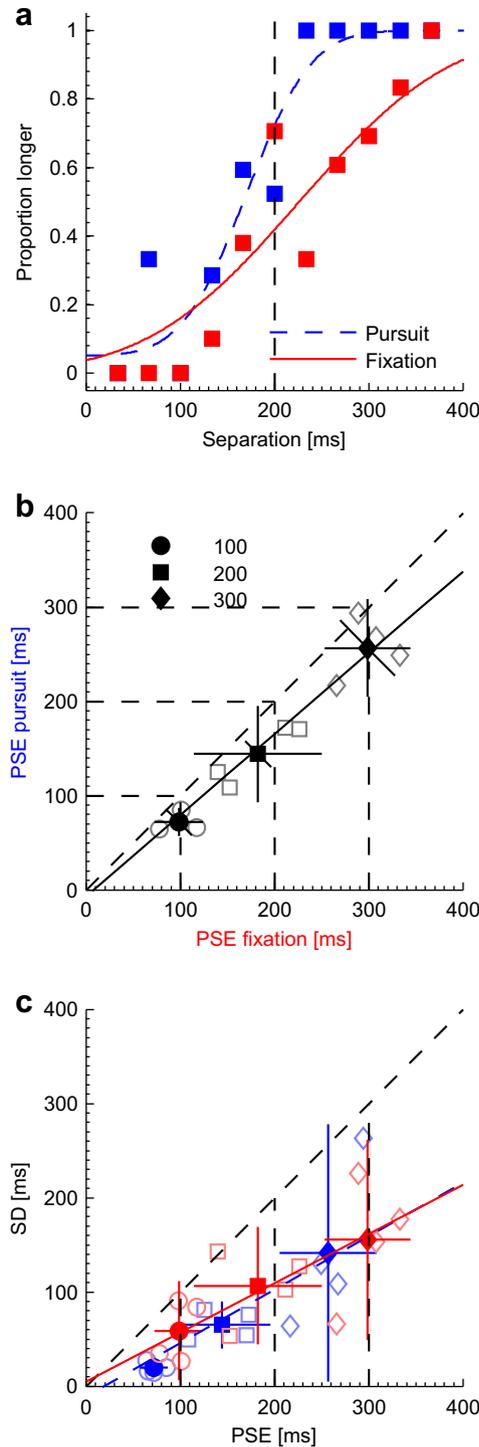


Fig. 5. Experiment using intervals marked by color bars. (a) Example of a psychometric function for a standard interval of 200 ms. (b) PSEs during fixation and pursuit for three standard intervals. (c) SD over PSE for fixation and pursuit. Conventions are the same as in Fig. 2.

this effect is probably not caused by catch-up saccades. The magnitude of the position error however corresponded to the perceptual effects, showing similar values for backward and forward steps.

3.8. The influence of retinal velocity error

In order to measure the contribution of retinal velocity errors to the compression effect (Fig. 8d–f), we added a speed change to the pursuit trajectory ($N = 7$). In all trials, the pursuit target started at a

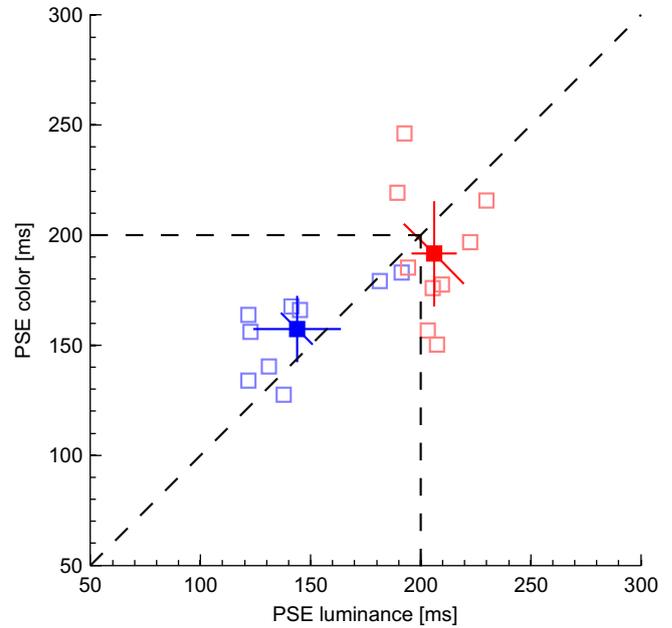


Fig. 6. Comparison of luminance and color results. PSE for color is plotted over PSE for luminance, for a standard interval of 200 ms. Pursuit data are plotted in blue and fixation data in red. Open symbols show individual subject data; the filled symbols the mean across subjects; the error bars the 95% confidence interval. The dashed black diagonal marks equal PSEs for color and luminance. The dashed vertical and horizontal lines mark the standard interval.

speed of 10 deg/s. In one-third of the trials each, the pursuit target accelerated to 14 deg/s, decelerated to 7 deg/s or continued to move with 10 deg/s. To evaluate the manipulation, we averaged the velocity error during the presentation of the standard interval and found an inverse relationship with pursuit target speed: 0.73 (SD 0.36), -0.52 (SD 0.61) and -2.03 deg/s (SD 0.92) for 7, 10 and 14 deg/s, respectively. We also analyzed the retinal position error, because a change in pursuit target speed inevitably affects the retinal position error until the eye speed matches the new target speed. Also for the average retinal position error, there was an inverse relationship with pursuit target speed: 0.07 (SD 0.26), -0.38 (SD 0.11) and -0.61 deg (SD 0.58) for 7, 10 and 14 deg/s, respectively. Like in the previous experiment, we also computed catch-up saccade frequency and amplitude. The average catch-up saccade frequency was 6.3% (SD 3.8), 7.0% (SD 5.8) and 16.0% (SD 7.9) for 7, 10 and 14 deg/s, respectively. The average catch-up saccade amplitude was 0.35 (SD 0.42), 0.88 (SD 0.30) and 1.19 deg (SD 0.28) for 7, 10 and 14 deg/s, respectively.

The average PSEs were 156.0 (SD 30.5), 156.0 (SD 25.3) and 114.1 ms (SD 21.1) for 7, 10 and 14 deg/s, respectively. To test the decline of the PSE with larger velocity error statistically, we computed a one-way repeated-measures ANOVA. The main effect of speed change was significant ($F(2, 12) = 20.532, P = 0.001$). These results indicate that larger velocity errors induced larger compression. However, only the magnitude of the velocity error mattered, not its direction, similar to the results for the position error.

The average SDs were not affected by the speed change. They amounted to 73.6 (SD 34.5), 57.9 (SD 12.8) and 52.5 ms (SD 18.8) for the three velocity conditions. An ANOVA showed no significant main effect of position change ($F(2, 12) = 1.442, P = 0.277$).

In this experiment, we found a stronger temporal compression in the condition with a speed increase and no difference between the other two conditions. This cannot be caused by catch-up saccades, because their amplitude was positively related to the speed change and different for all three conditions. The same is true for the retinal position error, which increased with increasing pursuit

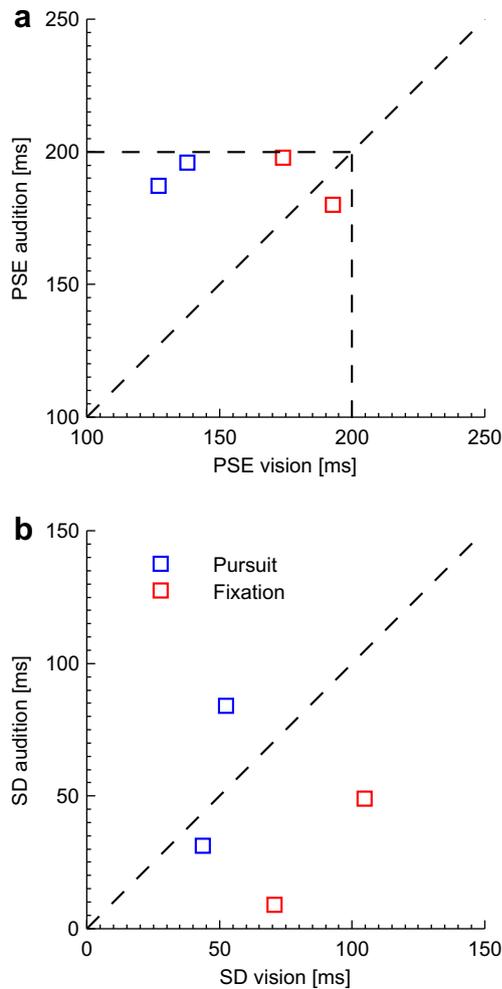


Fig. 7. Comparison of visual and auditory results for a standard interval of 200 ms. Pursuit data are plotted in blue and fixation data in red. The dashed black diagonal marks equal PSEs and SDs for vision and audition. (a) PSE for audition is plotted over PSE for vision. The dashed vertical and horizontal lines mark the standard interval. (b) SD for audition is plotted over SD for vision.

target speed. Strikingly, we found a temporal compression even for the speed decrement condition, in which we measured an average retinal position error of 0.

3.9. The influence of retinal eccentricity

Finally, we performed a control experiment (Fig. 8d–f) with parafoveal bars and a change in the pursuit speed ($N = 11$). Moving the bars closer to the pursuit target should reduce the potential detrimental effects of the lack of spatial attention in the periphery. However, it would also increase motion cues that could help in performing correctly the discrimination task. Like in the previous experiment, the pursuit target started at a speed of 10 deg/s. In one-third of the trials each, the pursuit target accelerated to 14 deg/s, decelerated to 7 deg/s or continued to move with 10 deg/s. We basically obtained similar retinal velocity errors as for the previous experiment with peripheral bars. The average values were 0.85 (SD 0.36), -0.37 (SD 0.30) and -2.02 deg/s (SD 0.53) for 7, 10 and 14 deg/s, respectively. Retinal position errors as well as catch-up saccade amplitudes were also very similar to the previous experiment.

As the perceived duration might be differently affected by the new parafoveal stimulus, we measured PSE during fixation. And in-

deed, there was a small time order error with 184.8 ms (SD 22.2) compared to the standard interval of 200 ms. During pursuit, the average PSE decreased with increasing pursuit speed: 177.2 (SD 42.5), 171.5 (SD 21.5) and 120.1 ms (SD 31.4) for 7, 10 and 14 deg/s, respectively. To test the decline of the PSE with pursuit speed statistically, we computed a one-way repeated-measures ANOVA. The main effect of pursuit speed was significant ($F(2, 20) = 13.415$, $P = 0.0012$). The overall compression seemed to be a bit smaller in this experiment. The time order effect during fixation could have masked the compression induced by pursuit.

In this experiment, the SD during fixation was 64.0 ms (SD 32.4), which was smaller on average than the values during pursuit: 93.2 (SD 52.5), 72.6 (SD 47.9) and 73.0 ms (SD 34.6) for 7, 10 and 14 deg/s, respectively. This indicates that the potential speed change of the pursuit target increased the interference between the eye movement and the duration judgment task. To test whether the magnitude of the speed change influenced the SD, we computed a repeated-measures ANOVA. The main effect of pursuit speed was not significant ($F(2, 20) = 1.781$, $P = 0.196$). As we find a stronger compression with increasing than decreasing speed, the constancy of the SD essentially leads to an increase in Weber fractions for a speed increase compared to a speed decrease.

4. Discussion

We investigated how pursuit affects the perception of time. To this end, we measured the perceived duration of intervals marked by visual targets during pursuit and fixation. We found a compression of time of about 32% for luminance stimuli and about 14% for color stimuli. The compression was proportional to the standard interval in the range of 100–300 ms. The SDs of the psychometric functions were also reduced during pursuit, indicating that the same Weber's law holds for both the discrimination during fixation and pursuit. However, the Weber fraction should be calculated using perceived duration rather than physical duration. The compression was constant for pursuit speeds from 7 to 14 deg/s. We did not find a compression for auditory stimuli, which shows that the compression effect is modality specific and not a global effect on all modalities. However, the SDs for auditory separation judgments increased during pursuit, which suggests that there was some interference between the two tasks.

Although, the compression effect is consistent and statistically significant, some subjects did not show a compression effect at all. These subjects either used a different method to estimate time or they used a different strategy for the pursuit task. Future research might specifically investigate these inter-individual differences in order to clarify whether they represent functional differences (Wilmer, 2008).

4.1. Saccades and retinal errors

The perceived duration of a time interval presented during a saccade is shorter than the same interval presented during fixation (Morrone et al., 2005), so one might argue that the observed compression in this study is caused by the catch-up saccades executed during non-perfect pursuit. We think that three reasons argue against this assumption: First, the compression was the same, when we excluded trials with catch-up saccades. This means that the occurrence of a saccade did not influence the judgment in a single trial. Second, the catch-up saccades occurred at different points in time relative to the standard interval, hence their effects on duration probably cancel out. Third, we believe that the catch-up saccade size was too small to generate compression, given that saccades smaller than 3 deg do not generate a spatial mislocalization (Morrone, Ross, & Burr, 1997).

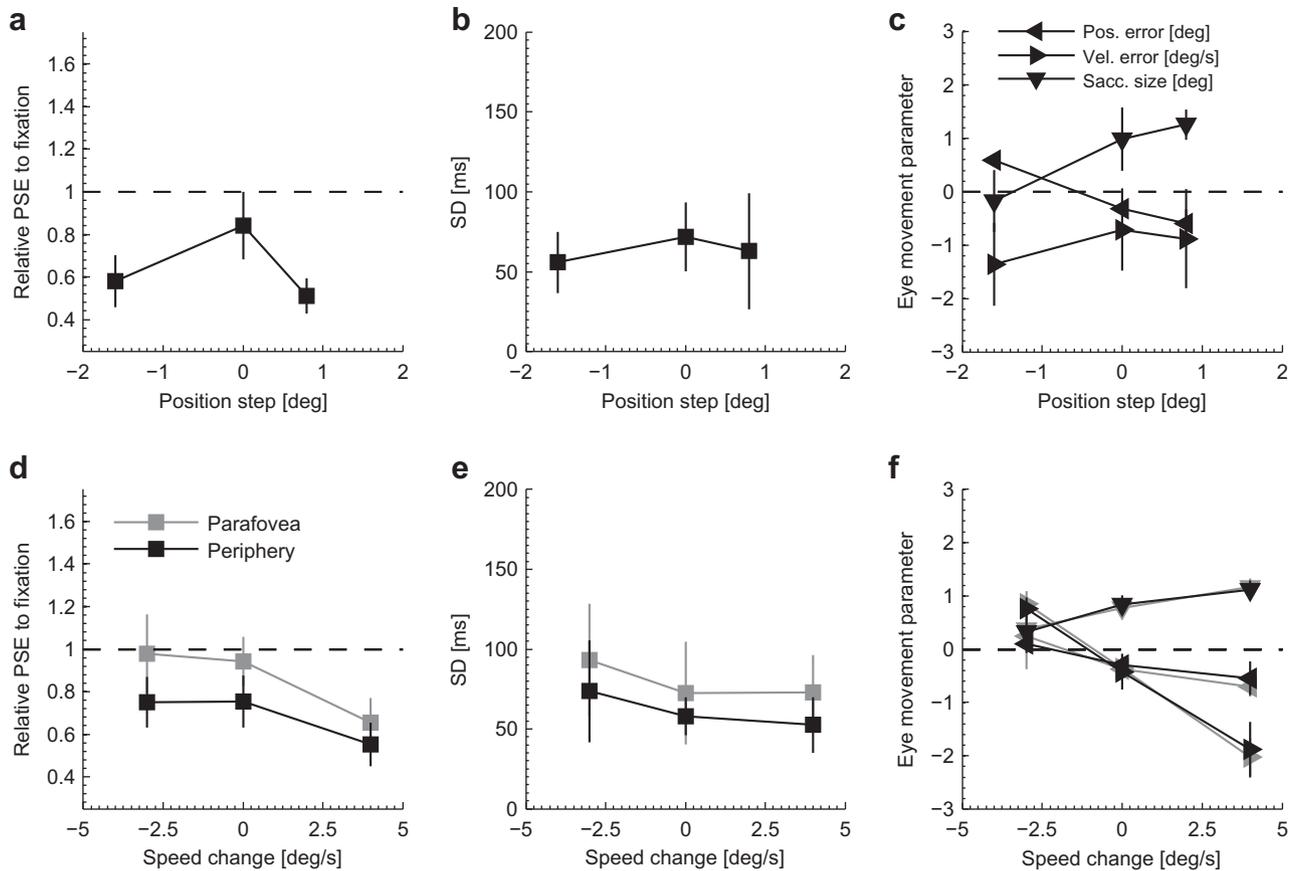


Fig. 8. Influence of position step (a–c) or speed change (d–f). (a and d) PSE relative to fixation. The horizontal dashed line indicates values with a PSE equal to fixation. (b and e) SD. (c and f) Eye movement parameters. Retinal position error is indicated by left-pointing triangles, retinal velocity error by right-pointing triangles and catch-up saccade size by downward-pointing triangles. (d–f) Data for peripheral bars are plotted in black, data for parafoveal bars are plotted in gray.

Although the compression of time during pursuit and saccades is similar, probably the phenomena reflect distinct mechanisms: First, the peri-saccadic compression is partially caused by the temporal mislocalization of one of the bars which marks the interval (Binda, Cicchini, Burr, & Morrone, 2009; Ibbotson, Crowder, Cloherty, Price, & Mustari, 2008; Ibbotson, Crowder, & Price, 2006). This is not plausible for the pursuit compression as both bars have been presented during steady-state pursuit and thus would have suffered from the same temporal mislocalization. Second, the temporal mislocalization during saccades is closely related to the spatial mislocalization (Binda et al., 2009). Although there are also spatial distortions during pursuit (Brenner, Smeets, & van den Berg, 2001; Kerzel, Aivar, Ziegler, & Brenner, 2006; Rotman, Brenner, & Smeets, 2002), these distortions are rather small in magnitude compared with the temporal compression we report here. A final difference is that saccades induce a constant loss of time, while the effect here is proportional to the interval duration.

In two experiments, we investigated the role of retinal position or velocity errors on perceived duration, by applying a position step or a speed change to the pursuit target. For position steps, the temporal compression during pursuit increased for both step directions, in and against pursuit direction. For the speed change, temporal compression increased only for speed increments but not for decrements. These modulations of perceived duration were not consistent with the effects on catch-up saccade frequency or size or the magnitude of retinal position or velocity errors. This indicates that the quality of pursuit does not contribute in an obvious way to the compression of perceived duration. However, we should note that the position step or the speed change might affect perceived duration indirectly via attention.

4.2. Spatial attention

Perceived duration is also influenced by the distribution of spatial attention. The allocation of attention to a stimulus increases its perceived duration and the precision of judgments (Mattes & Ulrich, 1998; Yeshurun & Marom, 2008). The lack of visuo-spatial attention causes a compression of time and a reduction of precision (Cicchini & Morrone, 2009). A crucial role for attention in visual time perception is also supported by electrophysiology (Chen, Huang, Luo, Peng, & Liu, 2010). Consistently with the experimental data, the role of attention has been simulated in models of time perception. For instance, the attentional-gate-model (Zakay & Block, 1997) is based on a pacemaker-accumulator model and assumes that every pacemaker's tick has to pass through an attentional gate to be counted. If attention is required by another task, the gate is not completely closed, which leads to missing ticks and a reduction in perceived duration. Now, several studies showed that spatial attention is bound to the pursuit target during smooth pursuit. On the one hand, perception of peripheral events is impaired during pursuit (Kerzel & Ziegler, 2005; Khurana & Kowler, 1987). On the other hand, a release of attention can lead to a reduction of pursuit gain (Kerzel, Souto, & Ziegler, 2008; Madelain, Krauzlis, & Wallman, 2005). Recently, it has been shown that attention is allocated exactly on the pursuit target (Lovejoy, Fowler, & Krauzlis, 2009). Consequently, it might be that the compression of time during pursuit is caused by a distraction of attention from the timing task. Several pieces of our data are consistent with this assumption. First, the effect size was smaller for parafoveal than for peripheral stimuli. However, this might also be caused by a stronger apparent motion cue for the parafoveal stimuli. Second,

the effect size was larger for conditions with a position step or a speed increment in the pursuit target. This might be taken as evidence for a contribution of attention because these manipulations presumably increase the attentional demand of pursuit. But there are also pieces of our data which are not consistent with a mere attention effect. First, we observed a reduction of the SD during pursuit, which is exactly the opposite of the typical attention effect (Cicchini & Morrone, 2009). Second, a small compression was also present for the parafoveal bars which were sufficiently close to the pursuit target (1 deg) to belong to the same attentional field. Hence, the present data does not allow a definite conclusion about the role of attention for the temporal compression during pursuit.

4.3. Stimulus visibility

Also the reduction of stimulus visibility has been identified as a factor compressing perceived time (Terao et al., 2008), so one could ask whether the compression during pursuit is related to a reduction of visibility. We think that two properties of the pursuit compression effect argue against this interpretation: First, if a reduction of stimulus visibility leads to more uncertainty about the precise on- and off-set of the time interval (Terao et al., 2008), one would expect rather a constant error for all time intervals than an effect proportional to the standard duration. Second, in our study, both color and luminance targets were compressed, albeit with a smaller effect on color, while pursuit acts differently on the contrast sensitivity for color and luminance. Whereas chromatic and high-spatial frequency luminance sensitivity is enhanced, sensitivity for low-spatial frequency luminance stimuli is reduced in the parafovea (Schütz, Braun, & Gegenfurtner, 2009b; Schütz, Delipetkos, Braun, Kerzel, & Gegenfurtner, 2007; Schütz et al., 2008). Hence, the sensitivity effects of pursuit show dissociation between color and luminance, while the compression is present for both. Thus, it seems unlikely that the compression is entirely caused by pursuit effects on visibility. The same holds true for the changes in the temporal impulse response function (TIRF) during pursuit. While the TIRF for luminance is either attenuated slightly (Schütz et al., 2007) or accelerated slightly (Tong, Ramamurthy, Patel, Vu-Yu, & Bedell, 2009), the TIRF for color shows a gain increase across all temporal frequencies (Schütz et al., 2009b). Such dissociation is also not compatible with the general time compression. Furthermore, the effects on contrast sensitivity scale with the pursuit speed (Schütz et al., 2008, 2009a), while we did not find any effect of pursuit speed on the magnitude of time compression. Still the smaller compression for color than for luminance suggests that the sensitivity changes during pursuit might have modulated the time compression effect.

4.4. Spatio-temporal interactions

Interestingly, we found lower PSEs for rightward than for leftward pursuit trials for a standard interval of 300 ms. This might be a mental-time-line effect and can be explained with the spatial arrangement of our stimuli: in leftward trials, the test interval was presented during right fixation, leading to mainly left-sided stimulation. Left seems to be associated with short durations, and consistently stimuli presented in left space are perceived shorter than stimuli presented in right space (Vicario et al., 2008). However, we found this effect only for a standard interval of 300 ms, which is not contradictory to the previous studies on spatial effects on time perception, because they tested only intervals of 300 ms and longer (Frassinetti, Magnani, & Oliveri, 2009; Vicario et al., 2007, 2008). The fact that we found a pursuit-induced compression of time for standard intervals of 100, 200 and 300 ms but the mental-time-line effect only for 300 ms indicates that these two effects act on different stages of temporal processing. Several studies suggested

a distinction of automatic timing for short intervals below 300 and 500 ms and a cognitive timing for longer intervals (Buonomano & Merzenich, 1995; Lewis & Miall, 2003b; Rammesayer & Lima, 1991). In that sense, it might be that only longer durations are prone to these spatio-temporal distortions.

4.5. Neural correlates and mechanisms

Several brain areas have been associated with temporal processing (Buhusi & Meck, 2005; Penney & Vaitilingam, 2008), here we will mention only areas involved in visual timing of sub-second intervals. Among these are the cerebellum (Lewis & Miall, 2003a), the caudate nucleus (Pouthas et al., 2005) and several cortical structures including the supplementary motor area (Ferrandez et al., 2003), the prefrontal, parietal (Leon & Shadlen, 2003) and temporal cortex, with strong evidence that the motion-sensitive medial temporal area is involved in humans (Buetti, Bahrami, & Walsh, 2008). Much of the neuronal circuitry implicated for time perception also is important for the generation of pursuit eye movements.

Although the neural structures involved in time perception are identified, there is still no consensus about the underlying computations (for a review see Ivry & Schlerf, 2008); on the one hand, there might be a dedicated mechanism which can be either located in one specialized region or distributed across several regions. These approaches typically postulate a centralized, supra-modal clock. Evidence for a centralized clock comes from cross-modal correlations in duration judgments (Keele, Pokorny, Corcos, & Ivry, 1985) and interval-specific learning which generalizes across modalities (Nagarajan, Blake, Wright, Byl, & Merzenich, 1998). The centralized clock is typically modeled as a pacemaker-accumulator (Creelman, 1962) or an oscillator process (Jones, 1976; Matell & Meck, 2004). As we find a modality-specific time compression during pursuit, a centralized clock would only be compatible, if it would have at least a modality-specific front-end. On the other hand, the timing might be an intrinsic property of the processing of other features. This view is supported by retinotopic adaptation effects on time perception (Burr et al., 2007; Johnston et al., 2006) and the stimulus dependence of duration judgments (Kaneko & Murakami, 2009; Terao et al., 2008; Xuan et al., 2007). Two different theories fit in that category. First, timing might be a property of a state-dependent network (Karmarkar & Buonomano, 2007). Second, duration might be represented by the magnitude of neural activity (Eagleman & Pariyadath, 2009; Pariyadath & Eagleman, 2007). Our results would be compatible with both intrinsic models.

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