



Spatio-temporal topography of saccadic overestimation of time

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ABSTRACT

Rapid eye movements (saccades) induce visual misperceptions. A number of studies in recent years have investigated the spatio-temporal profiles of effects like saccadic suppression or perisaccadic mislocalization and revealed substantial functional similarities. Saccade induced chronostasis describes the subjective overestimation of stimulus duration when the stimulus onset falls within a saccade. In this study we aimed to functionally characterize saccade induced chronostasis in greater detail. Specifically we tested if chronostasis is influenced by or functionally related to saccadic suppression. In a first set of experiments, we measured the perceived duration of visual stimuli presented at different spatial positions as a function of presentation time relative to the saccade. We further compared perceived duration during saccades for isoluminant and luminant stimuli. Finally, we investigated whether or not saccade induced chronostasis is dependent on the execution of a saccade itself. We show that chronostasis occurs across the visual field with a clear spatio-temporal tuning. Furthermore, we report chronostasis during simulated saccades, indicating that spurious retinal motion induced by the saccade is a prime origin of the phenomenon.

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1. Introduction

Saccades are fast ballistic eye movements that bring objects of interest into the fovea. With each saccade the projection of the visual scene sweeps across the retina at high speed. Yet, this drastic change in retinal input remains largely unnoticed and the world around us is perceived as stable. However, when probed with transient visual stimuli, perception is often far from veridical. As an example, the perceived location of flashed stimuli is shifted in the direction of the saccade (Honda, 1989) or compressed towards the saccade target (Morrone, Ross, & Burr, 1997; Ross, Morrone, & Burr, 1997). Sensitivity to luminance contrasts with low spatial frequencies is actively suppressed (saccadic suppression) while sensitivity to stimuli with high spatial frequencies, as well as to color contrasts remains unchanged (Burr, Morrone, & Ross, 1994) or is even enhanced shortly after the saccade (Burr & Morrone, 1996; Burr, Morrone, & Ross, 1994; Knöll et al., 2011). These changes to perception are hardly ever noticed during everyday life.

One saccadic misperception that is easily demonstrated in a modern environment is saccadic chronostasis, also called the *stopped clock illusion* (Yarrow et al., 2001). When making a saccade to a clock, the first second often seems to last longer than the subsequent ones. Yarrow et al. (2001) demonstrated this perceptual effect by asking subjects to saccade to a counter. At a set portion

of the saccade, the counter changed from '0' to '1' for a variable duration before it continued to count up to '4' in intervals of 1 s. Subjects judged whether the duration of the '1' was longer or shorter than the duration of the following 1 s intervals. Yarrow and colleagues found that the duration of the '1' had to be shorter than the subsequent intervals in order to be perceived as lasting equally long. That is, the duration of the first interval was overestimated compared to the other intervals. This overestimation exceeded the duration of the saccade by about 50 ms and increased by the same amount by which saccade duration increased (as induced by larger saccade amplitudes). Based on two further findings Yarrow et al. concluded that the onset of a stimulus at the saccade target is antedated to the time at which an efferent signal occurred (e.g. the efference copy of the saccade command) to preserve object-constancy across saccades. (i) When the stimulus was moved at about 200°/s with the eyes stationary, thereby simulating the visual consequences of a saccade, no chronostasis was observed. (ii) For two probe onset times (one fifth and four fifth of saccade duration), time was overestimated in a way that could be interpreted as antedating the onset of the stimulus to the same point in time prior to the saccade. When considering the physical duration of the stimulus, the overestimation was increased by the same amount the probe onset occurred later in the saccade.

Saccade induced chronostasis is not the only change in temporal perception during saccades. Morrone, Ross, and Burr (2005) reported that the perceived duration of an interval defined by

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two large horizontal bars, flashed in the retinal periphery around the time of a saccade, was compressed. In a critical time window just before saccade onset, the perceived temporal order of presentation of the two bars was even reversed. The underestimation of duration occurred for a period of about 300 ms around saccadic onset. This compression of perceptual time was also present when the interval was defined by vertical bars placed near the saccade target.

In order to disentangle these two seemingly contradictory results of *overestimation* (reported only at the saccade target) and *underestimation* of time around the time of saccades, Georg and Lappe (2007) asked whether chronostasis could also be found at positions other than the saccade target. The authors used the same paradigm as Yarrow et al. (2001), but with the counter placed either at the saccade target or midway along the saccade trajectory. Since Georg and Lappe only found an overestimation of duration at the saccade target, they concluded that chronostasis is, unlike the compression of time, a rather local mechanism. However, Yarrow (2010) recently described results of an experiment in which subjects were asked to saccade to a letter. The letter could be presented in isolation or was surrounded by four or eight other letters. During the saccade, one of the letters temporarily changed its color and subjects had to report the perceived duration of the color change. Since the magnitude of chronostasis did not depend of the number of letters, Yarrow concluded that chronostasis must have occurred at all letter positions. In a different experiment Yarrow also reported chronostasis for stimuli shown up to 7° beyond the saccade target.

Our groups recently studied the spatio-temporal profile of saccadic suppression (Knöll et al., 2011). We found that contrast sensitivity was reduced during saccades across the visual field by a constant factor in an eye-centered frame of reference. However, due to the differences in contrast sensitivity at different retinal eccentricities, the absolute sensitivity during the saccade was strongly dependent on the location of the stimulus in the outside world. Sensitivity was highest near the center of the saccade trajectory and reduced towards both sides (perpendicular to saccade direction) of this location. Perisaccadically, minimum sensitivity occurred later for stimuli near the fixations point as compared to stimuli near the saccade target. This temporal asymmetry occurred, however, only in a head-centered reference frame. The timing was symmetric for different positions in an eye-centered reference frame.

These results might be of critical relevance concerning the above mentioned study of Georg and Lappe (2007). It has been suggested by Yarrow and colleagues that the degraded perception of the stimulus onset, caused by saccadic suppression, might be a necessary condition for chronostasis to occur (Yarrow & Rothwell, 2003; Yarrow et al., 2006). One could thus expect chronostasis not to occur at the center of the saccade trajectory, where peri-saccadic contrast thresholds are lowest. Chronostasis could thus still be a global mechanism, but absent or reduced at some locations. In this case we should be able to find chronostasis at other positions where peri-saccadic contrast sensitivities were similar to that at the saccade target. The time at which chronostasis first occurs could also differ for different locations, given the differences in time course of peri-saccadic contrast sensitivity at different screen positions.

We thus aimed to investigate the influence of saccadic suppression on chronostasis. In the first experiment we tested for chronostasis at the point of initial fixation, where we expected peri-saccadic contrast sensitivity to be similar to that of the saccade target. In experiment two we expanded our sampling space by measuring the time course of chronostasis at the same two positions and additionally midway along the saccade trajectory. Experiment three aimed to investigate the visibility of the used

stimuli during the saccade and the dependence of chronostasis on saccadic suppression. Finally, experiment four explored the dependence of chronostasis on an eye-movement related signal by mimicking the visual consequences of a saccade by means of a fast rotating mirror.

2. General methods

2.1. Stimuli and procedure

All experimental procedures were in line with the declaration of Helsinki. Experiments 1 through 3 were performed at the Philipps-Universität Marburg (Germany). Experiment 4 was carried out at the Neuroscience Institute of the CNR in Pisa (Italy).

Experiments were conducted in a dark room with visual stimuli presented on a CRT screen (Experiments 1–3: Philips Brilliance 202P7; Experiment 4: Barco Calibrator) running at 100 Hz with a resolution of 1152 × 864 pixels and viewed from a distance of 57 cm, covering the central 39° × 29° of the visual field (Experiment 1: 33 cm and 62° × 49°, respectively). The stimuli were generated on a PC using the in-House OpenGL/C++ software Neurostim (<http://neurostim.sourceforge.net>). Timing of all stimuli was synchronized to the vertical retrace of the computer screen. Unless stated otherwise, randomization of temporal parameters was based on drawing from uniform distributions in steps of the duration of a single frame in the specified temporal ranges. Eye position data were recorded with an infrared eye tracker running at 500 Hz (Experiment 1: SR Research Eyelink II, Experiments 2–4: SR Research Eyelink 1000). They were used for online control of behavior and stored for later offline analysis.

The general paradigm used in our study was similar to a more abstract version of the task used in later studies by Yarrow and colleagues (e.g. Yarrow et al., 2006) for investigating chronostasis. In our task a *probe* stimulus with variable duration was shown around the time of the saccade and had to be compared with a single *test* stimulus of fixed duration (Fig. 1). In all experiments, subjects were either asked to fixate a given target or to make a visually guided saccade. A small square (constant stimulus, 1.5° × 1.5°, Experiment 1: 0.85° × 0.85°) was shown for the duration of a trial at one of three possible positions (*constant stimulus*). This square either served as the initial fixation point, as the saccade target or it was placed midway along the saccade trajectory. The square changed its appearance (decrease in luminance, except the second part of Experiment 3: change in color) at a variable time relative to the onset of the saccade. After a variable probe duration, it changed back to its original appearance for 1000 ms before changing the appearance (identical to that of the probe) for a test duration of 500 ms (Experiment 3.1: 50 ms). It finally returned to its initial appearance until the participant pressed a key indicating whether the probe or the test duration appeared to have lasted longer. In the first part of Experiment 3 participants additionally specified whether or not they had seen both stimuli.

In saccade conditions, depending on the location of the probe, the saccade was cued either by the disappearance of the fixation point (0.5° black disc), by the appearance of a saccade target (0.5° black disc) or both. The square, constantly shown throughout the trial, occluded the fixation point or saccade target when located at the same position, i.e., the cue at the location of the probe was omitted. We had chosen this approach to avoid visual changes at the location of the probe and target unrelated to the task of judging the duration.

In fixation conditions, visual stimulation was identical to saccade conditions, except that the onset of the probe was determined relative to the mean saccade latency and participants held fixation at the location of the saccade target throughout a trial, unless

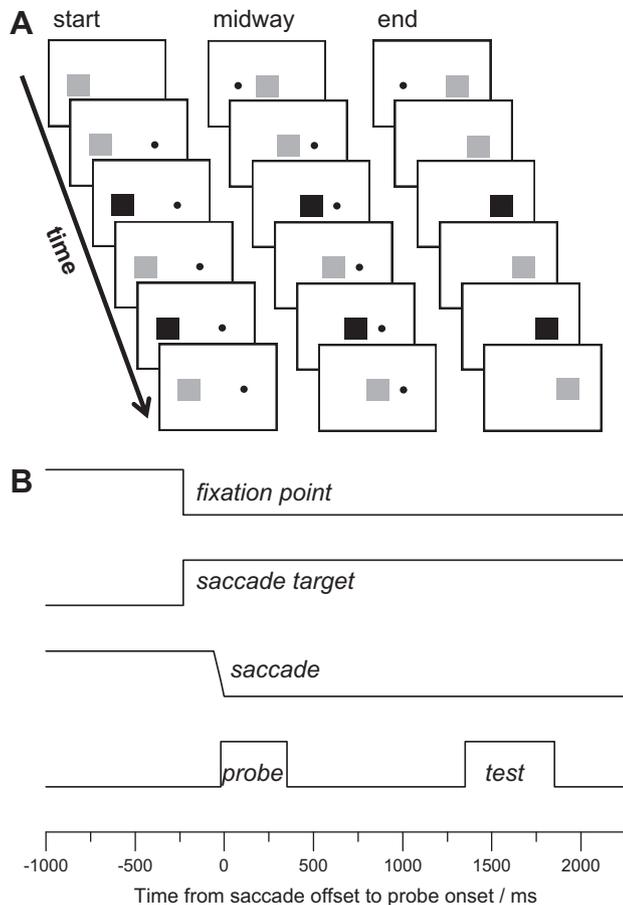


Fig. 1. A schematic representation of the stimuli and procedure used in this study (A). The images are not drawn to scale. Depending on the experiment the probe and test could be located either at the start or the end point of the saccade or midway along the saccade trajectory. (B) The time course of event occurrences. Participants initially fixated at the fixation point, which (if not occluded by the square) turned off while the saccade target simultaneously appeared (unless occluded). Participants saccaded to the saccade target. Around this time the square, constantly visible throughout each trial, changed in appearance for a probe duration. The duration had to be judged to an otherwise identical test duration that started 1000 ms after the offset of the probe.

stated otherwise. The fixation point at the location of the saccade target was visible throughout the trial, unless the probe was also placed at that location. In such case no fixation point was visible at the location of the saccade target, as it was occluded by the square.

Trials were automatically discarded and repeated later, if the participants showed an eye blink in the interval from the beginning of the trial to the end of the test duration, or if they failed to produce the required eye movement.

2.2. Data analysis

Eye traces from the left eye were analyzed offline. Saccades were detected by a velocity criterion of $200^\circ/\text{s}$. The start and end of a saccade were then defined by the last and first sample with a velocity below $20^\circ/\text{s}$, respectively. In saccade conditions, trials with saccade latencies less than 50 ms or more than 300 ms were discarded from further analysis. This was also done for trials where the start and end position of the saccade differed by more than 1° or 2° from the expected start and end point of the saccade, respectively.

In saccade conditions, trials were sorted according to the time of probe onset relative to the offset of the saccade and split into

bins of 20 ms. To obtain population results, data were pooled across participants. Datasets were balanced by reducing the number of trials from each participant in a given condition (fixation/saccade and stimulus position) to the minimum number of trials from any participant in that condition, but not for different bins within each condition. Psychometric functions were obtained by fitting cumulative Gaussians to the responses of the participants and the physical duration of the probe with the psignifit toolbox (Wichmann & Hill, 2001a, 2001b), which provided estimates of the 50% threshold (PSE) along with bootstrapped standard errors and 95% confidence intervals based on 1999 simulations. The distributions of the estimated parameters from these simulations were also stored for later statistical comparisons. The PSE of the probe describes the *subjective duration* at which it appeared identical to the test duration. It is important to note that a reduction in *subjective duration* implies an overestimation of the probe duration and vice versa.

While non-overlapping confidence intervals of different subjective durations already imply a statistical difference at a more conservative level than a corresponding *t*-test (Cumming, 2009), subjective durations were directly compared in order to quantify differences with corresponding confidence intervals. Comparisons between two subjective durations were done similar to a method described by Poe, Giraud, and Loomis (2005) in which two bootstrapped distributions (of simulated estimates) were subtracted from each other. That is, each estimate from one distribution was subtracted by each estimate from the other distribution, resulting in 1999×1999 estimates of the difference. The difference was considered significant if the 5% quantile was larger than zero (one sided test) or if the 2.5% and 97.5% quantiles had identical sign (two sided test). One sided tests were used to determine the point in time for which the subjective duration was for the first time lower than during fixation (onset of chronostasis) when analyzing the time course of chronostasis. Otherwise two sided tests were used.

3. Experiment 1

In this experiment we tested the hypothesis that chronostasis does not only occur in the spatial vicinity of the saccade target. Specifically, we tested perisaccadic duration perception with probes either at the saccade target or the fixation point and compared it to corresponding conditions during steady fixation.

3.1. Methods

3.1.1. Participants

Seven naïve observers participated in Experiment 1 (age range: 22–27, 4 female). All had normal or corrected-to-normal vision.

3.1.2. Stimuli and procedure

The general paradigm is depicted in Fig. 1. At 500–1000 ms after trial onset, participants were cued to make 25° horizontal rightwards saccades centered along the horizontal meridian. A gray square (0.85° width and height, 70% background luminance) shown throughout the trial on a white background (87 cd m^{-2}) was located either at the start or end point of the saccade (*constant stimulus*). The online detection of a saccade triggered the constant stimulus to change to a black *probe* ($<1 \text{ cd m}^{-2}$) for a duration of 200–800 ms chosen randomly for each trial. The change occurred between 30 ms and 10 ms before the end of the saccade. Subjects judged the duration of the probe relative to an otherwise identical *test* duration of 500 ms that started 1 s after the offset of the probe. As a control, duration perception was also measured during fixation for both probe positions while fixating at the location of the

saccade target. The four conditions were measured in separate sessions, with twice as many saccade as fixation sessions which were presented in pseudorandomized order. A single session consisted of 300 trials. A total of 12,143 valid trials were recorded with 10,269 contributing to the population analysis. The remaining 1874 trials were removed in order to consider the same number of trials per subject for each condition.

3.2. Results

The subjective durations, i.e. the points of subjective equivalence (PSE) of the probe duration, are shown for the population in Fig. 2. The perisaccadic PSE for probes located at the saccade end point (at 12.5°) was significantly reduced by about 110 ms compared to the PSE during fixation ($p < 0.05$; 95% CI: $[-126, -91]$ ms; see Section 2.2. for detail). In other words, the perisaccadic probe had to be shorter during the saccade to be perceived lasting as long as a stimulus shown during fixation, demonstrating chronostasis. As expected from our hypothesis, the PSE at the saccade start point (at -12.5°) was also significantly reduced compared to fixation (about 60 ms; 95% CI: $[-77, -42]$ ms). The extent of overestimation of duration was however significantly smaller compared to that at the saccade end point (difference about 50 ms; 95% CI: $[35, 69]$ ms). The average saccade duration was 72 ms.

3.3. Discussion

Chronostasis has previously been reported to occur at positions other than the saccade target that were either in the spatial vicinity of the target or exceeded its location (Yarrow, 2010). In our experiment we demonstrated for the first time that saccadic chronostasis is not limited to the region around the saccade target or exceeding it but occurs also at the location of initial fixation. The amount of temporal overestimation (compared to fixation) at the saccade end point was comparable to previously reported data. Yet at the saccade start point it was only half the value. Participants reported that the probe at the latter location was sometimes difficult to detect due to the combination of large eccentricity and

small stimulus size. However, any related changes in the visibility of the probe onset should have also affected the control condition.

4. Experiment 2

To further characterize temporal overestimation as a function of spatial position, we next measured the time course of chronostasis at the start and end point of the saccade and midway along the saccade trajectory.

4.1. Methods

4.1.1. Participants

Five new naïve observers participated in Experiment 2 (age range: 20–31, 4 female). All had normal or corrected-to-normal vision.

4.1.2. Stimuli and procedure

Stimuli and Procedure were identical to Experiment 1 with the following exceptions. In order to reduce detection problems due to retinal eccentricity, saccade size was reduced to 20° , and the size of the square was increased to 1.5° . The gray square remained at 70% of the background luminance, with the background luminance changed to 60 cd m^{-2} . The square could now also be located midway along the saccade trajectory (0°). In saccade conditions, the onset of the probe was timed to occur -150 ms to 100 ms around the expected offset of the saccade. This was achieved by adding a random value drawn from a uniform distribution in the specified range to each subject's average reaction time and saccade duration. As a control, duration perception was also measured during fixation for all three probe positions while fixating at the location of the saccade target. Trials were presented in blocks of fifteen trials with fixed probe location and saccade/control type within each block. The blocks were presented in pseudorandomized order with a ratio of six to one for saccade and control blocks. A total of 39,546 valid trials were recorded with 36,225 contributing to the population analysis.

4.2. Results

In Fig. 3 the subjective duration of the population is plotted for all three positions against the time of probe onset relative to saccade offset. Subjective duration was reduced not only at the saccade target (10° , cyan lines) and the saccade start point (-10° , orange lines), but also midway along the saccade trajectory (0° , magenta line). Well before the saccade (140 ms before saccade offset, mean saccade duration: 65 ms), subjective duration was similar to that observed during fixation. Subjective duration first dropped significantly below the value during fixation (one-sided comparison of bootstrapped distributions; see general methods, Section 2.2) at the saccade end point (-120 ms), followed by the central position (-80 ms) and finally at -40 ms relative to saccade offset at the saccade start point. It then progressed to drop at different rates to a peak reduction that occurred at about the time of saccade offset for all positions. Contrary to our expectation, the peak reduction as compared to fixation was stronger at the central position (-164 ms; 95% CI: $[-186, -145]$ ms) than at both the saccade target (-75 ms; 95% CI: $[-88, -60]$ ms) and the fixation point (-69 ms; 95% CI: $[-88, -49]$ ms). About 60 ms after the saccade, perceived duration was back to the level during fixation, but continued to an underestimation of duration afterwards. This underestimation compared to fixation was again stronger at the central position (118 ms; 95% CI: $[87, 153]$ ms) than at both the saccade target (42 ms; 95% CI: $[21, 65]$ ms) and the fixation point (45 ms; 95% CI: $[13, 78]$ ms).

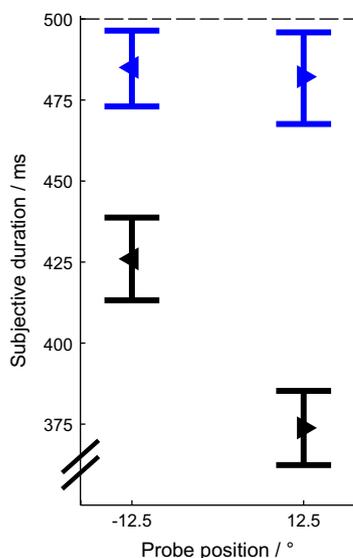


Fig. 2. Points of subjective duration equivalence at the fixation point (-12.5°) and the saccade target (12.5°) during fixation (blue lines) and perisaccadically (black lines) for the population. PSEs are reduced perisaccadically both at the saccade target and at the fixation point compared to PSEs during fixation. The dashed line indicates the test duration. Error bars show 95% confidence intervals.

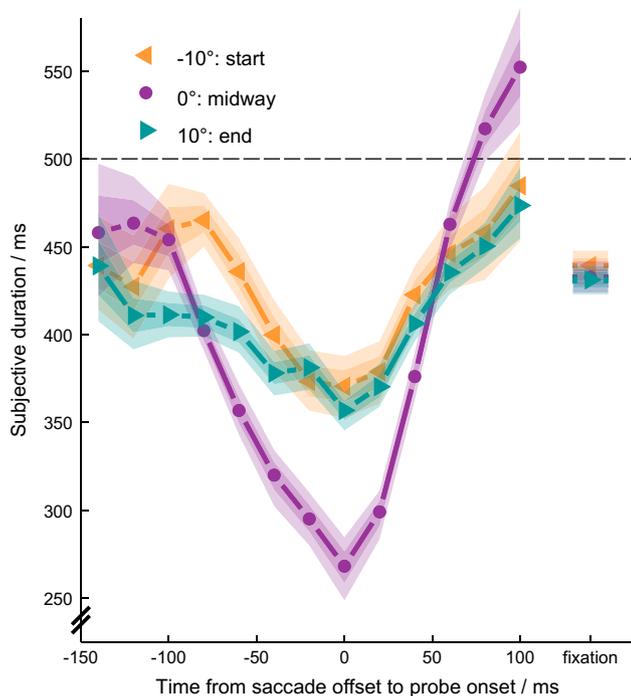


Fig. 3. Time course of chronostasis. Subjective durations (PSE) at the three measured positions (saccade start: orange, midway along the trajectory: magenta, saccade end point: cyan) as a function of probe onset relative to the offset of the saccade. These colors are also used in subsequent figures for corresponding conditions. PSEs are reduced perisaccadically at all three positions compared to PSEs during fixation (rightmost data points). The dashed line indicates the test duration. Dark shaded regions indicate the SEM, light shaded region the 95% confidence intervals.

4.3. Discussion

Perceived duration was overestimated at all three positions, peaking at the time of saccade offset. This finding was unexpected, given our hypothesis that chronostasis should be reduced midway along the saccade trajectory due to higher contrast sensitivity at this position compared to the other two. Instead we found the amount of chronostasis to be largest at this position. It has been demonstrated that the fast motion of an image can degrade visual perception independently of saccadic suppression under certain conditions (Campbell & Wurtz, 1978; Diamond, Ross, & Morrone, 2000). It is possible that the contrast sensitivity to the stimuli used in our experiment was not only affected by saccadic suppression, but also by these presumably passive modulations of perception (a more detailed consideration can be found in the general discussion).

It should be noted that the overestimation observed at the saccade target was reduced compared to the value found in Experiment 1. Perceived durations tested at the saccade target and the fixation point were similar near the end of the saccade. This difference to Experiment 1 might be a result of the slight change of the stimuli in Experiment 1 and Experiment 2 (larger stimulus in Experiment 2).

5. Experiment 3

In Experiment 2 we found chronostasis midway along the saccade trajectory with a maximum overestimation of duration of 164 ms as compared to fixation. We speculated that visibility of our stimulus was strongly reduced even at this point of the saccade trajectory. To test this explicitly, we measured the duration necessary to detect the probe at different times relative to the

saccade. The goal of this approach was also to determine what duration of a stimulus would go unnoticed and might thus not be available for later processing.

To test if chronostasis occurs also in the absence of saccadic suppression, we measured the perceived duration for isoluminant stimuli presented at the saccade target in a second part of this experiment. We chose for this approach because saccadic suppression had been shown to not affect the detection sensitivity of such stimuli (Burr, Morrone, & Ross, 1994).

5.1. Methods

5.1.1. Participants

The same participants as in Experiment 2 participated in the first part of this experiment, while only 4 of the 5 participants completed the second part.

5.1.2. Stimuli and procedure

The following differences to Experiment 2 were applied. Part 1: The probe was always located midway along the saccade trajectory, with a reduced test duration of 50 ms and range of probe durations from 0 ms (i.e. no probe was shown) to 100 ms. Participants stated whether or not they had seen both the probe and test duration but also reported the perceived duration. This procedure was chosen to ensure that the subjects were solving the same task as in the previous experiments. However, only the results of the detection task were analyzed. Trials were presented in several separate blocks of fifteen trials for control and saccade conditions. The blocks were presented in pseudorandomized order with a ratio of six to one for saccade and control blocks. A total of 12,262 valid trials were recorded with 11,035 contributing to the population analysis. Part 2: The probe was always shown at the saccade target. In half of the sessions, stimuli and background were identical to those used in Experiment 2. In the other half, the square was initially red, shown on a yellow background. During the probe and test duration the square was green, isoluminant to both the background and the previously red square. Isoluminance was established using the minimum flicker technique (Boynton, 1979). Sessions were recorded in alternating order, with a balanced starting with either type across subjects. Duration perception was tested during fixation at the corresponding post-saccadic probe location, as well as at three times relative to the saccade offset: 0, 70 and 420 ms, triggered by the online detection of the saccade and taking each subject's mean saccade duration into account. In each session, saccade and control conditions were presented in blocks of 15 trials in pseudorandomized order, with four saccade and one control block per session. A total of 9811 valid trials were recorded with 9588 contributing to the population analysis.

5.2. Results

5.2.1. Duration threshold

The duration necessary for a stimulus to be detected in 50% of the trials (duration threshold) is shown in Fig. 4A as a function of time relative to saccade offset. Well before and after the saccade as well as during fixation, the duration threshold was below 10 ms, i.e. stimuli were typically visible even if they were presented for only one frame. The duration threshold was first significantly higher than during fixation (one-sided comparison of bootstrapped distributions; see general methods, Section 2.2) 80 ms before saccade offset (or 20 ms before onset; mean saccade duration: 61 ms) peaking at –60 ms (saccade onset) with a value of 45 ms (95% CI: [43, 49] ms). The duration threshold then declined again and was not significantly higher than during fixation at 20 ms after saccade offset.

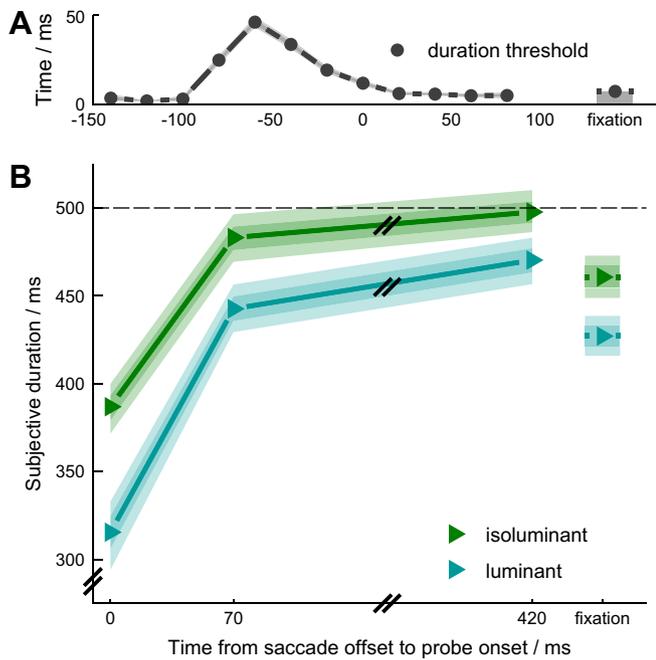


Fig. 4. (A) The duration threshold, i.e. the duration necessary for the probe to be visible in 50% of the trials, as a function of time relative to saccade offset. (B) Subjective duration for luminant probes (cyan lines) and probes isoluminant (green lines) to the constant stimulus and to the background. Dark shaded regions indicate the SEM, light shaded region the 95% confidence intervals.

5.2.2. Chronostasis for isoluminant stimuli

The subjective durations (PSE) for isoluminant (green) and luminant (cyan) stimuli are shown in Fig. 4B. PSEs obtained during fixation differed between the isoluminant and the luminant condition, with a lower subjective duration for luminant stimuli (34 ms difference; 95% CI: [17,50] ms). At saccade offset, the subjective duration was significantly reduced compared to fixation (luminant: 112 ms, 95% CI: [91,135] ms), isoluminant: 74 ms, 95% CI: [54,92] ms) and to post-saccadic probe onset times, for both luminant and isoluminant stimuli. Chronostasis was larger for the luminant than for isoluminant probes (72 ms difference; 95% CI: [49,97] ms). This difference remained significant, even when taking the differences in subjective duration during fixation into account (38 ms remaining difference; 95% CI: [10,68] ms).

5.3. Discussion

The duration threshold for detecting a stimulus was highly elevated during the saccade midway along the saccade trajectory. Elevation started about 80 ms prior to saccade offset, i.e. 20 ms prior to saccade onset. This implies that the probe onset could not be seen at a location where detection thresholds are known to be lower than at the saccade target. It supports the idea that saccadic suppression is not the only factor causing an imprecise percept of the probe onset in our experiment. The value of maximum duration threshold (45 ms) was less than the overall duration of the saccade. In other words: even if the probe onset coincided with saccade onset, a stimulus shown only for the duration of the saccade did not go completely unnoticed. The value of the maximum duration threshold was also significantly smaller than the amount of chronostasis (165 ms) found in Experiment 2. Accordingly, chronostasis can cause an overestimation of duration by more than about three times the duration that would go unnoticed if a stimulus appeared exclusively during the time of saccade onset.

The neglect of the peri-saccadic stimulus duration had been previously assumed and corrected for (e.g. Yarrow et al., 2001) to

estimate the magnitude of chronostasis at two different peri-saccadic probe onset times. With this correction, chronostasis appeared approximately constant for both probe onset times. Without the correction, the reported overestimation of the duration would have been increased for the later compared to the earlier probe onset time. Because two stimuli could be discriminated when shown briefly during a saccade in situations where no duration judgment task is involved, it has been argued that the correction was not justified (Hunt, Chapman, & Kingstone, 2008). In our experiment we showed that detectability of stimuli whose duration was to be judged was highly impaired during saccades. Thus for the stimuli used in this study, the results show that the assumption of the probe's undetectability during the saccade was generally correct, but might have slightly overestimated the magnitude of chronostasis.

Another important finding of this experiment was that chronostasis also occurred for isoluminant stimuli. Such stimuli are known to be unaffected by saccadic suppression (Burr, Morrone, & Ross, 1994). This result excludes saccadic suppression as a necessary condition for chronostasis to occur. It does, however, not exclude chronostasis to be caused by an imprecise perception of the onset of a stimulus. Given the reduced chronostasis for isoluminant as compared to luminant stimuli, we conclude that the motion of the retinal image probably caused a sufficiently unclear probe onset to allow chronostasis to occur for isoluminant stimuli, and that the additional reduction in visibility due to saccadic suppression for luminant stimuli increased the overestimation of duration observed in that condition.

6. Experiment 4

It is generally assumed that chronostasis relies on an eye-movement related signal. In previous studies, chronostasis did not occur when a probe was moved on the screen, while the participants kept fixation (Yarrow, Haggard, & Rothwell, 2004; Yarrow et al., 2001). It is possible that the speeds of 200–240°/s used in these experiments were not sufficient to cause an imprecise percept of stimulus onset. If chronostasis was to occur when the image is moved fast enough to be perceived as blurred, chronostasis would be a purely visual effect, independent of an efferent signal.

In this last experiment, we therefore tested if an eye-movement related signal was necessary for chronostasis to occur by using a mirror that moved the image of the screen at saccadic speeds.

6.1. Methods

6.1.1. Participants

Two naïve subjects and one author participated in this experiment. All had normal or corrected to normal vision.

6.1.2. Apparatus

A small galvanometer mounted mirror (M3S, GSI now Cambridge Technology) was placed closely before the participants' right eye, allowing participants to monocularly view a CRT placed at a total distance of 57 cm. The mirror was controlled by the stimulus presentation program by sending a sequence of target voltages (corresponding linearly to the angle of the mirror) using a 12-Bit USB-IO-Board (1208-FS, Measurement Computing). The signal was generated at 10 kHz in a way that moved the mirror with a Gaussian speed profile by 18° within 46 ms ($v_{\text{mean}} = 390^\circ/\text{s}$, $v_{\text{max}} = 890^\circ/\text{s}$). An identical second IO-Board was used to record a copy of that signal as well as the output of phototransistors placed on the CRT at 5 kHz. This allowed a precise synchronization of the signal to the time of the stimuli presented. The left eye was shielded from visual input and its movements were recorded. In

simulated saccade conditions, the recorded signal of the mirror command was analyzed analogous to the eye traces in saccadic conditions.

6.1.3. Stimuli and procedure

Two conditions were recorded in this experiment. Saccade conditions were identical to the saccade condition in Experiment 2, with three exceptions. The probe was always located midway along the saccade trajectory. Probe onset was timed to occur at 0, 70 or 420 ms after the offset of the saccades and participants made 18° leftward saccades (9° to -9°) instead of 20° rightward ones. The onset was triggered by the online detection of the saccade, taking each subject's mean saccade duration into account. In simulated saccade conditions participants kept fixation, while a mirror was moved to mimic an 18° leftward saccade. Possible probe onset times were 200, 100, 50, and 25 ms before and after offset of the simulated eye movement or directly at its offset. In order to suppress initiation of saccades upon appearance of the saccade target, the initial fixation point was not turned off in this condition. The different probe onset times were chosen in pseudorandomized order with identical likelihood. Simulated and saccade conditions were measured in separate sessions. A total of 6717 valid trials were recorded with 6678 contributing to the population analysis.

6.2. Results

When the image motion of a saccade was simulated by a rotating mirror, the mean eye position remained mostly unchanged with a small shift opposite to the direction of the motion (Fig. 5A, blue line). This shift however was small compared to the eye movement when participants viewed the screen monocularly through a mirror and performed 18° leftward saccades (magenta line). The subjective stimulus durations during these simulated and real saccades are shown in Fig. 5B. The magenta line depicts the subjective duration during real saccades. The onset of the probes could occur at three possible points in time with respect to the end of the saccade. As expected from the previous experiments, the subjective duration was reduced at the offset of the saccade, quickly recovering thereafter. The subjective duration for probes with an onset 420 ms after the end of the saccade was 535 ms (95% CI: [509,560] ms), but only 353 ms (95% CI: [317,389] ms) for probes starting at saccade offset. Subjective duration was also reduced when subjects kept fixation while the mirror was moved in a Gaussian speed profile at saccadic speeds (blue line). Like with saccades, the reduction was strongest at the offset of the mirror movement (373 ms; 95% CI: [347,398] ms), as compared to both 200 ms before (538 ms; 95% CI: [506,571]) and 200 ms after (501; 95% CI: [469,534] ms) the movement offset. The time course of this modulation was comparable to that observed during real saccades (see Fig. 3). Yet, the PSE did not recover as quickly, remaining strongly reduced until 50 ms after the movement. About 100 ms after the movement it was back to a level comparable to that before the movement. The results did not differ qualitatively when removing the author's data from the analysis.

6.3. Discussion

The results of this experiment clearly demonstrate that chronostasis can occur even in the absence of a saccade and thus in the absence of an efferent signal. The time course of chronostasis during simulated saccades, however, was prolonged, lasting up to 50 ms after the end of the mirror movement compared to real saccades (Experiment 2) where subjective duration started to return to normal immediately after saccade offset. This result is consistent with the small overestimation observed by Georg and Lappe (2007)

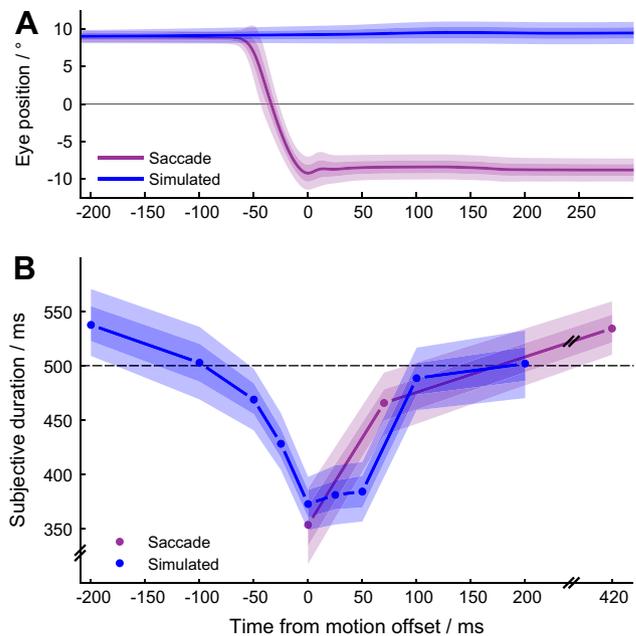


Fig. 5. Comparison of real (magenta lines) and simulated (blue lines) saccades. (A) The eye position during real and simulated saccades relative to motion offset. Dark shaded regions indicate the SD, light shaded regions the area that includes 95% of the recorded eye positions at a given point in time. (B) The subjective duration during real and simulated saccades as a function of the time of the probe onset relative to the motion offset. In both cases, strongest reduction of PSEs occurred at the end of the movement. Dark shaded regions indicate the SEM, light shaded region the 95% confidence intervals.

in the condition of simulated saccades. The overestimation in this case was smaller than the one we observed. However, in Georg and Lappe (2007) the retinal motion between the simulated and real saccade was not exactly equated. Given the pronounced temporal profile for simulated saccades, we can also exclude that the overestimation reflects an attentional or temporal order effect as observed during fixation for stationary stimuli (Rose & Summers, 1995).

In similar experiments where the visual motion of a saccade was also simulated with a mirror, neither saccadic suppression (Diamond, Ross, & Morrone, 2000) nor the peri-saccadic compression of space (Morrone, Ross, & Burr, 1997) was found to occur in the absence of eye movements. In another experiment the pattern of spatial mislocalization appeared to be compression-like for saccades but shift-like for simulated saccades (Honda, 1995). The dependence of temporal perception for stimuli similar to those used in experiments of compression of time and perceived inversion of temporal order (Morrone, Ross, & Burr, 2005), has also been investigated with simulated saccades (Binda et al., 2009). In an audio-visual temporal order judgment task, two subjects had to specify whether a transient isoluminant stimulus was presented earlier or later than a short sound. The visual stimulus was presented within 25 ms before a saccade. To be perceived as occurring synchronous, the stimulus had to be presented 100 ms prior to the sound. For simulated saccades, no such postdating was found. The independence of chronostasis on an eye-movement thus clearly dissociates it from many other saccadic misperceptions.

7. General discussion

In a set of experiments we demonstrated that chronostasis is neither limited to the region around the saccade target (Experiment 2) nor to the execution of saccades (Experiment 4). Also,

the peri-saccadic overestimation of durations does not just compensate for the duration of a stimulus that is perceptually 'invisible' due to saccadic suppression (Experiment 3), and differs for different positions (Experiment 2).

7.1. Visibility of probe onset without saccadic suppression

The amount by which the subjective durations were reduced, differed between single experiments of our study and also between different stimulus positions. Yarrow, Haggard, and Rothwell (2004) also reported different effect sizes in different experimental setups. They attributed this to subject specific differences given that distinct groups of subjects participated in the different experiments. This could also explain the differences found between Experiment 1 and Experiment 2 for stimuli at the saccade target. But it cannot explain the differences we found for the different positions within Experiment 2 and between luminant and isoluminant stimuli in the second part of Experiment 3, as these were carried out by the same group of participants. We rather consider chronostasis to be highly dependent on the visibility of the stimulus onset. The differences would then result from differences in visibility, which can be affected by a variety of factors such as eccentricity of the stimuli in the visual field. If an imprecise probe onset is modulating chronostasis, saccadic suppression alone thus cannot have been the source of the imprecise probe onset, as chronostasis also occurred during simulated saccades and for isoluminant stimuli.

It has been shown that a broad frequency stimulus (the image of a room), shown for the duration of a saccade, can be perceived as smeared due to the blurring of the retinal image (Campbell & Wurtz, 1978). While the image was not perceived as blurred when the presentation exceeded the duration of the saccade by about 20 ms, the peri-saccadic part of the stimulus was most likely not clearly perceived. The image was also perceived as undistorted when shown for only up to 5 ms during the saccade. This effect is thus likely to be independent of saccadic suppression, which also occurs for short stimulus presentations and stimuli optimized to reduce motion blur (Burr, Morrone, & Ross, 1994). In our experiment, a stimulus was constantly shown throughout a trial at the location of the probe and could thus contribute to motion blur even if the onset of the probe itself occurred at the very end of the saccade.

Another possibly related degradation of visual perception due to fast image motion has been reported by Diamond, Ross, and Morrone (2000) for stimuli presented on a patterned background. The background consisted of small patches, each with a luminance randomly chosen to be the minimum or maximum screen luminance. Contrast sensitivity was strongly reduced during a saccade but importantly, also when the image was moved by a mirror. The authors of this study demonstrated that the reduced visibility can be explained by the image motion of the patterned background. When the stimuli were shown on a homogenous background, decreased contrast sensitivity was only found during saccades. This clearly separates saccadic suppression from reductions in stimulus visibility due to image motion. As with chronostasis in our present study, the recovery of contrast sensitivity in their study was prolonged when the image was moved as compared to the saccadic condition. The background in our experiment was not patterned, yet the constant stimulus (the square) could have been sufficient to cause a (local) reduction in stimulus visibility.

It is thus likely that the onset of the probe was not optimally perceived even in the absence of saccadic suppression. While the conditions necessary for chronostasis to occur may typically only exist during saccades (imprecise percept of probe onset due to saccadic suppression and/or the high speed of the retinal image), it is definitely not dependent on the saccade itself.

Taking this consideration a step further, one could argue that it might be the background motion induced reduction in contrast sensitivity described by Diamond, Ross, and Morrone (2000) that mediates a large part of chronostasis. If a constant stimulus would cause a local reduction in contrast sensitivity, it could explain why chronostasis could not be found when the counter was displaced during the saccade (Yarrow et al., 2001). If this was the case, the constant stimulus would not be required for object constancy as previously assumed, but only to cause an imprecise onset of the probe. Other stimuli, where saccadic suppression alone causes such a sufficiently imprecise perception of its onset, might be able to cause chronostasis without a constant stimulus at the position of the probe.

It is important to note that the overestimation of duration was not necessarily completely unrelated to saccadic suppression. The overestimation was larger for luminant than for isoluminant stimuli. Also, the time at which chronostasis first occurred differed for the different stimulus positions with the same pattern observed for saccadic suppression (Knöll et al., 2011).

7.2. Chronostasis midway along the saccadic trajectory

At first glance our demonstration of chronostasis midway along the saccade trajectory appears to be contradicting the results of Georg and Lappe (2007), who did not find chronostasis at this location. In fact, our hypothesis based on the spatio-temporal profile of peri-saccadic contrast sensitivity (Knöll et al., 2011) was that stimuli shown during saccades midway along the saccade trajectory should have a higher visibility than at the saccade target. The stimuli used in our experiments however could not be detected at this location for a large proportion of the saccade (first part of Experiment 3), allowing for chronostasis to occur. We consider it plausible that the stimuli used by Georg and Lappe (2007) might have not been affected by motion blur as much as our stimuli and might thus have been peri-saccadically visible midway along the saccade trajectory, but not at the saccade target. The comparably high spatial frequencies of digits (the stimuli) might have allowed to adequately perceive the stimulus when it was foveated during the saccade. Given that the onset of the probe occurred after the eye passed the screen center (two thirds of saccade duration), it is possible that the visibility of the stimulus, during the saccade and before probe onset, might have limited the occurrence of chronostasis. Thus, visibility of the stimulus (a counter) might be the reason chronostasis midway along the saccade trajectory could not be found in their study. However we certainly cannot exclude other factors to be the cause of the discrepancy of our results to those of Georg and Lappe (2007). An experimental paradigm addressed at directly investigating the influence of these visual parameters on saccadic perception would be required to resolve this issue.

7.3. No common target of antedating

Yarrow and colleagues proposed that the onset of the perisaccadic probe is antedated to a fixed point in time relative to the onset of a saccade; namely, to the occurrence of an efferent trigger, e.g. an efference copy of the saccadic motor command (Yarrow, Johnson, et al., 2004). This view was further supported by an experiment in which they asked subjects to judge the onset of the probe relative to an auditory time marker (Yarrow et al., 2006). The authors confirmed that the overestimation of the duration is in fact caused by antedating the onset of the probe. While the fact that we found chronostasis for simulated saccades excludes an efferent signal as a 'target' for this antedating, the onset could still be antedated to the start of the image motion or the start of visual degradation of the stimulus onset.

The first possibility would predict the onset to be antedated to a fixed point in time. Our results show strong variations of the amount by which a stimulus is overestimated with stimulus positions, thereby excluding this option. This finding also supports the second possibility, as the time course of perisaccadic contrast sensitivity also varies with the location of a stimulus on the screen. Thus the onset of chronostasis varies in a similar pattern as visual degradation due to saccadic suppression. However, the visual degradation (the duration necessary for a stimulus to be detected) started to increase only at about 20 ms before saccade onset (Experiment 3), while the duration was overestimated by 100 ms in addition to the saccade duration. It thus seems unlikely that the onsets of the stimuli are antedated to a particularly marked event.

7.4. A possible mechanism of chronostasis

It has been demonstrated that the perceived temporal order of two stimuli, shown in rapid succession at the same location, can be reversed when the second stimulus had a lower contrast than the first (Bachmann, Pöder, & Luiga, 2004). If the reason for this reversal is that the onset is perceived to occur earlier for a stimulus with low than with high contrast, this explanation might also be able to explain chronostasis. The contrast sensitivity is reduced during the saccade and recovers afterwards. The onset of a probe that is switched on during the saccade might thus only be detected as soon as the contrast detection threshold returns to a value below the probe's contrast. It might thus be encoded like an onset of (subjectively) very low contrast. This could cause the onset to be perceived as earlier compared to the onset of the test stimulus and would result in chronostasis. It is, however, unclear if the changes in temporal perception described by Bachmann et al. can be as large as the overestimations in duration of up to 164 ms observed in this study.

Another probable possibility is that the speed of the constant stimulus (and of the probe) directly influenced the perceived duration. Motion is known to influence temporal perception. A stimulus with high speed is perceived to last longer than slow stimuli (e.g. Brown, 1931; Kaneko & Murakami, 2009; Tomassini et al., 2011). Watson and Krekelberg (2009) have demonstrated that a peri-saccadic stimulus that is not consciously perceived can nevertheless induce a shape contrast illusion. Even though the peri-saccadic part of the stimulus and its motion were not available to conscious perception, it might have still contributed to the perception of the probe's duration.

7.5. Other forms of chronostasis

Overestimation of durations have also been reported in the tactile (Park, Schlag-Rey, & Schlag, 2003; Yarrow & Rothwell, 2003) and auditory (Hodinott-Hill et al., 2002) domain. While Park, Schlag-Rey, and Schlag (2003) and Yarrow and Rothwell (2003) assumed that chronostasis may be a mechanism related to actions in general (as opposed to being specific for saccades); Hodinott-Hill et al. (2002) argued that the overestimation of durations is due to arousal. As evidence, that action is not a necessary condition for chronostasis to occur, they related the results of Yarrow et al. (2001) to those of Rose and Summers (1995) who had reported an increased perceived duration for the first and partly also the last of a sequence of visual stimuli. While this phenomenon could explain an overestimation of duration of a sequence, it should have also affected the control condition, in which the same sequence was shown while participants kept fixation. In fact, in all our control conditions, the first stimulus had to be slightly shorter to be perceived lasting as long as the second. But this overestimation was much smaller than the chronostasis found in the main

conditions. A follow up study, however, demonstrated duration overestimations unrelated to the execution of actions in the auditory domain (Alexander et al., 2005). The authors argued that the saccade acted as a cue as to when the duration judgment has to be done, causing an increase in arousal, which causes an increased rate of a hypothetical internal clock and thus, the duration to be overestimated. Some discrepancies however remained, making it unclear how these results translate to the visual system. First, arousal should also be increased when the counter is unexpectedly displaced during the saccade. Chronostasis, however, was not found under such circumstances. Secondly, arousal should be independent of the location of the counter in general. Yet, we and others found strong modifications of chronostasis with probe position. It is also unclear why the overestimation would scale with saccade duration in this framework, as small and large saccades should be similarly effective cues as to when the duration judgment is to be made. The demonstration that the duration overestimation is caused by an antedating of the stimulus onset (Yarrow et al., 2006) is another strong hint, that arousal cannot easily explain the results of saccade induced chronostasis.

7.6. Conclusions

Chronostasis is not a saccade-specific mechanism, limited to occur at the location of the saccade target. It rather reflects a global mechanism for duration estimation of visual stimuli. The overestimation of durations could be caused by an active compensation in conditions where the exact time of a stimulus onset is not clearly perceived, but it appears possible that it is a passive result of how the time of a stimulus onset is predicted by the visual system in general.

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