

Where does time go when you blink?

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Abstract

1 **Retinal input is frequently lost due to eye blinks, yet humans rarely notice these gaps in visual**
2 **input. While previous studies focused on the psychophysical and neural correlates of**
3 **diminished awareness to blinks, the impact of blinks on the perceived time of concurrent**
4 **events is unknown. Here, we investigated whether the subjective sense of time is altered by**
5 **spontaneous eye blinks, and how this link may inform mechanisms of time perception. We**
6 **found that participants significantly underestimated the duration of a visual stimulus when**
7 **a blink occurred during the stimulus. Importantly, this effect was not present when durations**
8 **of an auditory stimulus were judged. These results point to a link between spontaneous**
9 **blinks, previously demonstrated to induce suppression of activity in early visual cortex, and**
10 **a compression of subjective time. The findings suggest that ongoing encoding within**
11 **modality-specific sensory cortices, independent of conscious awareness, inform the**
12 **subjective sense of time.**

13 Spontaneous eye blinks trigger an occlusion of retinal input for a considerable duration, from tens
14 to hundreds of milliseconds (VanderWerf, Brassinga, Reits, Aramideh, & Ongerboer de Visser,
15 2003). Nevertheless, these frequent interruptions usually go unnoticed as our visual experience

16 remains continuous. Diminished awareness to visual stimulation during blinks was previously
17 validated in a psychophysical study that found a significant reduction in visual sensitivity during
18 voluntary eye blinks (Volkman, Riggs, & Moore, 1980). This suppression of visual detection
19 thresholds during blinks occurred when light was delivered through the roof of the mouth and was
20 therefore independent of eyelid position. Subsequent electrophysiological studies in cats
21 (Buisseret & Maffei, 1983) and in primates (Gawne & Martin, 2000, 2002) reported a decrease in
22 firing rates of neurons in the primary visual cortex during blinks. These studies also supported a
23 neural, rather than an optical, source of blink-related reduction in visual activity. Human studies
24 have provided further support of an extra-retinal suppression in early visual regions during
25 voluntary blinks, using fMRI (Bristow, Haynes, Sylvester, Frith, & Rees, 2005), as well as
26 suppression of transient activity in the visual cortex during spontaneous and voluntary blinks, as
27 revealed in intracranial EEG recordings (Golan et al., 2016).

28 Given the link between blinks and suppression of both visual sensitivity and neural activity, a
29 natural yet unexplored question concerns what happens to subjective time during spontaneous eye
30 blinks. This question offers a unique opportunity to study the link between mechanisms of time
31 perception and continuous processing of sensory input. The neural underpinnings of time
32 perception are an active, unresolved field (Ivry & Schlerf, 2008; Wittmann, 2013). *Dedicated*
33 *models* for timing postulate that duration estimation is implemented by a neural mechanism that is
34 fully designated to timing, for example, by postulating a neural pacemaker. In contrast, *intrinsic*
35 *models* assume that time is inherently encoded by the neural resources invested in sensory
36 processing. Whether neural mechanisms of timing are modality specific is somewhat related to the
37 distinction between dedicated and intrinsic models of timing: intrinsic models would postulate
38 timing as a modality specific computation. Investigating the link between suppressed neural

39 processing – indexed by spontaneous eye blinks – and sensory duration judgments can provide
40 important evidence for the role of ongoing perceptual encoding in informing temporal estimation.
41 Here we investigated how spontaneous eye blinks impact the subjective sense of time. An eye
42 blink during a visual stimulus leads to an unnoticed gap in retinal input. Importantly, we used both
43 visual and auditory stimuli as timed intervals in two separate experiments in order to test whether
44 time perception was affected by the input loss in a modality specific manner.

45 **Methods and Materials**

46 **Participants.** A total of 29 and 30 participants took part in the visual and the in the auditory
47 experiments, respectively. Inclusion criterion was defined prior to data analysis as having a
48 minimum of 10 percent blink and blink-free intervals. In both the visual and the auditory
49 experiments, 7 individuals did not meet this inclusion criterion and were therefore discarded from
50 all analyses. The analyses reported in this paper were thus carried out on 22 visual participants (14
51 females, 24 ± 2 years old) and 23 auditory participants (17 females, 22.5 ± 3 years old). Only for the
52 individual bisection point analysis (**Fig. 2c**) did we apply further exclusion criteria whereby
53 participants with a poor fit were discarded (see **Psychometric function fit**). A total of 18 and 15
54 participants in the visual and auditory experiments, respectively, (4 and 7 participants excluded,
55 respectively) were therefore included in this analysis. Written informed consent was obtained from
56 all participants in line with the institutional IRB approval from the Hebrew University of
57 Jerusalem.

58 **Stimuli.** The experiment was programmed in MATLAB (2017a, MathWorks) using
59 Psychtoolbox-3 (Kleiner et al., 2007). Oddball stimuli were 10 colored squares. For the visual
60 experiment, a white central disc was displayed for marking the timed interval. Both the squares

61 and the disc subtended a visual angle of 11.4° . For the auditory experiment, bursts of white noise
62 generated in MATLAB were delivered through headphones for marking the timed intervals.
63 Throughout both visual and auditory experiments, a random noise black and white pattern was
64 displayed as a background and a central red fixation point was presented.

65 **Experimental Procedures.** The experimental session began with a familiarization stage aimed to
66 introduce the participant with the duration of the short (0.6 sec) and long (2.8 sec) reference
67 intervals. The reference intervals were presented and the participant could replay them as many
68 times as he/she felt needed.

69 The main experiment was a dual task: each trial (400 trials in total) consisted of an oddball part
70 and a temporal bisection part (see **Fig. 1a** for a schematic illustration). A trial began with a jittered
71 sequence of 4-7 colored central squares, flashed for 250 ms each with a fixed ITI of 100 ms. The
72 participant was instructed to report how many red squares appeared during the entire oddball
73 sequences of the experiment. Immediately upon termination of the oddball part (i.e. without any
74 time delay), the timed interval was presented for one out of 9 possible durations spanning the range
75 between the two extreme reference intervals: 0.6 0.9 1.4 1.6 1.7 1.8 2 2.5 2.8 (sec). Upon the offset
76 of the timed interval, participants were instructed to indicate by pressing one of two possible keys
77 whether the current interval was closer in its duration to the short, or long, reference interval.
78 Response time was unlimited and response collection initiated the next oddball sequence (i.e. the
79 beginning of a new trial). All participants completed a short training prior to the main experiment.
80 To maximize the probability that spontaneous blinks would occur during timed intervals, oddball
81 task was emphasized as the main task whilst bisection was defined as secondary.

82 **Equipment.** We used a video-based eye tracker (Eyelink 1000, SR Research) to monitor
83 continuously eye position and pupil diameter of participants. Eye data was recorded binocularly at
84 a sampling rate of 1000 Hz. Messages were sent from the experiment PC to the Eyelink PC upon
85 stimuli presentation for offline alignment of the experimental log to eye tracking time series.

86 **Classification of blink and blink-free intervals.** The raw pupil time series of each participant
87 was processed offline in a semi-automatic blink detection procedure, composed of two stages.
88 First, blinks were automatically marked as all segments with missing pupil samples, with blink
89 onset corresponding to the point of maximal acceleration in the decrease of pupil size, and blink
90 offset corresponding to maximal de-acceleration point in increase of pupil size. These points
91 should reflect the time point in which the eyelid started covering the pupil and the time point in
92 which the pupil was fully exposed again, respectively. Second, we manually inspected the output
93 of the automatic detection on top of the raw pupil-size time series and disqualified segments
94 without a gradual decrease and increase in pupil size surrounding the putative blink. Disqualified
95 segments, as well as segments that exceeded 400 ms, were logged and excluded from all analyses.

96 Following temporal alignment of pupil time series to the experimental log, we divided timed
97 intervals into blink and blink-free. Importantly, blink intervals were defined only when a blink
98 occurred entirely within the interval - its onset detected at least 50 ms post the interval's onset, and
99 its offset preceding the interval's offset in at least 50 ms. Timed intervals in which a blink
100 overlapped with their onset or offset were logged and excluded from all analyses.

101 **Psychometric function fit.** Individual psychometric functions were estimated through a logistic
102 function fit based on a maximum likelihood criterion and executed by scripts available in the
103 Palamedes toolbox (Prins, 2014). Two free parameters were estimated - the threshold (i.e. bisection

104 point) and the slope, while the guess and lapse rate were fixed and predefined as equal to 1% each.
105 A measure of goodness of fit, pDev, was estimated for each fit. To estimate pDev, deviance values
106 of simulated data drawn from the best-fitting psychometric curve were computed over 1000
107 iterations. The proportion of simulated deviance values that were greater than the deviance value
108 of the original data corresponds to the pDev value. Thus, larger values of pDev reflect a better fit
109 to the measured data, while $pDev < 0.05$ indicates a poor fit of the data (Kingdom & Prins, 2010).
110 Since the individual bisection point (BP) analysis (**Fig. 1c**) relied on psychometric fits, participants
111 with poorly fitted functions ($pDev < 0.5$) were excluded from this analysis. Two additional
112 participants, one from the auditory and one from the visual experiment, had no blink intervals in
113 the two shortest levels (0.6 and 0.9 sec) and were therefore excluded from individual fitting
114 analysis as well. Thus a total of 3 and 7 participants were excluded from the visual and auditory
115 experiments, respectively, for the individual BP analysis. Notably, the results of the this analysis
116 remained unchanged also upon inclusion of poor fitted participants (paired t-test, visual: $p=0.007$,
117 $t(20)=3.02$; auditory: $p=0.54$, $t(21)=0.62$).

118 Group psychometric curves presented in **Fig. 2a** and **Fig. 2b** were estimated by fitting a logistic
119 function to the group mean proportion “long” in each interval duration. Importantly, this fit is
120 purely for visualization and does not contribute to any of the analyses presented here. The main
121 analyses presented in the results section, whether on probability “long” values or on BPs, took a
122 within subject approach with subjects as a random effect.

123 **Control analysis for unequal samples size.** Naturally, the number of blink- and blink-free
124 intervals was not matched within a participant or a specific interval level, with a bias towards
125 having fewer blink intervals. We therefore ran a control analysis to ensure this bias did not affect
126 the observed results. To this aim, we randomly subsampled the data such that each interval duration

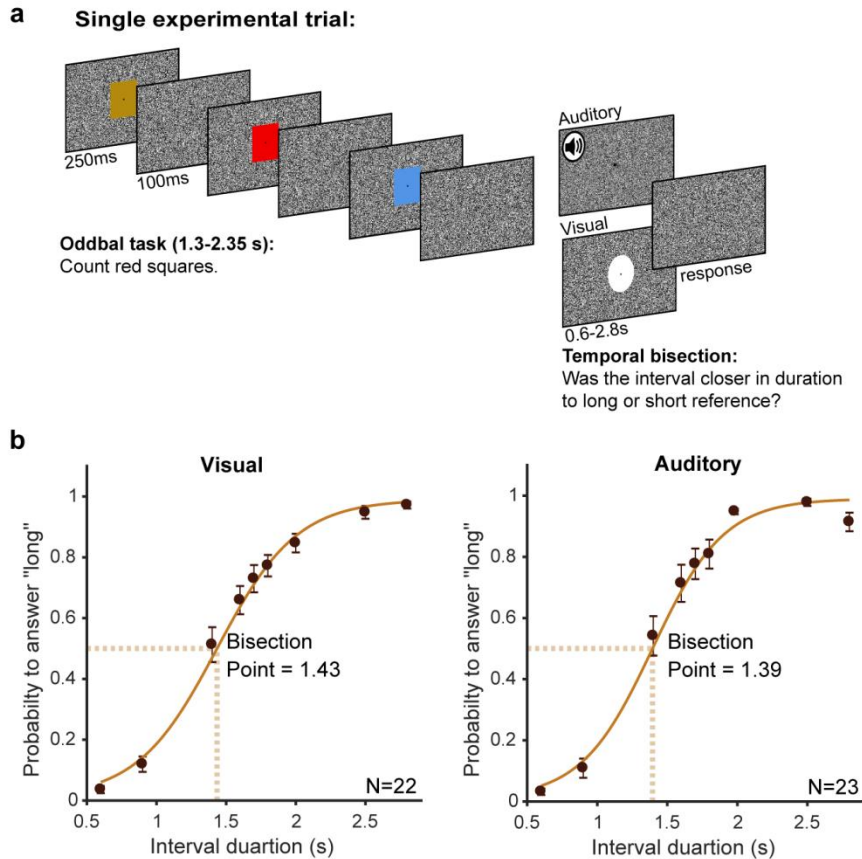
127 of each participant had an equal amount of blink and blink-free intervals. This essentially means
128 taking a random subsample of the intervals in the condition (blink/blink-free) with the larger n.
129 We then repeated the analysis presented in **Fig.1a**, performing a paired t-test on the proportion
130 “long” across the dynamic range in blink vs. blink-free intervals for this size-matched subsample
131 of the data. On each iteration (n=1000), the analysis was carried out on a size-matched random
132 subsample of the data, equating the number of blink and blink-free intervals for every participant
133 and interval duration. The resultant p-value distributions are presented in **Fig. S1**. For the visual
134 intervals, all resultant p-values were smaller than 0.05 (95th percentile = 0.004). In contrast, size-
135 matched sub-samples of auditory intervals resulted in a wide range of p-values, 98% of them larger
136 than 0.05 (95th percentile = 0.9).

137 **Results**

138 A major challenge in studying the impact of spontaneous blinks on duration estimation is that a
139 single-task approach leads to very few blinks during timed intervals, as participants naturally tend
140 to blink between the to-be timed intervals. We therefore combined a temporal bisection task in a
141 dual task paradigm. Upon mastering discrimination between long and short reference intervals (0.6
142 and 2.8 sec, respectively), participants proceeded to the main experiment. Each trial consisted of
143 two successive sub tasks: an oddball detection task during a rapid serial visual presentation (RSVP)
144 followed by a temporal bisection task (see **Fig. 1a** for a scheme of the experimental design). On
145 each temporal bisection trial, a timed interval was displayed for one out of nine possible durations,
146 ranging from 0.6 to 2.8 sec. Participants were instructed to report whether they perceived the
147 interval as being more similar to the long, or short, reference interval. Temporal bisection was
148 performed on visual or auditory intervals in two separate experiments, with all timing parameters

149 held constant. Visual-timed intervals consisted of a central white disc subtending 11.4° visual
150 angle, whereas auditory-timed stimuli were intervals of white noise.

151 Prior to inspecting the impact of blinks on duration estimation, we first observed the overall
152 performance of the group by collapsing data from all participants and plotting proportion “long”
153 responses as a function of stimulus duration (**Fig. 1b**). Based on individual logistic fits to all
154 intervals (blink and blink-free) of each participant, we estimated the mean bisection point (BP)
155 across participants. Interestingly, the mean BP was significantly shorter than the objective mid-
156 point between the two extreme reference intervals (1.7 sec) and was estimated to be 1.4 sec (95%
157 CI: 1.28-1.51) and 1.39 sec (95% CI: 1.27-1.5) for visual and auditory intervals, respectively. This
158 bias is in line with a previous meta-analysis linking intervals spread greater than two (quantified
159 as the long reference/short reference ratio) with an underestimation of the true bisection point
160 (Kopec & Brody, 2010) (see reference for a suggested model which accounts for this bias).



161 **Figure 1. Experimental design and group performance for both blink and blink-free intervals. a)** Schematic
162 illustration of a single trial. Each trial consisted of two combined sub-tasks appearing in continuous succession. The
163 oddball task was emphasized as the main task, whilst temporal bisection was defined as secondary. A white central
164 disc and a segment of white noise were used as the timed interval in the visual and auditory experiments, respectively.
165 On each temporal bisection trial, the timed stimulus was presented for one of 9 predefined durations (ranging from
166 0.6 to 2.8 sec). Participants judged whether the temporal interval was closer to the short or long reference interval,
167 with which they were familiarized during the initial stage. During the oddball task, central colored squares were
168 flashed for 250 ms with a fixed ITI of 100 ms. Participants were instructed to count the number of red squares that
169 appeared on every experimental block (4 blocks in total, each consisting of 100 trials). **b)** Group psychophysical
170 performance derived from all intervals (blink and blink-free) of all participants. Group psychometric functions and
171 bisection points (BP) for each modality were estimated by a logistic fit to the mean probabilities to answer long across
172 subjects. They are presented here for visualization only, note that all statistical tests took a within subject approach.
173 Error bars denote ± 1 SEM.

174 For the main analysis, timed intervals were classified as either blink or blink-free. Blink intervals
175 were defined as consisting of a full blink, which was initiated at least 50 ms after the onset of the
176 interval and terminated at least 50 ms prior to its offset. Twenty-two and 23 subjects who
177 participated in the visual and auditory experiments, respectively, met our predefined inclusion
178 criteria and were included in the analyses (see Methods for inclusion criteria). On average,
179 participants from the visual and auditory experiments had 126.7 ± 69.3 blink trials ($38.3 \pm 24\%$ of
180 the total trial count). There was no significant difference in the percent of blink intervals between
181 the visual and auditory experimental groups (independent samples t-test, $t(43)=1.009$, $p=0.32$).

182 In order to examine the impact of spontaneous blinks on duration judgments, we took two
183 complementary approaches: a direct quantification of individual performance and an estimation of
184 individual bisection points (BP) through a psychometric function fit. Accordingly, we first
185 computed the probability to answer “long” at each interval duration and condition (blink vs. blink-
186 free) per participant. As presented in **Fig. 2a**, this analysis revealed a clear reduction of the
187 probability to judge visual intervals as “long” in the presence of a spontaneous blink, as compared
188 with the same probabilities for blink-free trials. The probability to answer “long” across the
189 dynamic range (collapsing 5 intermediate levels for which judgment is more difficult, 1.4-2 sec)
190 was significantly smaller in blink, as compared to blink-free, intervals (**Fig. 2b**; paired t-test,
191 $t(21)=3.8$, $p=0.001$, Cohen’s $d = 0.81$). Here too, the effect was specific to the visual modality as
192 performance did not differ between blink and blink-free auditory intervals (paired t-test,
193 $t(22)=1.52$, $p=0.14$).

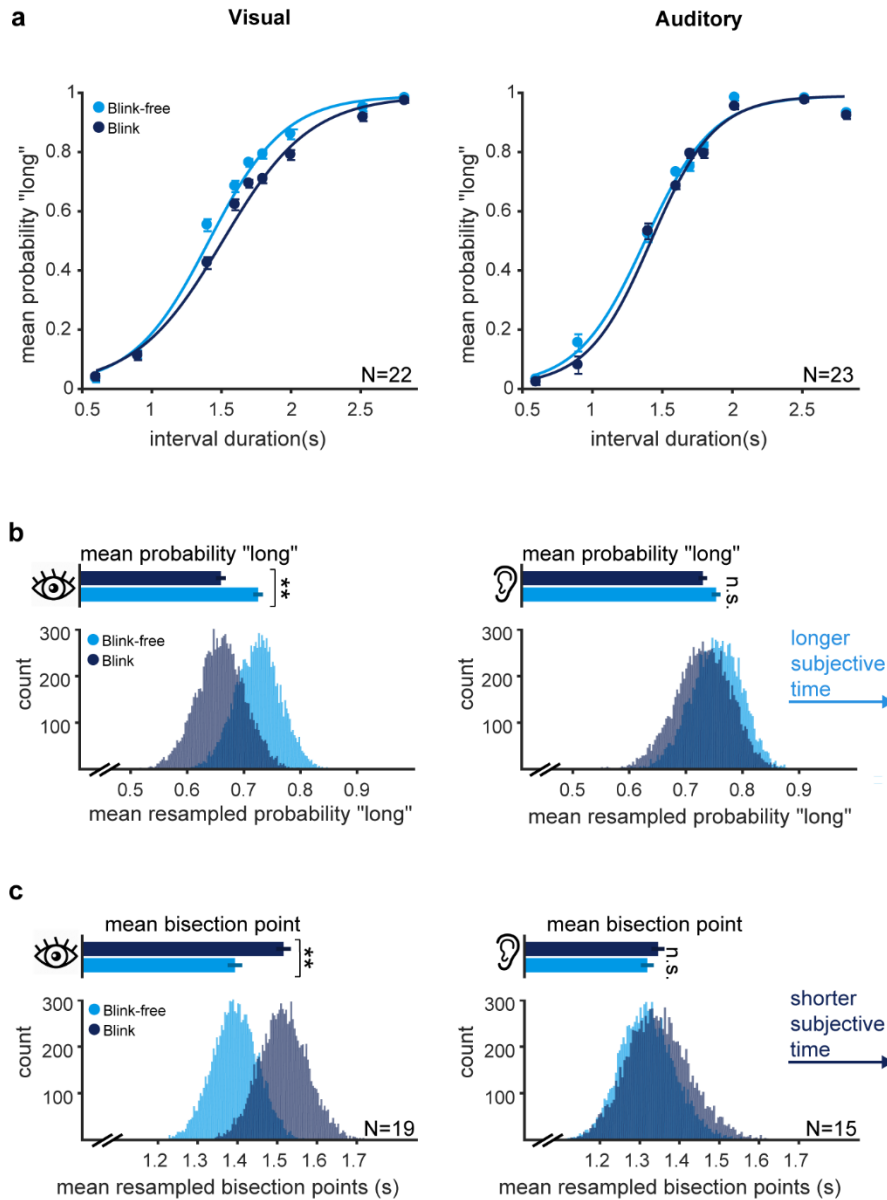
194 We next compared the bisection point (BP) between blink and blink-free data. The BP corresponds
195 to the interval duration which is equally likely to be judged as “long”, or as “short”. To this end,
196 we fit a psychometric function to each individual’s performance, for blink and blink-free intervals

197 separately, and derived the BP from the estimated function (see Methods). For visual intervals, we
198 found a significant increase in BPs for intervals containing blinks as compared to blink-free
199 intervals (**Fig. 2c**; paired t-test: $t(18)=3.4$, $p=0.003$, Cohen's $d=0.77$), further indicating a time
200 compression with blinks. It is noteworthy that the group average shift in BP (121 ± 36 SEM) was
201 similar in magnitude to the average blink duration (112 ± 9 SEM). Here too the effect was evident
202 only for visual intervals, as we did not observe any difference in BPs in the auditory experiment
203 (paired t-test: $t(14)=1.29$, $p=0.22$). Overall, there were significantly less blink intervals than blink-
204 free intervals in both the visual and the auditory groups (paired t test; visual: $t(21)=3.36$, $p=0.003$;
205 auditory: $t(22)=2.22$, $p=0.036$). In order to rule out the possibility that differences in trial-count
206 had contributed to the observed underestimation for blink-intervals, we repeated the main analyses,
207 presented in **Fig. 2a-b**, using a stratification approach that consisted of iteratively subsampling the
208 data to achieve an equal number of blink and blink free interval per participant and duration (see
209 Methods for details). The results of this analysis rule out smaller trial-count of blink intervals as a
210 confounding factor.

211 Since spontaneous blinks may also be coupled with attentional lapses, a possible explanation of
212 the observed time compression may be attenuated attention. The specificity of the effect to the
213 visual modality goes against such an attentional account. Nonetheless, to further test this
214 possibility, we compared the reaction times between blink and blink-free intervals. In both the
215 visual and auditory data, reaction times were not significantly longer following blink intervals, as
216 compared to blink-free intervals (paired t-test, visual: $t(21)=0.72$; $p=0.48$; auditory: $t(22)=1.51$,
217 $p=0.15$), arguing against decreased attention in blink intervals in either one of the modalities.

218 Finally, it could be argued that blinks during auditory intervals did not perturb duration judgments
219 since audition outperforms vision with regards to subsecond temporal resolution (Ortega, Guzman-

220 Martinez, Grabowecky, & Suzuki, 2014). However, we found no difference between individual
221 bisection points estimated on blink-free auditory intervals and blink-free visual intervals
222 (independent samples t-test, $t(36)=0.89$, $p=0.38$), or between the corresponding slopes of the
223 psychometric functions (independent samples t-test, $t(36)=-1.3$, $p=0.19$). This counters the
224 possibility that differences in task difficulty or performance precision underlie the modality
225 specificity aspect of the current finding.



226 **Figure 2. Temporal bisection performance in blink and blink-free intervals.** **a**) For each of the 9 possible interval
 227 durations (0.6 0.9 1.4 1.6 1.7 1.8 2 2.5 2.8), the mean probability to judge the duration as closer to the long reference
 228 interval is presented separately for blink and blink-free intervals. Results are presented separately for visual (left panel)
 229 and auditory (right panel) timed intervals. Note the visual-specific modulation of performance in blink intervals
 230 relative to the blink-free intervals. **b**) Histograms describe bootstrap distributions of the mean probability to judge a
 231 visual (left panel) or an auditory (right panel) interval from the dynamic range (5 intermediate levels) as long in the
 232 presence and in the absence of blinks. Top horizontal bars denote the original mean probabilities for blink and blink-

233 free intervals. Note that higher values for mean probability “long” reflect longer subjective time. c) Individual BPs
234 are larger in the presence of spontaneous blinks. Histograms describe bootstrap distributions of mean bisection point
235 as derived from individual psychometric function for blink and blink-free intervals, separately. Note that larger BP
236 corresponds to shorter subjective time. All error bars in the figure denote ± 1 SEM following Cousineau-Morey
237 correction for a within participant design (Morey, 2008). Figure design inspired by (Terhune, Sullivan, & Simola,
238 2016).

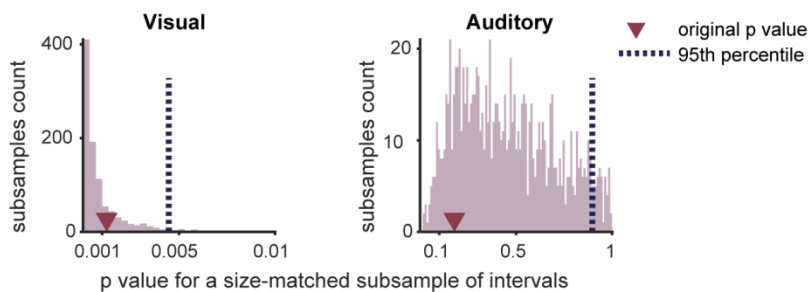
239 **Discussion**

240 The current results reveal that duration estimation of visual, but not auditory, input is significantly
241 reduced when a blink occurs within the estimated time interval. A converging line of studies has
242 shown that blinks induce a momentary reduction in visual sensitivity and a suppression of transient
243 neural activity in the visual cortex, both originating in an extra-retinal signal. The current findings
244 demonstrate that the unaware loss of visual sensitivity due to blinks is coupled with a loss of
245 subjective time of an equivalent duration. Importantly, the specificity of the effect to the visual
246 modality supports the view whereby the amount of neural processing invested in sensory encoding
247 of an incoming stimulus is an integral part of temporal estimation. Thus, a reduction in visual
248 processing, indexed by a blink, leads to the concurrent loss of subjective time.

249 Distortions of visual temporal estimation, at a shorter time scale than studied here, have been
250 linked to another type of eye movement - large saccades. Findings pointing to pre-saccadic time
251 compression (Morrone, Ross, & Burr, 2005; Terao, Watanabe, Yagi, & Nishida, 2008) and to post
252 saccadic time dilation (Yarrow, Haggard, Heal, Brown, & Rothwell, 2001) have been proposed to
253 relate to predictive shifts in spatial receptive fields. Specifically, underestimation of pre saccadic
254 intervals has also been suggested to relate to precision errors in encoding the onset and offset of a
255 stimulus (Terao et al., 2008), yet the impact of ongoing, cumulative, processing of the stimulus on

256 time distortion has not been tested. Importantly, saccades, different from eye-blinks, contain a
257 spatial element and are events tightly linked to visual awareness of the change in retinal input.
258 Here the use of blinks allowed the direct examination of input loss in the absence of retinal motion,
259 predicted or actual image displacement, awareness or any perceived discontinuity. Therefore, our
260 data speak to a purely temporal consequence of eye blinks and the accompanying loss of sensory
261 input at the supra-second time scale. We found that unconscious loss of visual input affects timing
262 of visual intervals, but not auditory intervals, supporting a central role for ongoing sensory
263 encoding in the subjective sense of time.

264 Supplemental figures



265 **Figure S1. Control analysis for unequal number of trials between condition types.** In order to ensure the effect
266 was not driven by a smaller amount of blink intervals relative to blinks-free intervals, we repeated the analysis
267 presented in **Fig.1b** 1000 times, each time subsampling the data to achieve a matched number of blink and blink-free
268 interval in each individual and interval level. The histograms present the distribution of the resultant p values in the
269 visual (right panel) and auditory (left panel) experiments.

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