



rijksuniversiteit
groningen

The Effect of Spontaneous Eye Blinks on Time Perception

Domenica Abad Malo

Master Thesis – Applied Cognitive Neuroscience

S3736083

December 2023

Department of Psychology

University of Groningen

Examiner/Daily supervisor: Dr. Hakan Karsilar

A thesis is an aptitude test for students. The approval of the thesis is proof that the student has sufficient research and reporting skills to graduate but does not guarantee the quality of the research and the results of the research as such, and the thesis is therefore not necessarily suitable to be used as an academic source to refer to. If you would like to know more about the research discussed in this thesis and any publications based on it, to which you could refer, please contact the supervisor mentioned.

Abstract

Our interaction with the world depends on our ability to process temporal information, which is a key component of human cognition that directly impacts decision-making, planning, and prediction of events. Visual information plays a crucial role in shaping our subjective perception of time, and even brief interruptions such as those caused by eye blinks, can disrupt the continuity of our perception and alter how we estimate durations. The purpose of this study was to investigate the relationship between spontaneous eye blinks and time perception by using a temporal bisection task. Particularly, we focus on how blinks preceding stimulus presentation impact the perceived duration of that stimulus. The results from fitting a generalized linear mixed-effects model revealed that blinking can influence duration estimation. Specifically, the presence of a single blink before the stimulus presentation had a significant effect on subjective time perception, participants were more likely to categorize the duration as shorter compared to when they did not blink. In contrast, two or more blinks before stimulus presentation did not have a significant effect compared to not blinking. This study emphasizes the subtle and complex interaction between the suppression of visual input and the perception of stimulus duration.

Keywords. time perception, spontaneous eye blinks, temporal bisection task

The Effect of Spontaneous Eye Blinks on Time Perception

The subjective experience of time passing is an essential component of human cognition that influences virtually all behavior (Meck, 1996). Within the context of time perception, ‘interval timing’ refers to the ability to estimate durations in the range of milliseconds to seconds, which is fundamental for abilities such as decision-making, strategizing, reasoning, motor perception, and speech (Buhusi & Meck, 2005; Namboodiri et al., 2014). From an evolutionary perspective, interval estimation allows us to predict the temporal statistics governing our surroundings; an essential skill for regulating goal-directed behaviors (Marshall & Kirkpatrick, 2015) such as finding and collecting food (Bateson, 2003), conditioning and learning (Balsam & Gallistel, 2009; Fung et al., 2021), and processing and responding to interpersonal cues during communication (Feldstein et al., 1993). Given its influence in such a wide range of behaviors, the conditions under which this ability may systematically be modulated constitutes an important question in the cognitive sciences.

Despite being a prevalent phenomenon that governs many aspects of our lives, explaining and describing how we perceive time is not as straightforward as it seems. Importantly, this phenomenon is not constant across dimensions of variables such as age (Zélanti & Droit-Volet, 2011), emotions (Gable & McCoy, 2023; Schirmer, 2011), arousal and attention mechanisms (Lake et al., 2016; Zhou et al., 2021), and psychopathology (Oyanadel & Buela-Casal, 2014). Moreover, time perception has revealed a complex interaction with factors such as brightness (Kinzuka et al., 2021; Matthews et al., 2011), size (Kanai et al., 2017), motion (Karşilar et al., 2018; Kroger-Costa et al., 2013), and numerosity of stimulus (Togoli et al., 2021; for a review see Eagleman & Pariyadath, 2009). Research on this area has established a directional relationship between higher magnitudes and longer perceived time.

A related area of research into how our perception of time dilates or constricts explores the relationship between time perception and various physiological reactions. For instance, studies have shown that higher body temperature, irrespective of whether experimentally or naturally induced, leads to time constriction (Tamm et al., 2014, 2015; van Maanen et al., 2019). Variations in cardiac activity influence the encoding and reproduction of time intervals, with temporal constriction during systole and dilation during diastole, which are further regulated by arousal (Arslanova et al., 2023; Meissner & Wittmann, 2011; Pollatos et al., 2014). Findings on eye movements and pupillary responses highlight the role of saccades and fixations on temporal processing (Balzarotti et al., 2021; Kruijne et al., 2021; Morrone et al., 2005; Suzuki et al., 2016; Wutz et al., 2016). While research in this area is sparse, a clear link exists between bodily responses to stimuli and how they are timed. One relatively less explored topic among these is the role of spontaneous eye blinks in altering time perception (Grossman et al., 2019; Terhune et al., 2016). This thesis attempts to further elucidate this potentially intriguing relationship by discussing the relevant literature and reporting the results of a controlled experiment.

Eye Blinks and Time Perception

Eye blinks occur around 12 times per minute (Carney & Hill, 1982), yet the brief loss of visual information is usually unnoticed (Volkman et al., 1980). During eye blinks two important phenomena come into play: visual continuity and suppression (Bristow et al., 2005a). Both of these processes are thought to explain why our impression of the world remains continuous despite the interruptions of visual signals to the brain (Grossman et al., 2019; Maus et al., 2020). Interestingly, the brain appears to ignore the gaps between blinks instead of attempting to fill them in with information (Duyck et al., 2021; Irwin & Robinson, 2016). Bristow and colleagues (2005a) suggest that a loss of visual sensitivity begins before the blink onset. One of their studies

combined pupil-independent retinal stimulation with fMRI and found that blinking suppressed neural activity in the visual, parietal, and prefrontal cortices. The reduced brain activity was associated with the extraretinal signal that occurs as a response to the motor command of blinking, resulting in an inability to detect visual changes (Bristow et al., 2005a). In addition, Irwin and Robinson (2016) pointed to the importance of the extraretinal signal for differentiating between internal and external sources of temporary object disappearance; this signal allows us to interpret natural and simulated blinks differently. These findings highlight the brain's ability to deal with problems effortlessly, ultimately creating our interpretation of the world.

Effect of Eye-blinks on Time Perception As Mediated by Dopamine

A connection between eye blinks, time perception, and the neurotransmitter dopamine has been proposed (Karson, 1988) and supported by empirical findings (Sadibolova et al., 2022). In particular, blinks serve as an indirect measure of the availability of dopamine receptors in the striatum, a brain area that is also known to be important for temporal accuracy in interval timing (Coull et al., 2010; Groman et al., 2014; Jongkees & Calzato, 2016). Higher eye blink rates are believed to indicate an increase in striatal dopamine release, which could give the impression that time passes more slowly than it actually does (Sadibolova et al., 2022). This pattern of behavior has been well-documented in disorders with dopamine dysregulation (e.g. Parkinson's disease, schizophrenia, autism, and attention-deficit hyperactivity disorder; Allman & Meck, 2011). For instance, patients with schizophrenia blink more frequently (Chan et al., 2010) and perceive time as passing slower, possibly due to hypervigilance (Bonnot et al., 2011; Ueda et al., 2018). In their review, Matthews and Meck (2014) examined individual differences in timing performance, one significant aspect of which involved the use of pharmacological treatment and genotype. They have reported studies showing that the alteration of dopamine levels by receptor

agonists and antagonists caused subjective time to appear slower or faster, respectively (Lake & Meck, 2013). Other studies have found further evidence for a double dissociation of dopamine genes as they relate to time perception, proposing separate mechanisms for the timing of short and long durations (Wiener et al., 2011; Wiener et al., 2014). Therefore, given the literature, it is apparent that eye blinks have the potential to impact how we interpret the duration of visual stimuli through their connection with the dopamine pathways.

Although the effect of eye blinks on time perception could be mediated by dopamine function, some recent evidence has challenged the relationship between eye blinks and dopamine (Dang et al., 2017; Sescousse et al., 2018). Nevertheless, researchers are still interested in the behavioral element of eye blinks and their possible implications on cognition and time perception, particularly, of spontaneous eye blinks that occur without any evident external stimuli (Stern et al., 1984). For instance, Grossman and colleagues (2019) conducted a study combining a temporal bisection task and an oddball task. They showed that when participants spontaneously blinked during a stimulus presentation, they underestimated its duration. It is important to note that individuals engage in strategic blinking depending on task demands as well (Hoppe et al., 2018). During stimulus presentation, individuals are likely to suppress their eye blinks because attention is required to not overlook the critical event (Murali & Händel, 2021). Hence, conclusions based on blinks during an event do not give sufficient insight into natural behavior, since these behaviors may be reflexive, caused by tiredness, an inherent need to pay attention, or dry eyes, rather than being truly spontaneous.

Pre-Stimulus Eye Blinks and Time Perception

The results presented above raise a crucial question: Can blinking just before a stimulus also alter how we perceive the duration of the interval it encompasses? Terhune and colleagues

(2016) investigated this question by using a temporal bisection task. They focused on how blinking during the inter-stimulus interval between stimulus presentation and judgment screen affected the duration estimate of the stimulus in the following trial. Participants overestimated the duration of stimuli when they blinked in the previous trial, compared to when they did not blink. The authors suggested that there is intra-individual variability in time precision due to fluctuations in dopamine levels as a result of blinking that may accelerate the neural oscillations of a hypothetical internal clock, leading to an overestimation of time (Terhune et al., 2016).

Interestingly, while Grossman (2019) observed underestimation when blinking during a stimulus presentation, Terhune (2016) reported overestimation in a subsequent trial when blinking before a stimulus presentation. This notable contrast in findings emphasizes the complex nature of blinking behavior in shaping our perception of time. Additionally, Suárez-Pinilla and colleagues (2019) failed to find a significant effect of eye blinks on participants' judgments of durations. Their task consisted of using videos with complex and dynamic images or static scenes with inanimate objects. Rather than categorizing the videos as 'short' or 'long' based on a reference duration, participants estimated the length of the videos using a visual analog scale. The researchers emphasized the role of external variables such as perceptual changes over internal factors like blinks in defining perceived time intervals (Suárez-Pinilla et al., 2019). The discrepancies between the results of these studies could be attributed to differences in the experimental design and paradigm.

This study aims to replicate and possibly expand upon prior findings regarding the role of spontaneous eye blinks in shaping the subjective experience of time. Specifically, the research question examines how the occurrence of spontaneous eye blinks before the presentation of a stimulus influences the perceived duration of that stimulus. The hypotheses proposed to address

this question are as follows: first, the presence of spontaneous eye blinks before stimulus presentation is expected to have a significant effect on time perception compared to trials without blinking. Participants' duration estimation is expected to differ depending on whether a blink occurs or not before the stimulus is presented. Second, a higher number of spontaneous eye blinks occurring before viewing the stimulus are expected to result in a higher probability of overestimating the time interval. In other words, it is predicted that participants who exhibit more eye blinks before the stimulus presentation will perceive the intervals as longer compared to when they have fewer blinks. The following sections describe the methods, results, and discussion of the findings.

Methods

Participants

A total of 30 healthy students (23 female; Mage = 20.95) from the University of Groningen participated in this study as part of a larger experimental session. They were compensated with 8 euros for their involvement in a one-hour session. All individuals had normal or corrected-to-normal vision. Each participant provided a written informed consent form before the beginning of the session. No participants were excluded from the analyses. The Department of Experimental Psychology of the University of Groningen evaluated and approved the experimental protocol and procedures (approval code: PSY-2223-S-0351), confirming that the study satisfied ethical and academic requirements.

Stimuli and Apparatus

The visual stimulus was a white circle displayed in the center of a 27" LCD monitor (1920 × 1080 pixels; 60 Hz). The central area of the background was black and shifted to gray towards the sides of the screen to reduce contrast effects. The stimuli and experiment were

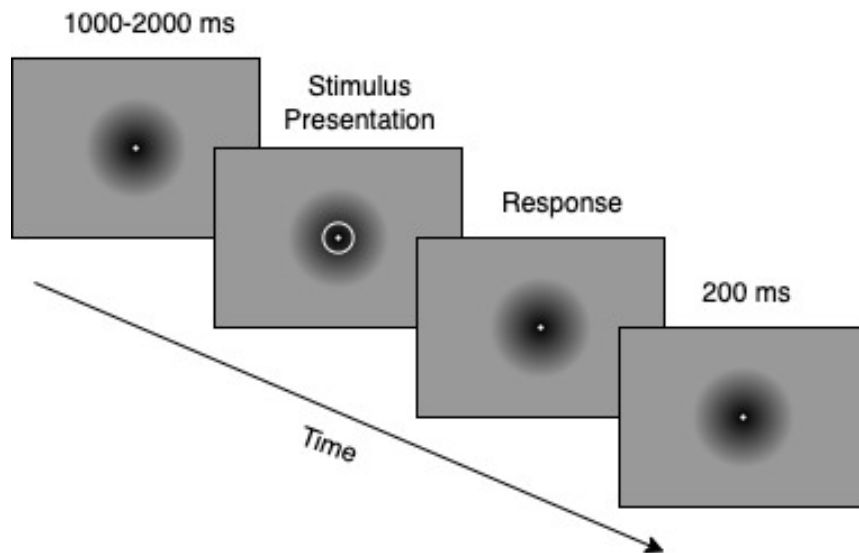
programmed in OpenSesame 3.3 (Mathôt et al., 2011; Mathôt & March, 2022) using the backend PsychPy (Peirce, 2007) and Python library PyGaze (Dalmaijer et al., 2014) for stimulus presentation and eye-tracking respectively. Participants stabilized their heads on a chin rest, limiting head movements and maintaining a consistent viewing distance of 60 cm to the monitor. Responses were collected using a wired keyboard and eye movements were recorded at 1000 Hz using the EyeLink 1000 (SR Research) system throughout the entire experimental session. The setting was carefully controlled by using a soundproof and lightproof booth during the task, ensuring a consistent sensory environment.

Procedure

The larger experimental session consisted of a temporal bisection task (see below) with a main block with changing background brightness and a shorter baseline block with fixed background brightness. The entire session lasted approximately one hour. For the purpose of this study, only data from the fixed-brightness baseline block at the end of the session were utilized (approx. 10 minutes). The block began with eye tracker calibration and an explanation of the task. Participants completed a training block until they had 10 consecutive correct trials. After meeting this requirement, they continued with the experiment consisting of 72 trials. Each trial involved three phases: fixation baseline to ensure participants focused their gaze on the dot at the center of the screen, stimulus presentation with varying probe duration, and keyboard response categorizing stimuli as either ‘short’ or ‘long’ based on prior training (see Figure 1). The inter-stimulus interval, the time between the offset and subsequent appearance of stimuli, was randomly assigned for each trial. Feedback on response accuracy was omitted to maintain natural temporal judgment without external input.

Figure 1

Single Trial Sequence in the Temporal Bisection Task



Temporal Bisection Task

The task started with the presentation of two reference durations of the stimulus (short = 200 ms and long = 800 ms). Participants were instructed to categorize future stimuli based on these by pressing the 'F' and 'K' keys on the keyboard to indicate stimuli as 'short' or 'long', respectively. The main goal was for participants to pay attention to how long the white circle remained on the screen and determine to which of the reference durations it was most similar. During the training block, participants familiarized themselves with the reference durations that were presented randomly and with equal probability. Moving to the experimental block, participants were asked to identify both the reference durations (200 and 800 ms) and additional probe durations (320, 440, 560, 680 ms) as closer to either the short or long reference durations, using the same keyboard responses established during the training block. The probe durations of the stimuli were randomized across trials to reduce predictability and any learning effects. Each probe duration was presented 12 times, resulting in a total of 72 trials for each participant. The

visual stimulus, represented by a white circle, remained consistent throughout the training and testing blocks.

Data Processing

Of interest for this study was the number of spontaneous eye blinks occurring immediately before stimulus presentation. The baseline for the blinking phase was set to the interval when the screen displayed a fixation cross from 1000 to 2000 ms before the stimulus presentation. Preprocessing was conducted in Python. Probe durations were transformed from milliseconds to seconds and were mean-centered. The dataset from Eyelink was processed using the `eyelinkparser` package in Python (Mathôt & Vilotijević, 2022). The eye blink occurrences were measured in arbitrary units, therefore they were further categorized into three groups: 0 (no blinks), 1 (one blink), and 2 (two or more blinks).

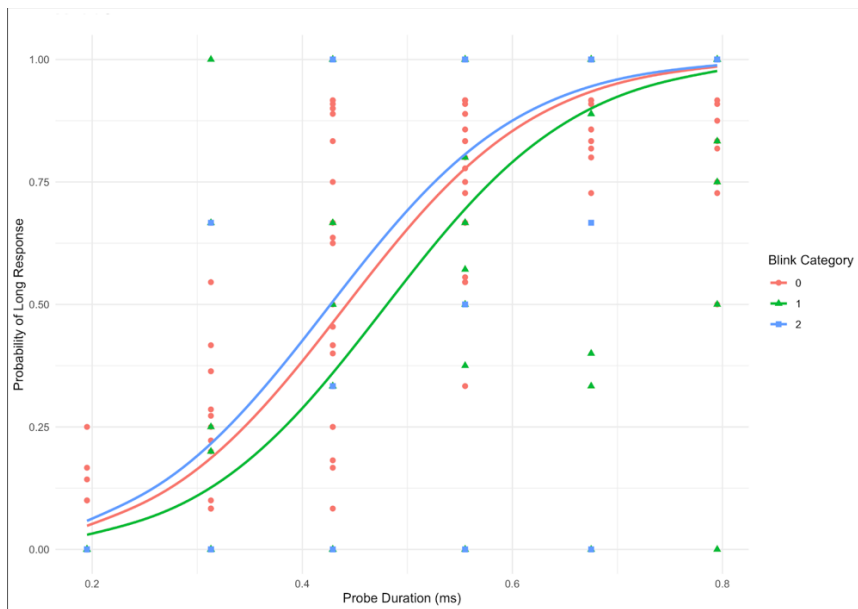
Results

The data were analyzed by fitting a Generalized Linear Mixed Effects (GLMER) model using the `glmer` function in the `lme4` package (Bates et al., 2015) in R (R Core Team, 2021) with a binomial distribution. The dependent variable was represented by the participant's probability of a 'long' response. The model included three predictor variables: probe duration, number of blinks before stimulus onset, and a random effect to account for individual differences. The reference was the no-blinks category, to which the other blink categories were compared. This modeling method is especially useful for behavioral studies, as it solves the multiple comparison problem and maintains the trial-by-trial variance (Mathôt & Vilotijević, 2022). The fixed effects of the model revealed statistical significance for both the intercept ($\beta = -5.96$, $SE = 0.326$, $p < .001$) and the probe duration ($\beta = 13.429$, $SE = 0.564$, $p < .001$). In terms of the effect of the number of blinks, compared to the no-blink category, the one-blink category showed a

statistically significant decrease in the probability of giving a ‘long’ response ($\beta = -0.514$, $SE = 0.221$, $p = .02$). In other words, participants who did not blink before the stimulus presentation were more likely to categorize a stimulus duration as ‘long’ compared to those who blinked once. However, the two-or-more blinks category had no significant effect on the perception of stimulus duration ($\beta = 0.209$, $SE = 0.471$, $p > .05$). In Figure 2, the data points represent the observed mean responses across all participants and the lines are the predicted probabilities derived from a GLMER model. The functions are plotted for each blink category represented by different colors, probe duration, and probability of having a ‘long’ response.

Figure 2

Subjective Perceived Time Duration as a Function of Spontaneous Eye Blinks



Discussion

The purpose of this study was to investigate the influence of spontaneous eye blinks on the perceived duration of stimuli by implementing a temporal bisection task by considering both blink presence and frequency. As predicted, the results showed that blinks do indeed alter time perception. The first hypothesis was supported, as the presence or absence of blinks before the

stimulus presentation had a significant effect on the judgment of duration, where participants who blinked once before the stimulus presentation were more likely to underestimate time intervals. This indicates that pre-stimulus spontaneous eye blinks influence probe duration judgment as compared to instances without blinking. Yet, contrary to the second hypothesis, the greater number of blinks preceding stimulus onset did not have a significant effect compared to not blinking. The presence of two or more blinks before stimulus onset, as opposed to no blinks, did not impact the perceived length of that stimulus. These findings question whether time perception and eye blink frequency have a linear relationship; while one blink appeared to influence time judgment, this effect did not increase with more blinks.

The observed impact of a single blink on time perception is consistent with previous research showing that blinks temporarily disrupt visual continuity and have implications for altering our sense of time (Grossman et al., 2019; Irwin & Robinson, 2016). However, the absence of an effect for two or more blinks reveals an interesting yet intricate insight into timing. It appears that beyond a certain threshold, more blinks do not distort the sense of time. One explanation would be that participants might have compensated for multiple blinks by cognitively combining the fragmented visual information, reducing the distorted sense of time and having a similar effect to no blinking (Maus et al., 2020). In addition, the lack of statistical significance might be related to having significantly fewer trials with more than two blinks. This was due to the inter-stimulus interval range being short (1000 ms to 2000 ms), which meant that the likelihood of participants blinking two or more times was considerably low. This result could also be interpreted as blinking behavior being affected by the distribution of event probabilities; blinking might have been suppressed in areas of high event probability, so participants had fewer blinks because they adapted to avoid missing the stimulus presentation (Hoppe et al., 2018). As a

result, there is an asymmetry of blinking, with more blinks after the stimulus presentation to compensate for blink suppression (Johns et al., 2009).

The findings of this study resemble those reported by Terhune and colleagues (2016) in the sense that blinking affects time perception of subsequent events; similarly, we also found a relationship between pre-stimulus blinks and time perception. In contrast to Terhune and colleagues (2016), however, we found that participants underestimated stimulus durations when they blinked, as opposed to overestimation. It is important to reiterate that our studies considered not only different inter-stimulus intervals but also the stimulus being estimated. This brings more complexity to the understanding of spontaneous eye blinks and timing, thus further research is needed to clarify these contradictory outcomes. Nevertheless, the observed effect of spontaneous eye blinks emphasizes the involvement of both sensory and cognitive processes in timing (Allman et al., 2014; van Bochove et al., 2012). These results may have theoretical implications, suggesting that models describing subjective time perception should integrate both neurobiological and behavioral mechanisms to a larger extent (Buhusi & Meck, 2005; Grondin, 2010). On a more practical level, a better understanding of blinking behavior might be beneficial in domains like human-computer interaction and building technological systems where precise timing is critical (Kadlec & Kirner, 2007), as well as dealing with clinical populations with dysregulated dopamine pathways and impaired timing abilities (Allman & Meck, 2011; Oyanadel & Buena-Casal, 2014).

While this study provides some insights into the effect of spontaneous eye blinks on time perception, it has some limitations that must be noted. This study assumed that all recorded blinks during the experiment were spontaneous, but it is possible that some were not truly spontaneous, possibly due to eye fatigue or dryness. Still, voluntary and simulated blinks have

also been shown to alter timing (Duyck et al., 2021). Moreover, the analyses focused on blinks occurring before stimulus presentation; during this period blinks may elicit saccadic movements that could also impact time perception (Johns et al., 2009). Future studies should define the conditions under which blinks alter both time estimation and reproduction. It could be interesting to consider all blink properties and how these affect timing differently within one study, including length of blinks, frequency, and when they occur in relation to the stimulus. Lastly, although eye blinks are believed to be an indirect measure of dopamine (Jongkees & Calzato, 2016; Karson, 1988; Taylor et al., 1999), this study only reports behavioral data, limiting the ability to make clear conclusions on the role of dopamine. The temporal bisection task considers various aspects of timing like assessing the duration of stimuli, storing and remembering duration information in memory, and comparing two durations (Kopeck & Brody, 2010). Therefore, combining behavioral data of this paradigm with neuroimaging techniques could reveal relevant details about brain activity and its link with the dopamine pathways.

Despite not having a distinct sensory center, time processing combines different sensory inputs like auditory and visual cues (Coull et al., 2012; Meck, 2005; Rammsayer, 1999). In particular, the processing of visual input is highly vulnerable to disruptions like those caused by eye blinks (Bristow et al., 2005b). This study provides empirical evidence that brief disruptions in visual input affect our sense of time. A single spontaneous eye blink changed the perceived duration of subsequent stimulus but multiple blinks did not have a noticeable impact. This illustrates the complex link between sensory and behavioral processes with time perception, emphasizing the need to continue research on this topic to understand how we perceive and interact with time in our daily lives.

References

- Allman, M. J., & Meck, W. H. (2011). Pathophysiological distortions in time perception and timed performance. *Brain*, *135*(3), 656–677. <https://doi.org/10.1093/brain/awr210>
- Allman, M. J., Teki, S., Griffiths, T. D., & Meck, W. H. (2014). Properties of the internal clock: First- and second-order principles of subjective time. *Annual Review of Psychology*, *65*(1), 743–771. <https://doi.org/10.1146/annurev-psych-010213-115117>
- Arslanova, I., Kotsaris, V., & Tsakiris, M. (2023). Perceived time expands and contracts within each heartbeat. *Current Biology*, *33*(7). <https://doi.org/10.1016/j.cub.2023.02.034>
- Balsam, P. D., & Gallistel, C. R. (2009). Temporal maps and informativeness in associative learning. *Trends in Neurosciences*, *32*(2), 73–78. <https://doi.org/10.1016/j.tins.2008.10.004>
- Balzarotti, S., Cavaletti, F., D'Aloia, A., Colombo, B., Cardani, E., Ciceri, M. R., Antonietti, A., & Eugeni, R. (2021). The editing density of moving images influences viewers' time perception: The mediating role of Eye Movements. *Cognitive Science*, *45*(4). <https://doi.org/10.1111/cogs.12969>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1). <https://doi.org/10.18637/jss.v067.i01>
- Bateson, M. (2003). Interval timing and optimal foraging. *Functional and Neural Mechanisms of Interval Timing*. <https://doi.org/10.1201/9780203009574.ch5>
- Bonnot, O., Montalembert, M. de, Kermarrec, S., Botbol, M., Walter, M., & Coulon, N. (2011). Are impairments of time perception in schizophrenia a neglected phenomenon? *Journal of Physiology-Paris*, *105*(4–6), 164–169. <https://doi.org/10.1016/j.jphysparis.2011.07.006>

- Bristow, D., Frith, C., & Rees, G. (2005a). Two distinct neural effects of blinking on human visual processing. *NeuroImage*, *27*(1), 136–145.
<https://doi.org/10.1016/j.neuroimage.2005.03.037>
- Bristow, D., Haynes, J.-D., Sylvester, R., Frith, C. D., & Rees, G. (2005b). Blinking suppresses the neural response to unchanging retinal stimulation. *Current Biology*, *15*(14), 1296–1300. <https://doi.org/10.1016/j.cub.2005.06.025>
- Buhusi, C. V., & Meck, W. H. (2005). What makes us tick? functional and neural mechanisms of interval timing. *Nature Reviews Neuroscience*, *6*(10), 755–765.
<https://doi.org/10.1038/nrn1764>
- Carney, L. G., & Hill, R. M. (1982). The nature of normal blinking patterns. *Acta Ophthalmologica*, *60*(3), 427–433. <https://doi.org/10.1111/j.1755-3768.1982.tb03034.x>
- Chan, K. K., Hui, C. L., Lam, M. M., Tang, J. Y., Wong, G. H., Chan, S. K., & Chen, E. Y. (2010). A three-year prospective study of spontaneous eye-blink rate in first-episode schizophrenia: Relationship with relapse and neurocognitive function. *East Asian archives of psychiatry*, *20*(4), 174-179.
- Coull, J. T., Cheng, R.-K., & Meck, W. H. (2010). Neuroanatomical and neurochemical substrates of timing. *Neuropsychopharmacology*, *36*(1), 3–25.
<https://doi.org/10.1038/npp.2010.113>
- Coull, J. T., Hwang, H. J., Leyton, M., & Dagher, A. (2012). Dopamine precursor depletion impairs timing in healthy volunteers by attenuating activity in putamen and supplementary motor area. *The Journal of Neuroscience*, *32*(47), 16704–16715.
<https://doi.org/10.1523/jneurosci.1258-12.2012>

- Dang, L. C., Samanez-Larkin, G. R., Castellon, J. J., Perkins, S. F., Cowan, R. L., Newhouse, P. A., & Zald, D. H. (2017). Spontaneous eye blink rate (EBR) is uncorrelated with dopamine D2 receptor availability and unmodulated by dopamine agonism in healthy adults. *Eneuro*, *4*(5). <https://doi.org/10.1523/eneuro.0211-17.2017>
- Dalmai, E. S., Mathôt, S., & Van der Stigchel, S. (2013). PyGaze: An open-source, cross-platform toolbox for minimal-effort programming of eyetracking experiments. *Behavior Research Methods*, *46*(4), 913–921. <https://doi.org/10.3758/s13428-013-0422-2>
- Duyck, M., Collins, T., & Wexler, M. (2021). Visual continuity during blinks and alterations in time perception. *Journal of Experimental Psychology: Human Perception and Performance*, *47*(1), 1–12. <https://doi.org/10.1037/xhp0000864>
- Eagleman, D. M., & Pariyadath, V. (2009). Is subjective duration a signature of coding efficiency? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1525), 1841–1851. <https://doi.org/10.1098/rstb.2009.0026>
- Feldstein, S., Jaffe, J., Beebe, B., Crown, C. L., Jasnow, M., Fox, H., & Gordon, S. (1993). Coordinated interpersonal timing in adult-infant vocal interactions: A cross-site replication. *Infant Behavior and Development*, *16*(4), 455–470. [https://doi.org/10.1016/0163-6383\(93\)80004-r](https://doi.org/10.1016/0163-6383(93)80004-r)
- Fung, B. J., Sutlief, E., & Hussain Shuler, M. G. (2021). Dopamine and the interdependency of time perception and reward. *Neuroscience & Biobehavioral Reviews*, *125*, 380–391. <https://doi.org/10.1016/j.neubiorev.2021.02.030>
- Gable, P. A., & McCoy, T. P. (2023). Editorial: Cognitive and emotional mechanisms of time perception. *Frontiers in Psychology*, *13*. <https://doi.org/10.3389/fpsyg.2022.1069460>

- Groman, S. M., James, A. S., Seu, E., Tran, S., Clark, T. A., Harpster, S. N., Crawford, M., Burtner, J. L., Feiler, K., Roth, R. H., Elsworth, J. D., London, E. D., & Jentsch, J. D. (2014). In the blink of an eye: Relating positive-feedback sensitivity to striatal dopamine D2-like receptors through blink rate. *The Journal of Neuroscience*, *34*(43), 14443–14454. <https://doi.org/10.1523/jneurosci.3037-14.2014>
- Grondin, S. (2010). Timing and time perception: A review of recent behavioral and neuroscience findings and theoretical directions. *Attention, Perception, & Psychophysics*, *72*(3), 561–582. <https://doi.org/10.3758/app.72.3.561>
- Grossman, S., Gueta, C., Pesin, S., Malach, R., & Landau, A. N. (2019). Where does time go when you blink? *Psychological Science*, *30*(6), 907–916. <https://doi.org/10.1177/0956797619842198>
- Hoppe, D., Helfmann, S., & Rothkopf, C. A. (2018). Humans quickly learn to blink strategically in response to environmental task demands. *Proceedings of the National Academy of Sciences*, *115*(9), 2246–2251. <https://doi.org/10.1073/pnas.1714220115>
- Irwin, D. E., & Robinson, M. M. (2016). Perceiving a continuous visual world across voluntary eye blinks. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(10), 1490–1496. <https://doi.org/10.1037/xhp0000267>
- Johns, M., Crowley, K., Chapman, R., Tucker, A., & Hocking, C. (2009). The effect of blinks and saccadic eye movements on visual reaction times. *Attention, Perception, & Psychophysics*, *71*(4), 783–788. <https://doi.org/10.3758/app.71.4.783>
- Jongkees, B. J., & Colzato, L. S. (2016). Spontaneous eye blink rate as predictor of dopamine-related cognitive function—a review. *Neuroscience & Biobehavioral Reviews*, *71*, 58–82. <https://doi.org/10.1016/j.neubiorev.2016.08.020>

- Kadlec, A., & Kirner, R. (2007). On the difficulty of building a precise timing model for real-time programming. *Kolloquium Programmiersprachen und Grundlagen der Programmierung* 99-105.
- Kanai, R., Dalmaijer, E. S., Sherman, M. T., Kawakita, G., & Paffen, C. L. (2017). Larger stimuli require longer processing time for perception. *Perception*, 46(5), 605–623. <https://doi.org/10.1177/0301006617695573>
- Karşılar, H., Kısa, Y. D., & Balçı, F. (2018). Dilation and constriction of subjective time based on observed walking speed. *Frontiers in Psychology*, 9. <https://doi.org/10.3389/fpsyg.2018.02565>
- Karson, C. N. (1988). Physiology of normal and abnormal blinking. *Advances in neurology*, 49, 25-37.
- Kinzuka, Y., Sato, F., Minami, T., & Nakauchi, S. (2021). Effect of glare illusion-induced perceptual brightness on temporal perception. *Psychophysiology*, 58(9). <https://doi.org/10.1111/psyp.13851>
- Kopec, C. D., & Brody, C. D. (2010). Human performance on the temporal bisection task. *Brain and Cognition*, 74(3), 262–272. <https://doi.org/10.1016/j.bandc.2010.08.006>
- Kroger-Costa, A., Machado, A., & Santos, J. A. (2013). Effects of motion on time perception. *Behavioural Processes*, 95, 50–59. <https://doi.org/10.1016/j.beproc.2013.02.002>
- Kruijne, W., Olivers, C. N., & van Rijn, H. (2021). Neural repetition suppression modulates time perception: Evidence from electrophysiology and pupillometry. *Journal of Cognitive Neuroscience*, 33(7), 1230–1252. https://doi.org/10.1162/jocn_a_01705
- Lake, J. I., & Meck, W. H. (2013). Differential effects of amphetamine and haloperidol on temporal reproduction: Dopaminergic regulation of attention and clock speed.

Neuropsychologia, 51(2), 284–292.

<https://doi.org/10.1016/j.neuropsychologia.2012.09.014>

Lake, J. I., LaBar, K. S., & Meck, W. H. (2016). Emotional modulation of interval timing and time perception. *Neuroscience & Biobehavioral Reviews*, 64, 403–420.

<https://doi.org/10.1016/j.neubiorev.2016.03.003>

Marshall, A. T., & Kirkpatrick, K. (2015). Everywhere and everything: The power and ubiquity of time. *International Journal of Comparative Psychology*, 28.

<https://doi.org/10.46867/ijcp.2015.28.02.03>

Mathôt, S., & March, J. (2022). Conducting linguistic experiments online with OpenSesame and osweb. *Language Learning*, 72(4), 1017–1048. <https://doi.org/10.1111/lang.12509>

Mathôt, S., & Vilotijević, A. (2022). Methods in cognitive pupillometry: Design, preprocessing, and statistical analysis. *Behavior Research Methods*, 55(6), 3055–3077.

<https://doi.org/10.3758/s13428-022-01957-7>

Mathôt, S., Schreij, D., & Theeuwes, J. (2011). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, 44(2), 314–324.

<https://doi.org/10.3758/s13428-011-0168-7>

Matthews, W. J., & Meck, W. H. (2014). Time perception: The bad news and the good. *WIREs Cognitive Science*, 5(4), 429–446. <https://doi.org/10.1002/wcs.1298>

Matthews, W. J., Stewart, N., & Wearden, J. H. (2011). Stimulus intensity and the perception of duration. *Journal of Experimental Psychology: Human Perception and Performance*,

37(1), 303–313. <https://doi.org/10.1037/a0019961>

- Maus, G. W., Goh, H. L., & Lisi, M. (2020). Perceiving locations of moving objects across eyeblinks. *Psychological Science, 31*(9), 1117–1128.
<https://doi.org/10.1177/0956797620931365>
- Meck, W. H. (1996). Neuropharmacology of timing and time perception. *Cognitive Brain Research, 3*(3–4), 227–242. [https://doi.org/10.1016/0926-6410\(96\)00009-2](https://doi.org/10.1016/0926-6410(96)00009-2)
- Meck, W. H. (2005). Neuropsychology of timing and time perception. *Brain and Cognition, 58*(1), 1–8. <https://doi.org/10.1016/j.bandc.2004.09.004>
- Meissner, K., & Wittmann, M. (2011). Body signals, cardiac awareness, and the perception of Time. *Biological Psychology, 86*(3), 289–297.
<https://doi.org/10.1016/j.biopsycho.2011.01.001>
- Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. *Nature Neuroscience, 8*(7), 950–954.
<https://doi.org/10.1038/nn1488>
- Murali, S., & Händel, B. (2021). The latency of spontaneous eye blinks marks relevant visual and auditory information processing. *Journal of Vision, 21*(6), 7.
<https://doi.org/10.1167/jov.21.6.7>
- Namboodiri, V. M., Mihalas, S., Marton, T. M., & Hussain Shuler, M. G. (2014). A general theory of intertemporal decision-making and the perception of time. *Frontiers in Behavioral Neuroscience, 8*. <https://doi.org/10.3389/fnbeh.2014.00061>
- Oyanadel, C., & Buela-Casal, G. (2014). Time perception and psychopathology: Influence of time perspective on quality of life of severe mental illness. *Actas españolas de psiquiatría, 42*(3), 99-107.

- Peirce, J. W. (2007). Psychopy—Psychophysics software in Python. *Journal of Neuroscience Methods*, 162(1–2), 8–13. <https://doi.org/10.1016/j.jneumeth.2006.11.017>
- Pollatos, O., Yeldesbay, A., Pikovsky, A., & Rosenblum, M. (2014). How much time has passed? ask your heart. *Frontiers in Neurobotics*, 8. <https://doi.org/10.3389/fnbot.2014.00015>
- Rammsayer, T. H. (1999). Neuropharmacological evidence for different timing mechanisms in humans. *The Quarterly Journal of Experimental Psychology: Section B*, 52(3), 273–286.
- R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Sadibolova, R., Monaldi, L., & Terhune, D. B. (2022). A proxy measure of striatal dopamine predicts individual differences in temporal precision. *Psychonomic Bulletin & Review*, 29(4), 1307–1316. <https://doi.org/10.3758/s13423-022-02077-1>
- Schirmer, A. (2011). How emotions change time. *Frontiers in Integrative Neuroscience*, 5. <https://doi.org/10.3389/fnint.2011.00058>
- Sescousse, G., Ligneul, R., van Holst, R. J., Janssen, L. K., de Boer, F., Janssen, M., Berry, A. S., Jagust, W. J., & Cools, R. (2018). Spontaneous eye blink rate and dopamine synthesis capacity: Preliminary evidence for an absence of positive correlation. *European Journal of Neuroscience*, 47(9), 1081–1086. <https://doi.org/10.1111/ejn.13895>
- Stern, J. A., Walrath, L. C., & Goldstein, R. (1984). The endogenous eyeblink. *Psychophysiology*, 21(1), 22–33. <https://doi.org/10.1111/j.1469-8986.1984.tb02312.x>
- Suzuki, T. W., Kunimatsu, J., & Tanaka, M. (2016). Correlation between pupil size and subjective passage of time in non-human primates. *The Journal of Neuroscience*, 36(44), 11331–11337. <https://doi.org/10.1523/jneurosci.2533-16.2016>

- Suárez-Pinilla, M., Nikiforou, K., Fountas, Z., Seth, A. K., & Roseboom, W. (2019). Perceptual content, not physiological signals, determines perceived duration when viewing dynamic, natural scenes. *Collabra: Psychology*, 5(1). <https://doi.org/10.1525/collabra.234>
- Tamm, M., Jakobson, A., Havik, M., Burk, A., Timpmann, S., Allik, J., Ööpik, V., & Kreegipuu, K. (2014). The compression of perceived time in a hot environment depends on physiological and psychological factors. *Quarterly Journal of Experimental Psychology*, 67(1), 197–208. <https://doi.org/10.1080/17470218.2013.804849>
- Tamm, M., Jakobson, A., Havik, M., Timpmann, S., Burk, A., Ööpik, V., Allik, J., & Kreegipuu, K. (2015). Effects of heat acclimation on time perception. *International Journal of Psychophysiology*, 95(3), 261–269. <https://doi.org/10.1016/j.ijpsycho.2014.11.004>
- Taylor, J. R., Elsworth, J. D., Lawrence, M. S., Sladek, J. R., Roth, R. H., & Redmond, D. E. (1999). Spontaneous blink rates correlate with dopamine levels in the caudate nucleus of MPTP-treated monkeys. *Experimental Neurology*, 158(1), 214–220. <https://doi.org/10.1006/exnr.1999.7093>
- Terhune, D. B., Sullivan, J. G., & Simola, J. M. (2016). Time dilates after spontaneous blinking [Supplemental material]. *Current Biology*, 26(11). <https://doi.org/10.1016/j.cub.2016.04.010>
- Togoli, I., Fornaciai, M., & Buetti, D. (2021). The specious interaction of time and numerosity perception. *Proceedings of the Royal Society B: Biological Sciences*, 288(1959), 20211577. <https://doi.org/10.1098/rspb.2021.1577>
- Ueda, N., Maruo, K., & Sumiyoshi, T. (2018). Positive symptoms and time perception in schizophrenia: A meta-analysis. *Schizophrenia Research: Cognition*, 13, 3–6. <https://doi.org/10.1016/j.scog.2018.07.002>

- van Bochove, M. E., Van der Haegen, L., Notebaert, W., & Verguts, T. (2012). Blinking predicts enhanced cognitive control. *Cognitive, Affective, & Behavioral Neuroscience, 13*(2), 346–354. <https://doi.org/10.3758/s13415-012-0138-2>
- van Maanen, L., van der Mijl, R., van Beurden, M. H., Roijendijk, L. M., Kingma, B. R., Miletić, S., & van Rijn, H. (2019). Core body temperature speeds up temporal processing and choice behavior under deadlines. *Scientific Reports, 9*(1). <https://doi.org/10.1038/s41598-019-46073-3>
- Volkman, F. C., Riggs, L. A., & Moore, R. K. (1980). Eyeblinks and visual suppression. *Science, 207*(4433), 900–902. <https://doi.org/10.1126/science.7355270>
- Wiener, M., Lee, Y.-S., Lohoff, F. W., & Coslett, H. B. (2014). Individual differences in the morphometry and activation of time perception networks are influenced by dopamine genotype. *NeuroImage, 89*, 10–22. <https://doi.org/10.1016/j.neuroimage.2013.11.019>
- Wiener, M., Lohoff, F. W., & Coslett, H. B. (2011). Double dissociation of dopamine genes and timing in humans. *Journal of Cognitive Neuroscience, 23*(10), 2811–2821. <https://doi.org/10.1162/jocn.2011.21626>
- Wutz, A., Muschter, E., van Koningsbruggen, M. G., Weisz, N., & Melcher, D. (2016). Temporal integration windows in neural processing and perception aligned to saccadic eye movements. *Current Biology, 26*(13), 1659–1668. <https://doi.org/10.1016/j.cub.2016.04.070>
- Zhou, S., Li, L., Wang, F., & Tian, Y. (2021). How facial attractiveness affects time perception: Increased arousal results in temporal dilation of attractive faces. *Frontiers in Psychology, 12*. <https://doi.org/10.3389/fpsyg.2021.784099>

Zélanti, P. S., & Droit-Volet, S. (2011). Cognitive abilities explaining age-related changes in time perception of short and long durations. *Journal of Experimental Child Psychology*, *109*(2), 143–157. <https://doi.org/10.1016/j.jecp.2011.01.003>