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Task-synchronized eye blink modulation neither requires visual stimulation nor active motor response and is modulated by task predictability

Stefan E. Huber [a,b,*], Markus Martini [a], Pierre Sachse [a]

[a] Department of Psychology, University of Innsbruck, Universitätsstraße 5-7, A-6020 Innsbruck, Austria
[b] Institute of Psychology, University of Graz, Universitätsplatz 2, A-8010 Graz, Austria

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ABSTRACT

It has been repeatedly shown that temporal task features are reflected in eye blink dynamics during attention tasks. Eye blinks occur with increased likeliness particularly when demands on external attention allocation are low. Both predictive, top-down and reactive, bottom-up processes were shown to be involved in blink regulation. However, whether temporal stimulus prediction is a generally active component of the attention system or rather specific to the visual domain has not been fully elaborated yet. By monitoring eye blinking of 99 students during an auditory attention task and analyzing particularly the dynamics of eye blink onsets relative to stimuli timings, we show here that prediction does, in principle, not require visual stimulation, and is also not merely a consequence of the involvement of manual responses during the task. We further show that both the inclusion of manual response to stimuli and elevated task predictability enhance the prediction component reflected in eye blink dynamics, whereas for the latter we experimentally manipulate objective task predictability by adjusting the frequency dependence of the power spectral densities of the series of inter-stimulus time intervals. This allows us finally to explain why, for specific choices of experimental conditions, the generally active and present prediction component involved in attention can become difficult to detect in non-visual, auditory tasks. Conversely, this comes with the important implication that, if tasks aim for elaborating particularly temporal prediction, distributing stimuli over time such that inter-stimulus-intervals conform to a sample of Gaussian noise represents a specifically unfavorable choice.

1. Introduction

Eye blinking has received considerable interest in cognitive psychology due to a steadily growing number of empirical studies suggesting it to serve as an easily accessible, non-invasive indicator for various intra-individual mental states and cognitive processes. In fact, of the 43 internal and external factors affecting eye blinking collected by Rodriguez et al. (2017), at least 17 are directly associated with specific mental states or cognitive processes (e.g. emotional state, mental fatigue and disorders, anxiety, concentration, deception, speech processing). In addition, many of the remaining factors such as hormonal changes, muscular fatigue and tension, illumination or noise are indirectly, yet clearly related to cognitive processing either.

Attention may serve as a common denominator underlying the variety of factors capable of affecting eye blinking and has, indeed, been suggested as one of the main psychological drivers of endogenous eye blink regulation for about a century (Haathi and Wuorinen, 1919; Ponder and Kennedy, 1927). For the intricate interrelations between attention and other cognitive processes it also stands to reason that eye blinking can be generally affected by a multitude of activities such as laboratory tasks including arithmetic operations, attention and memory tasks of varying difficulty (Holland and Tarlow, 1975; Tanaka and Yamaoka, 1993; Bacher et al., 2017; Fukuda et al., 2005; Irwin, 2014), resting, reading, listening and talking (Bentivoglio et al., 1997; Karson et al., 1981; Mori et al., 2008), or operation of vehicles including driving (Lal and Craig, 2002), flying (Morris and Miller, 1996), and air traffic control (McIntire et al., 2014). The close relations between attention and the dopaminergic system may further explain characteristic effects of certain pathological changes on eye blink rate like in Parkinson's disease or in schizophrenia (Green, 2006; Nieoullon, 2002; Maffei and Angrilli, 2018). A more comprehensive overview of the literature suggesting eye blink rate as a behavioral marker of dopamine function is provided by Jongkees and Colzato (2016).

That attention – rather than physiological purposes of cleaning and

* Corresponding author at: University of Graz, Universitätsplatz 2, A-8010 Graz, Austria.
E-mail address: stefan.huber@uni-graz.at (S.E. Huber).

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lubricating the surface of the eye for maintaining a stable tear film and good quality of vision (Sweeney et al., 2013; Montés-Micó, 2007) – mainly drives eye blink regulation can also explain why most people blink by far more often than physiologically necessary and why people blind from birth do hardly differ from people with vision in regard of blinking (Ponder and Kennedy, 1927). Although spanning an overall wide range of 3–48 blinks per minute, average blink rates were reported to about 14 blinks per minute (Doughty and Naase, 2006), accounting for a blink approximately every 4.3 s. In contrast, average tear film break-up times in healthy subjects were reported within a range of 19–42 s (Sweeney et al., 2013) depending on the choice of method for measurement. Although associated also with wide ranges of individual results (3–214 s), they typically exceed average inter-blink intervals by far, rendering tear film break-up unlikely to induce blinking (Norn, 1969).

Furthermore, eye blinks hardly occur randomly in time, but were reported to be temporally correlated with external stimulus onsets (Siegle et al., 2008), implicit breakpoints during movies (Nakano et al., 2013), smiling (Trutoiu et al., 2013), head movements and facial expressions during conversation (Ford et al., 2013), finger movements (Cong et al., 2010), verbal (Oh et al., 2012a) and manual responses during laboratory tasks (van Dam and van Ee, 2005; Oh et al., 2012b; Hoppe et al., 2018; Kobald et al., 2019; Huber et al., 2022). In a visual attention task (Hoppe et al., 2018) participants were required to detect temporary, very short visual events, and they quickly learned to time their blinking strategically, i.e. to blink rather when the respective events were unlikely to occur. In contrast, blinking was suppressed during phases in which events were highly likely. Such alignment of blink suppression with temporal task structure was also observed in auditory attention tasks (Oh et al., 2012b; Kobald et al., 2019; Brych and Händel, 2020; Huber et al., 2022). These findings suggest that the relation between blinking and attention is hardly constrained to the visual perception modality, but influences information processing via a general, cognitive, top-down mechanism such that eye blinking is suppressed particularly in phases when (task-)relevant information needs to be processed and is released directly afterwards (Wascher et al., 2015).

By contrasting results obtained from visual, auditory, and bimodal attention tasks, Brych and Händel (2020) managed to disentangle cognitive (top-down) from sensory (bottom-up) influences on eye blink timing. In particular, they identified three specific processes. First, a domain-specific, preparatory, top-down influence on blinking prior to sensory input, i.e. the likeliness to blink was decreased in preparation of visual input compared to auditory input. Second, a post-stimulus, early increase in blink likeliness after sensory input not requiring response (standard stimuli) if a task is involved for both modalities, and solely for the visual domain if no task is involved, suggesting a bottom-up influence specific to the visual domain in addition to a general top-down influence. Third, a reduction of this post-stimulus, early increase in blink likeliness given that the sensory input is comprised of a target stimulus requiring response in form of counting, an omission, or a distractor, accompanied by a late increase in blink likeliness in the case of target stimuli or omissions. According to the authors, this suggests a general, top-down influence based on the interpretation of the (missing) input. Brych and Händel (2020) conclude that their experiments reveal a modulation of eye blinking based on top-down, cognitive processes including prediction and attention in addition to bottom-up, sensory-based effects.

In our previous work on the dynamics of eye blinking (Huber et al., 2022), we could show that apparently strategic blinking in the form reported by Hoppe et al. (2018) for a visual task results also within the scope of a purely auditory attention task. We identified also a pre-stimulus decrease of blink likeliness dependent on the predictability of stimulus occurrences in time. In particular, pre-stimulus blink suppression was weaker for lower task predictability. Although based only on a tentative exploration, the post-stimulus increase in blink likeliness appeared rather orchestrated with the manual (keypress) responses by participants used to indicate detection of the short, transient stimuli like in the experiment of Hoppe et al. (2018). In addition, we noted a very weak, but noticeable post-stimulus effect on blink likeliness even under merely “passive” listening conditions. In comparison, the involvement of manual responses under active, task conditions exerted a strong influence on the magnitude, form, and coherence (across participants) of the temporal associations between stimulus onsets and eye blinks.

Overall, these recent investigations into the dynamics of eye blinking within laboratory attention tasks leave us with the following picture. Clearly, the intrinsic, temporal characteristics of attention tasks exert a modulating effect on eye blink dynamics (Hoppe et al., 2018; Brych and Händel, 2020; Huber et al., 2022). The mechanism further includes a general, modality unspecific component besides an effect-amplifying component specific for the visual domain (Brych and Händel, 2020). Both top-down, cognitive, and bottom-up, sensory processes are involved in the regulation of eye blink dynamics whereas top-down processing incorporates aspects of prediction and attention (Brych and Händel, 2020). Especially the top-down component associated with prediction is further affected by perception modality (Brych and Händel, 2020) and task predictability (Huber et al., 2022). Altogether, the domain within which stimuli are presented during a task, the task predictability and also the involvement of manual responses within the task (van Dam and van Ee, 2005; Huber et al., 2022) appear as important factors determining both magnitude and form of the effect that temporal task characteristics exert on eye blink dynamics under otherwise controlled laboratory conditions.

In the present work, we aim to add to this so far accumulated understanding, a specific clarification of the roles of task predictability and involvement of manual responses on eye blink dynamics. In particular, we hypothesize that (i) eye blink dynamics is affected by top-down, cognitive processing associated with prediction also in the case of an auditory attention task. However, we further hypothesize that this effect is modulated by both (ii) the involvement of manual response as well as (iii) task predictability, such that under conditions of low predictability and no involvement of manual response the influence of prediction, although yet present, becomes very weak and hence hard to detect. To this end, we build on the experimental design of our previous work (Huber et al., 2022), but extend the number of auditory signals differing in predictability from two to four signals and incorporate a second, mainly cognitive, counting task not involving any manual response as a contrast to the original detection task involving keypress responses upon stimulation. The increase in the variety of signals with different predictability shall allow us a refined view on how the temporal associations between external signal and eye blinking change upon small stepwise changes in signal predictability, a variable rarely explicitly investigated in psychophysiological experiments. Contrasting the results from a task involving manual response with the results from a task not involving a manual response under otherwise constant conditions will shed light directly on the influence of this factor. Altogether, we think to arrive thus finally at a more comprehensive picture of how the intricate interrelations between attention, perception and sensory-motor coordination are reflected in eye blink dynamics.

Due to the focus of our hypotheses on prediction, the primary focus of our analyses will be on pre-stimulus eye blink dynamics. Nevertheless, we will report and explore also how post-stimulus eye blinking is affected by varying involvement of motor response and task predictability. We note that there are no specific hypotheses involved in that respect though.

2. Method

2.1. Experimental setup

All participants were subject to two subsequent experimental conditions, each of a total duration of 12 min. During each of the experimental conditions, participants were seated at a distance of about 60 cm from a Tobii TX300 eye-tracker and instructed to direct their gaze towards the displayed, static image of a landscape (Kruczinsky, 2017). Besides, participants were presented 200 short sine tone bursts of 50 ms total duration with linear on- and offsets of 10 ms and a frequency of 440 Hz in each of the two experimental conditions. The tone bursts were presented diotically via headphones and sound levels were adjusted by each participant prior to the start of the experiment such that they could comfortably listen to the sine tone bursts for an extended period. In one of the experimental conditions, participants were required to indicate detection of each of the stimuli via a keypress. In the other condition, participants were required to silently count the stimuli. In order to keep concentration continuously high over the entire period of the counting condition, participants were instructed to count until they reached the number 17 and then restart at the number 1. The order of the two conditions was counterbalanced across participants.

Four different series of 200 sine tone bursts were prepared in order to vary predictability, i.e. how easy or difficult it is to predict when the next sine tone would occur based on the timings of the previous ones. Therefore, the time intervals between the onsets of two consecutive sine tone bursts were produced such that their predictability was located in the range between Gaussian noise and Brownian motion. In our earlier study (Huber et al., 2022), we had used Gaussian noise and Brownian motion as models for unpredictable and predictable tone series. To produce further time series with predictabilities between those two signal classes, we built on their spectral properties (Heneghan and McDarby, 2000). Whereas Gaussian noise exhibits a constant power spectral density, i.e. it is independent of frequency, the one of Brownian motion decreases proportionally to $1/f^{\beta}$ with f denoting frequency and the exponent $\beta = 2$. Signals decreasing at rates corresponding to β between 0 and 2 correspond to signals with intermediate predictabilities. Thus, we produced four samples of white noise with $n = 200$ and manipulated their power spectral densities such that they decreased proportionally to $1/f^{\beta}$ with $\beta = 0$, 0.6, 1.4 and 2.0. Subsequently, we adjusted the means and standard deviations of the four signals in the time domain such that they all accounted for 3.59 s and 0.8 s, respectively. Thus, the four signals, representing finally the four used series of inter-stimulus-intervals, were equal with respect to overall frequency and variability, but differed in predictability. The resulting signals are depicted in Fig. 1. Finally, we recomputed the spectral exponent of our four random samples by fitting a linear regression line to a double-logarithmic plot of frequency versus power spectral density resulting in $\beta = 0.02$, 0.75, 1.18 and 1.99. The differences between these exponents and the ones used for production are due to the finite sample size of the generated random numbers.

The four variations in predictability and the two possibilities of the order of keypress and counting conditions give rise to eight experimental groups in total. The participants were randomly assigned to one of those eight groups.

2.2. Participants

In total, 99 participants (64 female, 34 male, 1 not specified; mean age [*SD*]: 21.82 [1.84] years, range: 18–27 years) took part in the experiment in exchange for course credit. These do not include five more participants associated with unusable datasets (>15 % of missing data). All participants had normal or corrected-to-normal vision. No participant reported eye or ear diseases or difficulties. Participants were aware that their eye movements were recorded, but were not told details about the purpose of the task before the experiment was finished to prevent conscious control of blinking behavior. Written informed consent was obtained from all participants and all experimental procedures were carried out in accordance with the guidelines of the German Psychological Society and approved by the local ethics committee.

In our previous study (Huber et al., 2022), we had found that group sizes of about 20 participants each sufficed to reveal statistically clearly distinct pre-stimulus blink dynamics for very low ($\beta = 0.03$) and high ($\beta = 2.24$) task predictabilities under the condition of required manual responses. Hence, we concluded that a minimal sample size of 20 participants for each level of task predictability should suffice to at least reproduce that finding, assuming that it corresponded to a robust effect. In order to be able to capture eventually more subtle effects due to task order or participants only mentally responding to the stimuli we increased the envisaged sample size to 25 per level of predictability and stopped data acquisition as soon as the number of participants exceeded 100.

2.3. Data acquisition

Blink onsets were detected using an infrared eye-tracking device with a sampling frequency of 300 Hz (Tobii TX300; Tobii Technology AB, 2014) and the noise-based blink detection algorithm developed by Hershman et al. (2018). When closing the eyelids during blinking, the eye-tracking device loses track of the participants' pupils and these artifacts in the pupillometric data can be used to compute blink onsets. The

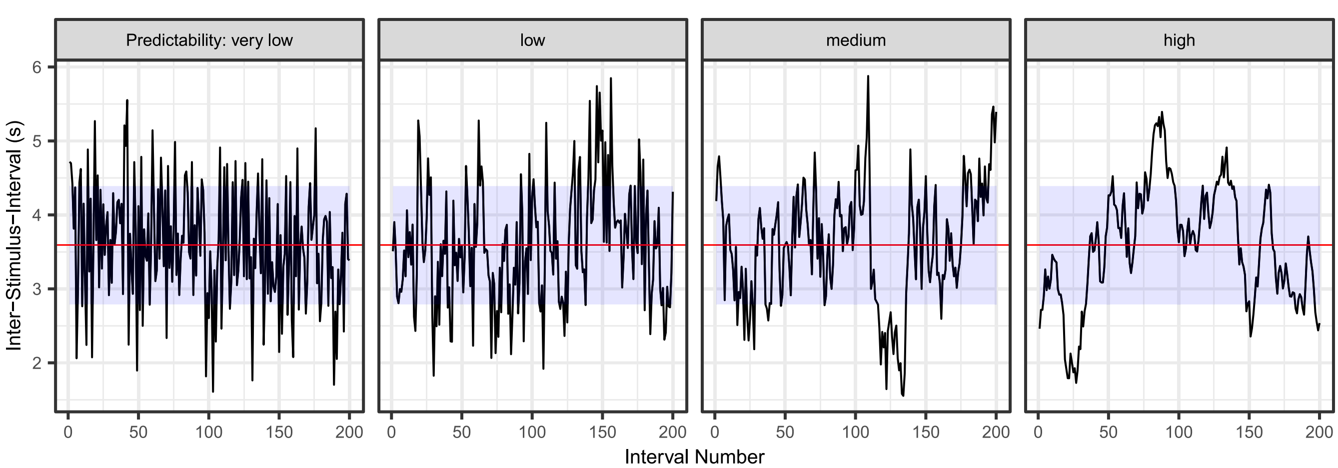

Fig. 1. Time intervals (in s) between two consecutive onsets of sine tone bursts versus number of appearance of the respective pair of tone bursts in the respective tone series. The first interval corresponds to the duration from the beginning of the respective experimental condition to the onset of the first sine tone burst. The means (red line) and standard deviations (blue shaded region) are the same for all four signal types, while their predictabilities are different which may be quantified by the exponent β characterizing their power spectral densities. The exponents for the depicted signals of very low, low, medium and high predictability were obtained to $\beta = 0.02$, 0.75, 1.18 and 1.99, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

blink onsets were then treated as point processes in our analysis of the temporal blink distributions with respect to the tone events (see below). Using this procedure, we found similar statistics concerning overall mean blink rates (mean [*SD*]: 20.69 [12.74] blinks/min) and fractal scaling (mean [*SD*]: 0.63 [0.12]) compared with studies using magnetic search coils (see e.g. Garcia et al., 2011), manual video analysis (e.g. Naase et al., 2005), EEGs and EOGs (e.g. Oh et al., 2012a; Oh et al., 2012b; Shin et al., 2015; Paprocki and Lenskiy, 2017).

We used only the pupillometric data of the dominant eye of each participant. The dominant eye of each participant was determined by a simple alignment test after the two experimental conditions. In particular, participants were asked to stretch out one of their arms and form a hole with their thumb and index finger. By looking through this hole with both eyes open they were then asked to fixate a plug socket located at the wall of the laboratory at a distance of about 3 m. Without moving, they were then asked to close one of their eyes and subsequently the other. Upon closing the dominant eye, the plug socket would appear to move out of the hole formed by the fingers, while upon closing the non-dominant eye it would not.

2.4. Data analysis

2.4.1. Mean blink rate

Besides pre- and post-stimulus blink distributions, we assessed also how the different experimental conditions affect the mean blink rate. Linear mixed-effects models were used to determine if and how mean blink rate depended on the involvement of a manual response (keypress condition versus silent counting condition; within-subjects factor), as well as the order of experimental conditions (first keypress, then counting condition versus first counting, then keypress condition; between-subjects factor) and the four levels of predictability (i.e. very low, low, medium, high; between-subjects factor), and all interactions between those three variables. In order to do so, we first constructed a complete model incorporating all three independent variables and their interactions as fixed factors, while random intercepts were included to take into account inter-individual differences in an overall propensity to blink. Subsequently, we constructed reduced models by step-wise removal of non-significant fixed factors. In order to investigate the influence of the predictability of the stimulus series, we considered the following orthogonal contrasts referring to the nomenclature provided in Fig. 1: very low and low predictability versus medium and high predictability, very low versus low predictability, and medium versus high predictability.

2.4.2. Pre- and post-stimulus blink distributions

In order to assess how blink likeliness is affected by the temporal distribution of the acoustic stimuli over the course of the experimental conditions, we first determined individual temporal blink distributions centered on the timings of the sine tone burst onsets. In order to do so, we subdivided all 1.5 s-intervals before and after each presented sine tone into 15 short 100 ms bins and counted the number of blink onsets in each of those bins over the full duration of 12 min for each experimental condition. Subsequently, we divided the resulting individual blink distribution by the total number of eye blinks during the respective experimental condition of the respective participant. Finally, we averaged these individual, normalized temporal blink distributions within each of the $2 \times 2 \times 4 = 16$ combinations of involvement of manual response, order of experimental condition, and predictability of sine tone series. These resulting averaged distributions for each combination of independent variables thus represent stimuli-centered temporal mean blink proportion (MBP) distributions specifying which proportion of all eye blinks occurred during a specific 100 ms interval in the two 1.5 s time windows before and after the onsets of sine tone bursts, giving rise to the denotation as *pre*-stimulus and *post*-stimulus blink distributions, respectively.

2.4.3. Statistical analyses

To analyze differences in mean blink proportion due to the three independent variables and their interactions we used again linear-mixed effects models as outlined above for mean blink rate but, in this case, for the mean blink proportions within each of the 15 time bins for both pre- and post-stimulus blink distributions. The time dependence of blink likeliness (with respect to stimuli onsets) was further explicitly modeled in both time windows and for each combination of independent variables based on our previous study (Huber et al., 2022). Pre-stimulus blink distributions were thus fitted with a linear regression model

$$B_{pre}(t) = c_1 + c_2 t \tag{1}$$

where t denotes the time relative to the onset of sine tone bursts, the intercept c_1 denotes a fit coefficient describing the strength of pre-stimulus blink suppression, and the slope c_2 denotes a fit coefficient describing the pre-stimulus (linear) rate of change in blink likeliness towards the onset of the next stimulus.

Post-stimulus blink distributions were fitted with the model introduced in our previous work (Huber et al., 2022), consisting of the superposition of a Fermi function taking into account the post-stimulus release of blink suppression, a Gaussian function accounting for the subsequent, transient blink overcompensation and an offset accounting for a minimal MBP:

$$B_{post}(t) = k_1 + \frac{k_2}{1 + exp\left(\frac{-t+k_3}{k_4}\right)} + k_5 exp\left(-\frac{(t-k_6)^2}{2k_7^2}\right) \tag{2}$$

Here, the various fit coefficients are denoted by k_i, i= 1, …,7, while t denotes again the time relative to the onset of sine tone bursts. Whereas k_1 describes the offset accounting for a minimal MBP, the Fermi function is described by the second term in Eq. (2) including a parameter k_2 to describe the magnitude of the release of blink suppression, a parameter k_3 determining the time of the release, and a parameter k_4 determining the time span over which the release occurs. The third term in Eq. (2) corresponds to the Gaussian function and includes a parameter k_5 describing the magnitude of blink overcompensation, a parameter k_6 determining when the overcompensation reaches its peak, and a parameter k_7 determining the width of the Gaussian curve.

2.4.4. Software

Production of the stimuli series and power spectral analyses were conducted with MATLAB (MathWorks, Natick, USA). All other data processing and statistical analyses were conducted using R (R Core Team, 2021) and RStudio (RStudio Team, 2021) using the packages tidyverse (Wickham et al., 2019), ggpubr (Kassambara, 2020), nlme (Pinheiro et al., 2021), pastecs (Grosjean and Ibanez, 2018), lme4 (Bates et al., 2015), performance (Lüdecke et al., 2021), RcmdrMisc (Fox, 2022).

3. Results

3.1. Mean blink rate (MBR)

MBRs (±standard errors) ranged from 13.52 ± 3.73 to 26.75 ± 4.93 blinks/min in the various experimental conditions realized in this experiment. MBRs showed significant variance across participants, SD = 11.86 blinks/min with a 95 %-confidence interval of [10.21, 13.78] blinks/min, $\chi^2(1) = 141.42$, $p < 0.0001$, $\Delta AIC = -139.4$. However, MBR turned out rather robust against differences between the various experimental conditions as none of the linear-mixed effects models including one or more of the three considered fixed factors (type of task, order of tasks, predictability) and their interactions resulted in a significant improvement over the baseline model incorporating, besides the grand mean, only random intercepts to account for inter-individual differences in MBR, see Table 1. None of the included factors or their

Table 1
Comparison of linear mixed-effect models for MBR in dependence of the considered independent variables and inter-individual differences. The baseline model including only random intercepts (besides the grand mean) yields an Akaike information criterion (AIC) of 1440.0. The numbers provided in the table for the degrees of freedom (df), the relative AICs (ΔAIC), the χ^2 statistics, and the p-values of the considered models account always for the relative difference of the respective model to the baseline model. The type of task is denoted shortly as the variable "type", while "predictability" denotes the predictability of stimulus series, and "order" denotes the order of tasks (keypress followed by counting versus counting followed by keypress).

MBR ~ 1 + (1|ID) + …	df	ΔAIC	χ^2	p-value
Type	1	1.7	0.28	0.60
Predictability	3	3.2	2.79	0.43
Order	1	1.9	0.12	0.73
Predictability*order	7	4.8	9.13	0.24
Order*type	3	1.0	4.97	0.17
Type*predictability	7	5.4	8.53	0.29
Type*predictability*order	15	6.9	23.04	0.08

interactions had a significant influence on MBR (using a Benjamini-Hochberg correction of significance levels with a false detection rate of 5 % for multiple comparisons). The marginal and conditional coefficients of determination obtained by the approach of Nakagawa et al. (2017) for a full model including all three fixed factors and their interactions yield r^2(marginal) = 0.09 and r^2(conditional) = 0.89, respectively, indicating the dominant contribution from inter-individual differences to the MBR in comparison to the impact of independent variables alone (marginal coefficient of determination).

3.2. Eye blink dynamics

We first investigated if there is a significant effect of task order on the eye blink proportion distributions centered on the occurrence times of the stimuli. Therefore, we evaluated a linear mixed-effects model including all three fixed factors (task order, task type, and predictability) and their interactions within each of the 100 ms time bins in both 1.5 s time windows before and after the stimuli. Significance levels were corrected for multiple comparisons following the procedure of Benjamini-Hochberg using a false detection rate of 5 %. Since neither task order nor any interaction including task order affected blink proportion at any of the time bins, we omitted task order from the fixed factors and repeated the procedure with mixed-effects models including the remaining two factors and their interactions at each time bin. Within time bins centered at −250 ms and at +150 ms (negative/positive signs indicate before/after stimulus onsets) mean blink proportions were significantly larger in the counting task than in the keypress task. Within the three time bins ranging from +700 to +1000 ms, the opposite was the case, i.e. mean blink proportions were significantly larger in the keypress task than in the counting task. Within the time bin centered at −150 ms, the mean blink proportion for the case of very low task predictability was significantly larger than the one for the case of low task predictability in the keypress task, but not in the counting task. Apart from these differences, bin-wise mean blink proportions were similar in both keypress and counting conditions as well as for different task predictabilities, see Fig. 2.

In Fig. 3(a), we compare the bin-wise mean blink proportions obtained for the keypress task with the ones obtained for the counting task, regardless of task predictability. We find that in the pre-stimulus region, mean blink proportions are larger in the counting task than in the keypress task. Differences are significant at the time bins centered at −450, −250 and − 150 ms (yellow shaded area in Fig. 3 for times <0). The mean blink proportion at the time bin centered at +150 ms is also significantly larger in the counting task than in the key press task (yellow shaded area in Fig. 3 for times >0), indicating that blink suppression is earlier released in the counting task than in the keypress task. The duration of post-stimulus blink compensation is longer in the keypress task than in the counting task, indicated by the mean blink proportions yielding significantly larger values from +700 to +1000 ms in the keypress than in the counting task (red shaded area in Fig. 3). In Fig. 3(a) also the linear and nonlinear functions fitted to the mean blink proportions according to Eqs. (1) and (2) for the time windows before and after stimuli onsets, respectively, are depicted. The intercepts and slopes of the regression lines fitted to the pre-stimulus distributions are depicted in Fig. 3(b) and (c), respectively. The fit coefficients for the nonlinear models fitted to the post-stimulus mean blink proportions are provided in Table 2. Note that we incorporated both nonlinear models in one combined model to assess the significance of the differences between the various coefficients. Fig. 3(b) and (c) illustrate that both intercepts and slopes of the linear fits to the pre-stimulus blink proportion distributions differ between the keypress and the counting task. Whereas in the keypress task the intercept yields 1.45 % with a 95 %-confidence interval of [1.37, 1.53] %, the intercept in the counting task yields 1.89

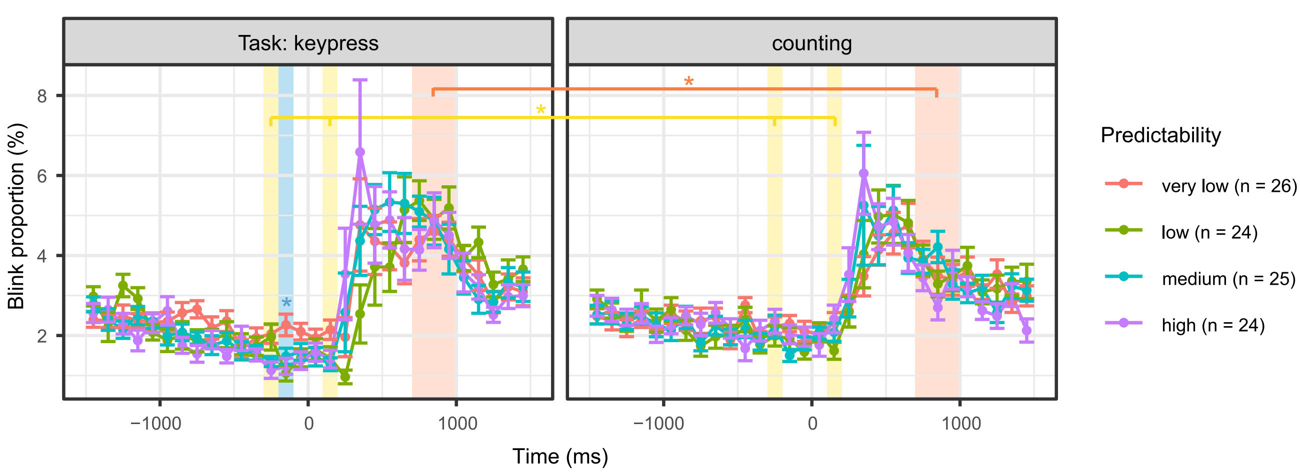

Fig. 2. Bin-wise mean blink proportions, for both keypress and counting conditions as well as for the four different task predictabilities, versus time before (negative sign) and after (positive sign) stimulus onsets. All 99 participants were subject to both the keypress and the counting task, whereas n denotes the number of participants being subject to the respective task predictability. Error bars represent standard errors of the means. Background colors indicate time bins in which mean blink proportions differed significantly: in the yellow shaded regions mean blink proportions were significantly larger in the counting task than in the keypress task; in the red shaded regions mean blink proportions were significantly larger in the keypress task than in the counting task; in the blue shaded region the mean blink proportion for the case of very low task predictability was significantly larger than the one for the case of low task predictability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

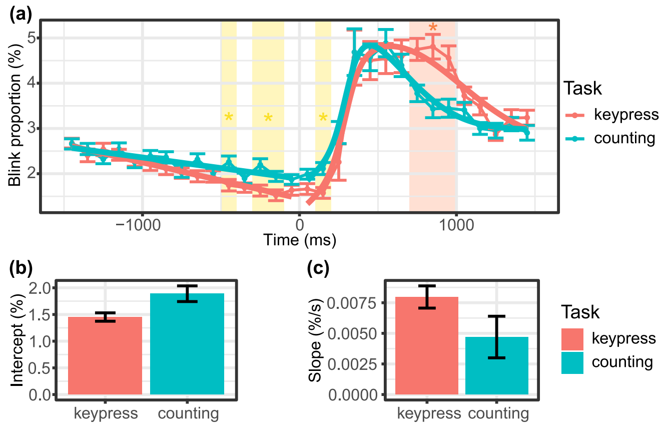

Fig. 3. Bin-wise mean blink proportions, for both keypress and counting conditions, versus time before (negative sign) and after (positive sign) stimulus onsets, regardless of task predictability, are shown in panel (a). Hence, the data points stem from all 99 participants included in the study. Background colors indicate time bins in which mean blink proportions differed significantly: in the yellow shaded regions mean blink proportions were significantly larger in the counting task than in the keypress task; in the red shaded regions mean blink proportions were significantly larger in the keypress task than in the counting task. The thick lines correspond to the linear (time < 0) and nonlinear (time > 0) models fitted to the blink proportion distributions according to Eqs. (1) and (2). The intercepts and slopes of the regression lines fitted to pre-stimulus blink proportion distributions and their 95 %-confidence intervals are depicted in panels (b) and (c) for both task types. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Coefficients of the nonlinear models fitted to the post-stimulus blink proportion distributions obtained for the two task types irrespective of predictability, see Fig. 2. Note that in order to assess the significance of differences between the two models, we incorporated both in a combined model. The coefficients of the model fitted to the post-stimulus distributions in the case of the keypress task are the k_i with $i = 1, \ldots, 7$ provided below. The coefficients of the model depicted in Fig. 2 for the post-stimulus distributions in the case of the counting task are given by $k_i + \Delta k_i$ with $i = 1, \ldots, 7$ and both the k_i and Δk_i provided below.

Coefficient	Estimate	Standard error	t-value	p-value
k_1 [%/100 ms]	0.100	2.450	0.041	0.968
Δk_1 [%/100 ms]	0.000	5.649	−0.018	0.986
k_2 [%/100 ms]	2.521	1.522	1.656	0.117
Δk_2 [%/100 ms]	0.449	5.204	0.086	0.932
k_3 [ms]	290.34	40.270	7.210	2.08×10^{-6}
Δk_3 [ms]	4.238	55.860	0.076	0.941
k_4 [ms]	50.000	36.633	1.365	0.191
Δk_4 [ms]	0.000	70.373	0.000	1.000
k_5 [%/100 ms]	2.205	1.196	1.844	0.084
Δk_5 [%/100 ms]	0.020	2.882	0.007	0.995
k_6 [ms]	562.12	237.75	2.364	0.031
Δk_6 [ms]	−282.69	758.03	−0.373	0.714
k_7 [ms]	468.28	362.66	1.291	0.215
Δk_7 [ms]	−104.48	483.71	−0.216	0.831

% with a 95 %-confidence interval of [1.74, 2.04] %. The slopes in the keypress and counting tasks yield 0.0080 %/s with a 95 %-confidence interval of [0.0071, 0.0089] %/s and 0.0047 %/s with a 95 %-confidence interval of [0.0030, 0.0064] %/s, respectively. Note that since the slopes always correspond to decreasing values of blink proportion, they were multiplied by a factor of −1 for convenience. Overall, pre-stimulus blink likeliness decreases faster and to smaller values in the keypress task than in the counting task. Post-stimulus blink likeliness increases sooner and yields a narrower region of blink compensation in the counting task than in the keypress task. However, due to large standard errors, the coefficients for the two nonlinear models fitted to post-stimulus blink proportion distributions do not differ significantly from each other. The only significant coefficients in Table 2 are k_3 and k_6 yielding a blink suppression release at 290 ms, t(16) = 7.21, p = 2.08×10^{-6}, and a blink compensation maximum at 562 ms, t(16) = 2.36, p = 0.031, respectively.

We also fitted regression lines to the pre-stimulus blink proportion distributions obtained for the four different task predictabilities in both the keypress and counting tasks. Their intercepts and slopes including their 95 %-confidence intervals are depicted in Fig. 4. In the keypress task, the intercepts (always directly followed by their 95 %-confidence intervals in the following) yield 2.03 % [1.79, 2.27] %, 1.28 % [0.89, 1.67] %, 1.31 % [1.14, 1.48] %, and 1.14 % [0.84, 1.44] %, for very low, low, medium and high task predictabilities, respectively. In the counting task, the intercepts yield 2.18 % [1.92, 2.43] %, 1.67 % [1.39, 1.94] %, 1.74 % [1.52, 1.96] %, and 1.96 % [1.71, 2.21] %, for very low, low, medium and high task predictabilities, respectively. Hence, moving from the keypress to the counting task does not only lead to an overall increase of the intercepts (indicating an overall decrease of blink suppression), but also to a loss in contrast between the influence of different task predictabilities. Note especially that the 95 %-confidence intervals of the very low task predictability and the higher task predictabilities do not overlap in the keypress task whereas they do in the counting task. A similar result is obtained in the case of the slopes. In the keypress task, the slopes (like the intercepts, they are always directly followed by their 95 %-confidence intervals, and they are multiplied again by −1 for convenience) yield 0.0032 %/s [0.0004, 0.0060] %/s, 0.0106 %/s [0.0061, 0.0151] %/s, 0.0087 %/s [0.0067, 0.0107] %/s, and 0.0098 %/s [0.0063, 0.0132] %/s, for very low, low, medium and high task predictabilities, respectively. In the counting task, the slopes yield 0.0018 %/s [−0.0012, 0.0048] %/s, 0.0072 %/s [0.0041, 0.0104] %/s, 0.0056 %/s [0.0030, 0.0081] %/s, and 0.0044 %/s [0.0015, 0.0073] %/s, for very low, low, medium and high task predictabilities, respectively. Besides an overall decrease of slopes and loss of contrast when moving from the keypress to the counting task, we also note that in the counting task, the 95 %-confidence interval of the very low task predictability includes zero, whereas in all other cases, the slopes differ significantly from zero.

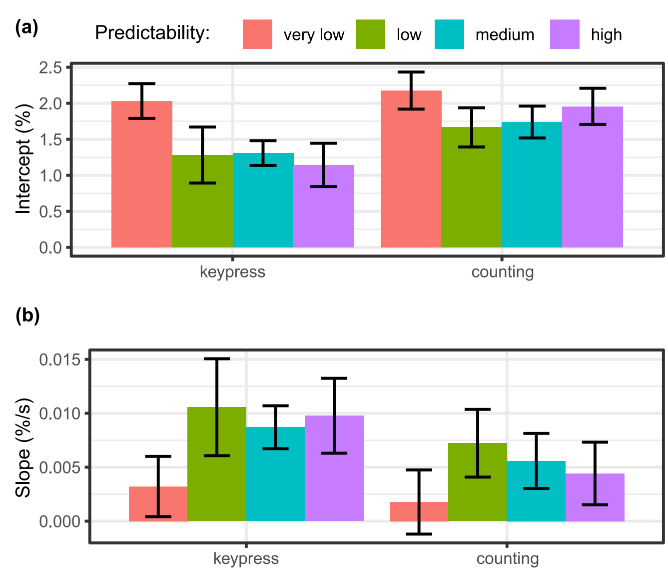

Fig. 4. The (a) intercepts and (b) slopes of the regression lines fitted to pre-stimulus blink proportion distributions and their 95 %-confidence intervals for the four different task predictabilities for both task types. The colour coding used to differentiate predictabilities is the same as in Fig. 2.

4. Discussion

4.1. Mean blink rate (MBR)

In line with the literature (Doughty and Naase, 2006) we found considerable inter-individual variation of MBR. Doughty (2001) provided evidence that MBR turns further out sensitive to the type of activity during which it is assessed, e.g. yielding 1.4–14.4 blinks/min during reading, 8.0–21.0 blinks/min during primary gaze or 10.5–32.5 blinks/min during conversation for normal adults. In the present study, MBR ranged overall from 13.5 to 26.8 blinks/min for the different implemented experimental conditions. However, MBR appeared rather robust against the rather subtle differences between these experimental conditions since neither the type of task, i.e. indicating detection of acoustic stimuli by a keypress or silently counting stimuli, nor the predictability of the stimuli series nor the order of the two conditions yielded a significant impact on MBR.

Also earlier studies employing similar types of attention tasks report similar values of MBR such as about 19.0 blinks/min (Hoppe et al., 2018), 14.3–24.4 blinks/min (Brych and Händel, 2020) or 20.2–30.0 blinks/min (Huber et al., 2022). While this could mean that MBR might be sensitive to structural or intrinsic temporal properties of an overall activity while being rather robust against slight changes given that the overall type of activity remains unchanged, it could also mean that it is less the type of involved activity than rather its intrinsic structural, temporal properties which in the first place determine the seemingly different ranges of MBRs associated with different types of activities. In the present study, the first two moments of the temporal distributions of stimuli, i.e. its mean and its standard deviation, were the same in all experimental conditions. This implies that the overall amount of information that was required to be processed as well as its overall variation was kept constant throughout the experiment, which may be a simple reason for the robustness of MBR against other structural properties of the task.

4.2. Eye blink dynamics

4.2.1. Influence of modality

In contrast to MBR, the dynamical features contained in the investigated temporal eye blink distributions could discriminate between the task variations realized by our different experimental conditions. Furthermore, our results show that significant pre-stimulus blink suppression is present in all but one of eight conditions, which, however, always represent realizations of *auditory* attention tasks. This suggests that a temporal prediction component of attentional processes contributes to the modulation of eye blinking also in the auditory domain and does, in principle, not require visual stimulation. However, taking into account the explicit comparison of visual and auditory domains provided by Brych and Händel (2020) then suggests that the effect is considerably enhanced in the visual domain, yet still present, although to a lower extent in the auditory domain. This is in line with both the notions of general attention exerting a dynamical, task-dependent modulation of eye blinking (Oh et al., 2012b) and attention as a proactively organizing mechanism elaborating a forecast of future stimuli in order to prepare an organism for optimal processing of sensory input (Sokolov, 1963; Klix, 1971). Such general attentional mechanisms should remain active also under conditions when stimuli are presented merely in the auditory domain since inattentiveness to external cues still increases the risk of missing relevant information.

It has been shown that during blinking neural activity is decreased in areas designated to the processing of environmental information such as particularly the primary visual area (Hari et al., 1994) and, more generally, the dorsal and ventral attention networks (Nakano, 2015; Nakano et al., 2013). At the same time, neural activity is increased in areas dedicated primarily to inner processing of information such as the default mode network, the hippocampus and the cerebellum (Nakano, 2015; Nakano et al., 2013). Upon re-opening the eyes, attention shifts back to neural areas for external information processing (Ang and Maus, 2020; van Bochove et al., 2013) while activity in non-sensory areas is reduced (Nakano, 2015). Hence, eye blinking in the “wrong” moment can be expected to exert a general, obstructive effect also on the processing of stimuli in non-visual domains which is indeed suggested by our results. A domain-specific enhancement of this effect in the case that stimuli are indeed presented in the visual domain can be expected due to the simple fact that in this case, the risk to miss relevant information by wrongly timed blinking is drastically increased due to the physical blockade of the visual input, i.e. a domain-specific additional risk factor.

4.2.2. Influence of active, manual response

Our results further revealed that the modulation of eye blink dynamics by temporal task structure, to which we referred as eye blink synchronization in our former work (Huber et al., 2022), is also enhanced if an active, manual response is required from participants compared to a mainly cognitive task (i.e. silently counting stimuli) besides another, weaker modulation by the predictability of the presented stimuli series. The difference between the two types of tasks manifests in both pre-stimulus and post-stimulus blink likeliness distributions. Concerning pre-stimulus distributions, the involvement of a manual response increases both the magnitude of the pre-stimulus blink suppression and the contrast between different levels of signal predictability. Concerning post-stimulus distributions, the release of blink suppression appears slightly earlier in the counting than in the keypress task, while the post-stimulus blink compensation is considerably less extended over time in the counting than in the keypress task.

Influences on eye blinking from other motor activity has been noted earlier (Ito et al., 2003; van Dam and van Ee, 2005; Cong et al., 2010). Particularly, Cong et al. (2010) suggest the orchestration of blinking and manual motor activity via the indirect influence of shared central clocking mechanisms determining the temporal regulation of both manual movements and eye blinking. In the present case, this could mean that preparation and timing of the manual motor response upon stimulus detection co-regulates the timing of blink execution enhancing thereby the synchronization with the external signal in contrast to the mainly cognitive task lacking the requirement of timing additional motor activity. This is line with the finding in our previous experiment (Huber et al., 2022) indicating a common neural process releasing simultaneously both the suppression of eye blinking and manual motor response. The apparently relatively earlier post-stimulus release of blink suppression in the case of the counting task also suggests the integration of both manual and eye movement motor pathways via a common, central bottleneck during the keypress task.

The less extended duration of blink compensation in the case of the counting task puts emphasis on the relation between cognition and eye blinking. Whereas in the case of the keypress task, cognitive evaluation of the stimulus temporarily concludes with detection and release of motor action, the counting task further requires continuous updating of the stimulus count. Eye blinks occur particularly at moments when information processing during a given task is transiently finished (Wascher et al., 2015). Nakano et al. (2009) showed that the eye blinks of participants watching movie clips were synchronized with implicit break points requiring less attention such as the conclusion of an action, during the absence of the main character, during a long shot, during repeated presentations of a similar scene, in addition to explicit break points such as scene changes. Siegle et al. (2008) suggested that blinks particularly flank moments of change in cognitive load in agreement with the notion of blinks representing the temporarily end of cognitive processing and a release of information from working memory (Ichikawa and Ohira, 2004).

Furthermore, although in the visual domain, eye blinking has been shown to be linked to mnemonic processes, resulting especially in a reduction in short-term memory capacity (Irwin, 2014), presumably caused by a reallocation of attention (Irwin, 2011) interfering particularly with rehearsal mechanisms (Awh and Jonides, 2001). This view is, however, contrasted by recent findings identifying particularly a positive association of spontaneous eye blink rate during delay periods and performance in a working memory task (Ortega et al., 2022). While this might be related to dopaminergic activity affecting the maintenance and updating of representations in working memory (Westbrook and Braver, 2016), the seemingly divergent findings may besides also point towards the relevance of a fine temporal attunement between a variety of periodically varying processes in a network of intricately related physiological, neurological, and cognitive mechanisms, on top or instead of time-independent rate modulations.

At least qualitatively, our results appear in line with these considerations, as particularly subvocal activity (verbal rehearsal) has been found to affect eye blinking (de Jong and Merckelbach, 1990). Furthermore, counting activity turned out especially associated to blinking since engaging in counting out loud increased blink rate significantly whereas reciting the alphabet had no comparable effect (Schuri and von Cramon, 1981). The moment between completed detection of a stimulus and updating of the stimulus count during our counting task might hence be seen as a natural breaking point at which blink likeliness is prone to accumulate. In the keypress task, the lack of the requirement to update the stimulus count and keep it actively in memory can, in contrast, lead to a more relaxed blink compensation before preparing for next stimulus. While this must remain speculation for now, it certainly puts further emphasis on the importance of examining phasic features of eye blinking in addition to tonic ones in future studies, especially when aiming for further resolving the intricate interrelations between eye blinking and cognitive processes.

4.2.3. Influence of predictability

Finally, our experiment revealed a weak yet noticeable effect also of the predictability of the stimuli series on the eye blink dynamics. This serves also as a replication of the result of our previous study (Huber et al., 2022), in which we already noted a significant difference between the pre-stimulus blink distributions obtained for stimuli series with low and high predictability.

In Fig. 5, we provide the intercepts and slopes of fitted regression lines to the pre-stimulus blink distributions obtained both in the present experiment and in our earlier work. Therein, the slopes and intercepts are plotted against the exponents β (characterizing the dependence of the power spectral densities on frequency) of the respective series of inter-stimulus-intervals used to vary task predictability within the two experiments. It is seen that the stimuli series with highest and lowest predictability in this study are very close to the ones of the earlier study in terms of predictability, i.e. $\beta = 0.02$ in the present study and $\beta = 0.03$ in our earlier study for low predictability and $\beta = 1.99$ in the present study and $\beta = 2.24$ in our earlier study for high predictability (note that there have been two groups subject to high task predictability in our earlier study and hence the two respective data points in Fig. 5). More importantly, the resulting intercepts and slopes are in very good agreement with each other yielding highly overlapping confidence intervals.

Although modulation of pre-stimulus blink suppression by task predictability is clearly apparent from these results, it is intriguing that, while blink suppression appears especially weak for low predictability, it seems of comparable magnitude for all other considered predictabilities. This might actually indicate a threshold at rather low levels of predictability, above which the influence of predictability on the eye blink dynamics remains stable. A possible explanation could be the influence of two opposed factors within predictability with one being the actual objective predictability of the signal facilitating temporal prediction, while the other might be related to the increasing monotony of the task with increasing predictability possibly attenuating sustained attention. A refined exploration of the dependence of eye blink dynamics on the dimension of task predictability remains thus an interesting pathway for future research.

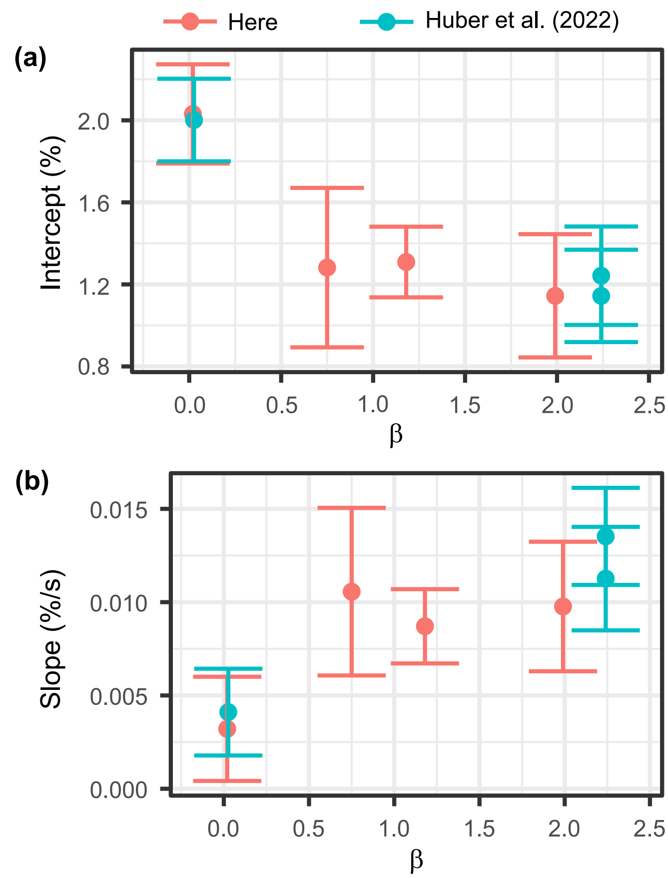

Fig. 5. (a) Intercepts and (b) slopes of regression lines fitted to pre-stimulus blink proportion distributions resulting from auditory attention tasks involving indication of stimulus detection via a keypress in the present experiment (red points and error bars) and in our previous experiment (Huber et al., 2022; blue points and error bars). The intercepts and slopes are plotted against the exponents β characterizing the dependence of the power spectral densities on frequency of the respective series of inter-stimulus-intervals used to vary task predictability within the two experiments. Low values of β indicate low predictability. Note that in our previous study, two participant groups were subject to the higher task predictability; hence, the two data points at $\beta = 2.24$ for both, intercept and slope. Error bars correspond to 95 %-confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Explicit consideration of the dimension of task predictability deserves attention also due to the particularly weak effect on eye blink dynamics in the case of low predictability. In this case, the inter-stimulus-intervals characterizing the timings of stimuli correspond to Gaussian noise. However, timings of consecutive stimuli according to Gaussian noise, i.e. inter-stimulus-intervals being distributed according to a normal distribution with the mean representing the average time interval between consecutive stimuli, represent a rather typical choice in experimental psychological research (e.g. in temporal jittering of stimulus onsets). Yet they turn out to be especially poorly suited to probe the temporal prediction component of attentional processes as our results suggest. In fact, our results show that prediction affects eye blink dynamics also during an auditory task involving no active, manual response to stimuli. However, if task predictability becomes as low as is the case for Gaussian noise, the effect appears insignificant, which is why we think that the small, yet still present effect could not be detected in the earlier study by Brych and Händel (2020). To their solid body of conclusions, we would hence add that pre-stimulus effects in preparation to sensory input are also in effect in the auditory domain, but to a considerably smaller extent. The perception modality clearly modulates the magnitude of the effect, but the general attentional mechanisms regulating eye blink dynamics remain probably unchanged.

4.2.4. Limitations and outlook

In our experiments, the eye blink dynamics has been explored via eye-tracking utilizing the transient loss of pupillometric data while blinking. Thus, different forms of eye blinking such as spontaneous, reflex or partial blinks (Ousler et al., 2014; Stern et al., 1984) cannot be distinguished and also sporadic departure of the gaze from the display cannot be entirely ruled out. Although it can be assumed that most of the temporarily missing pupillometric data stems from spontaneous eye blinking, attempts to replicate and refine our findings using other means of measuring eye blinking such as manual video analysis, EEG or EOG would appear valuable directions for future research. As summarized by Rodriguez et al. (2017), eye blinking is further influenced by many other internal and external factors like physiological or psychological disorders or diseases, age, or also physico-chemical, environmental conditions such as wind, temperature, illumination. An eventual further moderating or modulating impact of such factors on the modulation of eye blinking by task structural or temporal components could also not be resolved by our controlled laboratory experiments and hence remains open for future investigations.

5. Conclusion

We conclude that eye blink dynamics is affected by top-down, cognitive processing associated with prediction also in purely auditory attention tasks, although to a lesser extent than in visual attention tasks. The partial synchronization of eye blinking with temporal task characteristics is further modulated by the involvement of active, manual responses in the task, i.e. it is more pronounced in the case that a respective manual response such as pressing a key is required from participants than in the case that processing of stimuli can be done mainly cognitively by e.g. silent counting of stimuli. Task predictability turns out to be another, but weaker modulating factor of this eye blink synchronization. Especially under unpredictable conditions, e.g. when inter-stimulus-intervals are distributed according to Gaussian noise, the modulation of eye blink dynamics can become so weak that it could hardly be noticed. This has the important implication that, if especially this general, modality-unspecific prediction component involved in attention is what is aimed to probe, other forms of temporally distributing stimuli, or assessing even a range of tuned task predictability like in the present work, should rather be employed. Concerning particularly eye blinking this means, that prediction appears to remain an active, contributing factor for the moment-to-moment, dynamical regulation of eye blinking also in the case of non-visual tasks. Only its relative weight with respect to other regulative factors seems to be affected by modality, whereas the latter further depends on the eventual involvement of other, especially manual, motor response to stimuli, and the rarely explicitly considered predictability of the task at hand. Nevertheless, also in that case, general attentional processes and particularly prediction remain substantial factors underlying the dynamical regulation of eye blinking.

CRediT authorship contribution statement

Stefan E. Huber: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Resources, Software, Validation, Visualization, Writing – original draft. **Markus Martini:** Project administration, Resources, Software, Writing – review & editing. **Pierre Sachse:** Funding acquisition, Resources, Supervision, Writing – review & editing.

Declaration of competing interest

None.

Data availability

None-identified data underlying this work are available from the OSF website for this research: https://osf.io/v2bfn/.

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