Patterns of eye blinks are modulated by auditory input in humans

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ABSTRACT

Previous studies could elaborate a link between attentional processes and eye blinking in both visual and auditory attention tasks. Here we show that this link is active at a fundamental level of perception: presentation of a series of bare sine tones is sufficient to induce a modulation of temporal blink patterns, allowing to determine which series was presented to participants even when they are not required to interactively engage in processing the auditory input. In particular, we monitored eye blinking during an auditory attention task using two series of sine tones, differing in the predictability of the timing of tone onsets. Whereas inter-onset intervals in one tone series corresponded to uncorrelated samples from a normal distribution, they were distributed according to a Gaussian random walk in the other tone series. We find that blink patterns are dynamically modulated by both purely auditory inputs. The magnitude, form, and coherence of the temporal associations between tone onsets and blink events depend strongly on the requirement to respond to the presented stimuli. The predictability of the tone series appears to modulate pre-stimulus blink inhibition given that a response is required. Altogether, these findings suggest eye blink as a readily available, non-invasive behavioral marker for context-sensitive, moment-to-moment allocation of attention.

1. Introduction

Eye blink, i.e. the rapid, temporary closing of the eyelid, is one of the most frequent human behavioral processes, taking place on average about 12–15 times per minute (Doughty & Naase, 2006). Blink frequency usually exceeds the threshold related to its physiological purposes of cleaning and lubricating the surface of the eye to provide a stable tear film (Sweeney, Millar, & Raju, 2013), to prevent optical aberrations (Koh et al., 2006; Koh et al., 2008), and to maintain a good quality of vision (Montés-Micó, 2007). This is in accordance with the fact that the temporal patterns of eye blinks seem to be affected by a multitude of endogenous and exogenous factors (Cruz, Garcia, Pinto, & Cechetti, 2011; Rodriguez et al., 2017). In particular, besides physical or chemical, environmental conditions (Nakamori, Odawara, Nakajima, Mizutani, & Tsubota, 1997; Ponder & Kennedy, 1927; Tsubota, 1998; Tsubota et al., 1996), mean blink rate (MBR) was found to be affected by the degree of required attention (Baumstimler & Parrot, 1971; Cho, Sheng, Chan, Lee, & Tam, 2000; Drew, 1951; Gregory, 1952; Ponder & Kennedy, 1927; Poulton & Gregory, 1952), mental arousal (Březinová & Kendell, 1977; Stern, Walrath, & Goldstein, 1984; Telford & Thompson, 1933), emotional state (Ponder & Kennedy, 1927), fatigue (Kaneko &

Sakamoto, 2001; Maffei & Angrilli, 2018; Stern, Boyer, & Schroeder, 1994), sleep deprivation (Barbato et al., 1995, 2000; Barbato et al., 2007; Crevits, Simons, & Wildenbeest, 2003), task difficulty (Tanaka & Yamaoka, 1993), task nature such as arithmetic operations or memory tasks (Bacher, Retz, Lindon, & Bell, 2017; Fukuda, Stern, Brown, & Russo, 2005; Holland & Tarlow, 1975; Irwin, 2014), verbal activities (Bentivoglio et al., 1997; Karson et al., 1981; Mori et al., 2008), working at visual displays (Freudenthaler, Neuf, Kadner, & Schlote, 2003; Schlote, Kadner, & Freudenthaler, 2004; Tsubota, 1998; Tsubota & Nakamori, 1993), simulated driving (Lal & Craig, 2002), flying (Morris & Miller, 1996) and air traffic control (McIntire, McKinley, Goodyear, & McIntire, 2014).

One explanation for inter-individual differences in MBR is supposedly related to an association between MBR and dopaminergic activity, a specifically valuable finding in clinical contexts (Jongkees & Colzato, 2016; Taylor et al., 1999). In fact, pathologies associated with hypo-dopaminergic activity such as Parkinson's disease (Agostino et al., 2008; Biousse et al., 2004; Karson, LeWitt, Calne, & Wyatt, 1982; Korošec, Zidar, Reits, Evinger, & VanderWerf, 2006; Sandyk, 1990) or attention-deficit and hyperactivity disorder (Groen, Börger, Koerts, Thome, & Tucha, 2017; Konrad, Gauggel, & Schurek, 2003) are associated with

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reduced MBR, whereas pathologies associated with hyperdopaminergic activity like schizophrenia (Karson, 1983; Mackert, Flechtner, Woyth, & Frick, 1991; Mackert, Woyth, Flechtner, & Volz, 1990; Mackintosh, Kumar, & Kitamura, 1983), autism (Goldberg, Maltz, Bow, Karson, & Leleszi, 1987; Shultz, Klein, & Jones, 2011), depression (Mackintosh et al., 1983), panic disorder (Kojima et al., 2002) or Tourette's syndrome (Tulen et al., 1999) are associated with enhanced MBR. The dopaminergic function is also closely related to attention (Maffei & Angrilli, 2018), which manifests e.g. in cognitive difficulties associated with schizophrenia and Parkinson's disease (Green, 2006; Nieoullon, 2002). Whereas reduced dopaminergic activity in Parkinson's disease is associated with cognitive rigidity, the opposite is the case in schizophrenia (Nieoullon, 2002): attention seems to switch due to any perceivable environmental variation. Due to its capability of capturing these interrelations, MBR has been suggested as an ecological index for the dopaminergic component of attention allocation (Maffei & Angrilli, 2018).

Studies focusing on dynamic, moment-to-moment associations between the timings of blinks and temporal aspects of task structure or situational factors are scarcer than studies focusing on MBR, but could reveal that blink patterns are related to temporal characteristics of other motor behavior such as head or eye movements and variations in facial expressions during a conversation (Trutoiu, Hodgins, & Cohn, 2013), as well as speech content (Ford, Bugmann, & Culverhouse, 2013). Furthermore, the *synchronization* between event series of blinks of individual conversation partners or people jointly watching movies was also found to be modulated by the degree of shared interest in the common activity independently of the overall MBR (Nakano & Miyazaki, 2019).

A close association between eye blink and attention has been noted for a long time (Haathi & Wourinen, 1919; Ponder & Kennedy, 1927). More recent studies could add that blinking seems momentarily inhibited when relevant information is expected (e.g. Fukuda, 1994; Nakano & Miyazaki, 2019; Nakano, Yamamoto, Kitajo, Takahashi, & Kitazawa, 2009; Oh, Han, Peterson, & Jeong, 2012). Hoppe, Helfmann, and Rothkopf (2018) showed that participants, whose task was not to miss specific, temporary, short visual events, quickly learned to blink strategically, i.e. to blink rather when nothing task-relevant was supposed to happen than when a visual target event could probably occur.

Intriguingly, the close association between blinking and the timing of crucial task events was also found when merely acoustic stimuli were presented to participants (Fukuda, 1994; Kobald, Wascher, Heppner, & Getzmann, 2019; Oh, Jeong, & Jeong, 2012). In a comparison of results obtained via visual and auditory discriminative tasks, Fukuda (1994) noted that also auditory discriminative tasks resulted in an increased post-stimulus blink frequency compared to no-discrimination baseline conditions. Furthermore, the perception modality yielded no main effect and Fukuda concluded (Fukuda, 1994, S. 1607) that "the blink-rate peak is dependent upon stimulus discrimination and not upon stimulus modality". In the experiment of Oh, Jeong, and Jeong (2012) participants were asked to mentally count the number of tones of different pitches presented during stimulus periods and give their response via numbered keypads in subsequent response periods. Signaling cues were used to indicate the beginning of the different periods. The authors found that blinking was attenuated during stimulus periods as well as in the time between response cues and the participants' manual responses. The temporary suppression of eye blinks was in both cases followed by significant eyeblink facilitation. In a go-no-go task employing also exclusively auditory, particularly verbal stimuli, Kobald et al. (2019) also found that blinks were suppressed during stimulus presentation and that the temporary suppression was suspended significantly earlier in no-go than in go trials, i.e. when a signaling verbal cue had rendered subsequent information irrelevant. These results can hardly be explained solely on the basis of a principle of minimization of *visual* information loss. Instead, they accord with the notion that blinking is inherently and generally associated with the cognitive evaluation of environmental

stimuli (Wascher, Heppner, Möckel, Kobald, & Getzmann, 2015) and is actively involved in the dynamic allocation and deallocation of attention (Nakano, 2015; Nakano, Kato, Morito, Itoi, & Kitazawa, 2013).

Here, we also act on the premise that it is attention that constitutes an inherent, dynamic, moment-to-moment interrelation between the distribution of blinks over time and the structural characteristics of a task. Referring to Klix (1971), we call attention that functional system that *proactively* prepares the receptors of an organism such that (situationally) relevant information can be optimally processed - involving an appropriate timing of blinking. Since this function incorporates forecasting capabilities (Sokolov, 1963) and since stimuli cannot be generally assumed to indicate relevant information only along with their own modality – especially not under circumstances of everyday life – we expect that this results in a temporally tightly matched synchronization of eye blinking with task structure largely independent of the involved perception modality.

To this end, we designed an experiment in order to demonstrate the tight, moment-to-moment connection of blink patterns to temporal task structure for basic acoustic stimuli (sine tones) used as input. In addition, we varied the signal characteristics of the stimuli referring to the terminology of Sokolov (1963) such that *signal-stimuli* would require a (motoric) response by the participants whereas *non-signal-stimuli* would not. In particular, in the case of signal-stimuli participants were asked to detect each individual tone and indicate detection by a keypress. In the case of non-signal stimuli, tones were presented as well, but participants were not required to respond. In both cases, tones were presented consecutively in form of one of two series of 200 short, identical sine tones. The overall experimental setup is graphically illustrated in Fig. 1 (a) and will be explicated in detail in Section 2.1. The two tone series were further distinct with respect to their predictability providing a
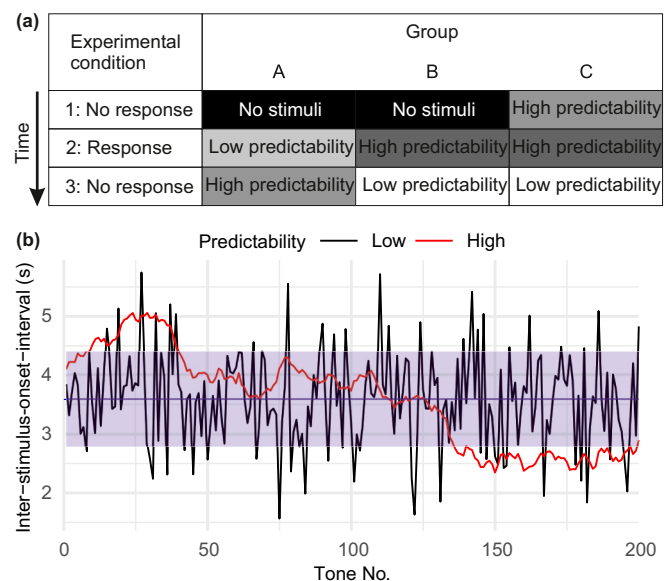

Fig. 1. (a) Experimental design: Participants were assigned to one of three groups A, B, or C which differed from each other with respect to the order in which two distinctly predictable series of acoustic stimuli were presented to the participants. Different background colors indicate different stimulus characteristics, i.e. the background color of two cells is the same if both predictability and requirement to respond are the same in the respective experimental conditions, and differs between two cells otherwise. (b) Inter-stimulus-onset-intervals between each pair of consecutive, identical sine tones presented to the participants for the tone series with low predictability (black line) and with high predictability (red line). The overall mean inter-stimulus-onset-interval and its standard deviation are indicated by the blue line and blue shaded region, respectively, and are the same for both tone series. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

distinctive measure of their temporal structure, in particular their predictability, i.e. how easy it would be to predict the time of occurrence of the next stimulus based on the timings of past stimuli, see Fig. 1(b). With this experimental framework we aimed to empirically test the following specific hypotheses:

(a) The synchronizing effect of task-structure on the timing of eye blinking identified and illustrated nicely by the analysis of Hoppe et al. (2018) for the visual modality exists and should be detectable also when using auditory stimuli.

(b) The synchronization is assumed to be caused by fundamental properties of attention for the organization of perception for the purpose of information processing. Hence, it should be present for any basic stimuli exhibiting sufficient salience to be processed at all. It should especially *not* necessitate any complex, eventually culturally primed, inner stimuli structure such as inherently prevalent for the use of verbal (Kobald et al., 2019) or musical (Oh, Jeong, & Jeong, 2012) stimuli associated also with more extensive cognitive evaluation (stimulus discrimination, verbal processing, counting, mnemonic processes, etc.).

(c) The magnitude of the modulation of temporal blink patterns by task structure should be associated with the requirement to respond to the stimuli as a measure of their signal characteristic. In particular, for stimuli which require a motoric response by the participants, the temporal distribution of blink patterns should be affected to a larger extent than for stimuli not requiring a response.

(d) Due to the proactive aspect of attention, i.e. as the functional system *preparing* the receptors for optimal information processing in a given situation (Klix, 1971; Sokolov, 1963), the modulation of blink patterns should also be associated with the temporal predictability of the series of the presented stimuli. Note that in the mentioned earlier studies employing auditory attention tasks (Fukuda, 1994; Kobald et al., 2019; Oh, Jeong, & Jeong, 2012) the usage of fixed time frames and signaling cues would naturally mask the influence of this fundamental aspect of organismic perception organization on the temporal orchestration of blinking.

In 2016, Bonneh, Adini and Polat stated that "spontaneous eyeblinks are known to serve important physiological functions, and recent evidence shows that they are also linked to cognitive processes. It is yet unclear whether this link reflects a crude rate modulation or, alternatively, an automatic and precise process, tightly linked to the low-level properties of sensory stimuli." We think that the results obtained by Hoppe et al. (2018) already allow to regard this question as answered and that the temporal regulation of blinking indeed represents such a precise process linked to low-level properties of sensory stimuli. With our experiment, we would like to add, however, that the inherent, dynamically fine-tuned concertation of cognitive and perceptual processes reflected in the temporal organization of eye blinking is very likely to go beyond the visual perception modality. Based on the results of our experiment we shall discuss that it rather appears related to the organization of perception in a very general way, encountered probably not only in human beings but eventually among all species equipped with vision, eyelid closure reflex, and orienting response.

2. Method

All experimental procedures were carried out in accordance with the guidelines of the German Psychological Society and approved by the ethics committee of the Leopold-Franzens-University Innsbruck. Written informed consent was obtained from all participants.

2.1. Experimental setup

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), throughout each of the three experimental conditions.

The acoustic stimuli represented by sine tones of a frequency of 500 Hz with a duration of 50 ms each were presented to the participants diotically via headphones at a sound level adjusted in a pilot phase of the experiment such that stimuli were audible at a comfortable level for the duration of one experimental condition for a few test subjects. The exact times, at which stimuli were presented, were distributed over the twelve minutes of each experimental condition [Fig. 1(a)] according to the two prepared tone series of low and high predictability [Fig. 1(b)]. For the tone series of low predictability, the durations between onsets of consecutive sine tones (inter-stimulus-onset-intervals) were temporally uncorrelated and drawn individually from a normal distribution (with a mean of 3.59 s and a standard deviation of 0.8 s). The intervals between onsets of consecutive tones for the series of high predictability corresponded to a Gaussian random walk (or Brownian motion) scaled such that the total series yielded the same overall mean and standard deviation as the series of low predictability.

During the second experimental condition [Fig. 1(a)], participants were asked to respond to each of the presented tones via a keypress, whereas during the other two conditions participants were not required to attend to the acoustic stimuli (if they were presented at all). The order in which tone series of low and high predictability were presented varied among groups.

Note that the inclusion of two conditions in which no tone series were presented to the participants at all [Fig. 1(a), groups A and B] was primarily due to our interest in the question of whether the auditory attention task would induce also a change in fractal regulation of eye blinking compared to a free viewing condition. Variations of fractal regulation of blinking in relation to task demands had been suggested in earlier studies (Lenskiy & Paprocki, 2016; Paprocki & Lenskiy, 2017). We could not identify any significant change in fractal regulation due to the auditory attention task and since this question is not in the focus of the present work, it will not be discussed further here. However, details on this issue can be found elsewhere (Huber, 2021).

2.2. Participants

In total, 55 participants (38 female, mean age [SD]: 22.96 [4.87] years) took part in the experiment in exchange for course credit. 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.

2.3. Data acquisition

The onsets of blinks were detected using an infrared eye-tracking device with a sampling frequency of 300 Hz (Tobii TX300; Tobii Technology AB, 2014) and the blink detection algorithm by Hershman, Henik, and Cohen (2018). When closing the eyes during blinking, the eye-tracking device loses track of the participants' pupils. These artifacts in the pupillometric data were used to compute the onsets of corresponding blinks. These onsets were then treated as point processes in our analysis of the temporal blink distributions with respect to the tone events. Using this procedure, we found similar statistics concerning overall blink rates (mean [SD]: 24.05 [12.27]; both given in blinks per minute), inter-blink-intervals (mean [SD]: 3.04 s [2.15 s]) and fractal scaling (mean [SD]: 0.66 [0.12]) compared with studies using magnetic search coils (see e.g. Garcia, Pinto, Barbosa, & Cruz, 2011), manual video analysis (e.g. Naase, Doughty, & Button, 2005), EEGs and EOGs (e. g. Oh, Han, et al., 2012; Oh, Jeong, & Jeong, 2012; Paprocki & Lenskiy, 2017; Shin et al., 2015). During four experimental conditions, however,

the pupillometric data exhibited short transient data loss more than a thousand times by the eye tracking device which we regarded as an unreasonable high number to be accounted for by blinking alone and thus excluded these 4 of in total 165 data sets. Only the pupillometric data of the dominant eye of each participant were analyzed. The dominant eye of each participant was determined by a simple alignment test after all three experimental conditions were finished. In particular, participants were first 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 further asked to fixate a plug socket located at the wall of the laboratory in a distance of about 3 m from them. Without moving, they were then asked to first close one eye and then 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 it would not.

2.4. Data analysis

2.4.1. Global blink characteristics

Individual blink behavior can vary widely among individuals. In order to control for these otherwise confounding factors, we determined the MBR, the median blink duration, and the first four moments of the inter-blink-interval (IBI) distribution for each of the participants in each condition. The IBIs are the time intervals between consecutive blinks, i. e. the durations from blink offset of the foregoing to blink onset of the subsequent blink for all pairs of consecutive blinks (Matsumoto-Oda, Okamoto, Takahashi, & Ohira, 2018), and as such the complement to the blink durations. The mean IBI is a similar measure as the inverse of the MBR, however, taking into account the times the eyelids were closed during blinks. The second moment of the IBIs-distribution, i.e. its standard deviation, is a global measure of the variability of how blinks are interwoven in time in the respective experimental condition. The third and fourth (standardized) moments of the IBIs-distribution are its skewness and kurtosis, respectively. Note that we particularly used the excess kurtosis but refer to it simply as kurtosis in the remainder of this work for convenience. Two-way, mixed ANOVA was used to test for main effects of experimental condition and group and their interaction for all considered control variables. Robust two-way, mixed ANOVA based on trimmed means (Mayr & Wilcox, 2020) was used if required assumptions for parametric tests were violated by the respective data.

2.4.2. Individual-level analysis

Our first hypothesis states the *existence* of temporal associations between presented tones and blink events without a priori specifying any specific type or form of such an association. To put this general assertion to the test, we investigated all *individual* temporal blink distributions for the indication of any temporal association with the series of occurrence times of the presented sine tones. In order to do so, we subdivided the 1.5 s intervals before and after each presented sine tone into 15 short 100 ms bins and counted how many eye closures occurred in each of these intervals over the full duration of 12 min, i.e. we "locked" the two 1.5 s time windows onto the occurrence times of the presented stimuli. It is very important to note that if there is no association between the two binary signals formed by the temporal blink patterns (blinks are either "on", i.e. the eyelid is closed, or "off", i.e. the eyelid is open) and the tone series (also the sine tones are either "on" or "off"), then onsets of one of the signals are equally likely to occur at every instance of time before or after the onsets of the other signal. Indeed, this is exactly the meaning of two signals being temporally independent of each other: How one of the signals varies over time is independent from the other. Hence, given temporal independence of the two considered signals, the frequency with which eye closures would occur during each of the 15 short 100 ms bins in the two time windows specified above should conform most likely with a uniform temporal distribution in both time windows. In contrast, any systematic association between the two signals should correspond to a systematic deviation from uniformity in at least one of

the two considered time windows. Thus, in order to scrutinize the mere *existence* of any temporal association between the tone onsets and blink events, the temporal distributions of eye blinks in each of the two considered time windows before and after the stimuli onsets were individually compared to a uniform distribution. The deviation from uniformity was tested for statistical significance using a χ^2-test. However, due to a non-zero error probability when testing the null hypothesis (i.e. that distributions are uniform) there is a proportionally small chance for a type I error, i.e. to reject the null hypothesis falsely. In fact, the probability P to arrive at m or more significant deviations from uniformity out of a total number of n performed χ^2-tests (on n distinct distributions) when the null hypothesis is, in fact, true in each case and given an error probability of α can be computed according to the binomial distribution:

$$P = \sum_{k=m}^{n} \binom{n}{k} \alpha^k (1-\alpha)^{n-k}. \tag{1}$$

Furthermore, given that no temporal association between the binary signals exists, the *p*-values of the conducted χ^2-tests should also represent a uniform distribution over the interval [0,1]. Each *p*-value should be equally probable and the probability that a χ^2-test yields $p \leq x$ should be equal to x, i.e. the cumulative distribution function (CDF) of resulting *p*-values should be linear with slope 1. The agreement between the empirically obtained distribution of *p*-values and the theoretical prediction can be assessed by a P-P-plot. For coinciding empirical and theoretical CDFs the resulting points should be located on the diagonal of the plot. Using Kolmogorov-Smirnov-tests (KS-tests) the deviation and its statistical significance of the empirical distribution of *p*-values from the theoretical distribution can be quantified.

For each combination of signal characteristic (i.e. motoric response required or not) and predictability we both computed P according to Eq. (1) using an error probability of $\alpha= 0.05$ and assessed the uniformity of *p*-values obtained via the conducted χ^2-tests by P-P-plots and KS-tests in order to evaluate the likeliness of that result in the case that there truly was no temporal association between tone onsets and blink events.

Taking a literature value for the mean blink rate of about 15 blinks per minute (see e.g. Doughty & Naase, 2006) let us expect about 180 eye blinks per participant during each experimental condition. Distributing this number of expected blinks uniformly over the entire 12 min of each of the experimental conditions would result in a total of 75 blinks over the five minutes for which each of the two observed 1.5 s intervals would account after aggregation over all 200 stimuli. Decomposing each of the time windows into 15 bins finally results in an expected value of 5 blinks per bin which represents a reasonable, albeit small number for computation of the χ^2-statistics. The decomposition into 15 bins hence represents a compromise between allowing a fine resolution of the temporal distribution of eye blinks with respect to the occurrence times of stimuli and yet providing enough observations per bin to allow for reasonable statistical analyses.

2.4.3. Group-level analysis

Hypotheses (c) and (d) given in the introduction state how an existent effect should *change* upon variation of other variables, in particular, how the temporal association between tone onsets and blink events should be affected by the requirement to motorically respond to the stimuli and the predictability of the tone series. Hence, the hypotheses make statements about the *form* of the temporal associations between tone onsets and blink events. In order to investigate the form of temporal association and how it is affected by the requirement to respond and predictability, we aggregate the individual temporal blink distributions obtained for the two time windows described above over each of the 3 × 3 cells of experimental conditions and groups given in Fig. 1(a). The rationale behind this approach is analogous to the one known from event-related potentials in EEG research (Gazzaniga, Ivry, & Mangun, 2014). It is known that blink behavior can vary substantially between

individuals in general and the same is likely to be the case for the stimuli-locked temporal blink distributions considered here. If however, there is some coherence in the effect which the stimuli, their predictability or the requirement to respond exert on the blink distributions, then by aggregation of the distributions other inter-individual fluctuations should cancel out with an increasing number of subjects in each group and an average effect should precipitate. However, absolute blink frequency distributions in the two considered time windows obviously depend largely on the overall likeliness of a subject to blink, i.e. they depend on the overall blink rate of the subject which is also known to fluctuate highly depending on both intra-individual and contextual factors (Doughty, 2001, 2002; Doughty & Naase, 2006). To take this into account we normalized each individual blink distribution before aggregation by dividing the absolute blink frequencies by the overall number of blinks of the respective subject in the respective condition. The resulting aggregated normalized distributions for each of the experimental conditions thus represent stimuli-locked temporal mean blink proportion (MBP) distributions specifying which proportion of all blinks occurred during a specific 100 ms interval in the considered time window. Linear mixed-effects models were used to determine if blink proportions varied significantly with experimental condition (and hence the requirement to motorically respond to the stimuli), group, time interval in the considered time window, and their interactions (fixed factors). Global descriptors of individual blink behavior were included in the model as covariates for controlling their eventual impact on blink proportions. Due to considerable collinearities between some of those covariates (see Results) only a subset of them was included in each of the models for the time windows before and after the occurrence times of stimuli. The included subset consisted of those combination of covariates reducing the residual error of the model the most. In the case of the model for the time window before the occurrence times of the stimuli the included covariates were the medians of the blink durations, the MBR and the skewness of the IBIs-distribution. In the case of the model for the time window after the occurrence times of the stimuli MBR was replaced by the standard deviation of the IBIs-distribution. The participant ID (nested within the experimental condition and time interval) was included in the model as a random effect (intercepts).

2.4.4. Statistical analysis

All statistical analyses were conducted using R (R Core Team, 2021) and RStudio (RStudio Team, 2021) using the packages dplyr (Wickham, François, Henry, & Müller, 2021), ggplot2 (Wickham, 2016), ggpubr (Kassambara, 2020), nlme (Pinheiro, Bates, DebRoy, Sarkar, & Core Team, 2021), pastecs (Grosjean & Ibanez, 2018), readxl (Wickham & Bryan, 2019), reshape2 (Wickham, 2007), rstatix (Kassambara, 2021), WRS2 (Mayr & Wilcox, 2020).

2.4.5. Data availability

Note that all pupillometric data, keypress timings and tone onset timings are available at the Open Science Framework (OSF) website for this research (Huber, Martini, & Sachse, 2021).

3. Results

3.1. Global blink characteristics

The means and their standard errors of the determined global descriptors of blink behavior, i.e. the MBR, the median of blink durations as well as the first four moments of the IBIs-distributions are supplied in Table 1.

Concerning MBRs, there was a significant main effect of the condition, $F(2, 96) = 5.174$, $p = 0.007$. Bonferroni-corrected pairwise comparisons revealed that MBRs were larger in condition 3 than in condition 1, $t(50) = 3.01$, $p = 0.012$, were close to a tendency to be larger in condition 2 than in condition 1, $t(52) = 2.12$, $p = 0.12$, but did not differ significantly between conditions 3 and 2, $t(52) = 1.34$, $p = 0.55$.

Concerning the medians of blink durations, Mauchly's test indicated that the assumption of sphericity had been violated for the main effect of the condition, $W = 0.836$, $p = 0.015$. Therefore, degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity. There was a significant main effect of the condition, $F(1.72, 82.45) = 10.086$, $p < 0.001$. Bonferroni-corrected pair-wise comparisons revealed that the medians of blink duration were larger in condition 2 than in condition 1, $t(52) = 4.97$, $p < 0.001$, yielded a tendency to be larger in condition 3 than in condition 1, $t(50) = 2.22$, $p = 0.09$, but did not differ significantly between conditions 3 and 2, $t(52) = 1.77$, $p = 0.25$.

Concerning the considered four moments of the IBIs-distributions, several of the assumptions for parametric ANOVA were violated, hence, the results of a robust, two-way, mixed ANOVA using trimmed means (Mayr & Wilcox, 2020) are reported in those cases.

Concerning the means of the IBIs, there was a significant main effect for group, $Q(2, 23.957) = 9.8715$, $p < 0.001$. Bonferroni-corrected pairwise comparisons revealed that the means of the IBIs were smaller in group A than in group B, $\widehat{\Psi} = 1.06$, $p < 0.001$, yielded a tendency to be smaller in group A than in group C, $\widehat{\Psi} = 0.88$, $p = 0.07$, but did not differ between groups B and C, $\widehat{\Psi} = 0.18$, $p = 1$.

Concerning the standard deviations of the IBIs, there was a significant main effect for group, $Q(2, 23.9109) = 5.2372$, $p = 0.013$. Bonferroni-corrected pairwise comparisons revealed that the standard deviations of the IBIs were smaller in group A than in group C, $\widehat{\Psi} = 1.27$, $p = 0.019$, were close to a tendency to be smaller in group A than in group B, $\widehat{\Psi} = 0.92$, $p = 0.12$, but did not differ between groups B and C, $\widehat{\Psi} = 0.35$, $p = 1$.

Concerning the skewness and kurtosis of the IBIs-distributions, neither one of the main effects of group and condition nor their interaction was significant. Hence, skewness and kurtosis were not significantly different across groups and conditions.

Overall means and standard deviations of the considered global descriptors of blink behavior are provided in Table 2. Also given are pairwise Pearson correlation coefficients corresponding each to regarding a pair of descriptors for one participant and condition as a single point on a scatter plot. The MBRs, the means of the IBIs, and the standard deviations of the IBIs were highly correlated among each other

Table 1

Number of included blink data, n, means of the mean blink rate (MBR) given in blinks per minute, means of the median of blink duration (MBD) given in ms, means of the mean of inter-blink-intervals (IBIs) given in s, means of the standard deviation (SD) of IBIs given in s, and means of the skewness and the kurtosis of IBIs (both dimensionless) for each experimental condition and each group. Standard errors of the respective means are given in parenthesis.

Condition	1			2			3		
Group	A	B	C	A	B	C	A	B	C
n	18	17	18	18	19	18	17	19	17
MBR [blinks/min.]	24.1 (2.1)	20.0 (2.2)	21.3 (3.3)	30.0 (3.1)	20.2 (1.8)	23.2 (2.5)	30.9 (3.4)	21.6 (2.8)	25.8 (3.8)
MBD [ms]	211 (11)	183 (8)	208 (10)	227 (13)	212 (9)	221 (12)	225 (15)	208 (11)	209 (10)
Mean (IBIs) [s]	2.72 (0.36)	3.40 (0.44)	4.23 (0.80)	2.42 (0.55)	3.24 (0.36)	2.83 (0.36)	1.75 (0.19)	3.59 (0.58)	3.07 (0.53)
SD (IBIs) [s]	2.68 (0.46)	2.90 (0.49)	4.22 (0.80)	1.95 (0.41)	3.18 (0.59)	2.71 (0.37)	1.86 (0.36)	3.54 (0.63)	3.58 (0.60)
Skewness (IBIs)	2.09 (0.36)	2.00 (0.25)	2.37 (0.29)	2.07 (0.50)	2.30 (0.26)	2.25 (0.27)	2.29 (0.34)	2.40 (0.42)	3.04 (0.42)
Kurtosis (IBIs)	8.82 (2.72)	6.96 (1.48)	9.75 (2.92)	12.85 (7.55)	9.40 (2.04)	9.24 (2.14)	9.49 (2.70)	11.01 (3.43)	16.06 (4.56)

Table 2

Overall means and standard deviations (second and third columns) as well as pair-wise Pearson correlations coefficients (six rightmost columns) of the considered global descriptors of blink behavior, i.e. the median of the blink durations (MBD) given in ms, the mean blink rates (MBR) given in blinks per minute, the means and standard deviations (SD) of the IBIs given both in s, as well as the skewness and kurtosis of the IBIs-distributions (both dimensionless).

Variables	Mean	SD	1	2	3	4	5	6
1. MBD [ms]	212	47	1					
2. MBR [blinks/min]	24.1	12.3	0.10	1				
3. Mean (IBIs) [s]	3.04	2.15	−0.29***	−0.78***	1			
4. SD (IBIs) [s]	2.96	2.36	−0.25**	−0.74***	0.85***	1		
5. Skewness (IBIs)	2.31	1.45	−0.08	0.02	−0.12	0.22**	1	
6. Kurtosis (IBIs)	10.4	15.5	0.03	0.11	−0.17*	0.06	0.92***	1

$N = 161$.
*** Correlation is significant at the 0.001 level (2-tailed).
** Correlation is significant at the 0.01 level (2-tailed).
* Correlation is significant at the 0.05 level (2-tailed).

with correlation coefficients of at least 0.74 (in absolute value), $p < 0.001$. Also, the skewness and the kurtosis of the IBIs-distributions were highly correlated with each other, $r = 0.92$, $p < 0.001$. Smaller correlations were found between the medians of the blink durations and the means of the IBIs, $r = -0.29$, $p < 0.001$, the medians of the blink durations and the standard deviations of the IBIs, $r = -0.25$, $p < 0.01$, the means of the IBIs and the kurtosis of the IBIs-distributions, $r = -0.17$, $p < 0.05$, the standard deviations of the IBIs and the skewness of the IBIs-distributions, $r = 0.22$, $p < 0.01$.

3.2. Individual-level analyses

3.2.1. Conditions without auditory stimuli

The fact that no auditory stimuli were presented in condition 1 in groups A and B, see Fig. 1(a), is used to illustrate the theoretical presumption that blink onsets should be distributed uniformly in the two time windows before and after stimuli onsets, given no temporal association between the tone and blink onsets. Since no stimuli were presented in this experimental condition, there are no tone onsets with which blink onsets could be temporally associated. Locking the two considered time windows, however, onto those timings of onsets of stimuli presented to each participant during the subsequent two conditions, should also result (mostly) in uniform, temporal blink distributions in both time windows, since blink onsets can by construction not be temporally associated with tone onsets from stimuli presented only during another experimental condition. When timings of tone onsets from stimuli presented in another than the actually considered experimental condition were used in this way for obtaining blink distributions, we refer to the stimuli as *virtual* (since not really presented in the respective condition) in the remainder of this work. By construction, any temporal association between these virtual stimuli and blink events of a participant must be random and occur only rarely within statistically reasonable bounds. In Fig. 2 we depict the resulting temporal blink distributions of two individual cases of group A [Fig. 2(a)] and B [Fig. 2(b)] which were chosen actually because of their responsiveness in the other experimental conditions in which some auditory stimuli had actually been presented. In particular, their individual blink distributions for conditions 2 and 3 exhibit features, such as a transient blink following tone occurrences, which qualitatively resemble those that will turn out as indicative of temporal associations between tone and blink onsets in the group-level analysis given in Section 3.3, compare especially Figs. 3(a)-6(a) and the corresponding panels in Fig. 7. Their blink distributions for condition 1 shown in Fig. 2, however, do not deviate significantly from uniformity, neither in the time windows before virtual stimuli onsets (i.e. t < 0 in the figure), $\chi^2(14) = 7.28$, $p = 0.92$ [Fig. 2 (a)], $\chi^2(14) = 5.06$, $p = 0.99$ [Fig. 2(b)], nor in the time windows after virtual stimuli occurrence times (t > 0), $\chi^2(14) = 17.86$, $p = 0.21$ [Fig. 2 (a)], $\chi^2(14) = 13.33$, $p = 0.50$ [Fig. 2(b)]. χ^2-tests were performed for all temporal blink distributions in both considered time windows, i.e. for t < 0 and t > 0, locked onto virtual stimuli occurrence times taken from

both tone series (i.e. the one with low and the one with high predictability) for all 35 participants in condition 1 in groups A and B. For t < 0 (before virtual stimuli onsets) 1 out of 70 distributions yielded a significant deviation from uniformity, yielding $P = 0.97$ according to Eq. (1). For t > 0 (after virtual stimuli onsets) 2 out of 70 distributions yielded a significant deviation from uniformity, yielding $P = 0.87$. Thus, both numbers of significant deviations are well within statistically reasonable bounds. Both p-value-distributions do also not differ significantly from uniform distributions. The corresponding P-P-plot is given in Fig. 2(c) and KS-tests yield $D = 0.15$, $p = 0.10$ when locking time windows on the stimuli of the series with high predictability ["x"-symbols in Fig. 2(c)], $D = 0.08$, $p = 0.75$ when locking time windows on the stimuli of the series with low predictability ["+"-symbols in Fig. 2(c)].

3.2.2. Signal-stimuli with high predictability

In groups B and C in condition 2 participants were subject to the presentation of series of auditory stimuli with high predictability and were required to respond to each of the presented stimuli with a keypress. Testing the uniformity of temporal blink distributions in the two considered time windows locked onto stimuli onsets resulted in 15 out of 37 distributions (6 out of 19 in group B, 9 out of 18 in group C) deviating from uniformity in the time window before stimuli onsets, yielding $P = 9.96 \times 10^{-11}$ according to Eq. (1). In the time window after stimuli onsets, 36 out of 37 distributions (18 out of 19 in group B, 18 out of 18 in group C) were significantly deviating from uniformity, yielding $P = 5.12 \times 10^{-46}$. If in contrast, time windows were locked onto stimuli onsets corresponding to the virtual series of low predictability (i.e. not presented in this condition), 0 and 3 out of 37 distributions deviated significantly from uniformity in the time window before and after virtual stimuli onsets, respectively, yielding $P = 1$ and $P = 0.28$. In Fig. 3 (a), the temporal blink distributions are shown for the same participant as was chosen for illustration already in Fig. 2(b) in the two time windows locked onto the real (presented) stimuli onsets, while in Fig. 3(b), the participant's blink distributions are shown in the time windows locked onto the virtual (not presented) stimuli onsets. In Fig. 3(c), a P-P-plot is provided comparing the empirical CDFs of obtained p-values for the time window after presented stimuli onsets (triangles), the time window before presented stimuli onsets (squares) and both time windows locked onto virtual stimuli onsets ("+"-symbols). The P-P-plots suggest that the obtained p-values neither for the time window before nor for the time window after presented stimuli onsets conform with a uniform distribution. This is in accordance with performed KS-tests yielding $D = 0.36$, $p < 0.001$ and $D = 0.92$, $p < 0.001$, respectively. In contrast, the distribution of p-values obtained for the time windows locked onto virtual stimuli onsets yields no significant deviation from uniformity, $D = 0.09$, $p = 0.60$.

3.2.3. Signal-stimuli with low predictability

In group A in condition 2 participants were subject to the presentation of series of auditory stimuli with low predictability and were
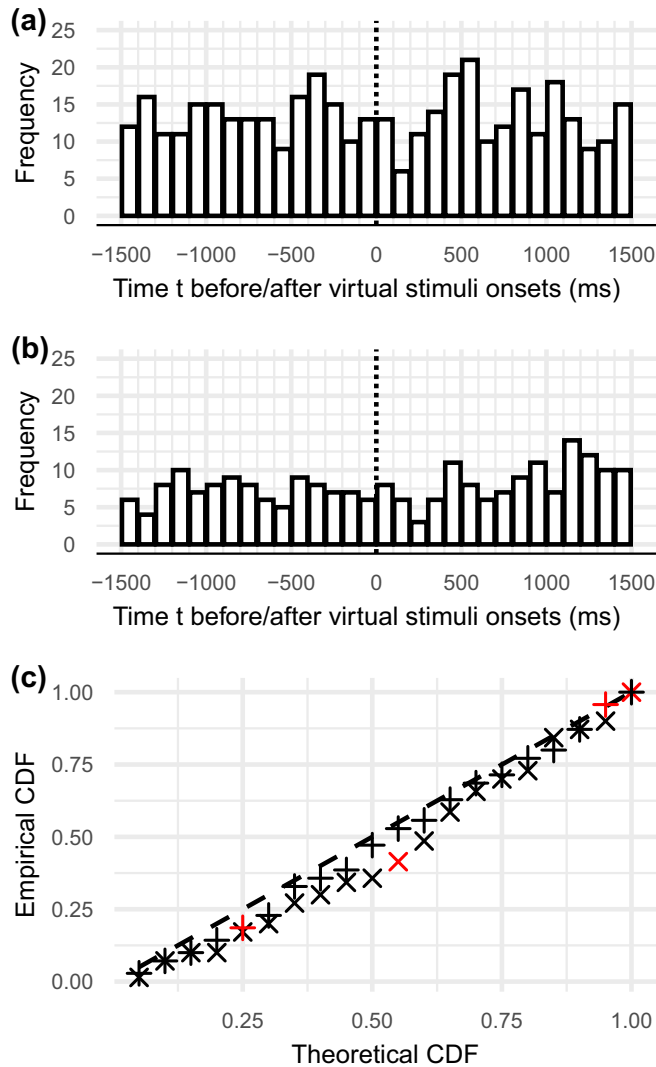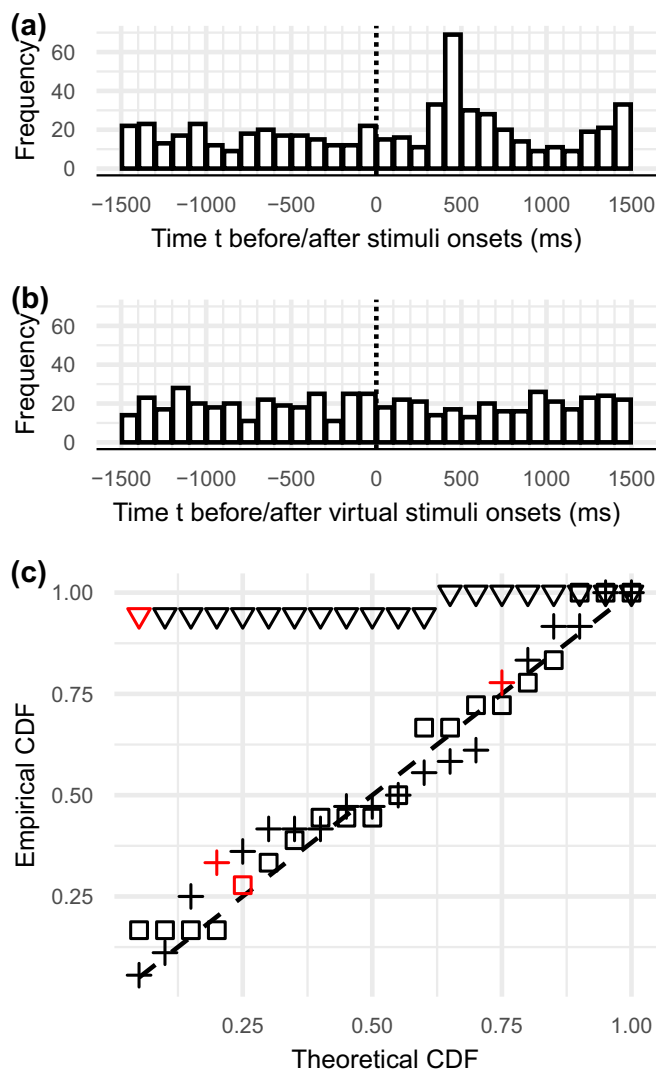
Fig. 2. Temporal blink distributions in the two considered time windows 1.5 s before (t < 0) and after (t > 0) stimuli onsets for two individual participants of (a) group A and (b) group B in condition 1. Note that in that condition in both groups no auditory stimuli were presented, because of which stimuli onsets were denoted as "virtual". Both distributions do not deviate significantly from uniform distributions in neither of the two time windows, $\chi^2(14) = 7.28$, $p = 0.92$ for $t < 0$ and panel (a), $\chi^2(14) = 5.06$, $p = 0.99$ for $t < 0$ and panel (b), $\chi^2(14) = 17.86$, $p = 0.21$ for $t > 0$ and panel (a), $\chi^2(14) = 13.33$, $p = 0.50$ for $t > 0$ and panel (b). In panel (c) a P-P-plot is shown comparing the empirical cumulative distribution functions (CDFs) of p-values obtained from χ^2-tests performed for all blink distributions in both groups in condition 1 in both time windows locked on stimuli of the series with high predictability ("x"-symbols) and low predictability ("+"-symbols) with the theoretical CDF of a uniform distribution. Note that the latter describes the expected distribution of p-values of the respective χ^2-tests if there is no temporal association between the tone and blink onsets. Data points corresponding to the results for the individual participant from group A shown in panel (a) and from group B shown in panel (b) are highlighted in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

required to respond to each of the presented stimuli with a keypress. Testing the uniformity of temporal blink distributions in the two considered time windows locked onto the stimuli onsets resulted in 3 out of 18 distributions deviating from uniformity in the time window before stimuli onsets, yielding $P = 0.06$ according to Eq. (1). In the time window after stimuli onsets, 17 out of 18 distributions were significantly deviating from uniformity, yielding $P = 1.31 \times 10^{-21}$. If in contrast, time
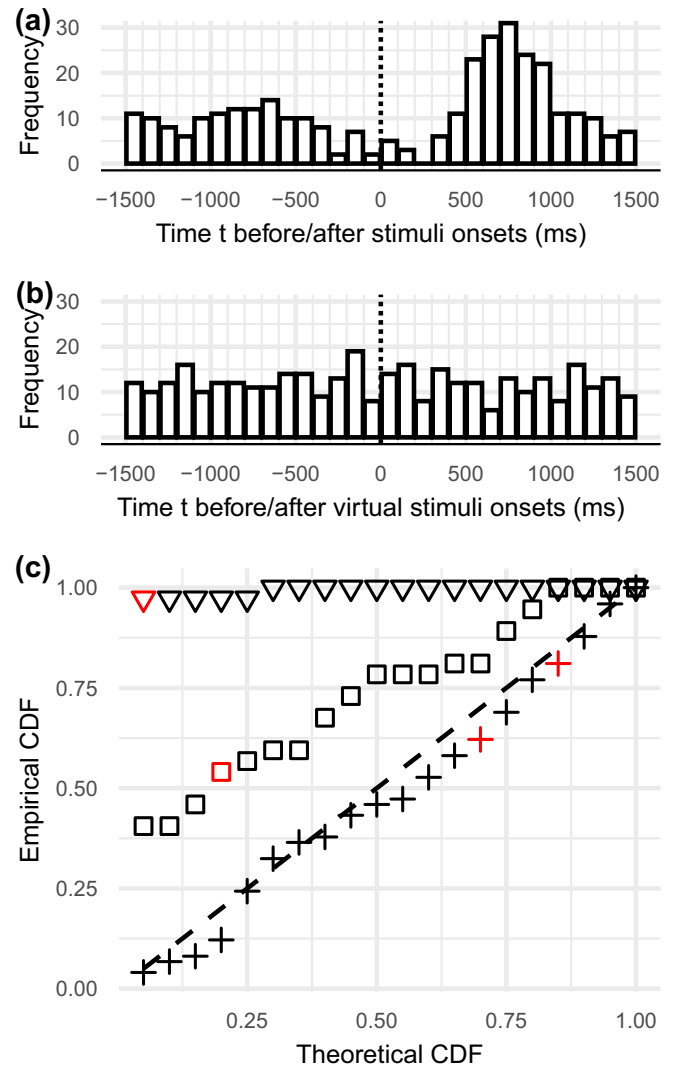
Fig. 3. (a) Temporal blink distributions in the two considered time windows 1.5 s before (t < 0) and after (t > 0) stimuli onsets for a participant of group B in condition 2, i.e. keypress responses were required and the presented series of stimuli had high predictability. Note that the participant is the same one as was chosen for illustration already in Fig. 2(b). The distribution does not deviate from uniformity in the time window before stimuli onsets, $\chi^2(14) = 18.92$, $p = 0.17$ for t < 0, but does in the time window after stimuli onsets $\chi^2(14) = 101.39$, $p < 0.0001$ for $t > 0$. (b) Resulting Blink distributions if time windows are locked on virtual, i.e. not presented stimuli onsets instead. The distributions do not deviate from uniformity in both time windows, $\chi^2(14) = 8.89$, $p = 0.84$ for t < 0, and $\chi^2(14) = 10.99$, $p = 0.69$ for t > 0. (c) A P-P-plot comparing the empirical cumulative distribution functions (CDFs) of p-values obtained from χ^2-tests performed for all blink distributions in groups B and C in condition 2 (i. e. keypress responses required and high predictability) in the time windows before (squares) and after (triangles) presented stimuli and in both time windows locked onto virtual stimuli ("+"-symbols; low predictability). Data points corresponding to the results for the individual participant shown in panels (a) and (b) are highlighted in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

windows were locked onto stimuli onsets corresponding to the virtual (i. e. not presented in this condition) series of stimuli with high predictability, 1 out of 18 distributions deviated significantly from uniformity in each of the two time windows, yielding $P = 0.60$. In Fig. 4(a), the temporal blink distributions are shown for the same participant as was chosen for illustration already in Fig. 2(a) in the two time windows locked onto the real (presented) stimuli onsets, while in Fig. 4(b), the

Fig. 4. (a) Temporal blink distributions in the two considered time windows 1.5 s before (t < 0) and after (t > 0) stimuli onsets for a participant of group A in condition 2, i.e. keypress responses were required and presented series of stimuli had low predictability. Note that the participant is the same one as was chosen for illustration already in Fig. 2(a). The distribution does not deviate from uniformity in the time window before stimuli onsets, $\chi^2(14) = 17.29$, $p = 0.24$ for t < 0, but does in the time window after stimuli onsets, $\chi^2(14) = 145.99$, $p < 0.0001$ for $t > 0$. (b) Resulting Blink distributions if time windows are locked on virtual, i.e. not presented stimuli onsets instead. The distributions do not deviate from uniformity in both time windows, $\chi^2(14) = 18.60$, $p = 0.18$ for t < 0, and $\chi^2(14) = 10.52$, $p = 0.72$ for t > 0. (c) A P-P-plot comparing the empirical cumulative distribution functions (CDFs) of p-values obtained from χ^2-tests performed for all blink distributions in groups A in condition 2 (i.e. keypress responses required and low predictability) in the time windows before (squares) and after (triangles) presented stimuli and in both time windows locked onto virtual stimuli ("+"-symbols; high predictability). Data points corresponding to the results for the individual participant shown in panels (a) and (b) are highlighted in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

blink distributions for the same participant are shown in the time windows locked onto the virtual (not presented) stimuli onsets. In Fig. 4(c), a P-P-plot is provided comparing the empirical CDFs of obtained p-values for the time window after presented stimuli onsets (triangles), the time window before presented stimuli onsets (squares) and both time windows locked onto virtual stimuli onsets ("+"-symbols). The KS-tests yield $D = 0.13$, $p = 0.88$, $D = 0.92$, $p < 0.001$, $D = 0.15$, $p = 0.34$ for

the p-values obtained for the time window before presented stimuli onsets, the time window after presented stimuli onsets and both time windows locked onto virtual stimuli onsets, respectively, suggesting that the p-values obtained for the time window after presented stimuli onsets are unlikely to conform with a uniform distribution.

3.2.4. Non-signal-stimuli with high predictability

In groups A in condition 3 and in group C in condition 1 participants were subject to the presentation of series of auditory stimuli with high predictability but were not required to respond to the stimuli. Testing the uniformity of temporal blink distributions in the two considered time windows locked onto stimuli onsets resulted in 1 out of 35 distributions (0 out of 17 in group A, 1 out of 18 in group C) deviating from uniformity in the time window before stimuli onsets, yielding $P = 0.83$ according to Eq. (1). In the time window after stimuli onsets, 11 out of 35 distributions (6 out of 17 in group A, 5 out of 18 in group C) were significantly deviating from uniformity, yielding $P = 6.64 \times 10^{-7}$. If in contrast, time windows were locked onto the stimuli onsets according to the virtual, i.e. not presented, series of stimuli with low predictability, 2 and 1 out of 35 distributions deviated significantly from uniformity in the time window before and after virtual stimuli onsets, respectively, yielding $P = 0.53$ and $P = 0.83$. In Fig. 5(a), the temporal blink distributions are shown for the same participant as was chosen for illustration already in Fig. 2(b) in the two time windows locked onto the real (presented) stimuli onsets, while in Fig. 5(b), the participant's blink distributions are shown in the time windows locked onto the virtual (not presented) stimuli onsets. In Fig. 5(c), a P-P-plot is provided comparing the empirical CDFs of obtained p-values for the time window after presented stimuli onsets (triangles), the time window before presented stimuli onsets (squares), and both time windows locked onto virtual stimuli onsets ("+"-symbols). The KS-tests yield $D = 0.12$, $p = 0.74$, $D = 0.44$, p < 0.001, and $D = 0.10$, $p = 0.45$ for the p-values obtained for the time window before presented stimuli onsets, the time window after presented stimuli onsets, and both time windows locked onto virtual stimuli onsets, respectively, suggesting that the p-values obtained for the time window after presented stimuli onsets are unlikely to conform with a uniform distribution.

3.2.5. Non-signal-stimuli with low predictability

In groups B and C in condition 3 participants were subject to the presentation of series of auditory stimuli with low predictability but were not required to respond to the stimuli. Testing the uniformity of temporal blink distributions in the two considered time windows locked onto stimuli onsets resulted in 2 out of 36 distributions (2 out of 19 in group B, 0 out of 17 in group C) deviating from uniformity in the time window before stimuli onsets, yielding $P = 0.54$ according to Eq. (1). In the time window after stimuli onsets, 12 out of 36 distributions (7 out of 19 in group B, 5 out of 17 in group C) were significantly deviating from uniformity, yielding $P = 9.87 \times 10^{-8}$. If in contrast, time windows were locked onto the stimuli onsets according to the virtual, i.e. not presented, series of stimuli with high predictability, 0 and 2 out of 36 distributions deviated significantly from uniformity in the time window before and after virtual stimuli onsets, respectively, yielding $P = 1$ and $P = 0.54$. In Fig. 6(a), the temporal blink distributions are shown for the same participant as was chosen for illustration already in Fig. 2(a) in the two time windows locked onto the real (presented) stimuli onsets, while in Fig. 6(b), the blink distributions for the same participant are shown in the time windows locked onto the virtual (not presented) stimuli onsets. In Fig. 6(c), a P-P-plot is provided comparing the empirical CDFs of obtained p-values for the time window after presented stimuli onsets (triangles), the time window before presented stimuli onsets (squares), and both time windows locked onto virtual stimuli onsets (plus signs). The KS-tests yield $D = 0.13$, $p = 0.55$, $D = 0.31$, $p = 0.001$, and $D = 0.08$, $p = 0.70$ for the p-values obtained for the time window before presented stimuli onsets, the time window after presented stimuli onsets, and both time windows locked onto virtual stimuli onsets, respectively,
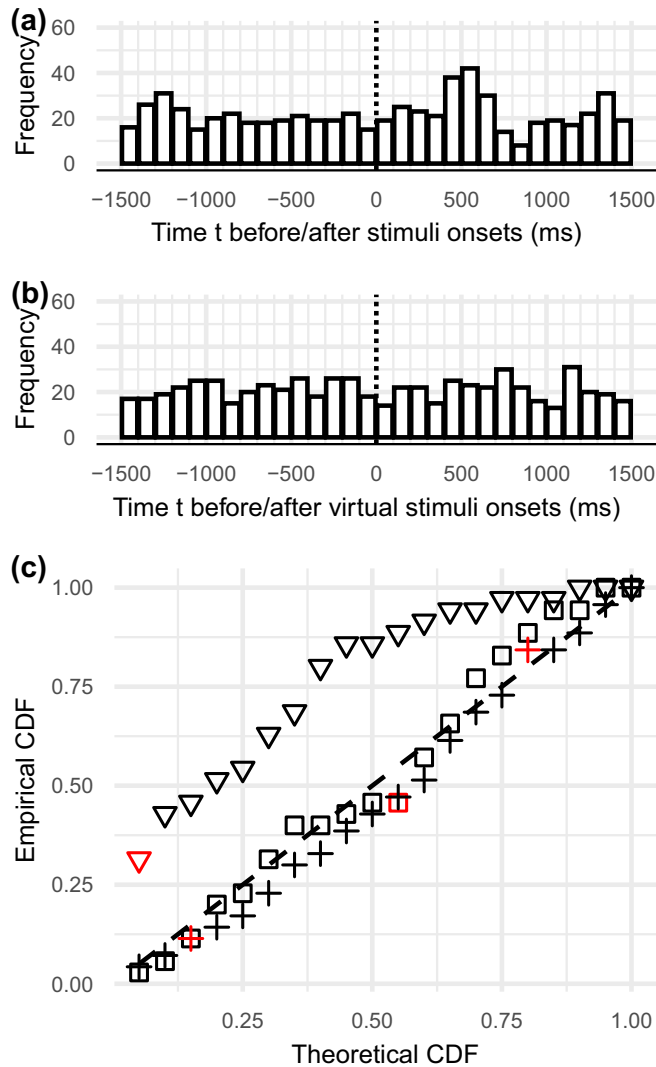
Fig. 5. Temporal blink distributions in the two considered time windows 1.5 s before ($t < 0$) and after ($t > 0$) stimuli onsets for a participant of group A in condition 3, i.e. keypress responses were not required and the presented series of stimuli had high predictability. Note that the participant is the same one as was chosen for illustration already in Fig. 2(a). The distribution does not deviate from uniformity in the time window before stimuli onsets, $\chi^2(14) = 12.66$, $p = 0.55$ for $t < 0$, but does in the time window after stimuli onsets, $\chi^2(14) = 48.68$, $p < 0.0001$ for $t > 0$. Note that the participant was chosen as an illustrative case exactly because the distribution was one of a few significantly non-uniform distributions in this condition while most distributions were in accordance with uniformity. (b) Resulting Blink distributions if time windows are locked on virtual, i.e. not presented stimuli onsets instead. The distributions do not deviate from uniformity in both time windows, $\chi^2(14) = 9.55$, $p = 0.79$ for $t < 0$, and $\chi^2(14) = 19.71$, $p = 0.14$ for $t > 0$. (c) A P-P-plot comparing the empirical cumulative distribution functions (CDFs) of p-values obtained from χ^2-tests performed for all blink distributions in group A in condition 3 and group C in condition 1 (i.e. keypress responses not required and high predictability) in the time windows before (squares) and after (triangles) presented stimuli and in both time windows locked onto virtual stimuli ("+"-symbols; low predictability). Data points corresponding to the results for the individual participant shown in panels (a) and (b) are highlighted in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
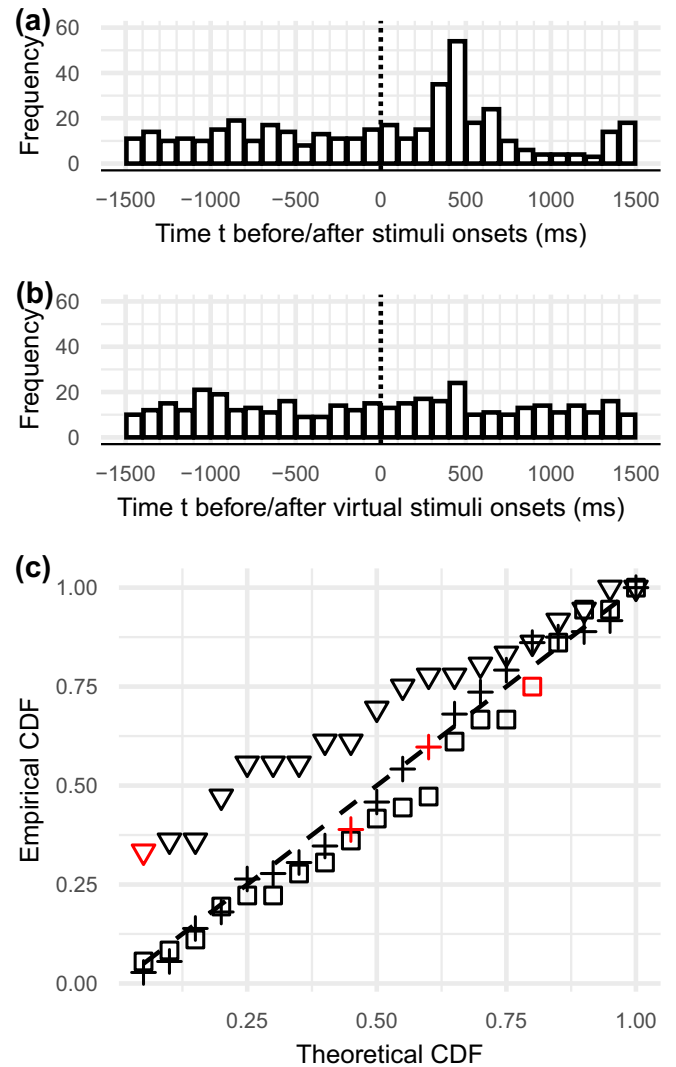
Fig. 6. Temporal blink distributions in the two considered time windows 1.5 s before ($t < 0$) and after ($t > 0$) stimuli onsets for a participant of group B in condition 3, i.e. keypress responses were not required and the presented series of stimuli had low predictability. Note that the participant is the same one as was chosen for illustration already in Fig. 2(b). The distribution does not deviate from uniformity in the time window before stimuli onsets, $\chi^2(14) = 10.13$, $p = 0.75$ for $t < 0$, but does in the time window after stimuli onsets, $\chi^2(14) = 167.37$, $p < 0.0001$ for $t > 0$. Note that the participant was chosen as an illustrative case exactly because the distribution was one of a few significantly non-uniform distributions in this condition while most distributions were in accordance with uniformity. (b) Resulting Blink distributions if time windows are locked on virtual, i.e. not presented stimuli onsets instead. The distributions do not deviate from uniformity in both time windows, $\chi^2(14) = 12.40$, $p = 0.57$ for $t < 0$, and $\chi^2(14) = 14.15$, $p = 0.44$ for $t > 0$. (c) A P-P-plot comparing the empirical cumulative distribution functions (CDFs) of p-values obtained from χ^2-tests performed for all blink distributions in groups B and C in condition 3 (i.e. keypress responses not required and low predictability) in the time windows before (squares) and after (triangles) presented stimuli and in both time windows locked onto virtual stimuli ("+"-symbols; high predictability). Data points corresponding to the results for the individual participant shown in panels (a) and (b) are highlighted in red. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

suggesting that the *p*-values obtained for the time window after presented stimuli onsets are unlikely to conform with a uniform distribution.

3.3. Group-level analyses

In Table 3 the step-wise constructed linear mixed-effects models for blink proportions in both considered time windows are compared. All models include participant ID (nested within condition and time) as a random effect, as intercepts varied significantly across participants for the time window before stimuli onsets, $\chi^2(3) = 67.52, p < 0.0001$ as well as for the time window after stimuli onsets, $\chi^2(3) = 125.07, p < 0.0001$. Including the global blink descriptors did not have a significant effect on blink proportions, neither in the time window before nor in the time window after stimuli onsets. Time and condition had significant effects on blink proportions for both considered time windows as well as the interactions between time and condition for the time window before stimuli onsets and both the interactions between time and condition as well as between time and group for the time window after stimuli onsets.

The variation of mean blink proportions (MBP) with time is shown for each combination of group and condition separately in Fig. 7. Significant differences with respect to the MBP closest to the stimuli onsets (t = 0) in each of the two time windows are indicated as well as and were computed via linear mixed-effects models including time and random intercepts for participant ID as predictors for each combination of group and condition. MBP distributions did not differ between time bins in both time windows in groups A and B, see Fig. 7(a) and (b). Note that for these conditions time windows were locked onto virtual stimuli onsets and were evaluated for both series of stimuli with low and high predictability. This is corroborated further by the linear regression models fitted to the MBP distributions in these conditions [blue lines in Fig. 7(a) and (b)], of which none yield slopes significantly different from zero (*p* < 0.05). The same was found for the slopes of linear fits in the time windows before stimuli onsets for non-signal-stimuli, irrespective of predictability, i.e. in group C, condition 1 [Fig. 7(c), t < 0], in group A, condition 3 [Fig. 7(g), t < 0], in group B, condition 3 [Fig. 7(h), t < 0], and in group C, condition 3 [Fig. 7(i), t < 0]. Although the fluctuations in the time windows after stimuli onsets (t > 0) for non-signal-stimuli shown in Fig. 7(c), (g)-(i) may partly and qualitatively appear distinct from the merely statistical fluctuations in the case of Fig. 7(a) and (b), they do not give rise to a specific pattern. Hence, we refrained from fitting any particular model to these MBP distributions.

This picture is, however, apparently different in the case of signal-stimuli, see Fig. 7(d)-(f). In the time windows before stimuli onsets, MBP distributions were decreasing as they approached the stimuli onsets and the linear regression slopes were significantly different from zero in all three groups. Furthermore, the linear fit for group A yielded an intercept of 2.00 ± 0.09%, *p* < 0.001 and a slope of −0.004 ± 0.001%/s, *p* < 0.01. Both, intercept and slope were significantly different from the ones obtained in groups B and C which was tested by

fitting a larger model to the data of all three groups and assessing the significance of the differences of model coefficients. In particular, the intercepts accounted for 1.24 ± 0.09%, *p* < 0.001, and 1.14 ± 0.10%, *p* < 0.001 in groups B and C, respectively, and the slopes for −0.011 ± 0.001%/s, *p* < 0.001, and − 0.014 ± 0.001%/s, *p* < 0.001 in groups B and C, respectively. This suggests that MBP distributions decrease faster and towards a lower value in groups B and C, i.e. when auditory input with high predictability was presented, than in group A, i.e. when an auditory input with low predictability was presented. In Fig. 7(d)-(f) we depict also models fitted to the MBP distributions in the time window after stimuli onsets which were constructed aiming for capturing the essentials of the apparent temporal pattern of the MBP distributions in all three groups. Omitting the error term, the model consisted of a sigmoid or Fermi function to take into account the post-stimulus release of blink suppression, a Gaussian function to take into account the subsequent, transient overcompensation of blinking and an offset accounting for a minimal MBP. The full model specification for the time-dependent MBP distribution, denoted as $B(t)$, for all three groups in condition 2 reads

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

where $k_i = b_i + s_A \Delta a_i + s_C \Delta c_i$, t denotes the time since stimuli onsets, b_i, Δa_i, Δc_i with $i = 1, ..., 7$ denote the model coefficients and s_A and s_C denote dummy variables equal to one when the fitted data refers to group A and C, respectively, and zero otherwise. The resulting model coefficients are provided in Table 4. The significant differences indicate that the transition corresponding to the sigmoid function appears later in group C than in groups A and B (see the entries for b_3, Δa_3 and Δc_3 in Table 4), that the compensation described by the Gaussian function appears later in groups A and C than in group B (see the entries for b_6, Δa_6 and Δc_6 in Table 4), and that the compensation duration is shorter in group A than in group B (see the entries for b_7 and Δa_7 Table 4).

In Fig. 8 we tentatively investigate the interplay between the motoric response of the participants and their eye blinking in condition 2. In Fig. 8(a)-(c) the MBP distributions in the two considered time windows locked on the stimuli onsets are depicted together with the keypress distributions (green dots and error bars) in the same time windows for groups A-C, respectively. In Fig. 8(d)-(f) we depict the MBP distributions resulting from locking two 1.5 s time windows onto the keypresses of each participant instead of the stimuli onsets. Blink distributions appear considerably shifted to the left, i.e. to smaller times, and most importantly the left flank of the compensatory peak seemingly crosses t = 0 in all three groups. The regression lines fitted in the time windows before the respective events (blue lines in Fig. 8) yielded less steep, i.e. more positive slopes in all groups (but not significant in group A, see below) for keypress-locked time windows than for stimuli-locked time windows while intercepts were not significantly different. Note that for fitting the

Table 3

Step-wise constructed linear mixed-effect models for blink proportions in both considered time windows. All models include participant ID (nested within condition and time) as a random effect. The degrees of freedom are denoted as df, AIC denotes Akaike's information criterion. Use of "…" denotes that all prior factors are retained in the model. Included global blink descriptors were medians of blink durations, and means and skewness of IBIs-distributions in the case of time windows before stimuli onsets, medians of blink durations, and standard deviations and skewness of IBIs-distributions in the case of time windows after stimuli onsets.

		Before stimuli onsets			After stimuli onsets		
	df	AIC	χ^2	*p*-value	AIC	χ^2	*p*-value
Global blink descriptors	8	9187.9	0.66	0.88	12791	125.07	0.33
… + time	22	9165.0	50.83	<0.0001	12688	131.17	<0.0001
… + condition	24	9083.8	85.19	<0.0001	12650	41.59	<0.0001
… + group	26	9084.9	2.93	0.23	12652	2.47	0.29
… + time × condition	54	9044.5	96.37	<0.0001	12484	223.25	<0.0001
… + time × group	82	9074.8	25.79	0.58	12462	78.21	<0.0001
… + condition × group	86	9081.0	1.78	0.78	12470	0.59	0.96
… + time × condition × group	142	9118.6	74.38	0.05	12530	51.79	0.63
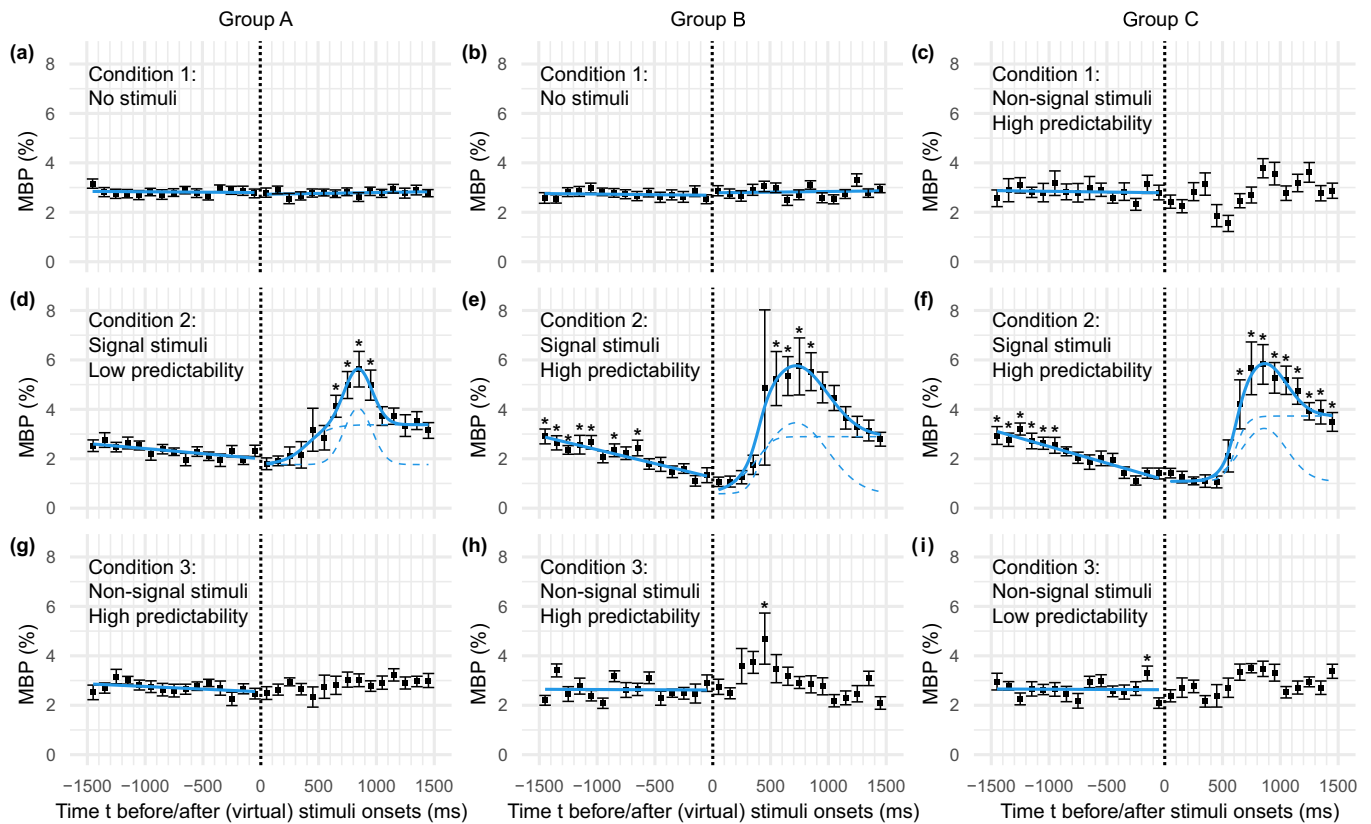
Fig. 7. Mean blink proportion (MBP; per 100 ms interval) distributions for all groups and conditions. Shown are means (averaged over all participants in the respective group and condition) and their standard errors (black dots and whiskers). Time windows before and after stimuli onsets are separated by the vertical, black, dotted line. Fit functions according either to linear models for t < 0 (and t > 0 in the case of condition 1 in groups A and B) or to models according to Eq. (2) for t > 0 are also indicated by blue, solid lines. The sigmoid and Gaussian portions of the models according to Eq. (2) are further indicated separately by blue, dashed lines for condition 2 in panels (d)-(f). The asterisks indicate MBPs significantly different ($p < 0.05$) from the value closest to the stimuli onsets (at t = −50 ms in the time window before stimuli onsets, and t = 50 ms in the time window after stimuli onsets; Bonferroni-corrected for multiple comparisons). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4

Coefficients of the model fitted to the MBP distributions of groups A, B and C in the time window after stimuli onsets according to Eq. (2).

Coefficient	Estimate	Standard error	*t*-value	*p*-value
b_1 [%/100 ms]	0.5822	0.4393	1.325	0.20
Δa_1 [%/100 ms]	1.1844	0.5904	2.006	0.06
Δc_1 [%/100 ms]	0.5061	0.4756	1.064	0.30
b_2 [%/100 ms]	2.3122	0.3863	5.985	< 0.0001
Δa_2 [%/100 ms]	−0.6994	0.5829	−1.200	0.24
Δc_2 [%/100 ms]	0.3296	0.4889	0.674	0.51
b_3 [ms]	396.4396	55.8130	7.103	< 0.0001
Δa_3 [ms]	0.5932	101.1885	0.006	1.00
Δc_3 [ms]	216.8283	82.9789	2.613	0.02
b_4 [ms]	50.0000	27.0404	1.849	0.08
Δa_4 [ms]	47.6649	85.0115	0.561	0.58
Δc_4 [ms]	0.0000	36.2134	0.000	1.0000
b_5 [%/100 ms]	2.8717	0.3415	8.408	< 0.0001
Δa_5 [%/100 ms]	−0.5966	0.4611	−1.294	0.21
Δc_5 [%/100 ms]	−0.7324	0.4770	−1.535	0.14
b_6 [ms]	716.2582	44.9813	15.923	< 0.0001
Δa_6 [ms]	125.0200	49.0382	2.549	0.02
Δc_6 [ms]	143.0481	66.8095	2.141	0.04
b_7 [ms]	277.8812	57.8349	4.805	< 0.0001
Δa_7 [ms]	−156.3054	62.0059	−2.521	0.02
Δc_7 [ms]	−82.8253	78.0143	−1.062	0.30

regression line in the time window before keypresses in group B we omitted the highly outlying data point at t = −50 ms. In particular, the differences in slope read 0.002%/s, $p = 0.41$ for group A, 0.005%/s, $p < 0.05$ for each of the groups B and C. We refrained from fitting the model

according to Eq. (2) to the MBP distributions for keypress-locked time windows as the "missing" left portion of the distribution in comparison to the stimuli-locked MBP distributions does not allow a reasonable fit concerning both the offset and the sigmoid function contained in Eq. (2).

4. Discussion

In accordance with our assumptions, our experiment shows that (i) purely auditory stimuli can dynamically modulate the distribution of eye blinks over time and it reveals that this synchronization is modulated both by (ii) the requirement to (motorically) respond to the presented stimuli and (iii) the predictability of the auditory input. Our findings indicate further that the presented series of stimuli are indeed anticipated when a motoric response is required. Blink suppression increases as the moment of the occurrence of acoustic stimuli approaches, which depends especially on the predictability of the presented tone series [compare especially Figs. 3, 4 and 7(d)-(f)]. This reduction of blink rate is compensated by an excess of blinking about 0.5–1 s after the occurrence of the tones. The release of blink suppression, as well as blink compensation, appear to be initiated rather concertedly with the release of keypress responses. In especially, keypress responses do not occur strictly in advance of the release of blink suppression, but appear to occur rather directly afterward (Fig. 8). This is an indication that both, keypress responses as well as eye blinking, are regulated by the cognitive evaluation of stimuli, and eye blinks are not merely a secondary motoric response in consequence of intentional keypress reactions. The short delay between the release of blink suppression and keypress responses
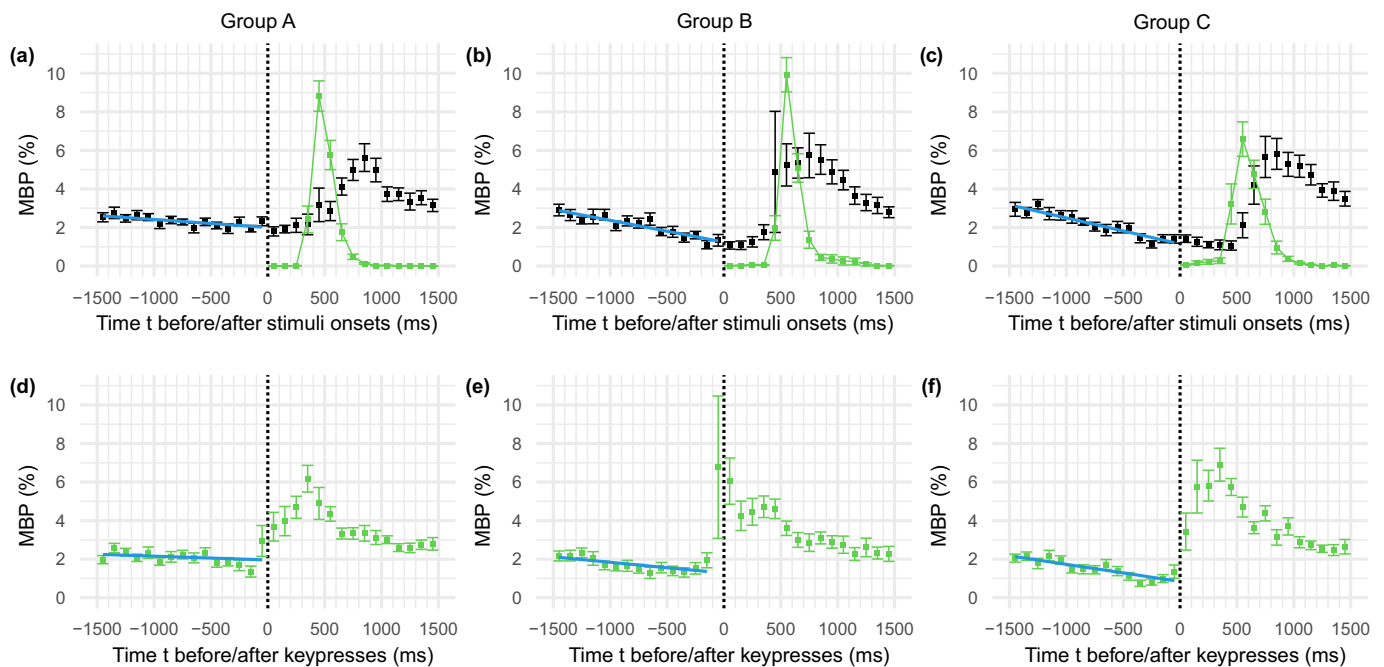
Fig. 8. Mean blink proportion (MBP; per 100 ms interval) distributions and standard errors in both stimuli-locked time windows (black dots and whiskers in top panels) for (a) group A, (b) group B, (c) group C, and keypress-locked time windows (green dots and whiskers in bottom panels) for (d) group A, (e) group B, (f) group C. In panels (a)-(c) the distribution of mean keypress proportions and their standard errors are also provided but was divided by a factor of 5 to fit on the same scale as the MBP distributions. Linear fits to the data are also given for $t < 0$ (blue solid lines). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

may have its cause simply in the fact of a larger distance of the effectors from the relevant cortical and subcortical centers in the case of the manual response than in the case of blinking and hence, longer transmission duration of the nerval impulses (Donders, 1969).

The requirement for a motor response appears to affect the temporal coherence of the blink responses with respect to the stimuli onsets. Whereas our individual-level analyses highly suggest that the temporal distributions of eye blinks of some individual participants are not independent from the occurrences of the presented tones also when no motoric response was required (compare especially Figs. 2, 5, and 6; in fact, our individual-level analyses can differentiate groups which were presented non-signal stimuli from groups which were presented no stimuli at all), the picture is less clear at the group-level. This is probably due to considerable inter-individual variations in the specific moment-to-moment response to the external stimuli, leading in fact to an impact on blink distributions hardly attributable to mere chance, but with too little coherence between individuals such that a common temporal pattern emerges from aggregating the individual data. In the case of a required motoric response, our group-level analyses definitely suggest such a common temporal pattern (Fig. 7), which indicates that the requirement to respond to the external stimuli acts as enhancement of the coherence between temporal blink distributions of different participants.

The reported blink proportion distributions do not vary significantly with the considered global descriptors of blinking behavior, i.e. MBR, blink duration, or the form of the IBIs-distributions as captured by their first four moments, which can be highly different across individuals, groups, and conditions. In fact, we note increasing MBRs and blink durations with increasing duration of the experiment. This is in agreement with earlier studies suggesting a relation between fatigue and blink rate especially in monotonic conditions (Fukuda et al., 2005; Kaneko & Sakamoto, 2001; Maffei & Angrilli, 2018; Stern et al., 1984; Stern et al., 1994). We also note differences in means, and standard deviations of IBIs between group A and groups B and C, which can, however, hardly be related to the different regularity of presented auditory input as they

are robust against varying experimental conditions (Table 1). We find also that MBRs, means and standard deviations of IBIs are highly correlated with each other (Table 2), although, in principle, describing different aspects of blinking behavior. Finally, we note that skewness and kurtosis of IBIs-distributions are similar in all groups and conditions and are highly correlated with each other. Both skewness and kurtosis are clearly positive, indicating that IBIs-distributions are both considerably positively skewed and leptokurtic, which is also in agreement with earlier assessments of the average form of IBIs-distributions (Cruz et al., 2011; Ousler III, Abelson, Johnston, Lane, & Smith, 2014).

A dynamic association between the occurrence of eye blinks and auditory task structure has been noted earlier (e.g. Fukuda, 1994; Kobald et al., 2019; Oh, Jeong, & Jeong, 2012). However, the *predictability* of the used auditory input was not systematically varied in said studies, thus not allowing to scrutinize the dynamically tight, temporal link between environmental input and behavioral response illustrating the moment-to-moment precision of temporal eye blink regulation. The modulation of blink patterns by the predictability of the auditory input indicates also a fundamental relation to organismic perception as a proactively organizing, functional system elaborating "a forecast of future stimuli" (Sokolov, 1963, S. 287). Furthermore, in contrast to musical or verbal stimuli, we used mere sine tones for acoustic stimulation in order to retain not more than a basic *salience*, i.e. stimuli being merely discernible from an otherwise empty or diffuse perception background. Altogether, this finally allows us to conclude that the dynamic regulation of eye blinking is an automatic and precise process, active at a *fundamental* level of perception.

We further note that the mathematical, explanatory model suggested by Hoppe et al. (2018) may be generalizable to non-visual tasks, i.e. when it is assumed that task-relevant information cannot only be missed by physically blocking the information stream but also by reducing attention even when the information may be physically accessible. In contrast to visual tasks, the physical blockade of the information stream is no consequence of blinking at all in non-visual tasks. If blinking is, however, tightly governed by attention, then missing task-relevant

information due to temporarily reduced attention remains linked to the distribution of blinks over time. Indeed, neural activity in the primary visual area is actively reduced during blinking which is why we are typically unaware of blinking (Hari, Salmelin, Tissari, Kajola, & Virsu, 1994). At the same time activity is also decreased in dorsal and ventral attention networks, while it is increased at the same time in the default mode network, hippocampus, and cerebellum (Nakano, 2015; Nakano et al., 2013). Upon opening the eyes, the opposite appears to be the case: processing sensory, particularly visual information (Ang & Maus, 2020) and cognitive control (van Bochove, Van der Haegen, Notebaert, & Verguts, 2013) are enhanced and activity in non-sensory areas drops (Nakano, 2015). Hence, overall, blinking seems, among other aspects, also closely associated with a dynamic shift of relative weight of neural activity from sensory to non-sensory areas and vice versa.

Our results also refuse the attribution of the effect to a consequence of the coordination of different motoric responses and also to learning or adaptation of the respective response behavior during earlier phases in the experiment. In earlier experiments blinking was often inevitably linked to motor responses by experimental design. Already 1971, Baumstimler and Parrot argued that voluntary motor action proactively suppresses blinking until a task-specific motor response has been completed. This is not in accordance with our analysis which rather suggests a concerted release of keypress and blink responses as discussed above. The requirement of a motoric response remained also by design confounded with the valence of the presented stimuli in our experiment and additional experiments are required, involving e.g. participants silently counting stimuli instead of pressing a key, to further scrutinize the influence of the motor component on temporal blink distributions as such. However, our results for those conditions, in which no keypresses were required, indicate already that dynamic, context-specific suppression of blinking may not necessitate any motor response as a prerequisite. This is in accordance with the conclusion made by Wascher et al. (2015) that blinks occur particularly at moments when all information processing during a given task is momentarily finished. Wascher et al. (2015) noted that similar time on task effects of blinks in no-go trials as of blinks in go trials indicated that it is not simply the manual response that initiates blinking, but it may be the completion of the cognitive evaluation of stimuli that triggers blinking. However, from a perspective of neuronal processing, it may still be argued according to Cisek's (2007) affordance competition hypothesis that tasks involving a decision component including any motor response are inevitably linked to motoric processing also when the motor response is finally inhibited like in no-go trials. Although blinking might then not be simply due to entrainment of manual responses as suggested by synchronization between blinking and finger tapping (Cong, Sharikadze, Staude, Deubel, & Wolf, 2010), it still could be associated with the completion of motoric processing of competing action programs in (pre-)motor regions. However, in the first condition of group C in our experiment, neither any response at all has at any point been required from the participants nor could any adaption of synchronization between blinking and stimulus occurrence due to prior conditions involving motor responses have been the case. Hence, our results provide a strong indication that blinking can indeed be initiated by the completion of cognitive stimulus evaluation per se. Thereby, in the absence of any external task, cognitive stimulus evaluation simply refers to the fundamental organismic capability to respond promptly to the questions "What is to be done?" or "What is this?" whenever a stimulus is associated with enough salience to evoke an orienting response to ensure a principal, organismic preparedness under steadily fluctuating environmental conditions.

During the orienting response, the receptor systems of an organism are adjusted for optimal processing of external information in the immediate future (Klix, 1971; Sokolov, 1963). This is accompanied by a variety of physiological changes such as dilation of pupils, a drop in the threshold of audibility, an increase of tonicity, etc. and also a temporary inhibition as well as subsequent enhanced activation of the *musculi orbicularis oculi* responsible for eyelid closure (Stekelenburg & Van

Boxtel, 2002) which might represent a possible mechanism underlying the moment-to-moment modulation of eye blinking by auditory or possibly, even generally non-visual stimuli. Illumination of such mechanisms capable of explaining the identified interrelations, however, certainly requires further experimental investigation specifically dedicated to this research question.

One limitation of our study is the operationalization of blink onset as the transient loss of pupillometric data by the eye-tracking device. As a consequence, different forms of eye blinks such as spontaneous, reflex, or partial blinks (Ousler III et al., 2014; Stern et al., 1984), or even sporadic departure of the gaze from the display cannot be discerned from each other. Although it seems reasonable to assume that most of the observed eye closures are due to spontaneous eye blinking, we cannot particularly attribute our findings to this specific form. Nevertheless, the close temporal associations between the series of tone onsets and the temporal pattern of eye closures remain and it is certainly unreasonable to assume this merely an artifact of a somehow favorable interaction of different kinds of eye blinks. Eye blinking is also affected by a variety of other factors like prevalent physiological, ophthalmological, neurological, psychiatric pathologies, age, or the variation of physico-chemical, environmental conditions (Rodriguez et al., 2017), all of which are also not particularly resolved in this work due to our choice of a random sample of a student population. Lastly, we investigated temporal associations between blink patterns and series of particularly acoustic stimuli. While we definitely expect a similar effect for stimuli of any modality, we cannot a priori rule out a modulation of the effect depending on modality or interactions between modalities in the case of more complex stimuli characteristics like typically met under everyday-life conditions.

Declaration of Competing Interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.cognition.2021.104982.

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