

Disentangling Top-down and Bottom-up Influences on Blinks
in the Visual and Auditory Domain

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Abstract

Sensory input as well as cognitive factors can drive the modulation of blinking. Our aim was to dissociate sensory driven bottom-up from cognitive top-down influences on blinking behavior and compare these influences between the auditory and the visual domain.

Using an oddball paradigm, we found a significant pre-stimulus decrease in blink probability for visual input compared to auditory input. Sensory input further led to an early post-stimulus blink increase in both modalities if a task demanded attention to the input. Only visual input caused a pronounced early increase without a task. In case of a target or the omission of a stimulus (as compared to standard input), an additional late increase in blink rate was found in the auditory and visual domain. This suggests that blink modulation must be based on the interpretation of the input, but does not need any sensory input at all to occur.

Our results show a complex modulation of blinking based on top-down factors such as prediction and attention in addition to sensory-based influences. The magnitude of the modulation is mainly influenced by general attentional demands, while the latency of this modulation allows to dissociate general from specific top-down influences that are independent of the sensory domain.

Keywords: Eye blinks, visual domain, auditory domain, attention, oddball

We spontaneously blink around 15 times a minute (Ponder & Kennedy, 1927). Only a fifth of that would be enough to maintain a tear film on the cornea (Norn, 1969). The surplus blinks are not just randomly executed in time, but seem to preferentially occur for example after sensory changes such as stimulus onset (Siegle, Ichikawa, & Steinhauer, 2008) or after verbal (Oh, Han, Peterson, & Jeong, 2012) and manual responses (van Dam & van Ee, 2005). Furthermore, blinks can be strategically executed during continuous sensory input, thereby collecting the highest amount of task-relevant information. Performing a detection task, participants blinked during low event probabilities (Hoppe, Helfmann, & Rothkopf, 2018), whereas participants consistently blinked at implicit breaks when watching a movie (Nakano, Yamamoto, Kitajo, Takahashi, & Kitazawa, 2009). In addition, not only the blink timing can be modulated, but also the blink frequency. While we blink more often during a conversation, we refrain from it during reading (Karson et al., 1981).

Not to blink is often attributed to optimizing the efficiency of visual information intake. Interestingly, the information deficit during blinking is accompanied by an inhibition of neural activity (Volkman, Riggs, & Moore, 1980). This was investigated in the visual domain by presenting light through the mouth, bypassing the eyelid. Results showed that small light changes are indeed less detectable when they co-occurred with a blink. This fits the common experience that blinks usually go unnoticed, i.e. processing of the internal blackening introduced by the blink is inhibited. Note that an external blackening of the visual field for the same duration as a blink is indeed detectable (Maus et al., 2017). This means that blinks not only shut out incoming visual information, but also co-occur with neuronal inhibition. While this suggests a strong link between the visual system (including information processing) and blinking, other research also show effects outside the visual domain. Auditory tasks are also accompanied by a suppression of blinks, e.g. before the presentation and pronunciation of

Japanese syllabary (Fukuda, 2001) or during pure auditory information display (Kobald, Wascher, Heppner, & Getzmann, 2019; Oh, Jeong, & Jeong, 2012). Moreover, this suppression holds until the end of stimulus presentation, where the probability of blink occurrence then strongly increases compared to baseline. Oh, Jeong, et al. (2012) conclude that high attentional demands go along with blink suppression, but as soon as the attentional demands drop, blink probability increases. These findings suggest that the modulation of blinking is based on more general mechanisms that are involved in the processing of visual as well as auditory information.

Our first aim was to understand if the underlying processes that influence blinking during visual and non-visual input could be the same. To this end, we systematically compared blink rate and timing during visual and/or auditory stimulation. Furthermore, we varied the overall attentional demands to be able to disentangle general sensory (bottom-up) from cognitive (top-down) influences on blinks. In addition, by using a novelty oddball paradigm, we investigated more specific top-down influences by comparing frequent standard stimuli and infrequent distractors and targets.

The novelty oddball paradigm we used is an experimental design that has been applied extensively to study the neuronal correlates of internal and external influences. In the second half of the 20th century, it was shown that components of the event-related signal such as the P300 are enhanced after an infrequent stimulus compared to a frequent one (Sutton, Braren, Zubin, & John, 1965) or when attention was actively drawn to the stimuli (Squires, Squires, & Hillyard, 1975). Other components like the mismatch negativity are known to be independent of attention and change in relation to the magnitude of difference between frequent and infrequent stimuli (for a review, see Pazo-Alvarez, Cadaveira, & Amenedo, 2003). Additionally, even the absence of a stimulus during a sequence can affect the event-related potential. Such

an influence which is not based on sensory input suggests that within a novelty oddball paradigm endogenous (top-down) and exogenous (bottom-up) contributions are distinguishable (McCullagh, Weihing, & Musiek, 2009). Following these neurophysiological results, researchers investigated the changes in eye movements like pupil responses and microsaccades during oddball tasks. While pupil dilation increases with decreased stimulus probability, microsaccades are longer inhibited after odd stimuli independent of the stimulus modality (Friedman, Hakerem, Sutton, & Fleiss, 1973; Valsecchi, Betta, & Turatto, 2007; Valsecchi & Turatto, 2009). Different bottom-up and top-down processes might therefore be distinguishable in neurophysiological signals, but also in changes in eye movements. Our second aim was to assess if also blink probability as well as their timing can depict internal and external mechanisms involved in oddball tasks.

Our first experiment focused on the comparison of blink behavior before and after stimulus occurrence in the visual, auditory or bimodal domain. In addition, we investigated task related effects on blinking by comparing frequent stimuli during active and passive conditions as well as frequent vs infrequent stimuli. We expected a blink modulation driven by sensory events for both sensory domains. We further predict an influence on blinking due to cognitive processes. Specifically, based on previous findings concerning eye movements, we expect that task demands increase the probability to blink in-between stimulus presentations, that blink frequency increases after target stimuli, and that blinking is delayed after infrequent stimuli in the auditory and visual domain alike. Our second experiment added task related influences independent of sensory input by adding stimulus omissions allowing us to further differentiate cognitive (top-down) from sensory (bottom-up) influences.

Methods Experiment 1

Participants

28 participants (26.71 years old, 6 male) took part in the study. These do not include seven other ones, of which six had unusable eye data recordings (more than 15% data missing) and one was excluded due to a blink rate lower than 2.5 per minute. All received payment or study credit for their participation. All participants had normal or corrected-to-normal vision, gave their written informed consent and the study was in line with the European data protection rules (DSGVO). The local ethics committee approved the study.

Stimuli

Visual stimuli consisted of black shapes and were presented in the center of a grey background using a standard computer screen (60Hz). The shape was either a triangle, a square, a circle (all 3°) or a small square (1.5°) (Fig. 1). The triangle was presented during no-task conditions, the square as the standards, the circle and the small square served as distractor or target (balanced across participants). Auditory stimuli were presented via headphones (Sennheiser PMX 95) and the tones had either a frequency of 440Hz (a', standard), 523Hz (c'', distractor/target), 349Hz (f', target/distractor) or 392Hz (g', standards during no task). Tones were faded in and faded out for 10ms. Bimodal stimuli are a combination of the described stimuli: The no task stimulus was the combination of the triangle and the g', standards were the square and the a'. During bimodal trials with the focus on visual stimuli, the distractor was the combination of the visual standard and the target tone and the target was the visual target combined with the auditory standard. During the bimodal focus on auditory trials, the distractor was the auditory standard with the visual target, the target the auditory target with the visual standard. Targets had a minimal distance of five stimuli in between each other, a maximal distance of 17 stimuli (mean \pm SD: 8.22 \pm 0.20% of all stimuli). Also, distractors had a minimal distance of five and a maximal distance of 17 stimuli between

each other ($8.20 \pm 0.28\%$ of all stimuli). Targets and distractors could follow one another. All other stimuli were standards (in task trials $83.57 \pm 0.32\%$, in no task trials 100%).











	Unimodal visual	Unimodal auditory	Bimodal visual	Bimodal auditory
No task	 Standard 100%	 Standard 100%	 Standard 100%	 Standard 100%
Task	 Standard Distractor Target 83.4% 8.3% 8.3%	 Standard Distractor Target 83.4% 8.3% 8.3%	  Standard Distractor Target 83.4% 8.3% 8.3%	  Standard Distractor Target 83.4% 8.3% 8.3%

Figure 1. Illustration of the stimuli used during the different conditions in experiment 1. Distractor and target features were balanced across participants. Percentages during task conditions are approximated and could minimally deviate from the given number. Stimuli were presented for 100ms followed by a 900ms break. One trial lasted for five minutes (300 stimuli). Subjects indicated the number of targets after the end of the task trials.

Procedure

One trial consisted of 300 stimuli. The presentation of each stimulus lasted 100ms followed by a 900ms break. During the four task trials (unimodal visual, unimodal auditory, bimodal with attention on visual, bimodal with attention on auditory), participants were asked to silently count the number of targets and type in their result after the final stimulus of the trial. We refrained from any explicit response during the trial (e.g. button press) in order to exclude motor related effects on blinking (Ito et al., 2003; van Dam & van Ee, 2005). During the four no-task trials (unimodal visual, unimodal auditory, 2 times bimodal), they were only

requested not to close their eyes and look at screen for the whole trial. The order of these eight trials was randomized. The whole experiment lasted for approx. 45 min. The experimental program was implemented in MATLAB (MathWorks, Natick, USA), using the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997).

Eye movement recording and blink detection

In the beginning and after every second trial, a calibration of the Eyelink 1000 (SR Research, ON, Canada) was performed. Eye movements were recorded binocularly at a sampling rate of 500Hz.

For blink detection, we z-transformed the pupil data. A blink was initially detected if the pupil size of both eyes was more than two standard deviations away from the mean. The blink was then extended until the z-transformed pupil data of one eye reached a size one standard deviation away from the mean. In a next step, blinks occurring less than 100ms apart from each other were combined, and finally blinks that lasted less than 50ms or more than 500ms were discarded.

Data analysis

For continuous blink alignments, each time point (every 2ms, as defined by the sampling frequency) during a blinks was set to 1, while 0s were set whenever there was no blink (Siegle et al., 2008). This approach is slightly different to the conventional one, where the blink rate during a set time window is often calculated, but increases the sensitivity to the latency of blink occurrence. We aimed to understand if our task manipulation would lead to a change in the absolute blink rate for which we compared the mean probability of ongoing blinks. On the other hand, we were interested in the modulation strength due to the task

manipulations. To this end, we compared the relative probability of ongoing blinks. To receive the mean probability of ongoing blinks at each point in time, the average over the binary coded time courses around all stimulus onsets in one condition was calculated (-200 until 800ms). The relative probability of ongoing blinks was computed as the mean probability of ongoing blinks of each point in time minus the mean probability of ongoing blinks of the first 50ms of the corresponding plot (-200 to -150ms before stimulus onset for all analyses between conditions, 0 to 50ms for comparing standards and odds). When comparing standards and odds, we decided to consider only the standard before the odd (Valsecchi et al., 2007) to have the same number of stimulus events and because of the comparably small amount of blink events. Consequently, both stimuli had a similar likelihood of a blink to occur. For analysis between standards in task and no task conditions, only the time around standard stimuli was taken into account if they were followed by another standard stimulus, so that no standard was used twice for statistical analysis.

To explore differences in blink response, we applied repeated measures ANOVAs for each point in time of the corresponding plots in the unimodal conditions with blink probability as dependent variable and visual/auditory as one factor and task/no task as second factor. Shaded areas mark time points where the level of significance survived the procedure described by Benjamini and Yekutieli (2001) controlling the false discovery rate (FDR) below 0.05 under any form of dependency. We did a separate analysis for the bimodal condition (rather than including unimodal vs bimodal as third factor) for three theoretical reasons. First, while the task condition in the unimodal condition only needed attention to the incoming stream, the task condition in the bimodal condition called for a concurrent suppression of the non-attended input stream. This introduces a qualitative difference between the two task conditions (unimodal vs bimodal). Secondly, while the comparison visual vs auditory in the

unimodal condition is mainly a comparison between different sensory inputs, the comparison between visual and auditory in the bimodal condition is one of attentional differences. Additionally, the quantity of sensory input is clearly different between uni- and bimodal conditions. Therefore, also the factor visual vs auditory should not be merged in a single analysis. Thirdly, possible sensory integration processes might be triggered in the bimodal condition only.

Nevertheless, we assumed that the same processes that modulate our blinking during visual/auditory input and task/no task demands in the unimodal condition are also present in the bimodal condition. Accordingly, the timing of the effects should be the same. To this end, we used the significant time points given by the ANOVAs and the FDR-procedure in the unimodal conditions to mark the time window of interest within the bimodal condition. The mean blink probability during attention on visual and attention on auditory as well as during task and no task was then compared with paired t-tests for this specified window in the bimodal conditions.

In addition to the time-resolved analysis, we compared blink occurrence and blink latency after the different stimulus types (standards, distractors and targets) in task conditions. Since we had on average 22.35 distractors and 22.42 targets in each task condition, we decided to combine all blinks after distractors and targets independent of the condition (visual/auditory, uni-/bimodal, only task trials) to increase the number of blinks.

Results Experiment 1

Participants of experiment 1 miscounted the correct number of targets by 0.47 ± 0.87 (mean \pm SD). In 5.36% of all miscounted cases, participants counted less than the correct number. They had a blink rate of 15.47 ± 9.70 blinks per minute (mean \pm SD). The blink rate during the unimodal, visual task trial was slightly lower (mean: 14.34 ± 10.24 SD) than during

the unimodal, auditory task trial (mean: 17.43 ± 10.11 SD). In a first analysis step, we compared the blink modulation around standard stimuli during unimodal no task conditions and unimodal task conditions. We additionally excluded participants who blinked less than 7 times in at least one of the compared conditions. Based on this threshold, for analysis in the unimodal domain as well as for analysis in the bimodal domain, two more participants were excluded.

Pre-stimulus modulation of absolute blink rate

To analyse the absolute blink rate during the pre-stimulus period (-200ms to 0ms), we calculated the probability of ongoing blinks for the unimodal visual and unimodal auditory trials (Fig. 2a) and ran a repeated-measures ANOVA with factors visual/auditory and task/no task for each point in time. For the main effect of modality, all time points before stimulus onset survived the FDR-procedure showing a much lower probability of ongoing blinks during visual stimulation than during auditory stimulation (Fig. 2b). Task vs no task did not show an effect before stimulus onset, neither did the interaction. On a descriptive level, it seems that a task during visual stimulation further decreases the probability of ongoing blinks compared to no task, but a task during auditory stimulation showed no such modulation, but rather the opposite.

In the next step, we tested if the decrease in the visual task was due to the physical presence of visual input or if the change is due to attention on this visual input. Therefore, we compared the means of blink probability in the bimodal conditions where always both sensory inputs were present, but attention was varied via the task. The window for this comparison was selected based on the results of the unimodal comparison, namely the significant time points when comparing auditory and visual input. . A t-test revealed that attention on the

visual task decreased the mean probability of ongoing blinks significantly more than when attention was on the auditory task ($t(25) = -5.05, p < .001, d = 0.99$) (Fig. 2d).

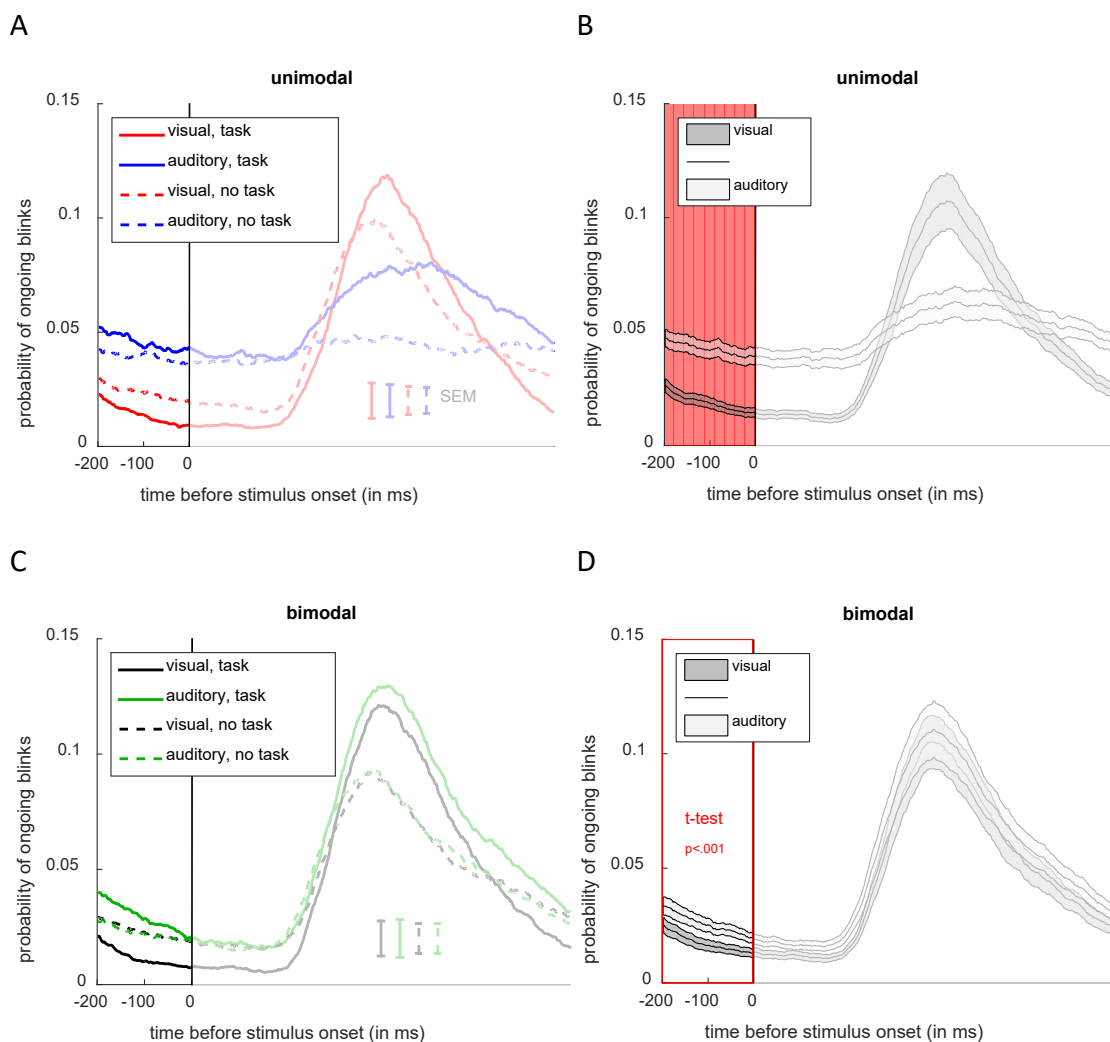


Figure 2. Pre-stimulus analysis of mean probability of ongoing blinks. A. Probability of ongoing blinks around stimulus onset during *unimodal* conditions. Error bars represent the averaged standard error over all time points. B. Main effect of probability of ongoing blinks during visual vs auditory stimulation. Red area marks the significant time points that survived the FDR-procedure. C. Probability of ongoing blinks around stimulus onset during *bimodal* conditions. Error bars represent the averaged standard error over all time points. D. Main effect of probability of ongoing blinks during bimodal stimulation with attention on visual vs attention on auditory. The probability of ongoing blinks during time points of significance (framed red)

taken from the unimodal analysis were averaged, and then visual vs auditory was compared with a paired t-test. The difference was significant. Grey shaded areas represent SEM.

Post-stimulus modulation of relative blink rate

To analyse how strongly the blink rate was changed due to sensory input and task, we subtracted the mean of 50ms before stimulus onset (-200 to -150ms) from all time points during the post-stimulus period, i.e. 0ms to 800ms after stimulus onset. We again ran a repeated measures ANOVA at each time point comparing visual/auditory unimodal stimulation and task/no task. The main effect of visual vs auditory survived the FDR-procedure for a long time, the blink modulation during visual conditions was much higher than during auditory conditions between 308 and 684ms as well as between 700 and 702ms after stimulus onset (Fig. 3b). In line with the pre-stimulus period, we found no interaction effect, but a significantly higher blink modulation between 486 and 488ms, 494 and 600ms as well as between 794 and 798ms, whenever participants had a task (Fig. 3c).

During bimodal conditions, we again calculated the mean for the time where we found a significant difference in the unimodal conditions and ran one t-test comparing attention on visual vs attention on auditory and another t-test comparing task vs no task. While we did not find a difference in blink modulation between attention on visual vs attention on auditory ($t(25) = 8.04, p = .429, d = 0.16$) (Fig. 3e), blinks were again more strongly modulated whenever there was a task ($t(25) = 3.76, p < .001, d = 0.74$) (Fig. 3f).

A

B

C

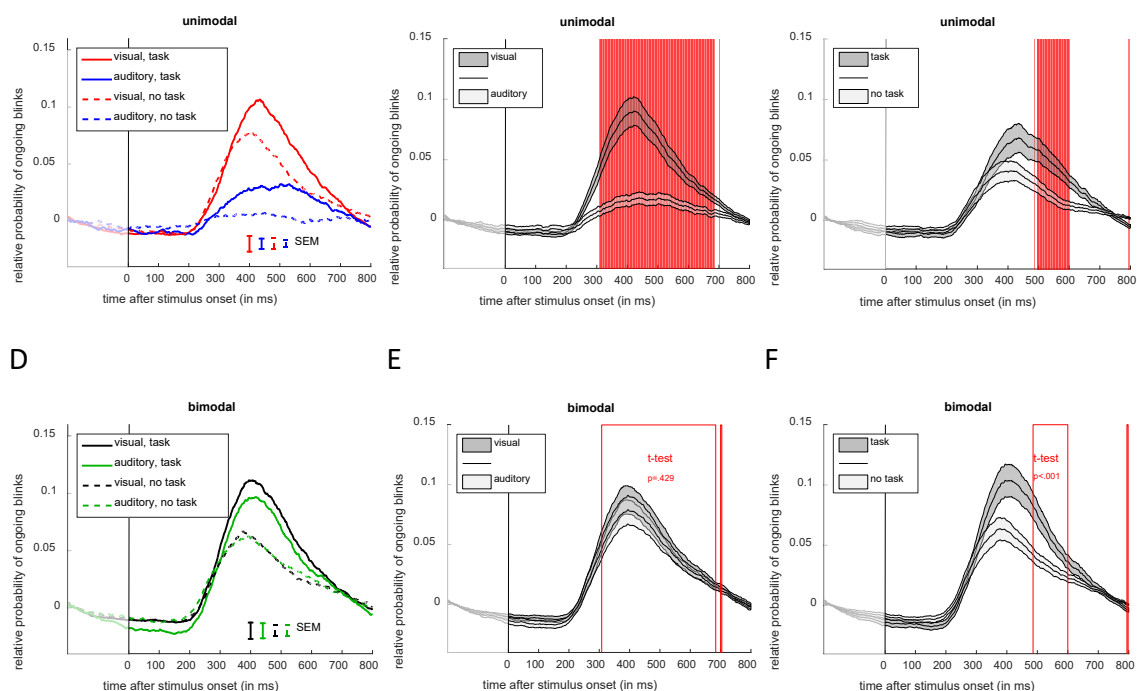


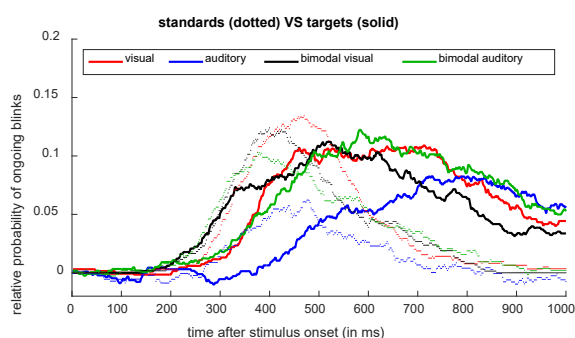
Figure 3. Post-stimulus analysis of relative mean probability of ongoing blinks. A. Probability of ongoing blinks around stimulus onset during *unimodal* conditions relative to the first 50ms of the graph. Error bars represent the averaged standard error over all time points. B. Main effect of probability of ongoing blinks during visual vs auditory stimulation. Red area marks the significant time points that survived the FDR-procedure. Grey shaded areas represent SEM. C. Main effect of probability of ongoing blinks during task vs no task. Red area marks the significant time points that survived the FDR-procedure. Grey shaded areas represent SEM. D. Probability of ongoing blinks around stimulus onset during *bimodal* conditions relative to the first 50ms of the graph. Error bars represent the averaged standard error over all time points. E. Main effect of probability of ongoing blinks around bimodal stimulation with attention on visual vs attention on auditory (mean \pm SEM). The probability of ongoing blinks during time points of significance (framed red) taken from the unimodal analysis were averaged, and then attention on visual vs attention on auditory was compared with a paired t-test. There was no significant difference. F. Main effect of probability of ongoing blinks around bimodal stimulation during task vs no task (mean \pm SEM). The probability of ongoing blinks during time

points of significance (framed red) taken from the unimodal analysis were averaged, and then the probability ongoing blinks during task vs no task was compared with a paired t-test. The difference was significant.

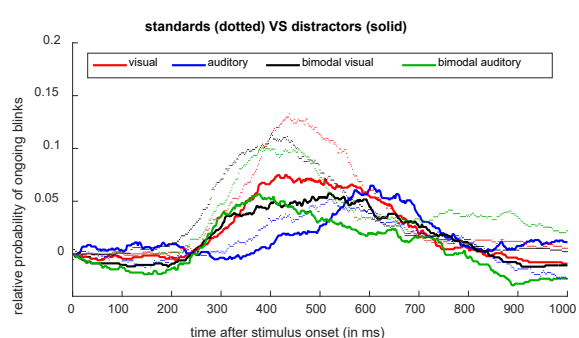
Stimulus type (target, distractor, standard)

In addition to the top-down modulation of blinks during a task, the specific sensory input, i.e. standards, distractors and targets, had an influence on the blinking behavior. Figure 3a shows the relative probability of ongoing blinks of distractors as well as the standards preceding the distractors separately for the four conditions. Figure 4b shows the same for targets and their predecessors. Since only 22.35 distractors / 22.42 targets appeared on average in each task condition, we combined the conditions for statistical analysis. Corrected pairwise t-tests revealed that participants blinked significantly more after a target than after a standard ($t(27) = 4.79, p < .001, d = 0.90$) and significantly less after a distractor compared to a standard ($t(27) = -3.50, p = .002, d = 0.66$) and compared to a target ($t(27) = -5.26, p < .001, d = 0.99$) (Fig. 4c). Interestingly, the latency of the first blink after a target was significantly higher than the blink latency after a standard ($t(27) = 6.68, p < .001, d = 1.26$) or after a distractor ($t(27) = 4.99, p < .001, d = 0.94$). Latencies after standard and after distractor did not differ significantly ($t(27) = -7.42, p = .94, d = 0.01$) (Fig. 4d).

A



B



C

D

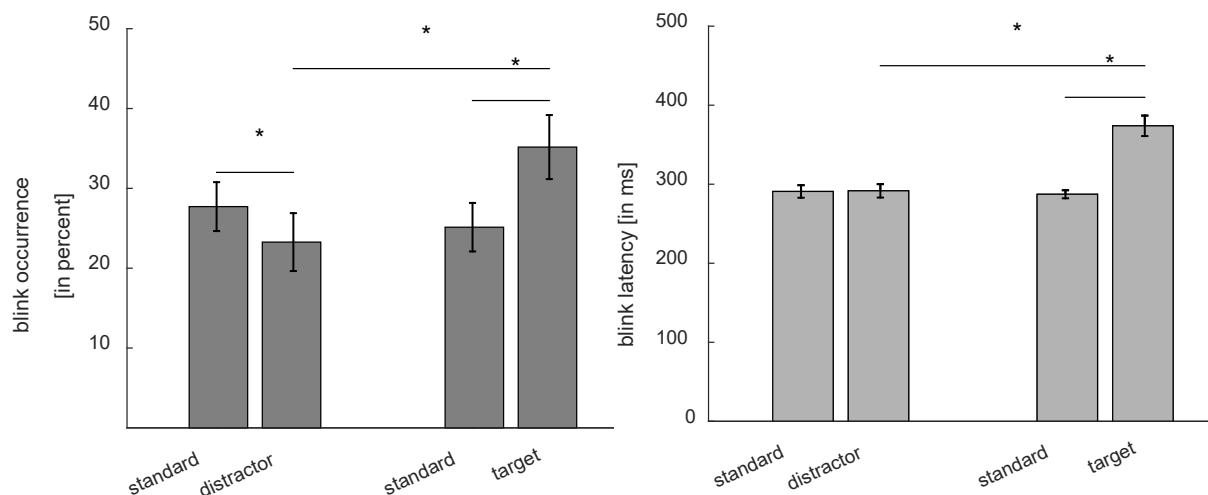


Figure 4. A. Probability of ongoing blinks after *target* (and preceding standard) onset relative to the first 50ms of the graph. B. Probability of ongoing blinks after *distractor* (and preceding standard) onset relative to the first 50ms of the graph. C. Blink occurrence after target, distractor and their preceding standards in percent. Paired t-test revealed significant differences in blink occurrences between standard-distractor, standard-target and distractor-target. Error bars represent SEM. D. Blink latency after target, distractor and their preceding standards. Paired t-test revealed significant differences in blink latency between standard-target and distractor-target. Error bars represent SEM.

Discussion Experiment 1

Our first experiment indicates that predictable sensory input modulates the probability of ongoing blinks before as well as after the sensory presentation. Firstly, we found a lower blink probability in preparation for the visual stimuli compared to the auditory stimuli. This reduction in blink probability was also found when participants attended to visual input compared to auditory input in a bimodal condition, i.e. when sensory stimuli from both domains were presented but only one was attended. Second, blink probability increased after stimulus presentation, even more so if a task drew attention to the sensory input, similarly in

both domains. Additionally, blink occurrence and blink timing following standards, distractors or targets were significantly different from each other.

Concerning the blink modulation before a stimulus, we need to consider processes based on prediction. Nakano et al. (2009) showed that when participants were watching video clips, they consistently blinked at breakpoints such as predictable actions, lifeless sequences or scenes without a character. Moreover, Fukuda (2001) reports that participants refrain from blinking before bimodal stimuli consisting of a visual Japanese syllabary and its pronunciation. In line with our findings, a reasonable interpretation could be that we do not execute our blinks at time points before or during highly relevant sensory input. Still, we found a difference with regard to the stimulus modality. We prepare for incoming visual information by not blinking, which is even intensified when a task is involved, but in preparation to auditory information, blink suppression seems to be little, and a task does not influence the blink probability in the same direction as in the visual domain. . Therefore, the visual input seems to be the driving factor for suppressing blinking in preparation to visual input. This fits well with the idea that not blinking is attributed to the optimization of visual information gathering as well as with the finding that blinking is accompanied by a reduction of neuronal activity in visual areas responsible for perceptual sensitivity (Bristow, Haynes, Sylvester, Frith, & Rees, 2005).

In addition to this pre-stimulus process, we found a second process, which increased blink probability after sensory input. Again, this modulation could be observed especially if a visual stimulus was presented. While this modulation might be partly sensory induced, since it was present under passive observation, task demands significantly enhanced this increase in blink probability, clearly indicating an additional top-down contribution. Concerning the auditory domain, such increase following sensory input was only visible if a task forced

attention to the stimulus. Stimulus evaluation accounts are unlikely to explain these results, because the standard stimuli during task conditions were not task relevant just like the stimuli in the no task conditions. The overall memory load, however, was slightly different between no task and task, since even if a standard did not lead to an update of the to-be-remembered number, the current number still had to be kept in memory. Nevertheless, attentional processes seem to be a more likely explanation since the memory load is the same during pre- and post-stimulus period, however, while post-stimulus period shows a significant increase during task vs no-task, there is no significant influence on the blink rate during pre-stimulus period. Additionally, we already found a specific attentional effect before stimulus onset when comparing bimodal conditions finding a lower blink probability for attended visual stimuli compared to attended auditory stimuli. Overall, the observed changes in the post-stimulus period indicate a task and the attentional demands introduced by it affect the modulation of blinks following sensory input similarly in the visual and the auditory modality. Changes in blink probability based on sensory input without a task, however, is only clearly visible for the visual domain.

When further analysing the post-stimulus period, we additionally find a differences in blink occurrence and latency dependent on the stimulus type. Our results on the differences in blink latency after the three stimulus types are similar to those found for other oculomotor behavior such as microsaccades. Comparable to the reported delay of microsaccade execution after target stimulus presentation (Valsecchi et al., 2007; Valsecchi & Turatto, 2009), we find that also blinks are delayed after target stimuli. Importantly, this increase in latency is not due to the infrequency of the targets, because the presentation of distractors, albeit similar in frequency, did not lead to a delay in blinking. Similarly, microsaccade execution is only slightly delayed after infrequent distractors (Widmann, Engbert, & Schröger, 2014). In addition, we

found a significantly higher blink occurrence after a target, but a lower blink occurrence after a distractor. In conclusion, microsaccades and blinks do not only react differently to different stimulus types, but they resemble each other in their behavior. In response to an event, microsaccades are first inhibited followed by a rebound phase and a return to baseline (e.g. Rolfs, 2009). Although blinks are less frequent, the probability of one to happen seem to have a similar decrease-increase-baseline signature. Consequently, Bonneh, Adini, and Polat (2016) proposition of a common inhibition mechanism for blinks and microsaccades is in line with our results.

In our second experiment, we wanted to further investigate the blinking behavior independent of sensory input. We therefore introduced stimulus omissions which were already shown to have an effect on our brain response (Tervaniemi, Saarinen, Paavilainen, Danilova, & Näätänen, 1994). While we should be able to replicate our results concerning blinking behavior around standards, we will get more insight on any non-sensory-driven influence.

Methods Experiment 2

Participants

18 participants (24.39 years old, 3 male) were analysed for experiment 2. Five additional were tested, but four had to be excluded due to unusable eye recordings and one because the target count was far off (on average 22% too many). None of them participated in experiment 1. All received payment or study credit for their participation and gave their written informed consent. The study was in line with the European data protection rules (DSGVO) and the local ethics committee approved the study.

Stimuli

The square and the circle from experiment 1 were used as visual stimuli, while the c'' (523Hz) and the f' (249Hz) served as auditory stimuli. Which stimuli were defined as targets (one visual, one auditory) and which as standards were counterbalanced across participants. The stimulus during the no-task condition matched the standard in task conditions. In addition, a stimulus was omitted unpredictably, which should be ignored. In bimodal conditions, neither the auditory nor the visual stimulus was presented. Targets had a minimal distance of five stimuli in between, a maximal distance of 17 stimuli (mean \pm SD: $8.57 \pm 0.18\%$ of all stimuli). Also, omissions had a minimal distance of five and a maximal distance of 17 stimuli between each other ($8.62 \pm 0.20\%$ of all stimuli). Targets as well as omissions appeared at least 25 times and could not immediately follow one another. All other stimuli were standards (in task trials $82.81 \pm 0.26\%$, in no-task trials 100%).

Procedure

The procedure was identical to Experiment 1.

Eye movement recording and blink detection

We used the same eye movement recording tools and the same algorithm for blink detection as in experiment 1.

Data analysis

Statistical analysis was based on the results of experiment 1. We took the means of the significant time points in the unimodal conditions of experiment 1 and evaluated the means with paired t-tests. In the bimodal pre- and post-stimulus analysis, we excluded one additional participant who blinked less than 7 times in one of the comparing conditions.

Results Experiment 2

Participants of experiment 2 miscounted the correct number of targets by 0.65 ± 1.01 (mean \pm SD). In 11.11% of all miscounted cases, participants counted less than the correct number. They blinked 22.23 ± 10.30 times per minute (mean \pm SD). The blink rate during the unimodal, visual task trial was slightly lower (mean: 18.78 ± 8.89 SD) than during the unimodal, auditory task trial (mean: 24.42 ± 12.25 SD).

Pre- and post-stimulus modulations

Replicating the results of experiment 1, the unimodal, visual condition had a stronger decrease in probability of ongoing blinks before stimulus onset compared to the unimodal, auditory condition ($t(17) = -6.42, p < .001, d = 1.51$) (Fig. 5ab). Again, we found the same effects during bimodal conditions before stimulus onset (visual vs auditory attention: $t(16) = -2.68, p = .016, d = 0.65$) (Fig. 5cd). In addition, the blink modulation effects after stimulus onset were also highly similar (Fig. 6a). We found a significantly higher blink modulation for unimodal, visual conditions compared to unimodal, auditory conditions ($t(17) = 4.43, p < .001, d = 1.05$) (Fig. 6b) and a higher modulation for task trials than for no task trials, which however did not reach significance ($t(17) = 2.09, p = .052, d = 0.49$) (Fig. 6c). In bimodal conditions, we again found no difference between attention on visual compared to attention on auditory ($t(16) = 1.48, p = .158, d = 0.36$) (Fig. 6e). Comparing the blink modulation between task and no task in bimodal conditions showed similar values as in the unimodal conditions ($t(16) = 2.07, p = .055, d = 0.50$) (Fig. 6f). Although the comparison between task and no task did not reach significance in the second experiment, blink modulation graphs look highly similar to our first experiment.

A

B

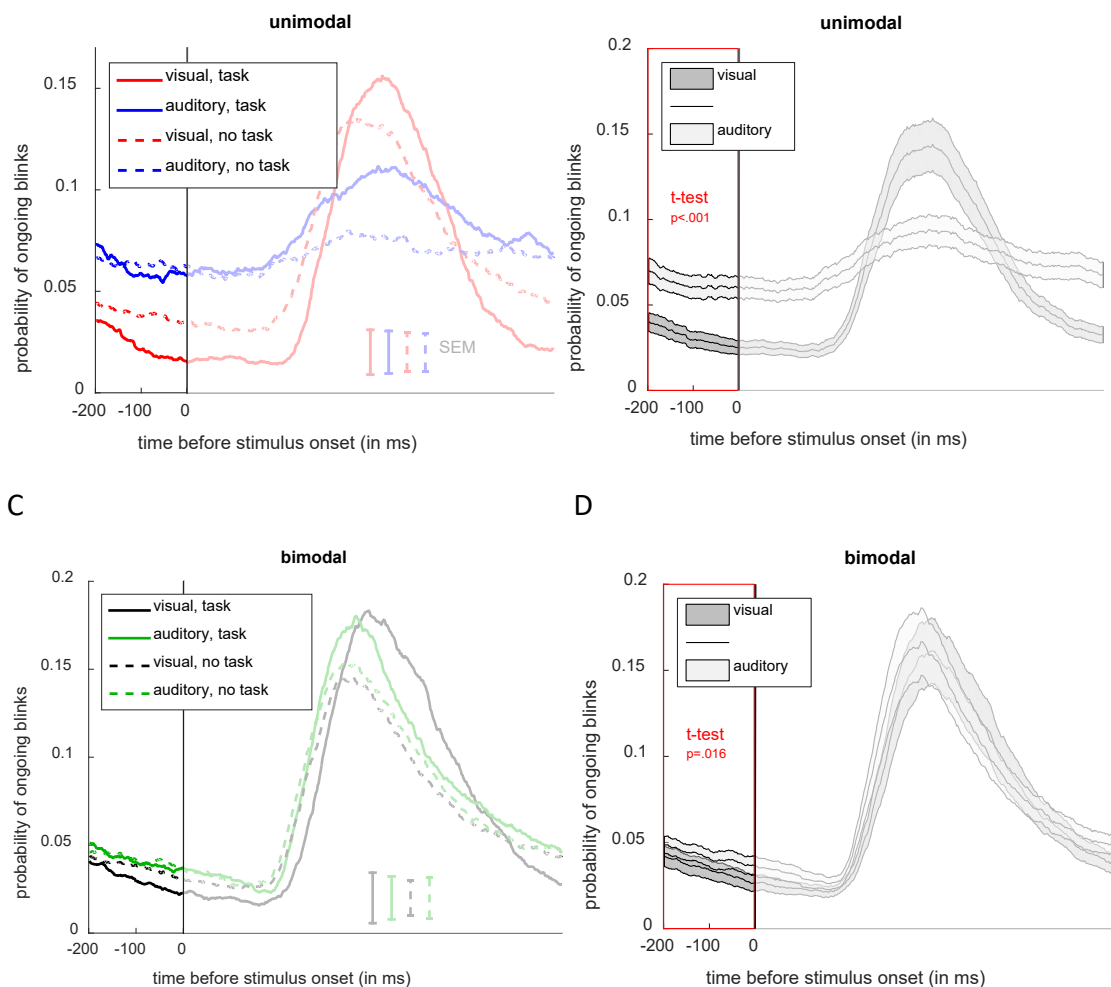


Figure 5. Pre-stimulus analysis of mean probability of ongoing blinks. **A.** Probability of ongoing blinks around stimulus onset during *unimodal* conditions. Error bars represent the averaged standard error over all time points. **B.** Significant main effect of the probability of ongoing blinks during visual vs auditory stimulation. The probability of ongoing blinks during time points of significance (framed red) taken from the unimodal analysis of experiment 1 were averaged, and then visual vs auditory was compared with a paired t-test. Shaded areas represent SEM. **C.** Probability of ongoing blinks around stimulus onset during *bimodal* conditions. Error bars represent the averaged standard error over all time points. **D.** Significant main effect of the probability of ongoing blinks during bimodal stimulation with attention on visual vs attention on auditory. The probability of ongoing blinks during time

points of significance (framed red) taken from the unimodal analysis were averaged, and then visual vs auditory was compared with a paired t-test. Shaded areas represent SEM.

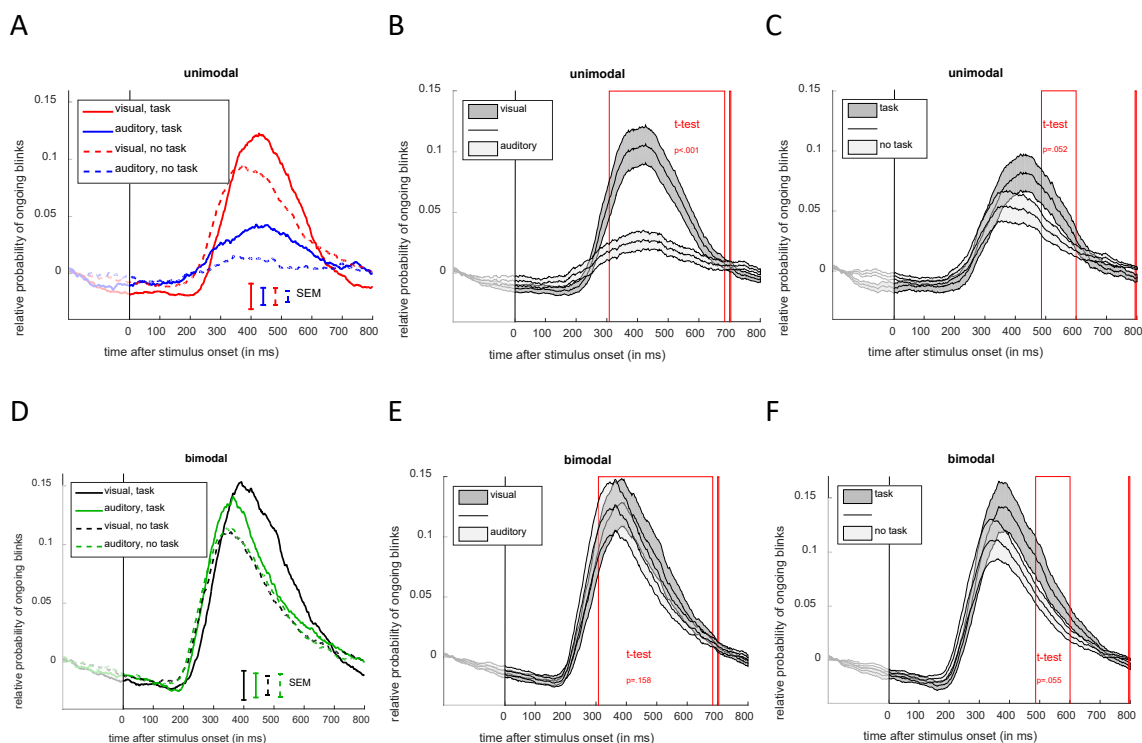


Figure 6. Post-stimulus analysis of relative mean probability of ongoing blinks. A. Probability of ongoing blinks around stimulus onset during *unimodal* conditions relative to the first 50ms of the graph in experiment 2. Error bars represent the averaged standard error over all time points. B. Significant main effect of probability of ongoing blinks around unimodal stimulation during visual vs auditory (mean \pm SEM). The probability of ongoing blinks during time points of significance (framed red) taken from the unimodal analysis of experiment 1 were averaged, and then the probability of ongoing blinks during visual vs auditory was compared with a paired t-test. The difference was significant. C. Main effect of probability of ongoing blinks around unimodal stimulation during task vs no task (mean \pm SEM). The probability of ongoing blinks during time points of significance (framed red) taken from the unimodal analysis of experiment 1 were averaged, and then the blink probability during task vs no task was compared with a paired t-test. The difference did not reach significance ($p=.052$). D.

Probability of ongoing blinks around stimulus onset during *bimodal* conditions relative to the first 50ms of the graph in experiment 2. Error bars represent the averaged standard error over all time points. E. Main effect of probability of ongoing blinks around bimodal stimulation with attention on visual vs attention on auditory (mean±SEM). The probability of ongoing blinks during time points of significance (framed red) taken from the unimodal analysis in experiment 1 were averaged, and then attention on visual vs attention on auditory was compared with a paired t-test. There was no significant difference. F. Main effect of probability of ongoing blinks around bimodal stimulation during task vs no task (mean±SEM). The probability of ongoing blinks during time points of significance (framed red) taken from the unimodal analysis in experiment 1 were averaged, and then probability of ongoing blinks during task vs no task was compared with a paired t-test. The difference did not reach significance ($p=.055$).

Stimulus type modulation

Interestingly, blink behavior after an omission was only partly similar to the results of blink behavior after a distractor. Figure 7 (ab) shows the relative probability of ongoing blinks after targets, omissions and their preceding standards separately for the four conditions. For statistical analysis, we averaged over conditions to have an appropriate amount of blinks per participant. After an omission, participants blinked on average 29.32 ± 4.89 times, after a target 46.00 ± 5.18 times. Testing the number of blinks, we found a significantly lower blink occurrence after an omission, but only compared to the blink occurrences after targets ($t(17) = -3.11$, $p = .006$, $d = 0.73$) and not compared to standards ($t(17) = -2.15$, $p = .046$, $d = 0.51$, critical $\alpha = 0.025$ due to correction for multiple comparisons). Also, the comparison of blink occurrence between targets and standards did not reveal a difference ($t(17) = 1.33$, $p = .200$, $d = 0.31$) (Fig. 7c). Blink latency after an omission was significantly higher than after a standard

($t(17) = 3.33, p = .003, d = 0.79$), which was not the case after a distractor in experiment 1. Similarly, to the first experiment, blink latency was significantly higher after a target compared to after a standard ($t(17) = 3.41, p = .003, d = 0.80$). Note that blink latencies after an omission was highly similar to latencies after a target ($331 \pm 10.77\text{ms}$ and $335 \pm 13.20\text{ms}$) (Fig. 7d).

Additionally noteworthy are the two peaks in the probability of ongoing blinks after a target. They can be seen most strongly during visual trials (red and black line in fig. 7a), one being in line with the peak after standard stimuli, the other shifted by approximately 300-400ms.

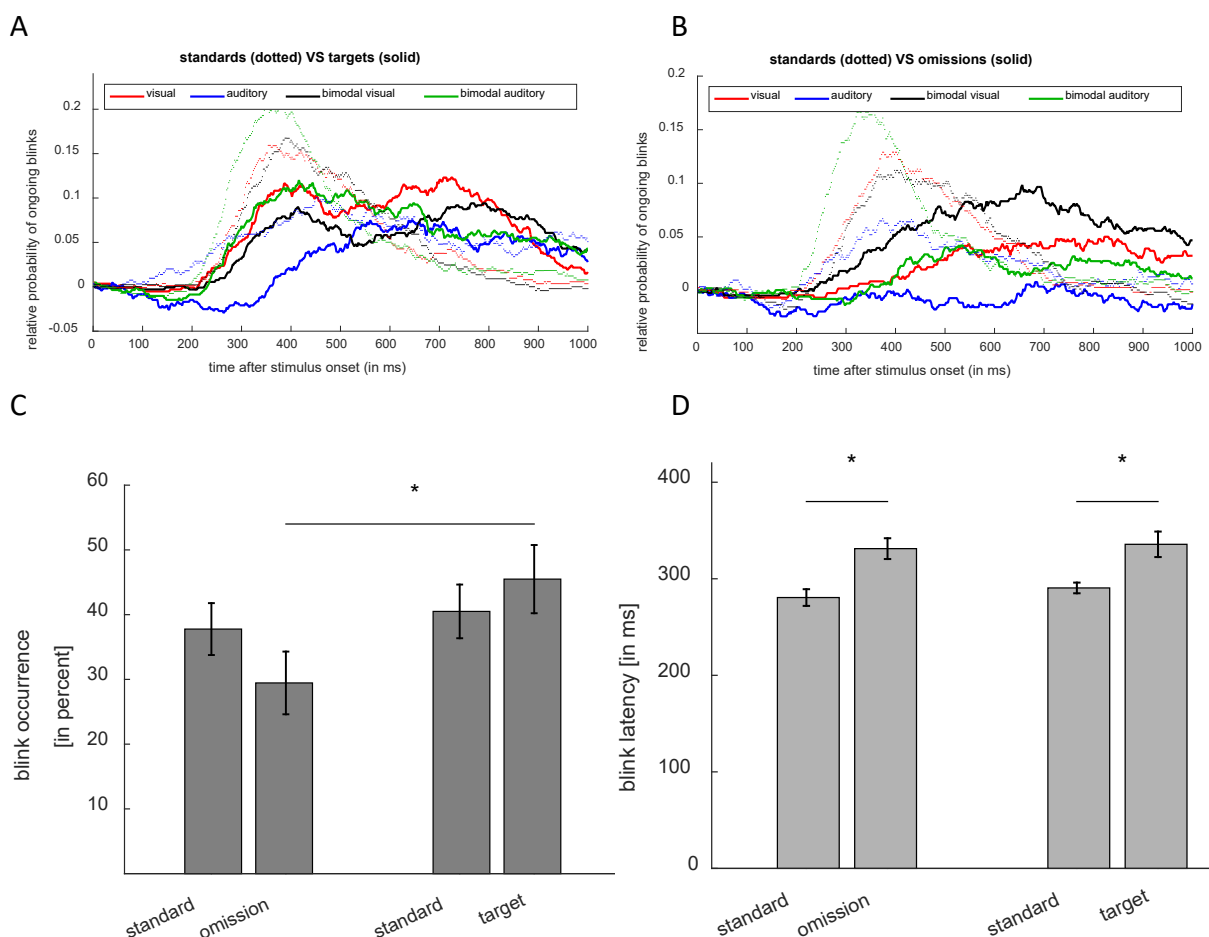


Figure 7. A. Probability of ongoing blinks after *target* (and preceding standard) onset relative to the first 50ms of the graph. B. Probability of ongoing blinks after *omission* (and preceding standard) relative to the first 50ms of the graph. C. Probability of ongoing blinks after target, omission and their preceding standards. Paired t-test revealed significant differences in blink

occurrence only between omission and target. Error bars represent SEM. C. Blink latency after target, omission and their preceding standards. Paired t-test revealed significant differences in blink latency between standard-omission and standard-target. Error bars represent SEM.

Discussion Experiment 2

We again found two independent processes that influence the probability of ongoing blinks, confirming the results of experiment 1. One process constitutes of a suppression of blinks before sensory input whenever attention is turned to visual stimulation, the other increases blink probability after sensory input, no matter if the task is in the visual or auditory domain. In addition, experiment 2 indicates that the post stimulus increase consists of two underlying processes, including an early, mainly sensory-based effect, and a slightly later purely top-down driven influence. This is indicated by the finding that there is a bimodal latency distribution for targets and an increased latency (overlapping with the second peak of this distribution) for omissions. This could mean that sensory input changes blink probability at an early time point, and that this change in blinking is already affected by general attentional processes, i.e. task vs no task. At a later time period a second influence is active, which is independent of sensory input (i.e. also the omission will lead to such an influence), but based on the interpretation of the stimulus (standard vs. omission vs. target).

The effect of stimulus omissions on electro-cortical event related potentials during oddball paradigms was intensively investigated. While the first studies showed that a P300 is produced when omitting any external stimulation (Stapleton & Halgren, 1987), later studies revealed lower amplitudes, poorer morphology and higher thresholds for the P300 to be elicited (McCullagh et al., 2009). The latter concluded that the P300 has an endogenous (internal or cognitive) component, which however is optimized when an external event is presented. The same logic would fit our blinking behavior. Both the recognition of a target as

well as the realization of time passing beyond the normal measure (omission) needs some kind of internal processing, which could introduce a higher blink latency. An actual stimulus presentation (external event) might enhance blink occurrence in comparison to no stimulus presentation.

General Discussion

The aim of this study was to understand if the influences on blinking behavior during visual and/or auditory input are the same. Moreover, we wanted to distinguish general bottom-up from top-down influences on blinks. The combination of both experiments made it possible to disentangle three partly independent processes. 1) In preparation of visual input there is a decreased blink rate compared to auditory input. This decrease is still present when attention is focused on visual input during bimodal stimulation indicating a domain-specific preparatory top-down influence. 2) Standard sensory input leads to an early increase in blink rate in both modalities if a task is involved. Visual input leads to a pronounced early increase even without task. This indicates a visual bottom-up influence in addition to a general top-down effect. 3) This early increase is further reduced (visual domain) or gone (auditory domain) if the sensory input is a target, an omission or a distractor. In the case of target and omission, an additional late increase in blink rate is found in both domains, which means it is based on the interpretation of the input, but does not need any sensory input at all to occur. This suggest a domain general, input specific top-down influence on blinking.

When trying to disentangle top-down from bottom-up influences on blinking, our experiment includes a variety of cases where a combined influence is possible. However, also two extremes are present; in one case, we present sensory input that can be ignored, since no task is involved. Here little to no specific cognitive process in response to the sensory input can be assumed. Nevertheless, blinks quickly follow such negligible input, however, only in the

visual domain. This indicates a relatively early, sensory driven response to processed, but task irrelevant input. On the other extreme, our paradigm included an omission of sensory input during a task. Interestingly, this non-sensory event still leads to an increased probability of ongoing blinks, however at a later time point. Since sensory input was missing, this effect must obviously be rather based on a cognitive top-down influence. It is now interesting to assess the blink modulation due to target presentation since target processing, in addition to the sensory input processing, is very likely accompanied by higher-order processing since target appearance must result in a response. Indeed, an early and a late peak was found in the time-resolved blink modulation following a target. Our findings therefore indicate that blinks are influenced by top-down and bottom-up processes in different time windows. This idea has already been suggested for other eye related movements such as saccades. Van Zoest and Donk (2006) investigated how saccades are affected by bottom-up and top-down control using a visual selection paradigm. They concluded that fast saccades were completely stimulus driven, whereas slower ones were goal driven. While they initially stated that these processes are completely independent, a follow-up study further developed their theory towards an interaction between bottom-up and top-down processes influencing saccadic behavior (Mulckhuyse, van Zoest, & Theeuwes, 2008). Furthermore, also microsaccades were suggested to be affected by an interaction of low- and high-level processes. While low-level visual properties are expressed by changes in microsaccade rate, attentional processes could be observed in microsaccade direction (Engbert, 2012). Since we show that also blinking follows such complex pattern influenced by bottom-up and top-down processes, a similar mechanism as discussed for saccades might underlie blinking. However, our results also show that a clear time-based separation of bottom-up and top-down influences might not always be possible, because standards and distractors show the same early blink latency, but differ

in the number of blink occurrences suggesting a top-down influence also at an early time point.

For our pre-stimulus results, we can further specify a general top-down process that has an influence on our blinking. Albeit identical sensory input in bimodal conditions, we found a difference between attention on visual and attention on auditory stimuli in preparation of stimulus occurrence. In more detail, attention on visual information decreases blink probability before stimulus occurrence. Attentional effects could also explain our second top-down post-stimulus influence, where we found a stronger blink modulation for task than for no task conditions. Furthermore, it is in line with research showing an effect of attention on microsaccades (Rolfs, 2009) as well as on event-related potentials (Squires et al., 1975). Nevertheless, other processes might have an additional impact on the modulation following sensory input, e.g. memory-comparison processes (Donchin & Coles, 1988; Jacobsen & Schröger, 2001) and decision making processes (McCullagh et al., 2009) have been suggested to play a role. Given the interaction between blinking and cognition, and the influence of blinks on brain activity (Bonfiglio et al., 2009; Liu, Ghosh Hajra, Cheung, Song, & D'Arcy, 2017), we advise caution in carelessly classifying blinks as artifacts. Further research is needed to identify the specific role of blinks in electrophysiological data.

Conclusion

Overall, our experiments show a complex modulation of blinking that is based on cognitive factors such as prediction and attention in addition to sensory-based effects. Such influences are present in blink rate as well as blink timing. We further show that the modulation of blinking is not restricted to the visual domain but also present in the auditory domain. However, pre-stimulus effects in preparation to sensory input are only visible in visual

tasks. We conclude that blinks are influenced by a variety of early sensory (bottom-up) and late cognitive (top-down) influences.

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