HOW MOVEMENTS AND COGNITION INTERACT:
AN INVESTIGATION OF SPONTANEOUS BLINKS

WIE BEWEGUNG UND KOGNITION INTERAGIEREN:
EINE UNTERSUCHUNG SPONTANER LIDSCHLÄGE

Doctoral thesis for a doctoral degree
at the Graduate School of Life Sciences,
Julius-Maximilians-Universität Würzburg,
Section Neuroscience

submitted by

Mareike Kimberly Brych

from

Hagen, Germany

Würzburg, 2021

Submitted on: ……………………………………………………………….........

Office stamp

Members of the Thesis Committee

Chairperson: Prof. Dr. Matthias Gamer

Primary Supervisor: Dr. Barbara Händel

Second Supervisor: Prof. Dr. Wilfried Kunde

Third Supervisor: PD Dr. Robert Blum

Date of Public Defence: 08.04.2022

Date of Receipt of Certificates: ……………………………………………

List of publications

Parts of this thesis have been published in the following references:

1) Brych, M., & Händel, B. (2020). Disentangling top-down and bottom-up influences on blinks in the visual and auditory domain. *International Journal of Psychophysiology*, 158, 400-410. https://doi.org/10.1016/j.ijpsycho.2020.11.002

2) Brych M, Murali S, & Händel B (2021) How the motor aspect of speaking influences the blink rate. *PLoS ONE*, 16(10): e0258322. https://doi.org/10.1371/journal.pone.0258322

3) Brych, M., Händel, B. F., Riechelmann, E., Pieczykolan, A., & Huestegge, L. (2020). Effects of vocal demands on pupil dilation. *Psychophysiology*, 58(2): e13729. https://doi.org/10.1111/psyp.13729

The publications listed above have been reproduced with permission from both the publishers and the co-authors.

Further publications

4) Brych, M.*, Murali, S.*, & Haendel, B. (2021). The influence of eye movements and their retinal consequences on bistable motion perception. *Frontiers in Psychology, 12:* 647256. https://doi.org/10.3389/fpsyg.2021.647256
*shared first authorship

A detailed statement of individual author contributions can be found in Appendix **C**.

ZUSAMMENFASSUNG

Während unseres natürlichen Verhaltens werden kognitive Prozesse und Körperbewegungen wie Kopf- oder Augenbewegungen oder Lidschläge parallel ausgeführt. Allerdings werden Bewegungen in experimentellen Untersuchungen zu kognitiven Prozessen meist stark eingeschränkt, was unnatürlich ist. Um natürliches Verhalten besser zu verstehen, wird in dieser Dissertation die Interaktion zwischen Kognition und Bewegung untersucht. Der Fokus liegt auf spontanen Lidschlägen, die auch mit anderen Körperbewegungen auf natürliche Weise interagieren.

Das Blinzeln ist unweigerlich mit dem Sehen verbunden, da bei jedem Lidschluss die Informationsaufnahme unterbrochen wird. Frühere Forschungsergebnisse zeigten, dass sowohl sensorische als auch kognitive Faktoren, wie beispielsweise Reizpräsentation und -evaluation, das Blinzeln beeinflussen können. Die erste Studie dieser Dissertation untersuchte, ob dieselben Einflüsse auf das Blinzeln wirken, wenn auch nicht-visuelle Informationen präsentiert werden. Das gewählte Versuchsdesign erlaubte rein sensorische von kognitiven Einflüssen auf das Blinzeln zu trennen. Diese Einflüsse konnten wiederum zwischen visuellem und auditivem Input verglichen werden. Unsere Ergebnisse zeigen, dass das Blinzeln stärker bei visuellem als bei auditivem Input angepasst wird, wenn dieser nur passiv verfolgt wird. Sobald allerdings Aufmerksamkeit auf den Input gerichtet wird, wird diese Anpassung an den sensorischen Input in beiden Modalitäten auf ähnliche Weise verstärkt. Zusätzlich wird der Zeitpunkt des Blinzelns durch die kognitive Bewertung der Reize verzögert - unabhängig davon, ob ein Reiz visuell oder auditiv präsentiert wird. Insgesamt legen unsere Experimente dar, dass das spontane Blinzeln und kognitive Prozesse über das Sehen hinaus miteinander verknüpft sind. Die zu

Grunde liegenden kognitiven Prozesse, die das Blinzeln beeinflussen, sind sogar weitgehend dieselben bei unterschiedlichem sensorischen Input. Das Blinzeln scheint demnach tiefgreifend in unser System integriert zu sein.

Ein weiterer wichtiger Aspekt natürlichen Verhaltens ist die gleichzeitige Ausübung mehrerer Bewegungen. Da diese Bewegungen miteinander interagieren und eine Verbindung zu kognitiven Prozessen besteht, erhöht sich die Komplexität unseres Systems. Im zweiten Teil der experimentellen Untersuchungen wurden daher Bewegungsinteraktionen in den Vordergrund gestellt. Die präsentierten Studien haben insbesondere den Einfluss verschiedener Bewegungsaspekte des Sprechens auf unser spontanes Blinzeln bzw. auf die Pupillengröße untersucht. Unsere Ergebnisse zeigen, dass sprechbezogene Bewegungen sowohl die Anzahl der Lidschlüsse als auch die Pupillengröße erhöhen, sowie den Zeitpunkt der Lidschlüsse beeinflussen. Auch andere Forscher fanden solche Zusammenhänge zwischen verschiedenen Körper- und Augenbewegungen. Da jede vom Körper verursachte Veränderung der Augenbewegung zudem unsere visuelle Reizaufnahme verändert, kann man schlussfolgern, dass verschiedene Bewegungen und deren komplexe Interaktionen eng mit unserer Wahrnehmung verbunden sind.

Alles in allem liefert diese Arbeit weitreichende Beweise, wie stark Bewegungen und kognitive Prozesse miteinander verwoben sind. Daher sollten Bewegungen als wesentlicher Teil unseres Systems angesehen werden. Wir müssen daher die Bedeutung von Bewegungen und deren Interaktionen in experimentelle Forschung einbeziehen, um ein realistischeres und kompletteres Bild unseres natürlichen Verhaltens zu enthüllen.

SUMMARY

During natural behavior, cognitive processes constantly coincide with body movements such as head or eye movements or blinks. However, during experimental investigations of cognitive processes, movements are often highly restricted which is rather unnatural. In order to improve our understanding of natural behavior, this thesis investigates the interaction between cognition and movements by focusing on spontaneous blinks, which naturally interact with other body movements.

Spontaneous blinks are inevitably connected to vision as they shut out incoming visual information. Both sensory-based and cognitive factors, for example, stimulus occurrence and evaluation, were reported to influence blink behavior. Our first study investigated if such influences are comparable for visual and non-visual input. The chosen experimental design allowed dissociating sensory-driven and cognitive influences, which then could be compared between the visual and auditory domain. Our results show that blinks are more strongly modulated during passive observation of visual input compared to auditory input. This modulation is however enhanced for both input modalities by an increased attentional demand. In addition, the cognitively defined meaning of a stimulus changes blink latency independent of the sensory domain. Overall, our findings show that spontaneous blinks and cognitive processes are linked beyond vision. Moreover, the underlying cognitive processes that influence blinks are largely the same across different sensory input indicating that blinks are profoundly integrated into our system.

When investigating natural behavior, it is important to consider that movements rarely occur in isolation, but are executed side by side. As these movements interact and have a link to cognitive processes, the complexity of our system increases. In order to take this complexity into account, the second part of the experimental research focused on movement interactions, more specifically on the interactions between blinks, pupil size and speaking. Our results reveal that speech-related motor activity increases blink rate and pupil size as well as modulates blink timing. This is in line with previous research that described a relation between different body and eye movements. Importantly, each bodily-induced change in eye movements affects visual information intake. Therefore, different movements can be tightly linked to perceptual processes through complex interactions.

Altogether, the work of this thesis provides rich evidence that movements and cognitive processes are deeply intertwined. Therefore, movements should be seen as an integral part of our system. Taking the relevance of movements and their interactions into account during experimental investigations is necessary in order to reveal a more realistic and complete picture of human natural behavior.

Table of Contents

1 GENERAL INTRODUCTION

When we are awake, our body is constantly moving. Even during periods of rest, our hearts are beating, we frequently execute very small eye movements and we blink every few seconds. During more active periods, larger movements, such as walking, head or larger eye movements are additionally executed. During natural behavior, our cognitive processes coincide with the execution of such body movements. However, when we experimentally investigate cognitive processes, participants are often asked to sit motionless, place the head in a headrest and/or fixate a small spot thereby suppressing blinks and restricting other eye movements. These are clearly unnatural situations. Therefore, it is time to understand cognition during more realistic behavior and that is during movement. The experiments of this thesis shed light on the interaction between cognition and subconsciously executed blinks and pupil size changes as well as how these small movements interact with consciously produced movements, more specifically speech-related motor activity.

Humans spontaneously blink every 3 to 4 seconds. An important function of blinks is to moisturize the eyes; however, these subconscious movements happen far more often than necessary (for more details, see Al-Abdulmunem, 1999). Nevertheless, spontaneous blinks are not randomly executed in time, but preferably around visual input (Bonneh, Adini, & Polat, 2016; Siegle, Ichikawa, & Steinhauer, 2008), which might be attributed to the optimization of visual information gathering. Furthermore, studies reported that blinks are modulated by cognitive processes, for example, at the end of stimulus evaluation processes (Fukuda, 2001; Wascher, Heppner, Möckel, Kobald, & Getzmann, 2015).

Interestingly, such cognitive effects were also shown outside vision, namely in the auditory domain suggesting a more general influence on blinks (Kobald, Wascher, Heppner, & Getzmann, 2019; Oh, Jeong, & Jeong, 2012). If sensory influences can be distinguished from cognitive ones and if blink behavior is indeed driven by a common mechanism that is involved in both visual and auditory information processing is not known. In order to shed light on these important questions, study 1 of this thesis investigated these questions with a setup that enabled a direct comparison of sensory and cognitive influences in the visual and auditory domain as well as in the bimodal domain. Our findings reveal an influence of cognitive processes on blink behavior beyond vision and how deeply blinks are integrated into our system.

Not only is there an integration of blinks into the cognitive system, but also in the motor system. Motor tasks such as walking or finger tapping increase the blink rate (Cao & Händel, 2019; Cong, Sharikadze, Staude, Deubel, & Wolf, 2010). Similarly, hand or finger movements were reported to increase pupil size (Richer & Beatty, 1985; Zénon, Sidibé, & Olivier, 2014). Previous studies also described an increase in the number of blinks during a conversation (Bentivoglio et al., 1997; Doughty, 2001; Karson et al., 1981), a phenomenon for which many possible explanations were reported (Doughty, 2001, 2018). Yet, no one investigated which components of speaking influence blink behavior and pupil size. Studies 2 and 3 of this thesis examined motor-related influences under strict control of sensory and cognitive factors that possibly act on blinks and pupil size during speaking. Our findings add insights on how movements interact, which is an important aspect of natural behavior. Furthermore, especially eye-body movement interactions are of high interest, since a change in eye movements is accompanied by a change in sensory information intake and consequently, influences perceptual processes.

Taken together, our research shows how spontaneous blinks are embedded in the cognitive and the motor system while thoroughly considering sensory influences.

This leads to a complex picture of cognition and movement including tight links and a large set of movement interactions. Altogether, movements should be seen as part of our cognitive system that need to be taken into account when studying natural behavior.

1.1 SPONTANEOUS BLINKS

1.1.1 ANATOMICAL AND NEURAL BASIS OF BLINKS

When investigating blinks, one need to keep in mind that three types of blinks can be distinguished. Firstly, involuntary blinks that protect the eyes are referred to as reflex blinks. They are elicited by external stimulation. Secondly, consciously executed blinks are called voluntary blinks. And thirdly, subconscious blinks, which happen approximately 18 times per minute (Al-Abdulmunem, 1999), are referred to as spontaneous blinks (VanderWerf, Brassinga, Reits, Aramideh, & Ongerboer de Visser, 2003). All blinks are characterized by the movement of the upper eyelid. The combination of the relaxation of the levator palpebrae superioris (LP) muscle and the activation of the orbicularis oculi (OO) muscle lowers the upper eyelid rapidly. As soon as the OO muscle relaxes and the LP muscle resumes its activation, the eyelid is again elevated (Evinger, 2010). The downward movement of the eyelid is similar between spontaneous, voluntary and reflex blinks, while the upward movement varies in duration, amplitude and velocity (VanderWerf et al., 2003). In addition, spontaneous blinks are associated with a small downward and inward eyeball rotation, whereas voluntary and reflex blinks show an additional, subsequent upward eyeball rotation (Collewijn, Van Der Steen, & Steinman, 1985; Iwasaki et al., 2005).

The blink generation pathway was predominantly studied by manipulating the excitability of reflex blinks in rodents. Successive experiments led to the assumptions that the basal ganglia, the superior colliculus in the mid brain and motor nuclei in the brainstem play key roles in the modulation of reflex blinks (figure 1). More specifically, neurons of the substantia nigra pars reticulata, an output nucleus of the basal ganglia, inhibit neurons in the superior colliculus. In turn, these neurons excite neurons in the nucleus raphe magnus in the brain stem leading to the inhibition of the neurons in the spinal trigeminal nucleus that are connected to the orbicularis oculi muscle via the facial motor nucleus (Basso & Evinger, 1996; Basso, Powers, & Evinger, 1996; Evinger et al., 1993). Additional pathways that connect the superior colliculus and the facial nerve were found comprising the reticular formation and the cervical spinal cord (Smit et al., 2006). Furthermore, studies in cats revealed that the cerebellum and its connection to the brainstem might be involved in the control of reflex blinks (Gruart & Delgado-Garcí, 1994). Overall, the reflex blink pathway is highly complex.

To bridge the gap to the human blink pathway, researchers looked at reflex blinks in Parkinson's disease patients. This disease has been related to the level of dopamine, a neurotransmitter that is produced in the substantia nigra pars compacta. This brain area is connected to the substantia nigra pars reticulata and thus, to the reflex blink pathway via an excitatory-inhibitory pathway through the striatum and the globus pallidus internal (areas of the basal ganglia, see figure 1) (Peterson & Sejnowski, 2017). If the dopamine level is decreased like in Parkinson's disease, the animal model suggests an increase in reflex blink excitability, which is indeed observed in human patients (Schicatano, Peshori, Gopalaswamy, Sahay, & Evinger, 2000). Therefore, the animal blink reflex model seems to hold for humans too. Surprisingly, the generation of spontaneous blinks is scarcely investigated. It has been assumed that a spontaneous blink generator circuit exists, in which the spinal trigeminal complex is a key element (Kaminer, Powers, Horn, Hui, & Evinger, 2011). Given that patients with Parkinson's disease show a reduced spontaneous blink rate, but dopaminergic medication increase it, an overlap with the reflex blink circuit is likely (Karson, Lewitt, Calne, & Wyatt, 1982). Furthermore, animal drug studies also postulate a relation between dopamine and spontaneous blink rate, however, human studies are less conclusive (for a review, see Jongkees & Colzato, 2016).

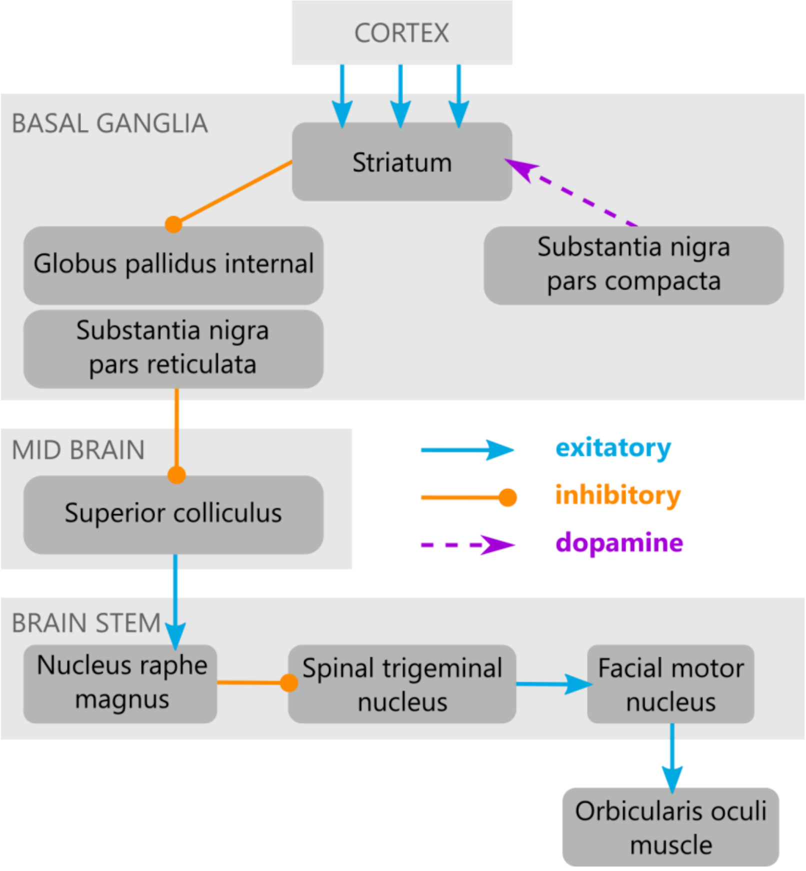

Figure 1. Reflex blink generation pathway (adapted from Peterson et al., 2017). This is a simplified graphical representation. The basal ganglia incorporates even more parts and segments, additional (indirect) pathways exist between the superior colliculus and the facial motor nucleus and the cerebellum is also likely involved in this pathway (see text). The generation pathway for spontaneous blinks is assumed to overlap with the reflex blink pathway.

1.1.2 PERCEPTUAL CONSEQUENCES OF BLINKS

During a spontaneous blink, vision is blocked for 100 - 300 milliseconds (Riggs, Volkmann, & Moore, 1981; Sun et al., 1997). While most blinks go unnoticed, an external darkening of the visual field for 30 ms is easily detectable (Riggs et al., 1981). Two phenomena of neural mechanisms were described to account for this phenomenon: blink suppression and visual continuity. The first to experimentally describe blink suppression were Volkmann and colleagues who placed a light in the oral cavity to stimulate the retina and bypass the eyelids. Few participants then had to detect light decrements, which varied in amplitude and time, during voluntary blinks. The sensitivity to the changes were found to be suppressed already before blink onset, reached a minimum before the lid covered the pupil completely and ended approximately 200 ms after blink onset (Volkmann, Riggs, & Moore, 1980). In a follow-up experiment, the authors showed that the closing eye is primarily linked to the insensitivity and less the eye opening, which rather facilitates the retrieval of visual information (Volkmann, Riggs, Ellicott, & Moore, 1982). Similar results were obtained when air puffs elicited reflex blinks (Manning, Riggs, & Komenda, 1983). In addition, Riggs and colleagues showed that simulated blinks produced by external darkening need to be shorter and of lower light reduction to match the visual effects of voluntary blinks (Riggs et al., 1981). Ridder III and Tomlinson (1993) added that the blink-related insensitivity is strongest for stimuli with low spatial frequencies such as introduced by the lowering eyelid. In sum, behavioral studies suggest that the darkening caused by the eyelid is not perceived due to the neural suppression during blinks. Indeed, there is evidence from neurological studies in primates that the absence of transient signals in the visual cortex (V1, V2, V3V, V4V, i.e. ventral stream of perceptual processing) of a small subset of neurons are responsible for the insensitivity to blink-related changes (Gawne & Martin, 2000, 2002). In humans, lateral parts of the temporo-occipital cortex including V3 and V5/MT showed a suppressed activity during blinking in the presence of a visual stimulus (Bristow, Frith, & Rees, 2005; Bristow, Haynes, Sylvester, Frith, & Rees, 2005). While blink suppression describes why we do not notice the darkening, it does not explain why we perceive a stable image although visual input is blocked during a blink. Such visual continuity mechanisms would be identifiable by an increased brain activity during blinks in combination with a visual stimulus compared to during blinks in complete darkness. The posterior parietal cortex was found to show such an increased activity during voluntary blinks (Hari, Salmellin, Tissari, Kajola, & Virsu, 1994) as was the medial parieto-occipital region (Bristow, Frith, et al., 2005).

1.1.3 RATE AND TIMING OF SPONTANEOUS BLINKS

When investigating influences on blinks, one can look at different blink parameters such as frequency, duration or amplitude. In this work, findings related to blink rate, i.e. the number of blinks in a certain time period, and blink timing, i.e. when are blinks suppressed, released or delayed, are presented. Please note that “blinks” refer to spontaneous blinks throughout this thesis if not otherwise indicated. Since the interest of this works lies in the interaction between blinks and cognition, especially perception, information processing and attention, the following section focuses on those processes. Nevertheless, studies investigating other factors that are possibly linked to blinks are shorty described.

Influences on blink rate

Ponder and Kennedy (1927) were one of the first to systematically investigate spontaneous blink rates. They found an effect neither of humidity nor of corneal anaesthetizing indicating that blinks are not solely a reaction to corneal irritation. Furthermore, they found that blink differences during light and total darkness are minimal and blink behavior is similar in the blind suggesting that blinking goes beyond the perception of light. Additional experiments led to the conclusion that mental tension, which includes attentional processes, but also excitement and anger, increases the blink rate (Ponder & Kennedy, 1927). Several studies also described an effect of fatigue on blinking, which likely includes the factor of time on task, but also factors such as visual input or task demands (for a review, see Stern, Boyer, & Schroeder, 1994). Indeed, visual demandingness has been frequently reported to decrease the blink rate. One of the most prominent findings is the decrease during reading (Bentivoglio et al., 1997; Cho, Sheng, Chan, Lee, & Tam, 2000; Doughty, 2001; Hall, 1945). Similarly, other visual tasks such as video watching (Nakano, Yamamoto, Kitajo, Takahashi, & Kitazawa, 2009) or visual search (Benedetto et al., 2011; Recarte, Pérez, Conchillo, & Nunes, 2008) were shown to decrease the blink rate. Additionally, a positive relation between the amount of visual information and the magnitude of the decrease was revealed (Cardona, García, Serés, Vilaseca, & Gispets, 2011; Drew, 1951; Nakano et al., 2009). The inhibition of blinks during such tasks might be attributed to the necessity of efficient visual information intake. Other sensory modalities are less studied. Concerning auditory studies, neither an auditory tracking task (Gregory, 1952), nor listening to an audio book (Nakano et al., 2009) or to different tones (Fukuda, 1994) significantly influenced the blink rate. Consequently, not every type of sensory input necessarily leads to an overall decrease in blink rate. Importantly, apart from the sensory influence, that is the transmitted and processed information from the senses without an interpretation thereof, all of the tasks above described likely involve at least some cognitive demands as well, for example, understanding the text or story or distinguishing between stimulus features or attentional demands. Therefore, these studies cannot entirely distinguish between sensory and cognitive influences, but sensory influences are typically put forth as a cause for the inhibition of blinks (e.g., Cardona et al., 2011).

In order to specify cognitive influences, it is necessary to control the external environment by holding the sensory input constant and investigate different cognitive task demands, for example, by presenting two tasks with different difficulty. The reported results so far are not entirely coherent. Several researchers claimed that cognitive demands increase the blink rate. For example, Tanaka and

Yamaoka (1993) asked participants to solve two arithmetic tasks written on a sheet of paper and found a significant increase in blink rate during the difficult compared to the easy task. Liu et al. (2019) even excluded sensory input except for a fixation spot and asked participants to perform mental arithmetic or passively wait. Again, the blink rate increased during the cognitive task. Other researchers assessed blink behavior during tasks requiring different amounts of cognitive control, such as during the Stroop task (Stroop, 1935). Here, color words are printed in either the same or another color and participants are asked to name the color (the word "blue"/"red" printed in blue requires the answer "blue"). Response time and errors are longer/higher when word and ink are incoherent indicating a higher amount of cognitive control that is needed. Using a slightly adapted visual Stroop task, Oh, Han, Peterson, and Jeong (2012) reported significantly higher blink rates during trials of high cognitive control compared to trials of low cognitive control. Yet, also several null findings with regard to the relation between blink rate and cognitive processes were described using a letter-search task (Tanaka & Yamaoka, 1993) or an adapted auditory Stroop task (Oh, Han, et al., 2012). Then again, few studies also showed a decrease in blink rate when comparing counting backwards and "clearing the mind" (Holland & Tarlow, 1975). Overall, influences of cognitive task demands on blink rate are rather inconsistent.

On the contrary, a consistent finding that has been reported repeatedly is the blink rate increase during a conversation or an interview (Bentivoglio et al., 1997; Doughty, 2001; Karson et al., 1981). Both sensory and cognitive influences are likely to be involved when seeing and hearing the conversational partner as well as understanding what is said and speaking in full sentences. Moreover, several other influences were suggested to affect blink rate during a conversation. Doughty (2001) pointed out a potential influence of opinions, emotions or interest. Also social factors were shown to be positively correlated with blink rates across primates (Tada, Omori, Hirokawa, Ohira, & Tomonaga, 2013). Furthermore, speech-related movements were suggested to increase the number of blinks during a conversation (Doughty, 2018; von Cramon & Schuri, 1980). Such a potential motor influence makes it difficult to interpret studies that tried to pinpoint cognitive influences on blinking using verbal responses and without a clear description if the amount of speaking was monitored (Bagley & Manelis, 1979 [negative relation]; Cho et al., 2000 [null results]; Recarte et al., 2008 [positive relation]; Rosenfield, Jahan, Nunez, & Chan, 2015 [negative relation]).

Studies 2 and 3 of this thesis aimed at dissolving several of those ambiguities. Apart from our main goal to study the interaction between movements and blinking, other influencing factors of a conversation on blinks were investigated. More specifically, auditory, cognitive and motor factors were tested, while controlling for social and emotional factors as well as for visual input. In addition, our results reveal insights on how vocal responses might affect the interpretation of cognitive influences on blink behavior during experiments.

Influences on blink timing

The previous section summarized findings on changes in the blink rate that is the number of blinks measured over minutes or at least several seconds. Consistent results were obtained with regard to visual information intake, namely blink rate decreases, and to conversational tasks, namely blink rate increases. Studies on auditory information intake are scarce, but the few existing ones reported no influence on the blink rate. The influence of cognitive task demands on blink rate is not entirely clear given inconsistent findings. However, researchers often additionally investigated changes in blink behavior within a task that is on a second to millisecond scale. In other words, researcher examined influences on blink timing. Both continuous tasks, that is the continuous presentation of a stimulus, and discrete-trial paradigms, that is the alternation of stimulus presence and absence, were used.

Continuous tasks have the advantage to be highly comparable to our natural behavior; however, it is more difficult to determine the exact time points of cognitive processes. Nevertheless, some studies reported consistent results. For example, during an ongoing, circular detection task with locally varied target probabilities, participants suppressed their blinks during high occurrence probabilities and released them after these periods (Hoppe, Helfmann, & Rothkopf, 2018). Similarly, blinks were primarily inhibited during important passages such as main character action while watching a comedy and were predominantly executed during implicit breaks (Nakano et al., 2009). Also, when reading, we tend to blink when turning the page or at the end of sentences (Hall, 1945). In addition, blink behavior seems to be comparable during continuous auditory tasks. More specifically, blinks were preferably executed during periods of lowest cognitive demands during an auditory tracking task (Gregory, 1952). Using a continuous speech processing task, Jin, Zou, Zhou, and Ding (2018) showed that blinks even tracked an attended syllable in a four-syllable sentence, that is blinks were suppressed during and released after the presentation of the attended one. Thus, this research suggests that blinks predominantly occur at optimal breaks within visual and auditory information processing which is likely driven by attentional and/or predictive processes.

Another interesting approach to study the influence of perceptual processes on blink timing is the use of bistable stimuli (also called ambiguous stimuli). During the continuous presentation of such a stimulus, the interpretation of this stimulus switches spontaneously every few seconds between two or more possible percepts albeit unchanging sensory input. A prominent example is the Necker cube (Necker, 1832). Here, the orientation of a wire frame drawing of a cube can be interpreted in two possible ways: The front side is either perceived on the lower-left or on the upper-right (e.g., see fig. 1 in Einhäuser, Stout, Koch, & Carter, 2008). Some studies reported a suppression of blinks before the button press that indicated a perceptual switch and a facilitation of blinks afterwards (Einhäuser et al., 2008; Ito et al., 2003; van Dam & van Ee, 2005). Studies of our lab extended these findings and showed that such a decrease in blink execution co-occurs with the actual perceptual switch (before the manual response) and the blink increase is not universal for all switches, but rather percept-specific (Brych, Murali, & Händel, 2021). Overall, a perceptual switch might be comparable to previously reported periods of high attentional demands, while the time after the switch is the least likely to contain another perceptual switch and is possibly of low attentional demand. Nevertheless, the percept-specificity suggests that also other cognitive processes are involved. In addition to the findings of continuous tasks with changing stimulation, bistable perception studies clearly show that the influence of perceptual processes on blink behavior exists independent of changes in sensory input.

Albeit reduced ecological validity, discrete-trial paradigms allow the experimenter to highly control the timing as well as the amount of stimulus events. This facilitates the determination of the exact time point of cognitive processes and enables averaging responses over a high number of identical inputs. Given that the blink rate likely decreases to optimize visual information input, it is little surprising that blinks are not executed during stimulus presentation, but rather in the absence of stimuli during such paradigms (Bonneh et al., 2016; Oh, Han, et al., 2012; Siegle et al., 2008). Using this sensory-driven influence as a reference, cognitive influences on blink timing during both the time period before stimulus onset as well as after stimulus offset can be examined. To investigate the influence of predictive processes, blink behavior before stimulus appearance needs to be analyzed. Researchers reported that predictive processes seem to inhibit blinks before visual stimulus onset for a duration that is dependent on the inter-stimulus-interval

(Bonneh et al., 2016; Wascher et al., 2015). Other researchers examined the influence of selective attention, that is focusing on relevant and ignoring irrelevant information, on blink timing after stimulus offset. Various experimental designs, such as visual continuous performance tasks (Pivik & Dykman, 2004; Sirevaag et al., 1999; Wascher et al., 2015) or a guilty knowledge test and a dual modal task (Fukuda, 2001) showed that blink execution is delayed after relevant compared to irrelevant stimuli. This suggests that stimulus evaluation has an influence on blink latency similar to the influence on reaction times (Fukuda, 2001). Instead of varying the relevance of the stimuli, differences in cognitive processing can also be measured by manipulating the amount of cognitive control that is needed to fulfill a task. Wascher et al. (2015) used a visual version of the Simon task, which is characterized by a conflict between stimulus location and response side (Simon & Rudell, 1967). In line with the other findings, blink latencies as well as reaction times were higher in trials of incompatible stimulus-response mapping requiring higher cognitive control. The authors concluded that blinks are inhibited until stimulus evaluation is finished. Less studied but apparently similar to visual stimulation is the influence of cognitive processes during auditory stimulation: Blinking was shown to be inhibited during auditory stimulus presentation and rebounds after stimulus offset whenever participants were engaged in a task (Fukuda & Matsunaga, 1983; Kobald et al., 2019; Oh, Jeong, et al., 2012). It was further revealed that the level of blink suppression during auditory stimulus presentation is positively correlated with cognitive task demands during stimulus presence (Kobald et al., 2019; Oh, Jeong, et al., 2012). Also, increased processing demands for highly relevant, auditory stimuli delay blink execution (Kobald et al., 2019).

Taken together, similarities in blink timing during visual and auditory tasks have been observed, such as the blink inhibition during stimulus presence and the release after stimulus offset as well as the delay in blink execution when higher cognitive demands are present. These findings suggest that blink behavior is modulated by general mechanisms that are involved in both visual and auditory information processing. Study 1 of this work further investigated this notion by systematically and directly comparing blink behavior during visual and/or auditory stimulation under varying cognitive demands ranging from passive observation to active task demands. Showing a common mechanism across sensory modalities would constitute a big step in understanding the link between cognition and eye/body movement and could be extended to other modalities such as the somatosensory domain.

1.2 THE PUPIL

1.2.1 ANATOMICAL AND NEURAL BASIS OF PUPIL SIZE

The pupil is the apparently black spot in the center of the eye. It is actually a hole, through which the light enters the eye. The opposing muscles of the iris, namely the constricting iris sphincter muscle and the dilating iris dilator muscle, change pupil size. Depending on the incoming amount of light, the human pupil can adjust from 1 to 9 mm in diameter, being small during bright light and large during dim light (Beatty & Lucero-Wagoner, 2000).

The parasympathetic constriction pathway and the sympathetic dilation pathway control the pupil size. Whenever light falls onto the retina, the constriction pathway is actived. From the retina, a signal is send to the pretectal olivary nucleus in the midbrain. From there, neurons project to the parasympathetic neurons in the Edinger Westphal nucleus and finally to the ciliary ganglion controlling the constricting iris muscle (Szabadi, 2012). Consequently, pupil size decreases and less light enters the eye. The dilation pathway does the opposite, namely increasing pupil size. Here, the hypothalamus excites the locus coeruleus, which projects to the sympathetic neurons in the intermedio-lateral column of the spinal cord (but also has an inhibitory influence on the Edinger Westphal nucleus). From the spinal cord, the signal is projected to the superior cervical ganglion innervating the iris dilator muscle (Mathôt, 2018; Szabadi, 2012). The superior colliculus, which receives input from the retina as well as from higher cortical areas and projects to both pathways, and the locus coeruleus, which is involved in both pathways, have been suggested frequently to be key structures for pupil responses (Mathôt, 2018; Wang & Munoz, 2015).

1.2.2 PUPIL CONSTRICTION AND DILATION

Three human pupil responses have been distinguished: the light response, the near response and the psychosensory response (Mathôt, 2018). In bright light, the pupil minimally constricts to approximately 1mm in diameter. In darkness, the pupil dilates up to 9mm in diameter (Beatty & Lucero-Wagoner, 2000). This response is mainly considered reflexive. Nevertheless, cognitive processes such as visual attention, mental imagery and working memory can modulate this light-dependent pupil response (for reviews, see Binda & Murray, 2015; Mathôt, 2018). Less known and little studied is the finding that the pupil also shrinks when we fixate on a near spot in our environment and dilates when fixating a far-away object. This near response is also considered reflexive. The influences of cognitive processes on this pupil response are not intensively investigated and rather unclear. Both the light response and the near response have a functional role in vision namely modulating visual sensitivity and visual acuity/ depth of field (Mathôt, 2018).

As the name suggest, the psychosensory response can be distinguished in a sensory and a cognitive response that are not luminance-related. They are typically less than 0.5 mm in size and thus, clearly less pronounced compared to the light or near response. Interestingly, the pupil always dilates to such events and never constricts. During constant light input, sudden, attention-grabbing sensory input independent of stimulus modality typically elicits a pupil dilation, a reaction that was described among other physical reactions as orienting response (Lynn, 1966; Sokolov, 1963). Finally, cognitively driven changes in pupil size were observed independent of light changes, fixation position or stimulus onset. They are slower in time compared to the influence of attention-grabbing sensory input. The interest in studying cognitively-driven pupil size responses started in the 1960s, when Hess and Polt published two studies showing first, that the interest in pictures was positively correlated with pupil size (Hess & Polt, 1960) and second, that mental arithmetic increased pupil size depending on the level of difficulty (Hess & Polt, 1964). The latter was replicated by other researchers, who also revealed that the magnitude of pupil size increases was related to the ability to perform such a task suggesting that the amount of information processing relates to pupil size (Ahern & Beatty, 1979). This conclusion is in line with studies using experimental designs of cognitive control such as the Stroop task (Laeng, Ørbo, Holmlund, & Miozzo, 2011; Siegle et al., 2008). Here, the incongruent condition (color word tinted in a different color) was associated with a stronger pupil dilation compared to the congruent (color word tinted in the same color). Likewise, other cognitive processes independent of visual input were found to be related to a sustained increase in pupil size. Examples are working memory demands (Karatekin, Marcus, & Couperus, 2007), auditory information processing and recognition (Weiss, Trehub, Schellenberg, & Habashi, 2016), decision making (Katidioti, Borst, & Taatgen, 2014), memory retrieval (Beatty & Kahneman, 1966) as well as visual target detection (Privitera, Renninger, Carney, Klein, & Aguilar, 2008).

As reviewed above, both pupil size changes as well as blinks are linked to sensory input and cognitive processes (e.g., Beatty & Lucero-Wagoner, 2000; Karson et al., 1981). Therefore, one needs to control for these influences, whenever studying other influences on such eye-related movements such as motor activity. In study 3 of this thesis, we investigated how defined speech-related motor output affects pupil size and blinks thereby minimizing any cognitive or sensory influence.

Importantly, sensory, cognitive and motor factors likely influence eye-related movements in a combined way during natural behavior. Consequently, study 2 additionally includes natural conditions such as normal speaking.

1.3 MOVEMENT INTERACTIONS

During natural behavior, cognitive processes and movements, for example spontaneous blinks and pupil size, are linked. In addition to this link, it is also important to take into account that during natural behavior, not only one movement is executed, but several are executed side by side. For example, we walk, turn our heads, and shift our gaze at the same time as we pay attention to our surrounding. Interestingly, such movements were shown to interact with each other. Thus, if we want to understand natural behavior, we also need to take into account movement interactions. In the following, research that focused on the interaction between different eye movements as well as between eye and body movements is reviewed. This is of special interest, because every eye movements is inevitably accompanied by a change in sensory information intake. Thus, by investigating eye movements and their interactions, we improve our understanding of how we perceive our surroundings.

1.3.1 THE LINK BETWEEN DIFFERENT EYE MOVEMENTS

Rapid eye movements, which are called saccades or microsaccades depending on their size, as well as lid movements during blinks are among the fastest movements of the body (Boghen, Troost, Daroff, Dell'Osso, & Birkett, 1974; VanderWerf et al., 2003). They induce fast changes to the retinal input, which could lead to perceptual blur. However, this visual challenge is likely dealt with by suppressing visual information processing during and around them. Consequently, our world remains stable and uninterrupted across eye movements to the detriment of concurrent sensory information processing (Volkmann, 1986). Both behavioral and neurophysiological studies provide evidence for this claim. For example, the ability to detect stimulus displacements (Higgins, Irwin, Wang, & Thomas, 2009), sensitivity to light changes (Volkmann, 1986) or to contrast changes (Ridder III & Tomlinson, 1997) are reduced during both saccades and blinks. Also, the neural suppression in response to the perceptual changes caused by saccades and blinks were found to be comparable (Gawne & Martin, 2002).

Beside these shared neural and perceptual characteristics, eye movements were shown to influence each other's occurrence. Large saccades are often accompanied by blinks, but these blinks are then of longer duration (Evinger et al., 1994; Fukuda, Stern, Brown, & Russo, 2005). Besides blinks and saccades, also other eye(-related) movements show an interaction. For example, blinks during smooth pursuit decrease the pursuit velocity (Rambold, El Baz, & Helmchen, 2005) and they induce a pupil size increase that likely goes beyond a darkness induced change (Fukuda et al., 2005). Yet, these movements are not rigidly coupled as each can be individually executed. However, in addition to a certain co-occurrence, a temporal relationship exists extending over a larger time period. For instance, saccades are less likely executed before or during a blink which was investigated with a method allowing to detect saccades when the eye is closed (Rambold et al., 2005). Using a video-based eyetracker, also microsaccade were found to be inhibited in preparation of a blink (Brych et al., 2021). Studies with intracranial neural recordings in primates suggest that the interplay between blinks and saccades form a complex circuity. It has been shown that blinks can inhibit saccade generation via the superior colliculus, but also facilitate the generation via omnipause neurons in the brainstem (Katnani, Van Opstal, & Gandhi, 2012). Overall, blinks, saccades and other eye movements not only share characteristics, but they also interact with each other.

1.3.2 THE LINK BETWEEN BODY AND EYE MOVEMENTS

Despite the described link between different types of eye and eye-related movements, also movements of other body parts were frequently found to be related to eye movements. Especially the interplay between saccades, blinks and head movements has been studied extensively. For example, small gaze shifts are executed by the eyes only, but the larger the shift, the higher the contribution of head movements (Stahl, 1999). Often, the head follows the saccade and in the end, a compensatory saccade in the opposite direction is added. This order can however change, when the target location is predictable (Bizzi, Kalil, & Tagliasco, 1971). This suggests that the eye-head coordination is highly flexible. Indeed, if the head is restrained, saccades adapt in a way that they are comparable to coordinated saccade-head movements in both their duration and speed (Morasso, Bizzi, & Dichgans, 1973). Also, larger head and eye movements are more likely to be accompanied by a blink (Von Cranach, Schmid, & Vogel, 1969). Apart from these eye-head movement interactions, researchers reported interactions between the eyes and other body parts. Some studies showed that blinks are more often elicited after button presses (Baumstimler & Parrot, 1971; van Dam & van Ee, 2005) or happened more frequently during finger tapping (Cong et al., 2010). Others described a mutual influence between eye and hand trajectories (Nissens & Fiehler, 2018) and concerning pupil size, a series of studies by Richer and Beatty (1985) revealed that the pupil dilates in preparation and execution of a hand or finger movement. Furthermore, the pupil dilation was reported to be dependent on the force and number of motor responses as well as grip and exercise intensity (Hayashi, Someya, & Fukuba, 2010; Richer & Beatty, 1985; Zénon et al., 2014). A study from our own lab also found that walking is related to a higher blink rate as well as to a higher saccade rate compared to standing still (Cao & Händel, 2019). These movement interactions might be explained by independent motor systems that are connected via feedback loops (Morasso et al., 1973), or an overlapping motor control mechanism (Cong et al., 2010). Important to note is that many movements occur repeatedly during natural behavior. Consequently, also the temporal relationship between concurrent movements is of interest in order to understand natural behavior. Several reports describe those relations. For example, blink rate is not only enhanced, but blinks are also phase-locked to the finger movements in the continuous tapping task (Cong et al., 2010). Moreover, blinks and saccades are less often executed during the swing phase of the legs during walking compared to the double support phase (Cao, Chen, & Haendel, 2020) and (micro-)saccades were shown to be preferably executed shortly after heartbeats (Galvez-Pol, McConnell, & Kilner, 2020; Ohl, Wohltat, Kliegl, Pollatos, & Engbert, 2016). These findings ask for an even more complex explanation for the interaction of movements possibly involving an internal timer or rhythm, which was suggested for individual types of movements (for saccades e.g., Engbert, Longtin, & Kliegl, 2002; for blinks e.g. Kaminer et al., 2011), but also for multiple movements, for example, eye and finger movements (McAuley, Farmer, Rothwell, & Marsden, 1999).

All in all, the complex circuity of suppression and facilitation between eye movements seems to be expendable to the whole body. While discrete tasks show that the execution of one movement often triggers another movement, temporal analysis of continuous tasks add that the movement interaction is precisely timed. Importantly, if a body movement influences an eye movement, this is accompanied by a change in visual information input. Moreover, the temporal coupling suggests that visual input is specifically sampled and thus, perception is influenced in a particular way. Overall, studying the interaction of eye and body movements helps to understand the natural interplay of movements and their connection to perception thereby improving our understanding of natural behavior.

Study 2 and 3 of this thesis investigated how spontaneous blinks and pupil size changes are embedded in natural behavior. To this end, we experimentally evaluated the relationship between these movements and speaking, which is an ecologically highly relevant behavior. More specifically, we tested how different motor aspects of speaking with and without vocalization influence blinks and pupil size and additionally examined sensory and cognitive influences.

1.4 OVERVIEW OF THE PRESENTED WORK

During natural behavior, our cognitive processes co-occur with body movements. However, body, head or eye movements are often restricted in experiments investigating cognitive processes, which is rather unnatural. The research presented in this thesis aimed to understand how movement and cognition interact, while taking the influence of sensory input, cognitive demands and movement interaction into account. More specifically, study 1 investigated sensory and cognitive influences on spontaneous blinks during a highly controlled visual and/or auditory task; study 2 examined cognitive, sensory and additionally motor influences on blinking during speaking allowing largely natural motor behavior and study 3 focused on influences of defined motor output as executed during speaking on blinks and pupil size.

Researchers investigated blink behavior inside and outside vision. Blinks are suppressed during visual input, but not necessarily during non-visual input (e.g, Bonneh et al., 2016; Nakano et al., 2009). As they shut out incoming visual information and are accompanied by a neural suppression of visual brain areas, a strong link between the eye-related movement and the visual system can be assumed (Gawne & Martin, 2000, 2002). Interestingly, cognitive effects on blink behavior were shown under visual and auditory stimulation. For example, in the visual domain, blinks are suppressed during periods of high attentional demands and released during breaks thereof (e.g., Hoppe et al., 2018); they are delayed until the end of stimulus evaluation processes (e.g., Fukuda, 2001) and suppressed before predictable stimulus onsets (Bonneh et al., 2016). Albeit fewer conducted studies, similar cognitive effects were shown in the auditory domain (e.g., Kobald et al., 2019; Oh, Jeong, et al., 2012). This suggest that blinks are modulated by more general mechanisms that are involved in visual, but also auditory information processing. Such general processes are referred to as top-down processes, while sensory-driven processes are referred to as bottom-up processes. The terms are inspired by the visual hierarchy of cell types and cortical areas. Neurons in the primary visual cortex respond to simple visual features such as lines of specific orientation and location. Going up in the hierarchy and the visual cortex (bottom-up), neurons integrate these features to form simple shapes, then objects and eventually categories. At this stage, previous knowledge, prediction, attention, and evaluation processes are included. Evidence suggests that we first perceive categories before perceiving individual features thereby descending the visual hierarchy (top-down) (Hochstein & Ahissar, 2002). Also the auditory pathway includes a core area in the primary auditory cortex responsive to simple tones which connects to a belt area integrating the tones to more complex stimuli. In a third stage, represented in the parabelt, the information is processed into patterns and objects are recognized. Finally, input from highest cortical areas such as auditory memory and speech perception is included in the parabelt (Kaas, Hackett, & Tramo, 1999). Consequently, the terms of sensory bottom-up and cognitive top-down processes can be used for both visual and auditory perception.

The main goal of the experiments presented in study 1 was to clearly distinguish sensory bottom-up from cognitive top-down influences on blinks and directly compare these influences between the visual and auditory domain. To do so, we used a classical experimental design, namely an oddball paradigm. In these paradigms, a standard stimulus is presented repeatedly intermitted by another, infrequent stimulus, also called “the odd”. Passive stimulation requires predominantly sensory processing, active counting of the odds (or “target stimuli”) incorporates sensory as well as cognitive processing and the detection of a stimulus omission mainly requires higher cognitive processing. Therefore, oddball paradigms allow to dissociate cognitive and sensory influences on blinks. In addition, they can be comparably used in all sensory domains. Our results show that general processes that are independent of vision modulate blink behavior. Since the influences on blinks are even comparable in the visual and auditory domain, our findings additionally indicate how deeply blinks are integrated in our perceptual system.

Importantly, spontaneous blinks are not only linked to the sensory and cognitive system, but also to the motor system. In order to reveal a complete picture of natural behavior is it therefore also necessary to investigate movement interactions. Various body movements were reported to facilitate eye(-related) movements. Moreover, the execution of different movements are not randomly placed in time, but are temporally interconnected. In study 2 and 3 of this thesis, specifically the influence of speech-related movements, an ecologically highly relevant movement, on eye-related movements was examined. In study 2, the focus lay on describing the motor-related influence on the blink rate thereby differentiating these from sensory and cognitive effects. While study 2 had a more natural setup, study 3 focused on specific motor output, which allowed to reveal a blink modulation over time. In addition, the relation between pupil size changes and speech-related motor activity was examined. Our results describe influences on blinks thereby clearly distinguishing between various factors and for the first time, reveal vocal motor influences. Interestingly, our research sheds light on the blink rate increase during conversation, which has been discussed for a long time (e.g., Doughty, 2001). Overall, our studies highlight motor interactions between eye-related movements and other motor outputs. It is essential to remember that a change in eye movement also changes sensory information intake and thus, affects perception. Consequently, movement interactions are an important phenomenon of natural behavior, which needs to be considered during experimental investigations.

2 STUDY 1: DISENTANGLING TOP-DOWN AND BOTTOM-UP INFLUENCES ON BLINKS IN THE VISUAL AND AUDITORY DOMAIN

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 dissociating general from specific top-down influences that are independent of the sensory domain.

The official citation that should be used in referencing this material is: Brych, M., & Händel, B. (2020). Disentangling top-down and bottom-up influences on blinks in the visual and auditory domain. *International Journal of Psychophysiology*, 158, 400-410. https://doi.org/10.1016/j.ijpsycho.2020.11.002. Headlines and figure numbering were adapted to exclude ambiguities in this thesis.

2.1 INTRODUCTION STUDY 1

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 et al., 2008) or after verbal (Oh, Han, et al., 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 et al., 2018), whereas participants consistently blinked at implicit breaks when watching a movie (Nakano et al., 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 (Volkmann et al., 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 et al., 2019; Oh, Jeong, et al., 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.

2.2 EXPERIMENT 1

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°) (figure 2). 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 ± SD: 8.22 ± 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 ± 0.28% of all stimuli). Targets and distractors could follow one another. All other stimuli were standards (in task trials 83.57 ± 0.32%, in no task trials 100%).

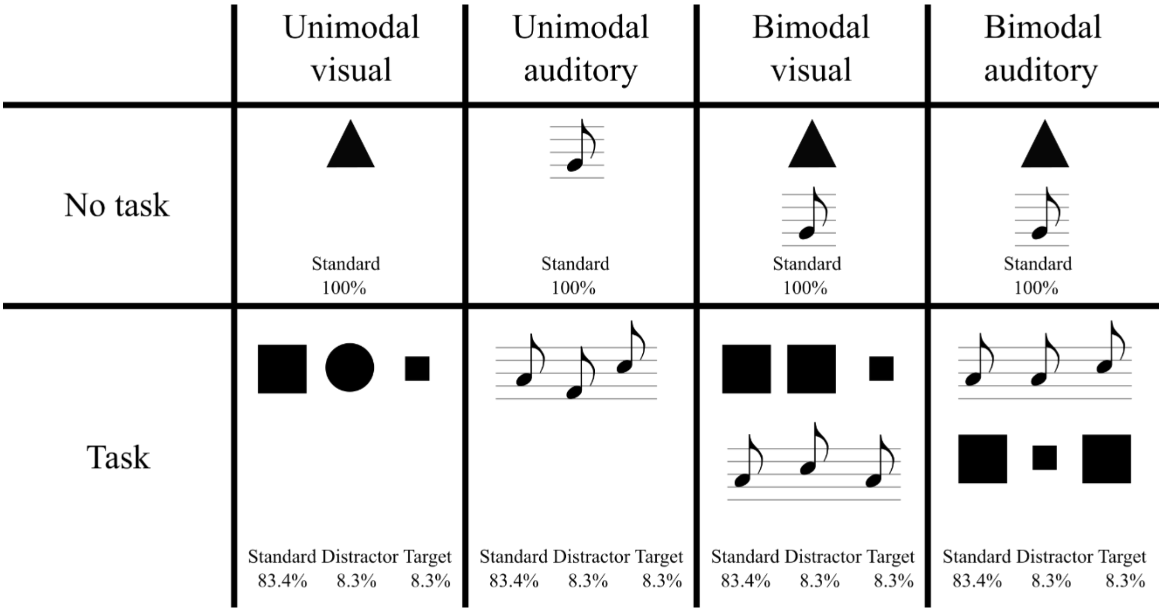

Figure 2. Illustration of the stimuli used during the different conditions in experiment 1. Distractor and target features were balanced across participants. Percentages during task conditions are approximated and could minimally deviate from the given number. Stimuli were presented for 100ms followed 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 ± 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 ± 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 (figure 3a) 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 (figure 3b). 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 ($t(25) = -5.05$, $p < .001$, $d = 0.99$) (figure 3d).

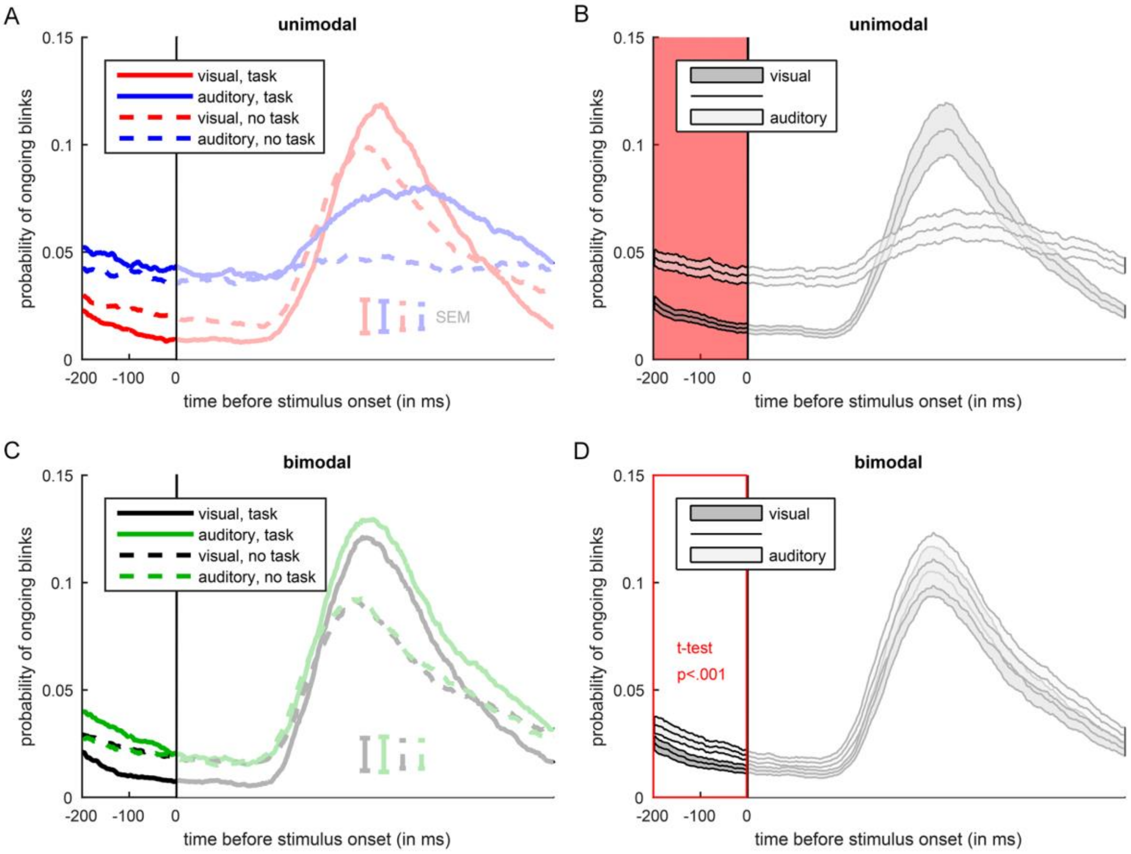

Figure 3. Pre-stimulus analysis of mean probability of ongoing blinks. A. Probability of ongoing blinks around stimulus onset during *unimodal* conditions. Error bars represent the averaged standard error over all time points. B. Main effect of probability of ongoing blinks during visual vs auditory 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 (figure 4b). 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 (figure 4c).

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 ($t(25) = 8.04$, $p = .429$, $d = 0.16$) (figure 4e), blinks were again more strongly modulated whenever there was a task ($t(25) = 3.76$, $p < .001$, $d = 0.74$) (figure 4f).

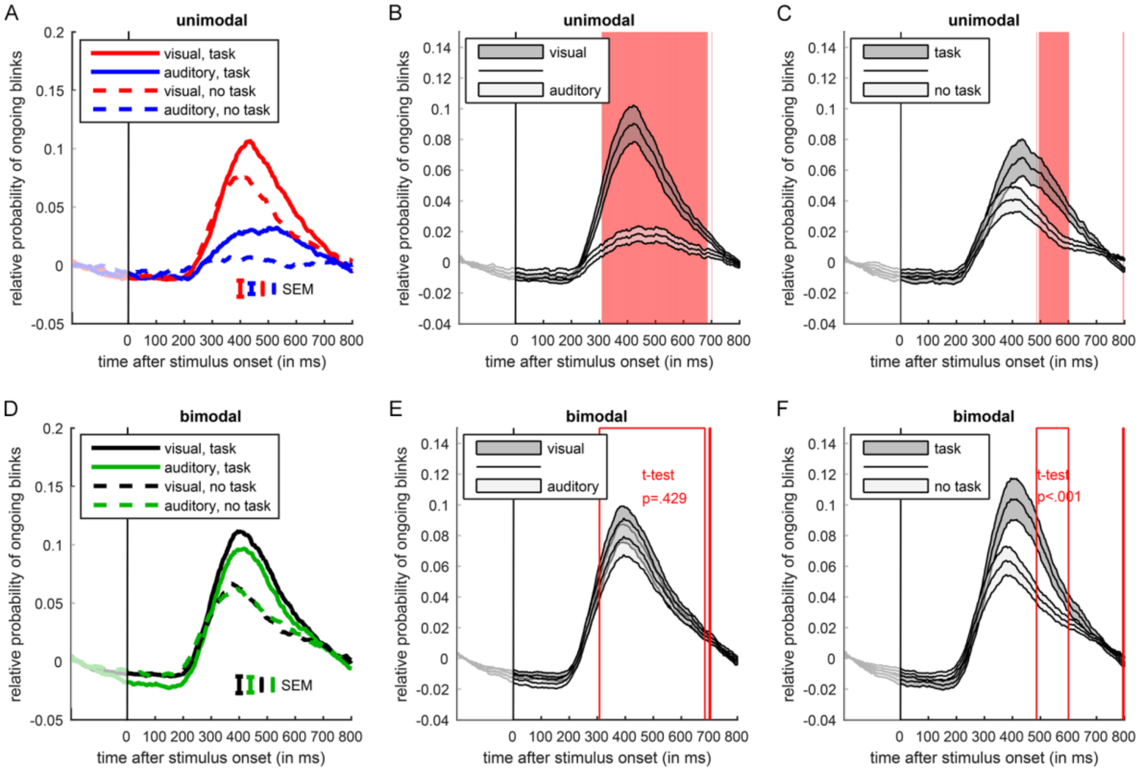

Figure 4. Post-stimulus analysis of relative mean probability of ongoing blinks. A. Probability of ongoing blinks around stimulus onset during *unimodal* conditions relative to the first 50ms of the graph. Error bars represent the averaged standard error over all time points. B. Main effect of probability 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±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±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 5b shows the relative probability of ongoing blinks of distractors as well as the standards preceding the distractors separately for the four conditions. Figure 5a 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 ($t(27) = -5.26$, $p < .001$, $d = 0.99$) (figure 5c). 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 ($t(27) = -7.42$, $p = .94$, $d = 0.01$) (figure 5d).

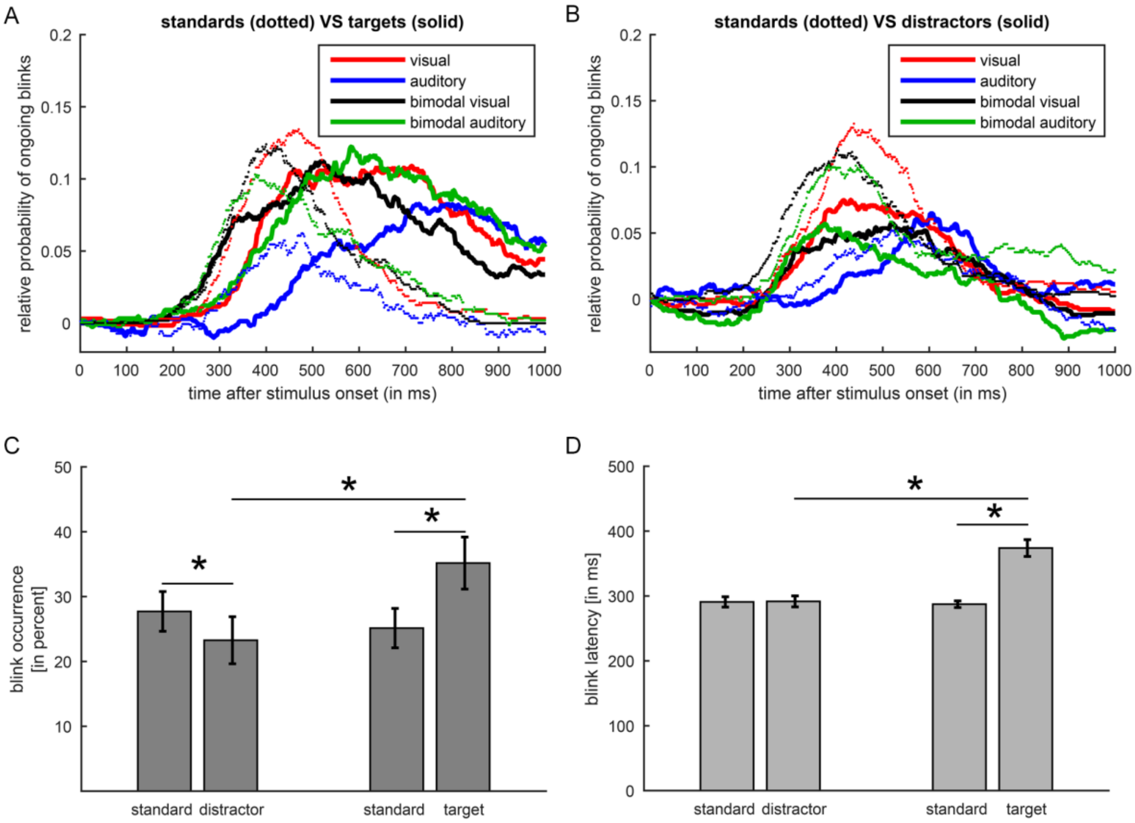

Figure 5. A. Probability of ongoing blinks after *target* (and preceding standard) onset relative to the first 50ms of the graph. B. Probability of ongoing blinks after *distractor* (and preceding standard) onset relative to the first 50ms of the graph. C. Blink occurrence after target, distractor and 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, et al., 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 et al. (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.

2.3 EXPERIMENT 2

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 ± SD: 8.57 ± 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 ± 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 ± 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 ± 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 ± 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) (figure 6ab). 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) (figure 6cd). In addition, the blink modulation effects after stimulus onset were also highly similar (figure 7a). 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) (figure 7b) 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) (figure 7c). 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) (figure 7e). 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) (figure 7f). 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.

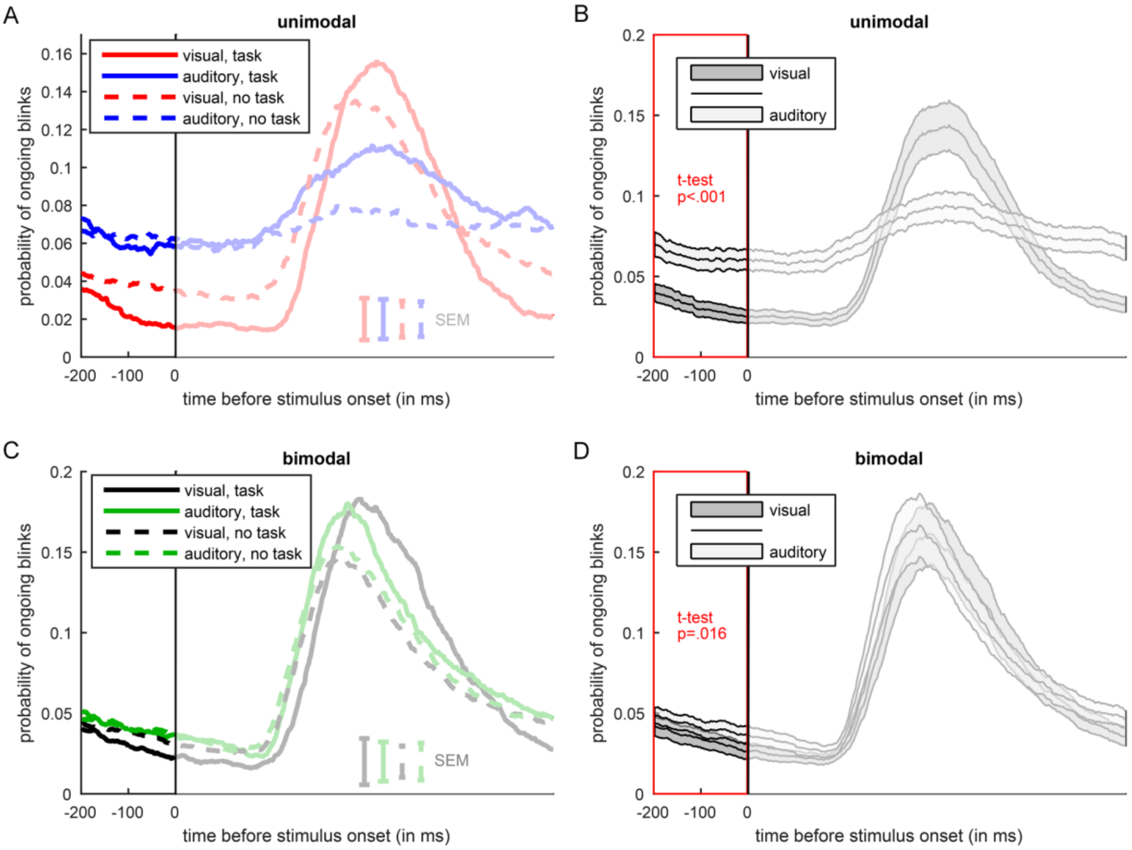

Figure 6. Pre-stimulus analysis of mean probability of ongoing blinks. A. Probability of ongoing blinks around stimulus onset during *unimodal* conditions. Error bars represent the averaged standard error over all time points. B. Significant main effect of the probability of ongoing blinks during visual 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.

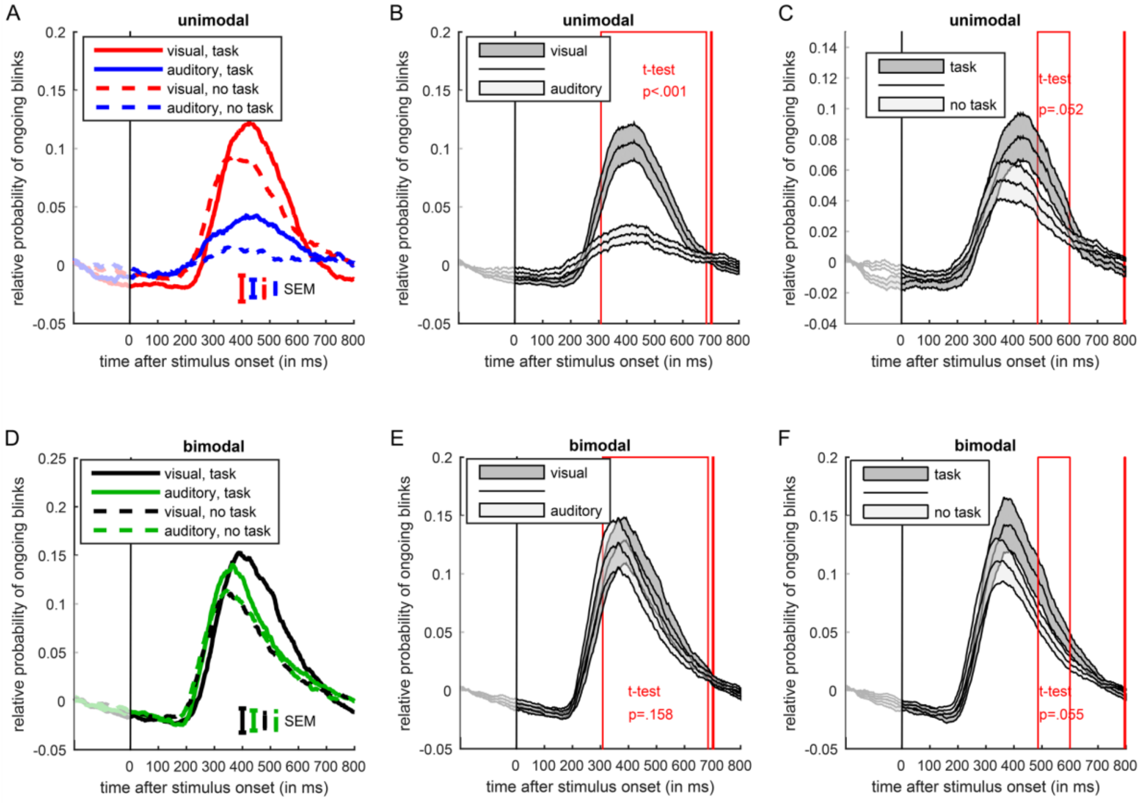

Figure 7. Post-stimulus analysis of relative mean probability of ongoing blinks. A. Probability of ongoing blinks around stimulus onset during *unimodal* conditions relative to the first 50ms of the graph in experiment 2. Error bars represent the averaged standard error over all time points. B. Significant main effect of probability of ongoing blinks around unimodal stimulation during visual vs auditory (mean±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±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 8 (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, $d = 0.31$) (figure 8c). 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±10.77ms and 335±13.20ms) (figure 8d).

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 figure 8a), one being in line with the peak after standard stimuli, the other shifted by approximately 300-400ms.

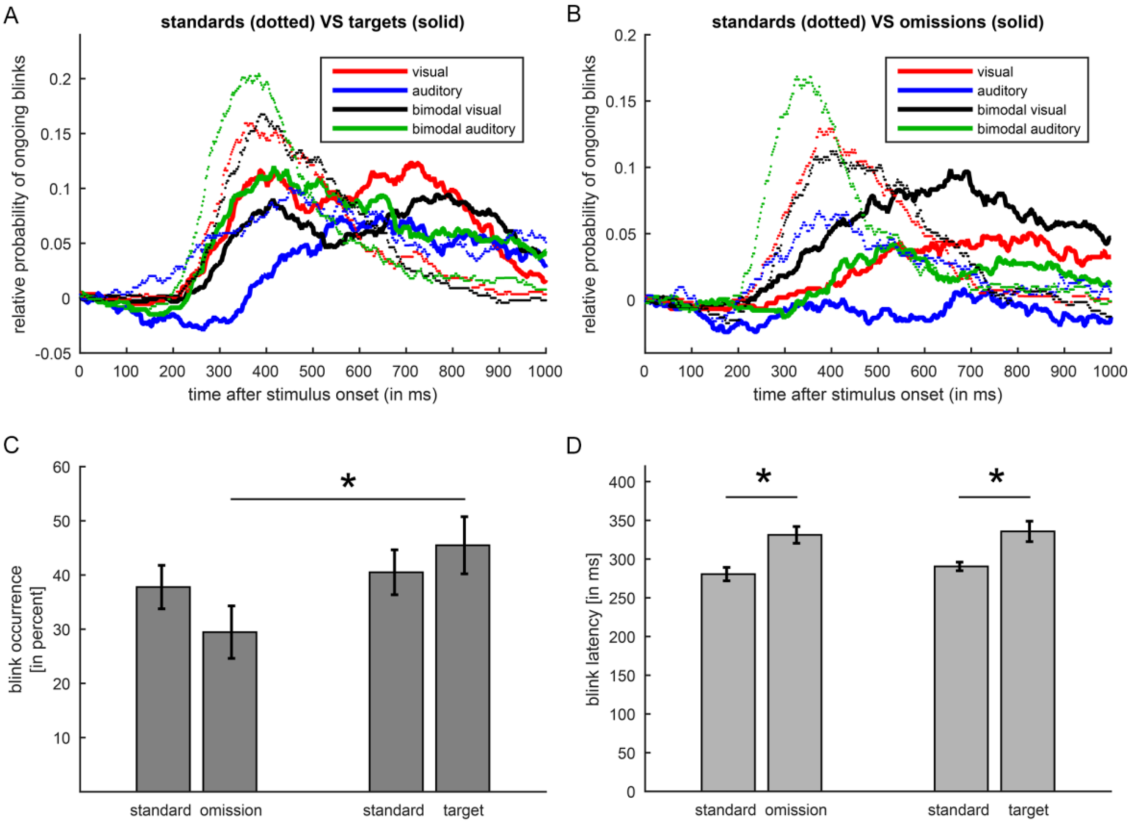

Figure 8. A. Probability of ongoing blinks after *target* (and preceding standard) onset relative to the first 50ms of the graph. B. Probability of ongoing blinks after *omission* (and preceding standard) relative to the first 50ms of the graph. C. Probability of ongoing blinks after target, omission 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.

2.4 GENERAL DISCUSSION STUDY 1

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.

3 STUDY 2 & 3: SPEECH-RELATED INFLUENCES ON SPONTANEOUS BLINKS AND PUPIL SIZE

3.1 HOW THE MOTOR ASPECT OF SPEAKING INFLUENCES THE BLINK RATE

The blink rate increases if a person indulges in a conversation compared to quiet rest. Since various factors were suggested to explain this increase, the present series of studies tested the influence of different motor activities, cognitive processes and auditory input on the blink behavior but at the same time minimized visual stimulation as well as social influences. Our results suggest that neither cognitive demands without verbalization, nor isolated lip, jaw or tongue movements, nor auditory input during vocalization or listening influence our blinking behavior. In three experiments, we provide evidence that complex facial movements during unvoiced speaking are the driving factors that increase blinking. If the complexity of the motor output increased such as during the verbalization of speech, the blink rate rose even more. Similarly, complex facial movements without cognitive demands, such as sucking on a lollipop, increased the blink rate. Such purely motor-related influences on blinking advise caution particularly when using blink rates assessed during patient interviews as a neurological indicator.

The official reference for this material is: Brych, M., Murali, S., & Händel, B. (2021). How the motor aspect of speaking influences the blink rate. PloS one, 16(10): e0258322, https://doi.org/10.1371/journal.pone.0258322. Headlines, figure and experiment numbering were adapted to exclude ambiguities in this thesis.

3.1.1 INTRODUCTION STUDY 2

Humans blink approximately every 3-6 seconds, which is far more than needed to keep a constant tear film on the cornea (Al-Abdulmunem, 1999). Blink behavior is known to be affected by multiple factors, including external sensory (e.g., Bonneh et al., 2016; Nakano et al., 2009) and internal cognitive factors (e.g., Karson et al., 1981; Liu et al., 2019). During visually demanding tasks such as reading, the blink rate drops from approximately 17 blinks per minute during rest to approximately 4 to 5 blinks per minute. Conversely, the blink rate increases during conversation to approximately 26 blinks per minute (Bentivoglio et al., 1997). This increase has been proposed to reflect various internal processes such as engagement, emotions or opinions (Doughty, 2001). Hömke, Holler, and Levinson (2017) further showed that blinks can serve as communicative signals between conversation partners. Findings as to the role of motor execution on blink rate are inconsistent. Research has shown that the motor act of speaking (von Cramon & Schuri, 1980), but not jaw movements as produced during gum chewing (Karson et al., 1981) or the mere act of keeping the mouth open (Doughty, 2018) increased blinking. Interestingly, in the latter study, a small group that exhibited notable mouth and jaw movements during a no-task condition nearly had a doubled blink rate compared to those who did not show such movements. A clarification of the influence of motor activity seems relevant, especially since blinks serve as neurological indicators in clinical settings. For example, very low blink rates are observed in patients with Parkinson’s disease (Karson et al., 1982), which is possibly due to dopaminergic hypoactivity (questioned by Dang et al., 2017; review by Jongkees & Colzato, 2016; Sescousse et al., 2018). The patient’s response to medication can be assessed by the increase in blink rate, which is often measured during the conversation with the physician (Karson et al., 1982). Consequently, if other factors such as speaking increases blink rate in the same direction, this might lead to inaccurate medical examinations. In healthy humans, blink rate is often used as an indicator of cognitive load (e.g., Karson et al., 1981; Liu et al., 2019; Wascher et al., 2015). A speech-related motor influence might therefore affect experimental outcomes using verbal responses.

We set up an experiment to systematically investigate the influences of facial motor activity on blinking behavior, while at the same time controlled cognitive and auditory influences. Several anatomical findings reveal that the eyelid and facial muscles are connected. Speaking involves various motor processes including the respiratory system, larynx and vocal tract, which is shaped by the lips, jaw and tongue (Smith, 1992). In the human brain, the area for vocalization is located inferior to the area for eyelid movements and superior to the areas for mouth movements including tongue and lip movements. The area for jaw movements is inferior to the mentioned mouth movements (Penfield & Boldrey, 1937). Considering human facial anatomy, the facial nerve (7th cranial nerve) innervates the muscles for facial expressions and eyelid closing, but is not directly involved in chewing movements (Sanders, 2010). Whenever the facial nerve malfunctions, blinking is ceased and the corner of the mouth drops on the affected side (Gilden, 2004). During surgeries, facial nerve stimulation is also used to predict the postoperative function by checking motor-evoked potential in the eye ring muscle (orbicularis oculi) and the kissing muscle (orbicularis oris) (Fukuda, Oishi, Takao, Saito, & Fujii, 2008). The above reviewed work clearly shows a proximity of the anatomical substrate of blinking and other facial movements. Our experiments particularly test the influence of motor activity on the blink rate including the isolated movements of the lips, jaw and tongue as well as speech-related movements with and without vocalization. Apart from the new insights on how blinks and other body movements are related, our work seeks to clarify the validity of blinks as a marker for pathological states as well as for sensory and cognitive processing in experiments using verbal responses.

3.1.2 EXPERIMENT 3

In a first experiment, we tested for influences of motor output during speaking. In order to account for the auditory and cognitive aspect, we included conditions in which we varied the cognitive as well as the auditory input normally introduced by speaking. We hypothesize that the blink rate is mainly increased by motor related factors as indicated by the proximity of anatomical conditions (Penfield & Boldrey, 1937; Sanders, 2010) as well as by previous research concluding a motor effect, but without strict control of other possible influences (von Cramon & Schuri, 1980). Only few studies investigated blink behavior under auditory stimulation. Concerning the number of blinks during a task, these studies reported no significant changes compared to rest (Gregory, 1952; Nakano et al., 2009) and studies testing for cognitive influences are inconsistent (Oh, Han, et al., 2012; Tanaka & Yamaoka, 1993). Therefore, we assume that auditory input or cognitive aspects of speaking only have a minor effect on blinking. Visual stimulation as well as social influence were minimized in our experiment.

Method Experiment 3

Participants

30 psychology students of the University of Würzburg (mean age: 20.17 years ± 1.86 SD, 2 male) took part in the study. All participants gave their written informed consent and received study credit for their participation. The study was approved by the local ethics committee (Institute for Psychology of the Faculty for Human Sciences of the Julius-Maximilians-University of Würzburg; project protocol number: GZEK 2015-01) and was in line with the European general data protection regulations (DSVGO).

Procedure

Participants sat alone in a noise shielded, very small, dimly lit room. They were allowed to freely move their eyes and head. Auditory instructions were given by a Sennheiser PC3 Chat headset. Binocular eye movements were recorded with the 120Hz SMI eye tracking glasses (figure 9).

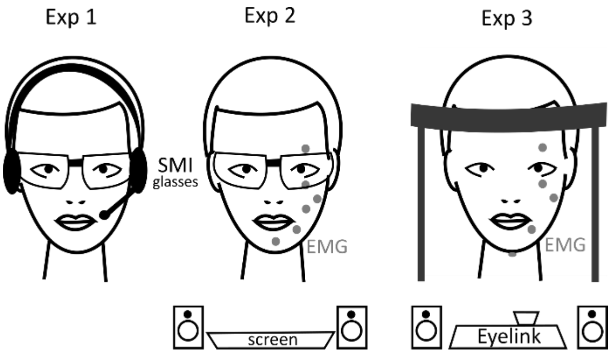

Figure 9. Experimental setup for the three experiments. In experiment 1, we recorded eye movements with SMI eye tracking glasses. In experiment 2, we added EMG and in experiment 3, we used an Eyelink eye tracker and EMG.

When measuring blink rate during a conversation, there are several possible influences. Our different experimental conditions were designed to test for influences of the cognitive load during speech production (with and without vocalization), of motor output (mouth movements, with focus on lip or jaw movements) and of auditory input (due to one's own speaking or someone else). The study consisted of eight different tasks, which were repeated 5 times (except for the baseline, which was repeated 15 times) and each lasted for 1 minute. The tasks were "normal talking", "talking inside the head", "talking without sound", "lip movement", "jaw movement", "listen to someone else", "listen to oneself" and "baseline" (being at rest). Table 1 summarizes all tasks. During "normal talking", "talking inside the head" and "talking without sound", participants were instructed to talk about easy topics like "Describe your apartment" or "Describe your last holiday". Topics were defined by us and randomized across tasks and participants. "Talking inside the head" involved no mouth movement and no sound production, but required cognitive processes that are comparable to the cognitive processes during "normal talking". „Talking without sound" referred to simply mouthing words mimicking mouth movements during "normal talking" but omitting auditory stimulation. To induce lip movements independent of talking, participants were asked to suck on a real lollipop ("lollipop"). In another condition ("gum"), chewing a gum resulted in jaw movements. We chose sucking on a lollipop as an easy way to induce mouth and especially lip movements. Respectively, gum chewing intended to mainly introduce jaw movements. However, we are aware that also other movements such as tongue movements and swallowing are likely executed as well. In the auditory conditions, auditory input was either a monologue of a young woman ("listen to someone else") or a playback of their own monologue recorded from a previous "normal talking" trial ("listen to oneself"). "Listen to oneself" therefore is the same auditory input as during the "normal talking" condition, however, "listen to someone else" was added to mimic the auditory input experienced during a conversation with another person. During the baseline conditions, participants should not stand up or close their eyes, but had no additional task, which will be referred to as 'resting'. "Baseline 1" consisted of 5 randomly selected minutes of the 15 baseline minutes, "baseline 2" of 5 randomly selected minutes of the 10 remaining minutes and "baseline 3" of the lastly 5 remaining minutes. This was done to prevent multiple testing of the same data. The order of tasks was fully randomized to exclude any time related effects, except that the task "listen to oneself" needed to be placed after the "normal talking" condition. Participants were able to start each trial at their own pace by pressing a button followed by a starting tone. The end of the trial was signaled by another tone.

Table 1. List of tasks, their description and their use in the analysis.

Task	**Description**	**Analysis of which effect**
"normal talking"	Talk about a given topic **with** mouth movements and **with** vocalization	Cognitive (Fig. 10)
"talking inside the head"	Talk about a given topic **without** mouth movements and **without** vocalization	Cognitive (Fig. 10)
"talking without sound"	Talk about a given topic **with** mouth movements, but **without** vocalization	Motor (Fig. 11)
"lollipop"	Sucking on a lollipop to induce lip movement	Motor (Fig. 11)
"gum"	Chewing a gum to induce jaw movement	Motor (Fig. 11)
"listen to someone else"	Listen to an unknown monologue of a woman	Auditory (Fig. 12)
"listen to oneself"	Listen to own monologue recorded during "normal talking"	Auditory (Fig. 12)
"baseline 1-3"	Resting	All (Fig. 10,11 & 12)

Data analysis

Four participants were excluded (three due to more than 20% eye data loss, one due to an extremely high mean blink rate >50 blinks/min). Additionally, the eye recording of one participants was lacking two trials. The blink rates over the five repetitions of each task were averaged before comparing between tasks. Since we did not have the participant's permission to listen to the monologues, we plotted the recorded sound signal and visually inspected the amplitude of the signal representing speech to control for task fulfillment in the "normal talking" condition. Repeated measures ANOVAs and corresponding post-hoc analyses for blink rate were computed. The epsilon for Huynh-Feldt correction is given in case of violation of sphericity. Bayesian analysis was added as a supplement to the classical frequentist statistics to get insights on the credibility of the alternative as well as the null hypotheses. The experimental program was implemented and analyzed in MATLAB R2015b (Mathworks). Bayesian analysis was performed with JASP (JASP Team (2019), Version 0.11.1.0).

Blink detection

When the eyelid occludes the pupil during a blink, pupil size recordings of video-based eye tracker quickly and strongly decrease until the pupil is undetectable. Using this characteristic, our blink detection algorithm is based on the recorded pupil size. Blinks were initially detected when both z-transformed pupil radii were below a threshold of -2 standard deviations or when the pupil data was marked as lost. The start and the end of the blink were then shifted to the time point when the radii were higher than half the threshold. Blinks less than 50ms apart from each other were concatenated. Blinks longer than 1000ms and shorter than 50ms were discarded.

Results Experiment 3

To test for cognitive influences on the blink rate, we compared "baseline 1" (no task) with "talking inside the head" (only the cognitive component of speaking) and with "normal talking". A repeated measures 1-factor ANOVA compared the blink rate between these tasks and revealed a significant main effect ($F(2,50) = 25.22$, $p < .001$, $\eta_p^2 = .502$, $\varepsilon = .679$, Huynh-Feldt correction (HF)). Post-hoc pairwise t-tests revealed a significant higher blink rate during "normal talking" than during "talking inside the head” (*p* < .001) as well as a significantly higher blink rate during “normal talking” than during “baseline 1”(*p* < .001) (figure 10a).

In addition to the classical Frequentist analysis, a Bayesian analysis was performed to improve possible interpretations of the results. Comparing the model with the predictor, that the tasks (“baseline 1”, “normal talking” and “talking inside the head”) have an effect on the blink rate, to the null model, overwhelming evidence for the alternative was revealed (Bayes Factor: $BF_{10} = 3.636*10^5$). Post-hoc tests showed strong evidence that the blink rate during “normal talking” differed to the blink rate during “baseline 1” as well as to the blink rate during “talking inside the head” (adjusted posterior odds of $2.507*10^3$ and $1.818*10^2$). Additionally, there was evidence that the blink rate during “baseline 1” and “talking inside the head” were the same (adjusted posterior odds of 1/0.529 = 1.890) (figure 10b).

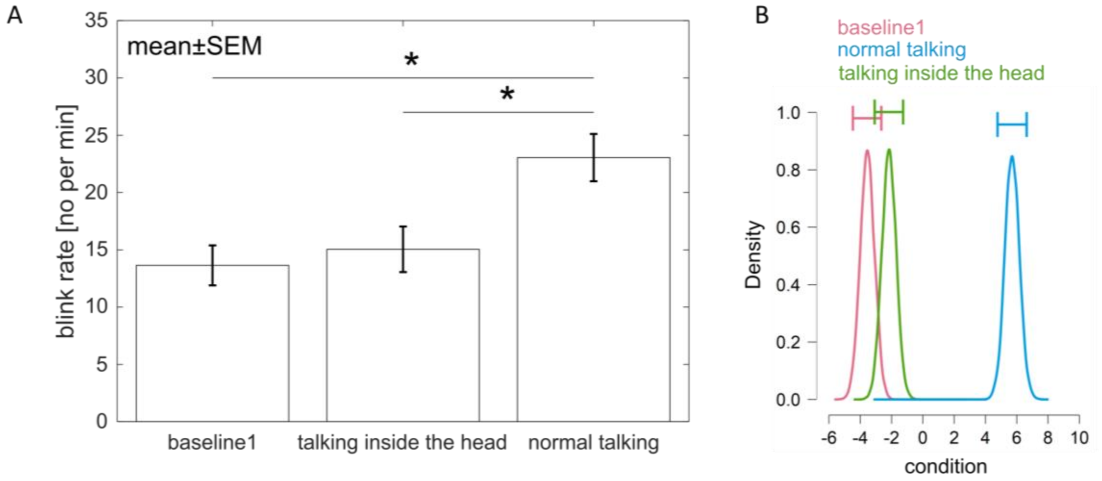

Figure 10. Influence of the cognitive component on the blink rate. A. Blink rate during “baseline1” (being at rest), “talking inside the head” and “normal talking”. Error bars represent one standard error of the mean (SEM). Stars mark significant differences revealed by parametric statistics. B. Posterior distributions of the effect of each condition on the blink rate. “Normal talking” has highest effect on blink rate followed by “talking inside the head” and “baseline1”. The horizontal error bars above each density represent 95% credible intervals.

In a next step, the influence of different motor components on the blink rate was investigated. Figure 11a shows a high blink rate during "talking without sound", followed by lip movements during "lollipop" sucking and jaw movements during "gum" chewing. The "baseline 2" condition with no movement showed the lowest blink rate. A repeated measures ANOVA showed a significant main effect of tasks on blink rate ($F(3,75) = 8.94$, $p < .001$, $\eta_p^2 = .263$, $\varepsilon = .800$ (HF)). Post-hoc tests specified this effect. The blink rate was significantly lower during the "baseline 2" compared to "lollipop" ($p = .016$) and compared to "talking without sound" ($p = .003$). Neither did the difference between "gum" chewing and "baseline 2" reach significance ($p = .106$), nor did any other comparison between movements ($ps > .105$).

Again, Bayesian ANOVA was additionally conducted to assess the differences in blink rate between tasks. Given the predictor of tasks ("baseline 2", "lolli", "gum" and "talking without sound"), strong evidence for the alternative was found when comparing the model with the predictor to the null model (Bayes Factor: $BF_{10} = 5.371*10^2$). Post-hoc comparisons revealed moderate evidence for differences in blink rate between "baseline 2" and "lollipop" as well as between "baseline 2" and "talking without sound" (adjusted posterior odds of 6.086 and 29.963). The evidence for differences in blink rate between "baseline 2"and "gum" as well as between "gum" and "talking without sound" was rather inconclusive (odds of 1.212 and 1.222). Blink rate between "gum" and "lollipop" as well as between "lollipop" and "talking without sound" was not different from each other (odds of 1/0.609=1.642 and 1/0.278=3.597) (figure 11b).

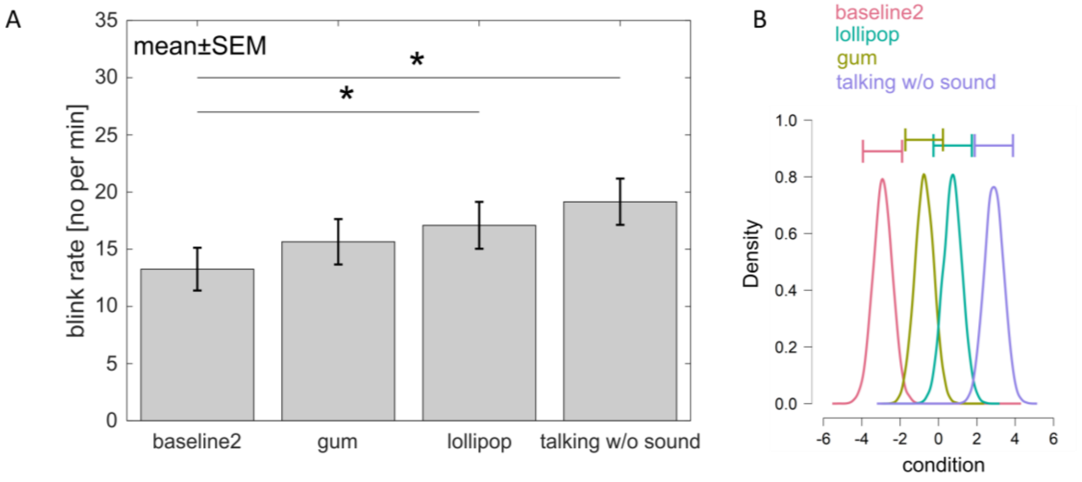

Figure 11. Influence of motor tasks on the blink rate. A. Blink rate during the second baseline (being at rest), moving the lips during lollipop sucking, moving jaw muscles during gum chewing and talking without sound production. Error bars represent one SEM. Stars mark significant differences revealed by parametrical statistics. B. Posterior distributions of the effect of each condition on the blink rate. Talking without sound has highest effect on blink rate followed by lip movement during lollipop sucking, jaw movement during gum chewing and baseline. The horizontal error bars above each density represent 95% credible intervals.

Finally, the influence of auditory input on blink rate was examined with a repeated measures ANOVA comparing the blink rate between the conditions “baseline 3”, “listen to oneself” and “listen someone else”. The main effect suggesting a difference between conditions was significant ($F(2,50) = 3.96$, $p = .036$, $\eta_p^2 = .137$, $\varepsilon = .790$ (HF). Post-hoc tests did not reveal a difference in blink rate between the “baseline 3” condition and any auditory input (*p*s > .089), but a significant difference between “listen to oneself” and “listen to someone else” (*p* = .027) (figure 12a).

Bayesian analysis revealed evidence that the model with the predictor of tasks on the outcome of the blink rate is better than the null model ($BF_{10} = 2.022$). Post-hoc tests revealed that the blink rates between “baseline 3” and “listen to oneself” are not different from each other (1/0.163=6.135), while the blink rates between “listen to someone else” and “listen to oneself” are different (odds of 2.992). The data does not seem to be sufficiently informative to show whether there is a difference between “baseline 3” and “listen to someone else” or not (odds of 1.127) (figure 12b).

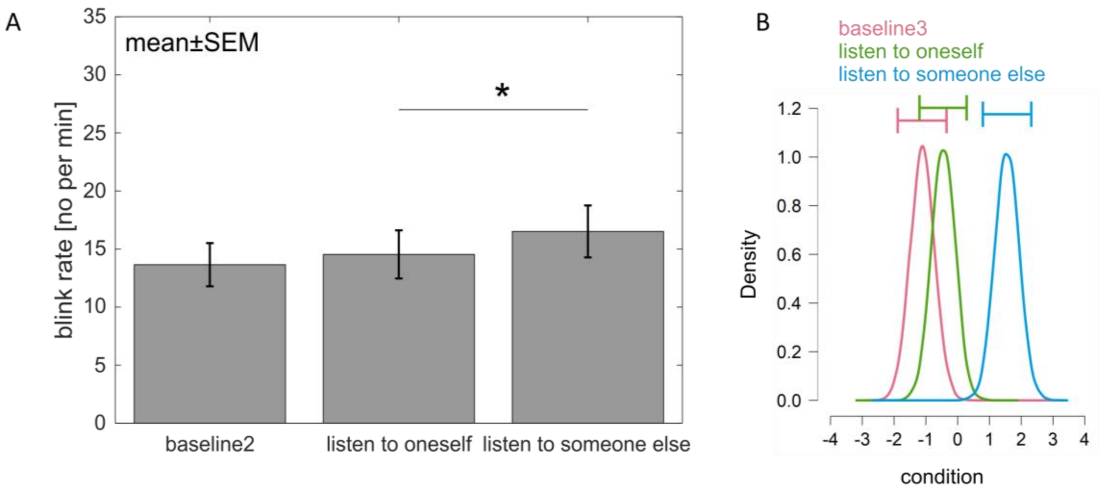

Figure 12. Influence of auditory input on the blink rate. A. Blink rate during the rest (“baseline 3”), “listen to someone else” and listening to a previously recorded monologue. Error bars represent one SEM. Stars mark significant differences revealed by parametric statistics. B. Posterior distributions of the effect of each condition on the blink rate. The blink rate between “listening to someone else” was not different to “baseline3”, but the blink rate between “listening to oneself” and ”listen to someone else” was different. The horizontal error bars above each density represent 95% credible intervals.

Discussion Experiment 3

Our results replicated previous findings that talking is accompanied by an increase in blink rate compared to baseline (e.g., Karson et al., 1981). More specifically, our results suggest that neither the cognitive processes nor the auditory input, but rather, the motor activity of the mouth has the main influence on our blink rate.

The conditions “talking inside the head” and “normal talking” differed in terms of motor output and auditory input but not cognitive processes, which are needed for the production of meaningful sentences. Since the blink rate was significantly lower during “talking inside the head” than during “normal talking” and highly similar to “baseline 1”, cognitive processes without motor output seem to have, if at all, little effect on our blinking. Various researchers have investigated the influence of cognitive load on blink rate, but even the use of similar tasks across different studies, e.g. mental arithmetic, revealed contradictory outcomes. While some researchers showed a negative correlation between blink rate and cognitive load during mental arithmetic (Bagley & Manelis, 1979; Holland & Tarlow, 1972), other studies found an increase in blink rate for difficult arithmetic compared to rest or easy arithmetic (Liu et al., 2019; Tanaka & Yamaoka, 1993). The advantage of an arithmetic task, in comparison to our task, namely talking about a given topic, is that one can receive feedback as to the solution for such a task and easily control for the task fulfilment. In experiment 3, we were not able to control for task fulfillment especially during “talking inside the head”. We specifically focused on this aspect in experiment 4. However, given the above reviewed work and the contradictory findings, a clear-cut influence of cognition is not indicated.

Similarly, auditory input during listening and self-induced auditory input during talking does not seem to be the cause for the increase in blink rate during a conversation. Listening had no significant effect on blink rate as supported by Bayesian analysis showing that the effect on the blink rate during being at rest (“baseline 3”) and during “listen to oneself” is the same. The findings of Bailly, Raidt, and Elisei (2010) not only fail to show an increase in blink rate due to auditory input, but further suggest an inhibition of blinking during listening periods within a conversation compared to waiting periods. While one is bound to attend to the auditory input of the conversation partner in order to respond accordingly, in our experiment the auditory input was not task relevant. Such a difference in attentional demand might explain the different observations. The differences might also be explained by the fact that our experiment explicitly excluded social interaction. Indeed, it was shown that the duration of blinks can serve as a feedback signal for the conversation partner (Hömke et al., 2017), serving a role in social communication. If social aspects are missing, the reduction of blink rate during listening might also cease. The finding, that “listening to someone else” showed a slightly but significantly increased blink rate compared to “listening to oneself” suggests that the content or characteristics of the auditory stimulation can at least weakly influence blinking.

Our results also indicate that the self-induced auditory input during talking is not the driving factor for the pronounced increase in blink rate, because blinking was significantly enhanced during “talking without sound” (mean: 19.15, SEM: 2.03) which was only slightly less than during “normal talking” (mean: 23.05, SEM: 2.07). Therefore, auditory input as introduced through speaking seems not to exert substantial influences on the blink rate. Importantly, auditory input might alter blink behavior in terms of blink timing. During an attended and continuous stream of auditory input, blinks are seldom elicited shortly before or during stimulus presentation, but rather after stimulus offset (Brych & Händel, 2020). Furthermore, it was shown that blinks are synchronized to the rhythm of auditory presented sentences or even to a specifically attended syllable within a heard sentence (Jin et al., 2018). When listening to a monologue, blinks occur predominately at breakpoints of speech or are synchronized with the speaker’s blinks (Nakano & Kitazawa, 2010).

Our findings strongly suggest that motor related factors during talking exert the main influence on the blink rate independent of cognitive or auditory factors. This is indicated by increased blinking during “talking without sound” as well as during the “lollipop” condition. More specifically, by separately investigating the influence of different muscle groups, our results suggest that not all types of motor output are equally linked to blinks. Chewing movements did not significantly increase the blink rate when using a parametric statistical approach, a finding that is in line with previous research (Karson et al., 1981). The mouth movements during “lollipop” on the other hand showed a clear effect on blink rate. The prevalent lip movements during “lollipop” and the closeness of motor cortical areas for the lip and eye lid (Penfield & Boldrey, 1937) or the innervation of the same nerve (Sanders, 2010) might be responsible for this influence. This will be further clarified in experiment 2 and 3.

3.1.3 EXPERIMENT 4

Experiment 3 provides evidence that the motor activity during speaking has a major influence on blinking, while auditory input and cognitive processes only have a minor effect. Our second experiment was designed to replicate the findings of experiment 3, and additionally to describe the underlying causes of the blink rate modulation in greater detail. Concerning cognitive influences, we experimentally manipulated cognitive load by using easy and difficult mental arithmetic tasks and controlled for task fulfillment. In the auditory task, we ensured that participants carefully listen to the spoken words by means of experimental tasks. Concerning motor influences, we isolated defined facial movements, namely lip and jaw movements.

Method Experiment 4

Participants

A power analysis using the effect size of the second analysis of experiment 1 (n_p^2 = .263, alpha = .05 and a power of 0.95) suggested a minimum sample size of 22. We tested 23 new participants (mean age: 25.78 years ± 7.60 SD, 6 male) compensating for one potential exclusion. None of the participants took part in experiment 3. All participants gave their written informed consent, agreed to voice recordings and received payment for their participation. The study was conducted in line with the European data protection rules and was approved by the local ethics committee

(Institute for Psychology of the Faculty for Human Sciences of the Julius-Maximilians-University of Würzburg; protocol number: GZEK 2020-52).

Procedure

Participants sat alone in a moderately lit room. Instructions prior to the task were presented on an Eizo LCD monitor, which was controlled by a Dell Precision M6700 laptop. The monitor turned black during the tasks. The start and end of each trial was marked with a short tone (500 Hz, 100 ms). Binocular eye movements were recorded with 120 Hz using the SMI eye tracking glasses. To record electromyographic (EMG) activity with a sampling rate of 500 Hz, electrodes were placed on the chin, under the left lip corner, on the left cheek, on the left musculus masseter and above and below the left eye (figure 9). Two participants lost their chin and lip electrodes during the recording probably due to movement, so we did not attach these electrodes to the last nine participants, in order to prevent them from focusing on the electrodes instead of the task requirements. There was no obvious differences in blink behavior between subjects with four or six electrodes.

The study consisted of nine tasks. Similar to the first experiment, each task was repeated 5 times (except for the baseline, which was repeated 15 times) and lasted for 1 minute each. For an overview of tasks, please refer to table 2. During "calculating aloud - easy", participants had to count upwards continuously adding one (starting from one) in a normal voice. During "calculating aloud - difficult", they had to continuously subtract seven starting from 200. The same tasks had to be performed in the "calculating inside the head – easy" and "calculating inside the head – difficult", except that they were to perform the arithmetic in their head without moving the mouth and without producing any sound. At the end of these silent trials, participants were asked which number they had reached and how well they performed on a scale from one to seven, where 1 meant "I haven't done the task" and 7 "I was highly concentrated most of the time". During "calculating without sound", participants had to mouth the numbers from one in steps of one without producing any sound. To induce lip movements independent of talking, participants were asked to open and close their lips without moving the jaw ("lip movement"), and to move the jaw up and down without moving the lips during the "jaw movement" task. Again, they scaled their performance from 1 (very bad) to 7 (very good). During the "listen" task, participants had to listen to a voice counting upward (from one in steps of one) leaving out one number that had to be reported after the trial. Again, self-rated concentration had to be indicated on the above-mentioned scale between one to seven. The left out number differed between trials, but was always placed in the second half of the trial. Each analysis included a baseline task where participants were at rest without task. As in experiment 1, the different baseline conditions (1-3) consisted of five randomly, but exclusive, selected minutes out of the 15 minutes. The order of tasks was completely randomized. Participants started each trial by pressing a button at their own pace. The experiment lasted for approximately 65 minutes.

Blink detection

We detected blinks based on pupil size as described for experiment 3. In addition, we used the low-passed filtered (20 Hz) data of the electrodes around the eye and detected blinks according to the EOG blink detection described by Wascher et al. (2015). However, we defined the blink on- and offsets as the point where the peak amplitude decreased by three quarters, which slightly differs from the approach used by Wascher and colleagues. For most of the participants, both blink detection methods revealed similar blink numbers, but the eyetracker data was unusable for three participants and therefore, we present the results based on the EOG blink detection.

Table 2. List of tasks, their description and their use in the analysis of experiment 4.

Task	Description	Analysis of which effect
“calculating aloud – easy”	Add 1: 1, 2, 3, …	Cognitive (Fig. 13)
“calculating aloud – difficult”	Subtract 7: 200, 193, 186, …	Cognitive (Fig. 13)
“calculating inside the head – easy”	Add 1 internally: 1, 2, 3, …	Cognitive (Fig. 13)
“calculating inside the head – difficult”	Subtract 7 internally: 200, 193, 186, …	Cognitive (Fig. 13)
“calculating without sound”	Mouthing numbers: 1, 2, 3, …	Motor (Fig. 14)
“lip movement”	Open and close lips	Motor (Fig. 14)
“jaw movement”	Move jaw up and down	Motor (Fig. 14)
“listen”	Listen to someone adding 1 leaving out one number: 1, 2, … 22, 23, 25 …	Auditory (Fig. 15)
“baseline 1-3”	Resting	All (Fig. 13,14 & 15)

Data analysis

We excluded one participant due to a very low blink rate (3.80 blinks/minute) from all analyses. We also excluded trials where participants evaluated their own performance equal or less than 3 on the scale from 1 to 7. This resulted in a list-wise exclusion of two participants from the analysis of cognitive influence on blink rate. One trial of one participant with a blink rate of 110 was also excluded (participant’s mean: 27.9 blinks/min). Blink rate during the five minutes of one task were averaged for each participant before the comparisons between conditions.

To evaluate the task demands on performance, we took the entered last number during “calculating inside the head” conditions and extracted the last spoken number that was recorded during “calculating aloud” conditions. This allowed to quantify calculations in the same way for both conditions. If the last number was not a number obtained after correct calculation (only difficult conditions), we counted calculations that were possible up to this point. For example, after 14 calculations, the participant should have arrived at 102, but entered 105. Then, 13 correct calculations were possible and minimally one error. In case of 100, 14 correct calculations were possible. Please note, that this quantification could only result in an overestimation of correct calculations in case of an incorrect last number, and thus, was rather conservative as it made the analysis less likely to find a difference between easy and difficult mental arithmetic. The error identification in the “calculating aloud – difficult” condition, where participants made approximately one error per trial (mean: 1.32, SD: 1.11), supported our approach to only assume one error if the last number was incorrect. As for the blink rate analysis, trials were excluded after which participants evaluated their performance less or equal than 3 on a scale from 1 to 7 (i.e. two participant were excluded for this analysis).

Electromyographical (EMG) data of each electrode was preprocessed by subtracting the mean of all other electrodes in a first step. Subsequently, the data was bandpass filtered between 20 and 90 Hz and a Hilbert transformation was applied. Finally, the resulting EMG amplitudes were averaged over facial electrodes excluding eye-related electrodes.

Implementation and analysis of the experiment was done with MATLAB R2015b (The MathWorks Inc., Natick, MA, USA) in combination with Psychtoolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997).

Results Experiment 4

We tested performance with the number of correct calculations based on the last number given by the participants. A repeated measures ANOVA with factors difficulty (easy vs difficult) and condition (calculating aloud vs calculating inside the head) revealed that participants made significantly more calculations during the easy task (add 1) compared to the difficult task (subtract 7) ($F(1,19) = 71.91$, $p < .001$, $\eta_p^2=.791$) as expected. Moreover, the performance was not significantly better during "calculating inside the head" than during "calculating aloud" ($F(1,19) = 2.89$, $p = .106$, $\eta_p^2 = .132$). Additionally, the interaction was significant ($F(1,19) = 11.83$, $p = .003$, $\eta_p^2 = .384$) showing that participants added more numbers in the "calculating inside the head" condition compared to the "calculating aloud" condition, but made less calculations in the more difficult subtraction task during the "calculating inside the head" condition than during the "calculating aloud" condition (figure 13a).

Comparable to the analysis of the influence of task demands on performance, the impact of cognitive load on blink rate was examined. To see whether blink rate was increased or decreased during task compared to baseline, we subtracted the blink rate during baseline from the blink rate during the tasks "calculating aloud" and "calculating inside the head" (figure 13b). While the blink rate increased during "calculating aloud - difficult", the blink rate seemed to be only slightly affected during "calculating inside the head" conditions as well as during "calculating aloud – easy". A repeated measures ANOVA on blink rate with factors aloud/inside the head and easy/difficult revealed a significant increase for aloud tasks compared to quiet tasks (F(1,19) = 10.43, *p* = .004, η_p^2 = .354). In addition, blink rate was higher during difficult tasks compared to easy tasks, but the difference was not significant (F(1,19) = 2.61, *p* = .123, η_p^2 = .121). Also, the interaction was not significant (F(1,19) = 1.35, *p* = .260, η_p^2 = .066).

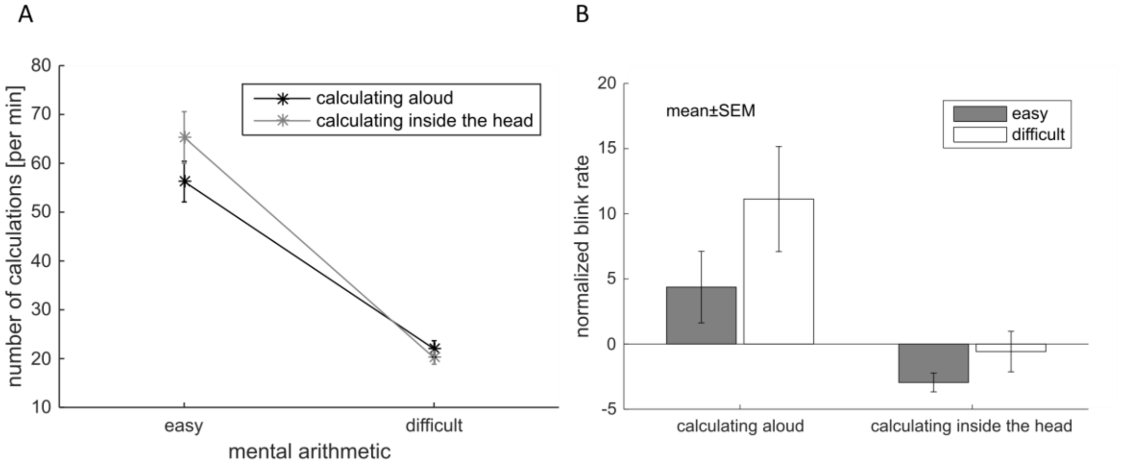

Figure 13. Results of cognitive tasks A. Performance assessment during cognitive tasks. B. Influence of cognitive task demands on the blink rate. Blink rate during "baseline 1" was subtracted from the blink rate in each task showing that only the blink rate in the "calculating aloud – difficult" task was strongly increased. Only the main effect of "calculating aloud" vs "calculating inside the head" was significant (*p* < .004).

EMG activity was analyzed in a 1-factor repeated-measures ANOVA across these five tasks ("calculating aloud – easy/difficult", "calculating inside the head – easy/difficult", baseline 1), which revealed a significant difference between the tasks (F(4,76) = 9.55, *p* <.001, η_p^2 = .334, ε = .598 (HF)). Bonferroni-adjusted post-hoc tests revealed increases in EMG activity during "calculating aloud" tasks compared to "calculating inside the head" tasks and all baselines (*p*s < .045) except for the comparison between "calculating aloud - difficult" and "calculating inside the head - easy" (*p* = .437). "Calculating inside the head" tasks did not significantly vary in EMG activity compared to baseline 1 (*p*s = 1) as expected.

Concerning motor tasks, the repeated measures ANOVA comparing the blink rate between motor tasks (“calculating without sound”, “lip movement”, “jaw movement”, “baseline 2”) did not reveal a significant effect across tasks ($F(3,63) < 1$) (figure 14). Neither the “lip movements” nor the “calculating without sound” tasks increased blink rate. The ANOVA comparing EMG activity between these tasks showed a significant main effect ($F(3,63)=9.73$, $p = .001$, $\eta_p^2 = .317$, $\varepsilon = .525$ (HF)). Bonferroni-adjusted post-hoc tests revealed that the activity during the motor tasks (“lip movement”, “jaw movement” and “calculating w/o sound”) was significantly increased compared to baseline (*p*s < .017).The EMG activity between the motor tasks did not differ (*p*s > .060).

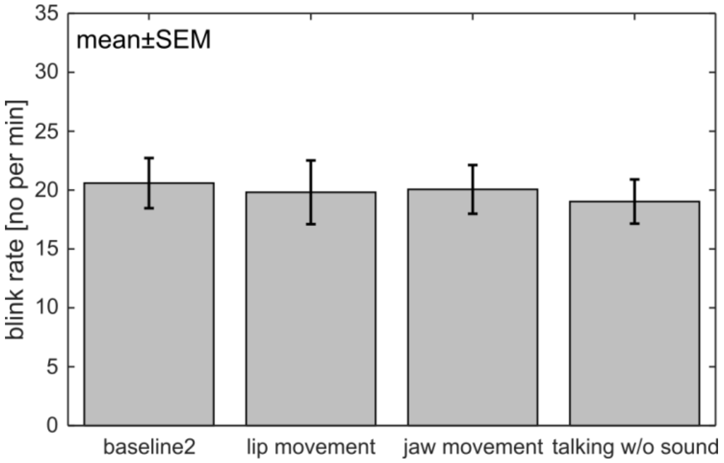

Figure 14. Influence of motor activity on the blink rate. Neither isolated “lip movements”, nor isolated “jaw movements” influenced the blink rate compared to baseline. During “calculating without sound” participants performed the easy ‘Add 1’ task, which did not increase the blink rate.

Finally, participants performed perfectly on the auditory task (100% correct) and always rated their concentration higher or equal to 4 on the 7-point scale (except for two trials). This proves that the cognitive load was quite low and that participants actually listened to the presented numbers. A t-test comparing the blink rate between “listen” and “baseline 3” did not reveal a significant difference (*t*(1,21) = 1.53, *p* = .141, d = .326) which replicates the results of experiment 1 (figure 15). As expected, EMG activity during these tasks was not significantly different (t(1,21) = 1.60, *p* = .124, d =.341).

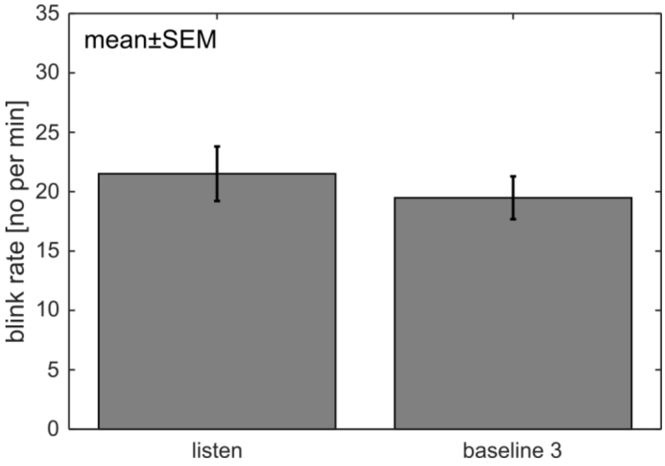

Figure 15. No influence of auditory input on the blink rate. Participants listened to the easy 'Add 1' task, where one number was skipped. This number had to be reported afterwards. Blink rate between "listen" and "baseline 3" was not significantly different from each other.

Discussion Experiment 4

Our second experiment focused on the cognitive aspects during speaking controlling for task performance. First, trials with low subjective ratings on attentional involvement in the task were excluded. Second, participants had to report the last number of their calculations, which was used to measure performance based on the number of sub-calculations. Participants performed significantly better during easy compared to difficult mental arithmetic tasks. This confirms that the addition task was indeed easier than the subtraction task. Importantly, performance was comparable or better during silent conditions compared to normal vocalization showing that participants followed task instructions even during silence. This clearly indicates that the cognitive load was not particularly increased during normal vocalization. After this important step, we did not find a significant difference in blink rate between the easy and difficult task, but there is a tendency towards a higher blink rate during difficult tasks, which has been reported previously (Liu et al., 2019; Tanaka & Yamaoka, 1993; Wood & Hassett, 1983). Our results further showed that an increase above baseline and a clearly visible modulation due to task difficulty was only observed when the task was performed with vocalization. The difference in blink rate between the easy and difficult mental arithmetic when performed in silence was substantially smaller and stayed around baseline level. This small difference of less than five blinks per minute is in line with previous studies using no visual stimulation and no hand movement (Liu et al., 2019; Wood & Hassett, 1983). These findings would suggest that the influence of cognition on blink rate is dependent on additional factors. Indeed, reviewing work on the relation between blink rate and task difficulty shows a rather complex picture. Neither the reading of words compared to the reading of mirror images of the same words (Cho et al., 2000), nor an easy compared to a difficult letter search task revealed any difference in blink rate (Tanaka & Yamaoka, 1993). Some other tasks like driving in open country vs in heavy traffic (Drew, 1951) and an easy vs difficult tone counting task (Oh, Jeong, et al., 2012) show a negative correlation between blink rate and task difficulty. Except for studies investigating conversations (e.g. Bentivoglio et al., 1997; Doughty, 2001; Karson et al., 1981) or tasks involving spoken responses (Oh, Han, et al., 2012), only few studies show an increase in blink rate during a task compared to rest (Pivik & Dykman, 2004). In conclusion, whether the blink rate is influence by the cognitive demands of a task seems to be dependent on the specific task requirements. The combined results of experiment 3 showing that "talking inside the head" about an easy topic did not increase the blink rate, and experiment 4 showing that neither easy nor difficult mental arithmetic during silence substantially increased the blink rate compared to baseline, suggest that the cognitive component during a conversation alone is not the driving influence on the blink rate.

Experiment 4 further strengthened the findings of experiment 3 that auditory input during listening does not substantially alter the blink rate. Importantly, this time we controlled if participants indeed attended to the auditory input, because they had to report the number that was left out in the stream of easy calculations. While performance and self-rated concentration on the task was very high, blink rate was not significantly increased. This shows that attending auditory input is not the driving factor for the often reported blink rate increase during conversation.

Experiment 4 additionally broke down speaking into isolated facial movements to concretize our finding that motor output influences blinking. Interestingly, neither isolated lip movements, nor isolated jaw movements increased the blink rate. Consequently, other aspects of speaking modulate blinking behavior. One possibility could be that motor output needs to be combined with a certain amount of cognitive demand. Our results that the blink rate was not substantially affected by "calculating aloud – easy" would point in that direction. However, experiment 3 showed that movements introduced by simply sucking on a lollipop are sufficient to increase the blink rate, which clearly argues against the necessity of cognitive demands. A second possible aspect might be the complexity of movement. Lollipop sucking, as used in the first experiment, does not solely activate isolated lip movements but involves complex muscular activity. Forming full sentences during talking with and without sound as in experiment 3 can also be considered complex motor output (Smith, 1992) and to a certain extent, the utterance of mainly two- and three-digit numbers during the "calculating aloud – difficult" task is possibly more complex than mainly one- and two-digit numbers during the "calculating aloud – easy" task. Unfortunately, to quantify movement complexity, a more sensitive methods, than the EMG data collection as applied by us would be necessary. A third possibility is a specific involvement of the tongue, as surely can be found during lollipop sucking, but not during isolated lip and jaw movement.

The shape and position of the tongue further has a primary function during speech as it shapes the vocal tract (Smith, 1992).

3.1.4 EXPERIMENT 5

In a last experiment, we set out to test a possible involvement of isolated tongue movement on the blink rate increase during speaking and confirm again that motor execution during a complex (cognitive/motor) task leads to an increased blink rate. More specifically, our third experiment compared "normal talking" and "talking without sound" during forming meaningful sentences, with isolated tongue movements and being at rest. In addition to the approach applied in experiment 3, we control for task fulfillment by recording facial EMG activity.

Method Experiment 5

Participants

24 new participants (mean: 25.00 years, SD: 5.63, 6 male) took part in the third experiment. None of them took part in experiment 1 or 2. The number of participants was chosen upon the power analysis described in experiment 2, which was based on the data of experiment 1 and resulted in 22 participants (+ 2 potential dropouts). All gave their written informed consent and received payment for their participation. The experiment was conducted in line with the European data protection rules.

Procedure

Participants sat alone in a moderately lit room. Auditory instructions were presented via two loudspeakers left and right to the Eyelink 1000 eyetracker (SR Research, ON, Canada). Eye movements were recorded binocularly at a sampling rate of 500Hz. Participants had to touch a horizontally mounted bar with their forehead fixing the distance of the eyes to the eyetracker minimizing large head movements. In addition, electrodes were placed above and below the left eye, under the left lip corner, on the left musculus masseter and below the chin to record the muscular activity of the face and tongue (figure 9). EMG activity was recorded with 500 Hz. The experiment was controlled by a Dell Precision M6700 laptop.

The study consisted of four tasks (see table 3). Each task lasted for 1 minute and was repeated five times. As in experiment 3, participants had to talk about easy topics (e.g. "Describe your apartment") during the "normal talking" condition and during the "talking without sound" condition. During the "tongue" condition, participants had to write the numbers from 0 to 9 with their tongue towards the palate in the oral cavity with the mouth closed. Participants had no task and rested during the "baseline" condition. Participants started each trial by pressing a button at their own pace. The trial was preceded and followed by a short auditory tone. The experiment lasted approximately 25 minutes.

Table 3. List of tasks and their description of experiment 5.

Task	**Description**
"normal talking"	Talk about a given topic **with** mouth movements and **with** vocalization
"talking without sound"	Talk about a given topic **with** mouth movements, but **without** vocalization
"tongue"	Write the numbers from 0-9 with the tip of the tongue
"baseline"	Resting

Data analysis

Two participants were excluded, because neither the eyetracking data nor the EMG data was usable for blink detection. We used the same EOG and video-based blink detection algorithms as in experiment 4 and the same preprocessing of electromyographical data for muscle activity. The eyetracker data for two other participants showed reduced accuracy, which is why we present the results of the EOG blink detection. Please note that the results are similar between the different methods. Again, the implementation and analysis was done with MATLAB R2015b (The MathWorks Inc., Natick, MA, USA).

Results Experiment 5

Figure 16 shows the blink rate during the four tasks. It was highest for "normal talking" followed by "talking without sound". "Tongue" and "baseline" blink rates were nearly equal and lower than for the other two tasks. A repeated-measures ANOVA comparing the four tasks revealed a significant difference between tasks ($F(3,63) = 24.57$, $p < .001$, $\eta_p^2 = .539$). Bonferroni-adjusted post-hoc tests revealed that every combination is different from the other (*p*s < .019) except for "tongue" vs "baseline" ($p = 1$). EMG activity analysis, taking into account the jaw, lip and tongue electrode, revealed a significant difference between tasks (repeated-measures ANOVA: $F(3,63) = 84.54$, $p < .001$, , $\eta_p^2 = .801$, $\varepsilon = .591$ (HF)). Bonferroni-adjusted post-hoc tests showed the expected significant difference between all movements and the baseline (*p*s < .003), no difference between "talking without sound" and "normal talking" ($p = 1$) and a significant difference between "tongue" and the other two movements (*p*s < .001).

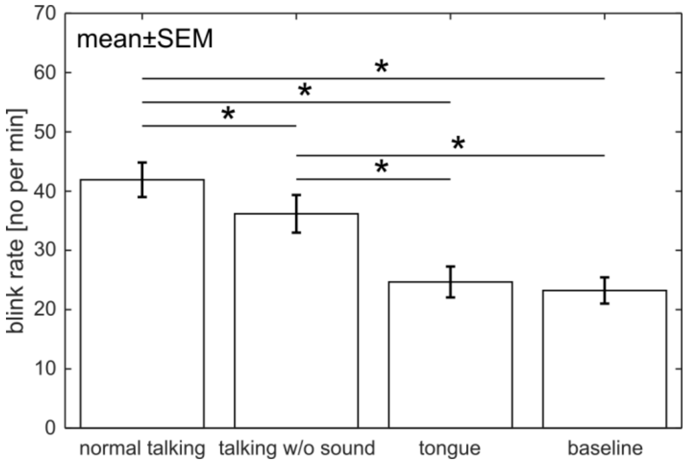

Figure 16. Influence of motor activity varying in complexity on the blink rate. All pair-wise post-hoc tests revealed a significant difference in blink rate except for the tasks “tongue” and “baseline”. EMG analysis showed that participants fulfilled task requirements.

Discussion Experiment 5

Our third experiment replicated the findings of experiment 3 and other studies showing that “normal talking” about a specified topic (Bentivoglio et al., 1997; Doughty, 2001; Karson et al., 1981) increased the blink rate. Moreover, experiment 5 showed again that “talking without sound” requiring similar cognitive effort and motor activity as “normal talking” but lacking auditory components, also significantly increased the blink rate. Adding to experiment 3, this time, task fulfillment was controlled using EMG, which showed that all talking conditions had increased muscle activity compared to baseline. Further, experiment 5 showed that isolated tongue movements were not the driving factor for the increase in blink rate.

Given the finding of experiments 3 and 4 that cognitive demand had only a minor influence on blinking, we assume that complex motor output is the relevant modulator of the blink rate during speaking. The increased complexity of the facial movements during forming sentences compared to counting upwards in experiment 4 (“calculating aloud – easy” and “calculating without sound”), could therefore explain the difference in blink rate modulation between conditions. Accordingly, the additional motor activity (e.g. of the respiratory system and larynx) during vocalization leading to an increased complexity of motor activity as compared to “talking without sound”, could explain the stronger increase in blink rate for “normal talking” compared to “talking without sound”.

3.1.5 GENERAL DISCUSSION STUDY 2

In sum, we found that neither cognitive demands without verbalization, nor isolated movements of the lips, jaw or tongue, nor the auditory input during vocalization or listening influenced the blink rate. However, our three experiments clearly showed that complex motor tasks as well as verbalization of cognitively demanding tasks increased the blink rate.

During a conversation, we speak at a rate of 3-5 syllables per second (Ramig, 1983), which refers to approximately 200 words per minute (language dependent). Given the amount of muscles that are involved in speech production, this motor activity can be described as complex (Smith, 1992). In our experiments, “normal talking” is the most complex movement followed by “talking without sound”, “lollipop”, “gum” chewing and finally isolated facial movements. Since we could find blink rates during these tasks in descending order, the complexity of facial motor activity is likely a relevant factor for the amount of blink rate enhancement. An influence of articulation complexity on blinking was touched by von Cramon and Schuri (1980) who compared the possibly more complex mouth movements during reciting numbers from 100 upward and the simpler movements during reciting the alphabet. We added a stringent control for auditory and cognitive influences, and excluding these as possible explanations strengthened the evidence that motor activity influences blinking.

Previous research revealed various interactions between different types of movements. For example, blink and saccade rate increases with walking speed (Cao & Händel, 2019) and is especially high around the stance phase of the gait cycle (Cao et al., 2020). Furthermore, finger tapping entrains spontaneous blinking (Cong et al., 2010) and a large saccade size holds an increased blink probability (Fogarty & Stern, 1989). (Micro-)Saccades further co-occur with head movements (Collewijn & Kowler, 2008; Kowler, 1991) and saccades and reach movements can influence each other's trajectories (Nissens & Fiehler, 2018). This suggests a common phenomenon of motor interaction beyond speaking and blinking. Moreover, our results add to theories on cross-modal multiple action control that demonstrated that eye-related responses are linked to other effector systems such as manual or vocal responses (e.g., Huestegge, 2011; Huestegge & Koch, 2013). Finally, understanding the interaction of movements might advance the realistic visualization of human behavior in artificial avatars thereby possibly improving engagement and/or acceptance of such systems.

Given our results, we advise caution when using blinks as neurological indicators during patient interviews or as indicators of cognitive load during tasks involving verbal responses. In order to obtain optimized blink rate measurements, we suggest to carefully monitor and take into account the duration and complexity of talking, as well as the actual execution of motor output during the evaluation.

3.2 EFFECTS OF VOCAL DEMANDS ON PUPIL DILATION

Pupil dilation is known to be affected by a variety of factors, including physical (e.g., light) and cognitive sources of influence (e.g., mental load due to working memory demands, stimulus/response competition etc.). In the present experiment, we tested the extent to which vocal demands (speaking) can affect pupil dilation. Based on corresponding preliminary evidence found in a re-analysis of an existing data set from our lab, we set up a new experiment that systematically investigated vocal response-related effects compared to mere jaw/lip movement and button press responses. Conditions changed on a trial-by-trial basis while participants were instructed to keep fixating a central cross on a screen throughout. In line with our prediction (and previous observation), speaking caused the pupils to dilate strongest, followed by non-vocal movements and finally a baseline condition without any vocal or muscular demands. An additional analysis of blink rates showed no difference in blink frequency between vocal and baseline conditions, but different blink dynamics. Finally, simultaneously recorded electromyographic activity showed that muscle activity may contribute to some (but not all) aspects of the observed effects on pupil size. The results are discussed in the context of other recent research indicating effects of perceived (instead of executed) vocal action on pupil dynamics.

The official reference for this material is: Brych, M., Händel, B. F., Riechelmann, E., Pieczykolan, A., & Huestegge, L. (2021). Effects of vocal demands on pupil dilation. *Psychophysiology*, 58(2): e13729 https://doi.org/10.1111/psyp.13729. Headlines, table and figure numbering were adapted to exclude ambiguities in this thesis.

3.2.1 INTRODUCTION STUDY 3

Apart from its sensitivity to physical sources of influence (e.g., light), pupil dilation has been shown to be affected by mental processing load (e.g., Hess & Polt, 1964; see Laeng, Sirois, & Gredebäck, 2012; Mathôt, 2018). Specifically, pupils are sensitive to executive or working memory load (e.g., Beatty & Kahneman, 1966; Chatham, Frank, & Munakata, 2009; Karatekin, Couperus, & Marcus, 2004; Katidioti et al., 2014) and to the relation between stimuli and responses as measured by the Stroop-task (Laeng et al., 2011) or by a finger response-cuing paradigm (Moresi et al., 2008). Pupil size was also linked to the preparation and execution of self-triggered finger flexions. Specifically, pupil diameter increases for more complex movements (Richer & Beatty, 1985). In addition, hand movement imagery was related to an increase in pupil diameter compared to no task (Rozado, Duenser, & Howell, 2015). It was also shown that pupil size during imagery was slightly smaller, but not significantly different to real executed hand movements (O'Shea & Moran, 2016).

Recently, it has additionally been demonstrated that pupils are possibly related to speech or speech processing, as pupil dilation increased when listening to vocal as opposed to instrumental music (Weiss et al., 2016). However, the question of whether producing instead of listening to vocal output can also affect pupil responses has not been systematically addressed yet. While the presence (vs. absence) of vocalization demands should generally increase executive load, we here for the first time study specific effects of vocalization, and in particular the motor aspect of it, on pupil dynamics.

On a general level, the idea that different behavioral systems may strongly interact is supported by research on cross-modal multiple action control. Specifically, it has been shown that eye-related responses such as saccade latencies interact with even simple additional concurrent action demands in other effector systems such as a manual key press or a basic vocal response (Huestegge, 2011; Huestegge & Koch, 2013; Huestegge, Pieczykolan, & Koch, 2014; Pieczykolan & Huestegge, 2014). However, up to now, studies on the effects of vocal actions, that is, the motor activity during speaking, on pupil size are still lacking.

Taking the idea of a strong interaction between various behavioral domains seriously, we decided to additionally assess the blinking behavior during vocalizations. Indeed, similar to pupil dilation, blink rate has also been discussed as an index of perceptual and cognitive load (e.g., Fogarty & Stern, 1989; VanderWerf et al., 2003), and has also been studied in the context of verbal (dyadic) communication (e.g., Bentivoglio et al., 1997). However, corresponding research is less extensive and systematic than that on pupil dilation, and research on the interaction between pupil and blink responses in particular is even more rare (e.g., Siegle et al., 2008).

In a first step towards addressing the influence of vocalization on pupil size and blink rate, we re-analyzed a set of data from a previous, unpublished study that was not originally designed to address effects of vocal demands on pupil responses. Participants (N = 18, 13 female, mean age = 23, SD = 2.9) randomly switched between single manual (left/right key press), single vocal (uttering the words "left"/"right"), and dual (manual + vocal) response demands on a trial-by-trial basis while fixating a central fixation cross (green on black background) throughout. The pitch of a lateralized tone (200 Hz, 600 Hz, 3200 Hz) indicated the response condition (single manual, single vocal, vocal+manual; mapping counterbalanced across participants), while tone presentation side (via headphones) indicated the response identity (e.g., tone on left ear indicated to execute a left key press, saying "left", or doing both). Each trial lasted 3 sec, with 540 trials in total. An EyeLink II eye tracker (500 Hz, SR Research, Canada) was used. Results revealed an effect of response condition on pupil dilation, $F(2, 34) = 6.64$, $p = .004$, $\eta_p^2 = .281$: Pupils dilated more in both the vocal+manual and single vocal conditions than in the single manual condition (*p* = .023, *p* = .011; see figure 17). Thus, vocal demands in terms of corresponding motor activity related to the mouth and vocal tract appeared to increase pupil dilation. An additional analysis of blink rates also revealed an effect of response condition, *F*(2, 34) = 4.36, *p* = .021, η_p^2 = .204: Conditions involving vocal demands involved higher blink rates than the single manual condition (although post hoc contrasts revealed that only the difference between the single manual and the dual condition was significant, *p* = .027).

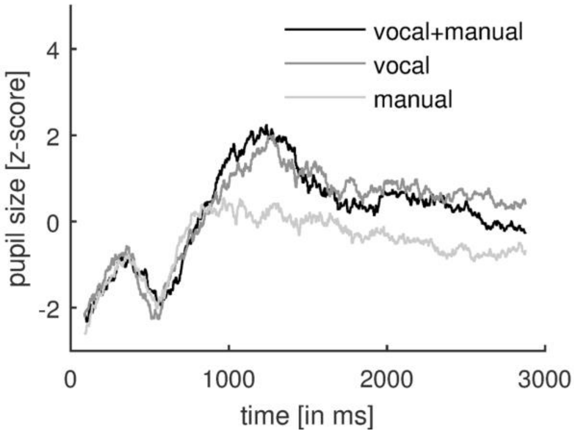

Figure 17. Exploratory analysis of a previous data set showing pupil dynamics within each trial as a function of response condition. We plotted the mean pupil diameter (here: z-standardized across all conditions) as a function of time elapsed in a trial. All trials involving a blink (65.8 %) were removed for this analysis. This rather strict criterion was applied to ensure that blinks cannot possibly contribute to the observed effects. Pupil diameter was baseline-corrected (based on the dilation data during the first 100ms of each trial prior to stimulus onset). Thus, the dependent variable was the maximum baseline-corrected diameter increase (measured in arbitrary raw data units as provided by the eye tracker) within each (error-free) trial. Note that the lines diverge at around 1s (i.e., around the time of the mean vocal response onset of 1150ms), and the effect extended until the end of the trial.

Based on this re-analysis of previous data (which served as an exploratory starting point to come up with specific hypotheses), we set up a new experiment to rigorously test whether and how vocal demands indeed increase pupil dilation. This new experiment erased several limitations of the previous (exploratory) re-analysis study. First, trial duration was increased to ensure that an increase in pupil size due to the task will return to baseline before the start of the next trial. Second, a proper baseline condition without any response demands was added, and third, a pure motor condition requiring mouth movements without auditory output was included to possibly pinpoint other types of influence of vocalization on pupil dilation and to exclude any effects that might merely be driven by differences in overall task demands. Specifically, we included the following conditions: Two vocal conditions targeting different mouth movements (lip loud: uttering "boo", jaw loud: uttering "mmh" while clenching teeth), three non-vocal movements (lip silent: lip movements of "boo" without producing sound, jaw silent: clenching teeth without producing sound, key press: finger movement) and a baseline condition (no response at all). We hypothesized that pupil dilation should be greatest for the two vocal response conditions, followed by the non-vocal movement conditions, and finally, the baseline condition without any response requirements.

3.2.2 EXPERIMENT 6

Method Experiment 6

Participants

25 participants (20 female, mean age: 24.2, SD: 5.2) took part in the study. A power analysis based on the effect size in the previous data set (see above) revealed that this sample size is sufficient to detect a pupil size effect with > 95% probability. One additional participant was excluded due to the execution of > 55blinks/minute. All gave their written informed consent and received payment or study credit for

their participation. The study was conducted in line with the European data protection rules.

Apparatus and Stimuli

Participants sat in a moderately lit room in front of a standard computer screen wearing Sennheiser PMX 95 headphones. Their forehead touched a bar fixing the distance of the eyes to the screen and eye tracker. Binocular eye movements were collected at a sampling rate of 500Hz using an EyeLink II (SR Research, Canada). A single key was placed on the table connected to a BBTK response box (model: K-RB1-4; The Black Box ToolKit Ltd, UK). A green fixation cross (0.6°) was continuously presented on black background at the center of the screen. Auditory instruction words ('lip loud', 'lip silent', 'jaw loud', 'jaw silent', 'key' and 'pause' in German) were presented (500ms) prior to a go signal (frequency: 300Hz, 50ms). To record electromyographic (EMG) activity in the face, three electrodes were placed around the right eye, another one below the left lip corner and a last one above the left musculus masseter. Reference and ground electrodes were fixed on the earlobes (figure 18). The experimental program was implemented using Psychtoolbox-3 in MATLAB R2015a (Brainard, 1997; Pelli, 1997; The MathWorks Inc., Natick, MA, USA).

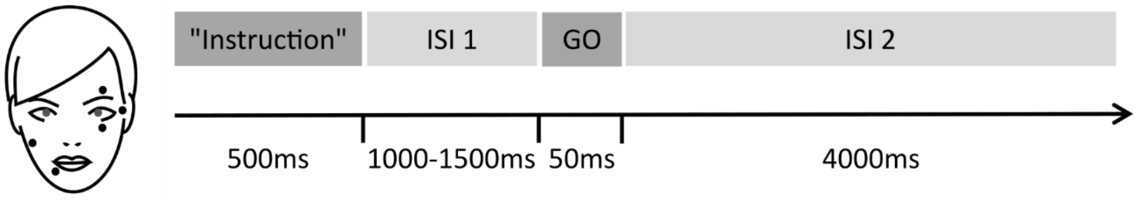

Figure 18. Electrode placement and trial structure. After the auditory instruction, subjects had to wait for a jittered time period (ISI 1) until the go signal, after which the movement (based on the instruction) should be executed. Trials ended four seconds after the go signal (ISI 2).

Procedure

Each trial involved the presentation of one auditory instruction followed by the go signal after 1000 to 1500ms (jittered in steps of 100ms). The next trial started after four additional seconds. Oral presentation of the words 'lip loud' or 'lip silent' signaled to utter the word 'boo' vocally or without producing sound. The instruction 'jaw silent' referred to clenching one's teeth, while 'jaw loud' required saying 'mmh' in addition. The word 'key' indicated pressing a response button with a finger, and the word 'pause' suggested to withhold any response (baseline). Each participant completed 15 blocks consisting of 30 trials each. Within a block, each condition was performed five times in randomized sequence. Prior to each block, subjects underwent a calibration routine for the eye tracker. Participants underwent (at least once) a practice block, in which all conditions occurred twice. The experiment lasted approximately 50 minutes.

Blink detection

Whenever the z-transformed pupil diameter decreased more than two standard deviations (SD) away from the mean in both eyes, a blink was detected. This time range was extended until the z-transformed pupil data of both eyes reached a threshold of one SD away from the mean (verification of our custom blink detection by comparing it to the internal EyeLink blink detection as well as EOG blink detection is presented in supplementary material). Blinks occurring less than 100ms apart from each other were combined. Those that lasted less than 50ms or more than 500ms were discarded.

Data analysis

MATLAB R2015a (The MathWorks Inc., Natick, MA, USA) was used for data analysis. Pupil loss, e.g. due to blinks, was linearly interpolated before averaging over both eyes. Linear interpolation was performed from the time point of 20ms before data loss until the time point of 20ms after data loss. Trials that included more than 30%

of interpolation were excluded (maximally 38/450 trials). Pupil diameter was baseline-corrected by subtracting the mean pupil size of the time interval between -1000 and -900ms before the go signal. We used the maximum baseline-corrected diameter increase as dependent variable, which enables an analysis over the complete time range of a trial instead of manually selecting a time window. However, Supplementary information also includes an analysis of mean baseline-corrected pupil diameter between -1000 and 2000ms (revealing similar results). For each participant, we excluded trials that showed a maximum diameter increase that was 3 times larger than the interquartile range (maximally 5/450 trials).

Blink rate was calculated over the time window from -1000 to 4000ms. Continuous blink graphs were obtained by coding all time points with zeros, whereas blinks were marked with ones (Siegle et al., 2008). These binary coded trials were averaged and baseline-corrected by subtracting the mean of -1000 to -900ms before the go signal to obtain a mean proportion of blinks at each time sample.

The EMG signal of one participant was excluded due to technical problems. For all other data sets, each channel of the EMG was normalized by subtracting the mean of the other channels. After that, the signal was band-pass filtered (20-90Hz) and the Hilbert transformation was applied. This signal was again low-pass filtered (10Hz) and baseline-corrected by subtracting the mean of -1000 to -900ms before the go signal. Graphs show the signal change of the electrode that was placed close to muscles executing the movement (electrode below the lip for lip movements, electrode on the musculus masseter for jaw movements).

Results Experiment 6

Pupil dilation

Pupil size increased after the instruction word, but quickly decreased during the baseline condition ('pause'). In contrast, pupil size increased until after the go signal for all other conditions (figure 19). A repeated-measures ANOVA using the maximum pupil dilation as dependent variable revealed a significant main effect of conditions ($F(5,120) = 36.74$, $p < .001$, $\eta_p^2 = .605$). Bonferroni-adjusted post-hoc tests confirmed our main hypothesis: The pupil dilation increase was significantly greater for both vocal tasks ('lip loud' and 'jaw loud') and for non-vocal movements ('lip silent', 'jaw silent' and 'key press') compared to the baseline condition ('pause'). The two vocal tasks did not significantly differ between each other. The same holds for the three non-vocal tasks, suggesting that the 'key press' condition was comparable to the other (lip/jaw) silent conditions. Critically, maximum pupil diameter for 'jaw loud' was significantly greater than for 'jaw silent' and 'lip silent'. The diameter was also significantly larger for 'lip loud' than for 'jaw silent'. Only the tendency towards a greater diameter for 'lip loud' than for 'lip silent' failed to reach the significance threshold. Detailed p-values are depicted in Table 4.

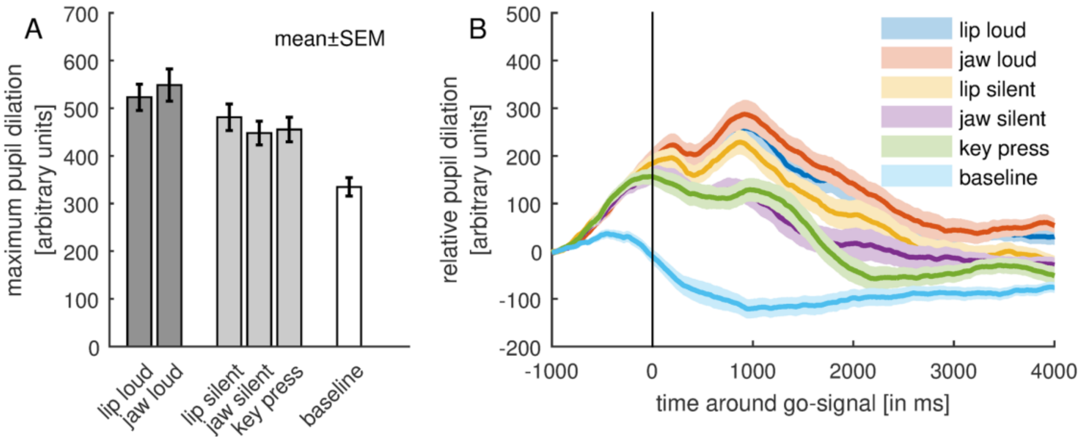

Figure 19. A. Maximum pupil dilation for the six different conditions (± SEM). Statistical comparisons between the individual conditions are presented in Table 1. B. Mean pupil diameter for the different conditions relative to the first 100ms of the graph. Shaded areas represent ±SEM. C. Mean pupil dilation between -1000ms and 2000ms during the six different conditions.

Table 4. P-values of the Bonferroni-adjusted post-hoc tests comparing the maximum pupil dilation across conditions.

	Lip loud	**Jaw loud**	**Lip silent**	**Jaw silent**	**Key press**	**Baseline**
Lip loud	---	1	.222	.017*	.051	<.001*
Jaw loud	---	---	.002*	<.001*	.005*	<.001*
Lip silent	---	---	---	.837	1	<.001*
Jaw silent	---	---	---	---	1	<.001*
Key press	---	---	---	---	---	<.001*

Blinks

First, we calculated the number of blinks per minute for each condition. A repeated-measures ANOVA with the number of blinks per minute as dependent variable revealed a significant difference between conditions ($F(5,120) = 2.94$, $p < .033$, $\eta_p^2 = .109$, $\varepsilon = .662$ (Greenhouse-Geisser correction applied). Bonferroni-adjusted post-hoc tests only showed a significantly higher blink rate during vocal conditions ('lip loud' and 'jaw loud') compared to the 'jaw silent' condition ($p < .008$ and $p < .034$), while all other comparisons were non-significant.

Second, we analyzed blink dynamics (figure 20), which can be described along three sub-patterns. While a peak after the instruction word could be detected in all conditions, this increase was strongest (and the only peak) in the baseline condition. In the key press condition, a second, strong and rather long-lasting increase (between 500-1500ms) could be identified following the go signal. In contrast, all conditions involving facial muscle activity (both loud and silent) showed two local peaks after the go signal. The first was located at approximately 500ms, the second at 1500ms. While the first seemed rather comparable in size and shape between verbal conditions, the second peak varied considerably in its latency and strength. In sum, the blink analysis suggests that although the overall frequency of occurrence does not strongly differ between conditions, the timing of the blinks appears to be quite sensitive to the different contextual (facial and manual) motor demands.

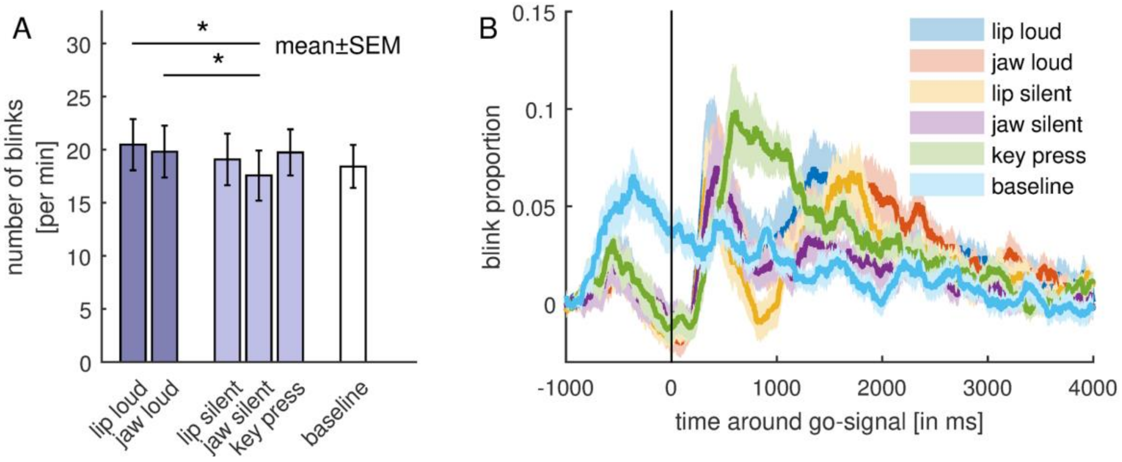

Figure 20. A. Mean number of blinks per minute for the six different conditions (± SEM). B. Mean averaged blink proportion of the conditions as a function of time. Shaded areas represent ±SEM.

Electromyographic activity

We measured EMG activity to approximate the on- and offset of mouth movements as well as to assess differences between loud and silent conditions. Interestingly, blinks seem to have occurred either before or at the beginning of the mouth movement (500ms after the go signal) or after the end of the movement (around 1500ms). Comparing loud and silent conditions revealed a stronger and longer lasting EMG-signal during 'lip loud' compared to 'lip silent', but the signal was highly similar during 'jaw loud' and 'jaw silent' conditions (figure 21).

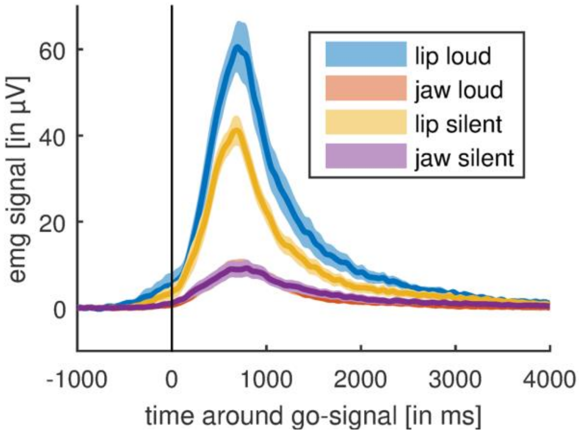

Figure 21. Electromyographic activity during mouth movements. While the activity seems to differ between silent and loud lip movement conditions, they highly overlap during jaw movements. Please note that the difference in peak amplitude between lip and jaw movements is not informative, since the signal stems from different electrodes.

3.2.3 DISCUSSION STUDY 3

The present study focused on the analysis of pupil dilation as a function of different types of vocal-related demands. Our re-analysis of a previous, existing data set suggested that vocalization indeed leads to a significant increase in pupil dilation compared to a condition without vocal demands. We replicated these findings in a follow-up study, and to pinpoint the underlying mechanisms and to exclude a range of potential confounds, we included several control conditions.

The experiment showed that pupil responses were indeed sensitive to the presence of vocal demands: Conditions with vocal demands were associated with the greatest increase in pupil dilation, followed by the conditions requiring a facial movement without oral sound production. All of the crucial comparisons were significant (‘jaw loud’ vs. ‘jaw silent’, ‘jaw loud’ vs. ‘lip silent’, ‘lip loud’ vs. ‘jaw silent’) except for one contrast (‘lip loud’ vs. ‘lip silent’), which nevertheless pointed into the expected direction. The manual movement condition was comparable to the silent facial movement conditions. Pupil dilation was minimal in the baseline condition without any response requirements. As vocal demands typically consist of at least two components, namely mouth-related movements and the production of sound (involving the vocal tract), the results suggest that both aspects contribute to the observed overall effects of vocal demands on pupil dilation.

Concerning lip movements, the difference in amplitude of the EMG signal between loud and silent lip conditions might be explained by the direct involvement of the lips during sound production known as bilabial plosive (Ladefoged & Maddieson, 1996). Uttering "boo" during the lip loud condition involves constricting the airflow out of the mouth by pressing the lips together. Since the airflow is likely less present during the silent condition, this likely explains the difference in motor activity. In contrast, jaw muscles are not involved in sound articulation of "mmh" (bilabial nasal articulation, Ladefoged & Maddieson, 1996), thereby resulting in a highly similar amplitude in the EMG signal between loud and silent conditions. Due to our electrode placement, we cannot specify the influence of motor activity of the vocal tract, but we assume that there should also be a difference between loud and silent conditions. The difference in pupil diameter between all loud conditions and all silent conditions (except for 'lip loud' vs 'lip silent') suggests that not only the movement itself, but also the articulation of sound, the facial movement and the motor activity of the vocal tract, increase the pupil diameter.

While our overall result pattern is well in line with our predictions, one might still further speculate why the pupil dilation between the lip loud and lip silent condition did no significantly differ. O'Shea and Moran (2016) suggested that mental imagery of actions may have similar effects on the pupil as "real" actions. Thus, mental imagery of producing "boo" while moving the lips accordingly in the silent condition might have increased pupil size similar to the real utterance of "boo". This might also explain the difference in the nature of lip and jaw movements. While clenching ones teeth (jaw movement) is not clearly associated with a sound, the lip movements are clearly associated with the sound "boo". Overall, while the complexity of the task itself (detect a cue and choose a simple motor output as response) is roughly comparable for all task conditions, apparently even slight differences in motor output demands lead to a change in pupil dilation. Therefore, we advise to be cautious when using pupil size as a marker of cognitive aspects of a task whenever differences in motor activity exist between task conditions.

While in a future study one might want to additionally assess whether a sound-inducing button press or non-vocal auditory input would lead to a similarly strong pupil dilation response, previous research already demonstrated that pupil dilation is greater for listening to vocal than to instrumental music (Weiss et al., 2016) suggesting a specific role of vocalization rather than auditory input per se. Interestingly, our setup did not include social or higher order cognitive aspects, since neither was the elicited sound meaningful, nor was any sort of communication involved. Therefore, it is neither the interpretation of the vocal input nor the social context that leads to the modulation of pupil dilation here. Our findings might rather point to an interaction between auditory vocal input and the motor aspect of vocalization, such that the increased pupil dilation for listening to vocal compared to instrumental music (Weiss et al., 2016) might depict common (and automatic) coding of vocal perception and action (Hommel, Müsseler, Aschersleben, & Prinz, 2001).

It is further important to consider the modulation of the pupil diameter in the light of blinking. Blinks change the light input, thereby leading to a slight change in pupil size. Additionally, blinks can lead to a miscalculation of pupil size if the algorithm used by the eye tracker does not fully take the pupil coverage during a blink into account. Since we did not find consistent significant differences in the number of blinks between vocal and baseline conditions (unlike the substantial corresponding effect in pupil diameter), blinks are very unlikely to account for the reported effects on pupil dilation here. This is further confirmed by the exploratory data re-analysis (presented in the introduction), in which we deliberately decided not to implement any data interpolation regarding blinks and only analyzed blink-free trials to minimize any possibility that the effect on pupil size might be driven by blinks. The results were highly similar to the results of our newly designed experiment, where we generously interpolated blinks. While this again strongly suggests that blinking behavior cannot account for the observed effects on pupil dilation, a replication study of the present experiment might include an explicit instruction to avoid blinking. However, while blinking does not seem to drive the pupil dilation changes during vocalization, we observed a complex temporal pattern of blinking that is clearly distinct for vocal motor output compared to, for example, a button press. Such time-critical motor-based modulation can be of importance for studies on blink rate during verbal (dyadic) communication. For such studies, which assess blink rates during a conversation (e.g., Bentivoglio et al., 1997) or eye-blink behavior at breakpoints of speech (Nakano & Kitazawa, 2010), it appears important to consider that vocal demands per se can affect ocular parameters on a fine-grained temporal scale.

3.2.4 SUPPLEMENTARY MATERIAL

Analysis of mean pupil dilation over the time window between -1000 and 2000ms

In addition to the analysis of maximum pupil dilation, we analysed the mean pupil dilation over the time window between -1000 and 2000ms (similar to Laeng et al., 2011). Mean pupil dilation was baseline-corrected by subtracting the mean pupil dilation of the first 100ms of the selected time window. A repeated-measures ANOVA using mean pupil dilation as dependent variable revealed a significant main effect of conditions ($F(5,120) = 45.53$, $p < .001$, $\eta_p^2 = .655$, $\varepsilon = .681$). The pupil increased the most during vocal conditions ('lip loud' and 'jaw loud') followed by 'lip silent' and the other two non-vocal movements ('jaw silent' and 'key press'). The pupil even showed a decrease over the selected time window during the baseline ('pause') condition (Fig. S1). P-values of Bonferroni-adjusted post-hoc tests are presented in Table S1.

Table S1. P-values of the Bonferroni-adjusted post-hoc tests comparing the maximum pupil dilation across conditions.

	Lip loud	**Jaw loud**	**Lip silent**	**Jaw silent**	**Key press**	**Baseline**
Lip loud	---	1	1	.025*	.020*	<.001*
Jaw loud	---	---	.213	.001*	.006*	<.001*
Lip silent	---	---	---	.085	.058	<.001*
Jaw silent	---	---	---	---	1	<.001*
Key press	---	---	---	---	---	<.001*

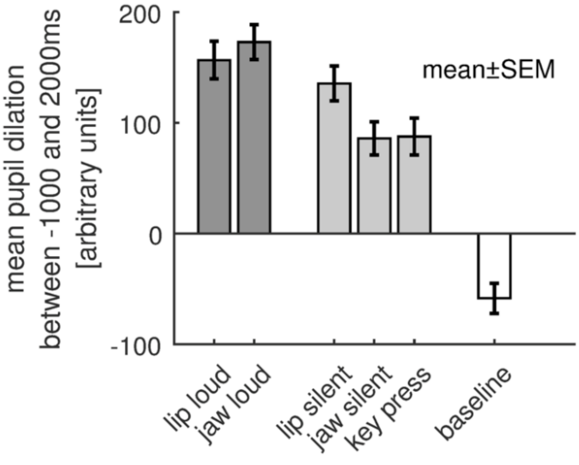

Figure S1. Mean pupil dilation during the six different conditions.

Blink detection: Comparison of different blink detection algorithms

The internal EyeLink algorithm only detects blinks of each eye separately. Therefore, only data of the left eye (of one random participant) is presented (Table S1). For comparison, our custom blink detection was also run on the left eye only. Internal EyeLink blink detection revealed similar number and duration of blinks compared to our custom blink detection. As an additional comparison, we used the low-passed filtered (20Hz) electromyographic data of the electrodes below and above the left eye to detect blinks with the EOG blink detection described by Wascher et al. (2015). In addition to this procedure, we changed blink on- and offsets. Instead of the minimum time point in a specified window, the decrease of the peak amplitude by three quarters was used. This resulted in a reduction in blink duration. While blink number was similar to the other blink detection algorithms, the duration of blinks slightly increased. Since the EOG recording was recorded with a different time stream, blink on- and offsets cannot be compared to the other two detection algorithms.

Table S2. Comparison of internal EyeLink blink detection, EOG blink detection after Wascher et al. (2015) to our custom blink detection. Detections based on the data of the left eye of one participant. *all blinks with a duration between 50 and 500ms

	Internal EyeLink *	**Custom**	**EOG ***
Number of blinks detected	531	535	559
Blink duration (mean ± SD)	142.26 ± 47.11ms	159.02 ± 51.98ms	177.45 ± 39.99ms
Blink onset difference	4.97 ± 5.21ms (EyeLink - custom)		
Blink offset difference	-12.73 ± 4.19ms (EyeLink - custom)		

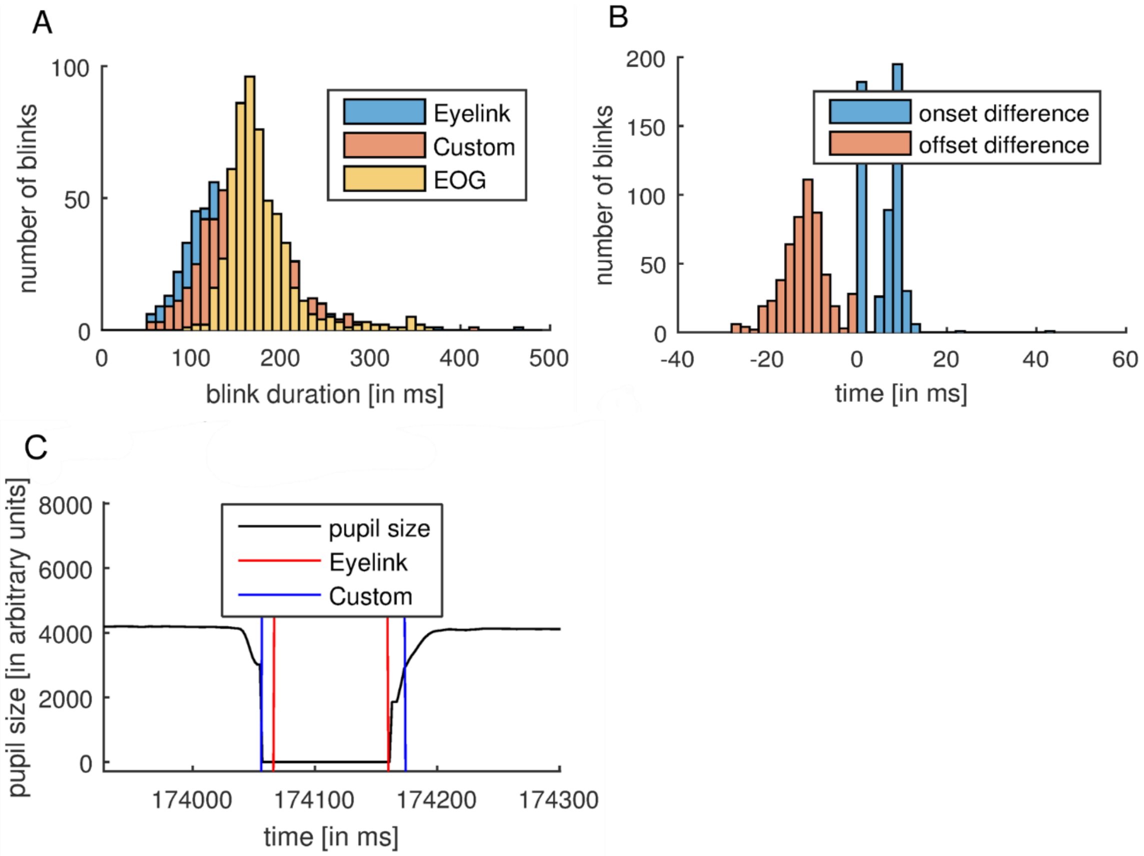

Figure S2. A. Number of blinks with different blink durations. Comparison of internal EyeLink, custom and EOG (Wascher et al., 2015) blink detection. B. Blink on- and offset difference between EyeLink and custom blink detection. C. Example blink detection of EyeLink and custom algorithm in relation with pupil size (blink 17: difference onset 10ms; difference offset -14ms).

4 GENERAL DISCUSSION

4.1 SUMMARY OF THE RESULTS

The presented studies systematically investigated the interaction between cognition and spontaneous blinks and how those eye-related movements are embedded within other motor output. More specifically, we examined sensory and cognitive influences on blink rate and timing during a perceptual task (study 1), evaluated how speaking and blinking is related (study 2), and studied the influence of defined speech-related motor output on blink timing and pupil size (study 3). The experiments provide strong evidence that movements and cognitive processes are deeply intertwined. Before embedding the insights into the bigger picture, the most important findings are shortly summarized below.

The aim of study 1 was to disentangle sensory-driven bottom-up and cognitive top-down influences on blinks. In addition, we wanted to understand if the influences on blinks during visual and/or auditory input are the same by directly comparing the influences between modalities. The results of study 1 can be summarized by three key findings. First, blink probability decreased before visual compared to auditory stimulus onset. This was also the case in the bimodal condition, when the visual compared to the auditory stream was attended. Second, blink probability was clearly increased shortly after passively observed visual or audiovisual stimulus offset, but not or only weakly after unimodal auditory stimulation. However, this modulation was enhanced in all domains or became clearly visible, respectively, if a task was assigned. Third, blink probability and latency increased after the offsets of relevant stimuli compared to irrelevant or distracting stimuli in all domains. The omission of a stimulus resulted in a lower blink occurrence, but in a higher blink latency. Overall, the findings suggest a complex interplay of different influences on blink behavior, which can be grouped into sensory driven, attentional and task specific effects. While the sensory driven effect differs between stimulus modalities being more pronounced when a visual stimulus was presented, the enhanced blink rate modulation due to the increased attentional demand is similar in both domains. Stimulus specific top-down processes based on the evaluation of task specific sensory information are domain general and influence blink rate and latency even in the absence of sensory input (stimulus omission). We concluded that visual input plays a special role in blink modulation. In addition, the magnitude of sensory-induced blink rate modulation is influenced by domain general attentional demands, while particularly the latency of blinks is influenced by domain general information evaluation processes.

The goal of study 2 was to understand the interaction between speaking and blinking while assessing cognitive demands, sensory input and different motor aspects of speaking. The results showed that the observed blink rate increase during speaking was mainly driven by complex motor activity of the mouth, whereas simple motor output, cognitive demands or auditory input only had a minor or no effect on the number of blinks during speaking. More precisely, neither simple movements of the jaw, lip or tongue nor cognitive task demands without verbal responses, nor self- or foreign-produced auditory input had a strong effect on the blink rate. In contrast, complex facial movements as executed during lollipop sucking or unvoiced speaking strongly increased the blink rate. The strongest effect was found during the most complex and most natural condition, namely speaking with a normal voice.

Extending these findings, study 3 showed that speech-related motor output not only enhanced blink rate, but also modulated the timing around such movements. Moreover, blink dynamics introduced by verbal output were distinct from the blink modulation around a manual response. In addition, study 3 demonstrated that pupil size changes are comparable to blink rate changes: the pupil was increased the most by spoken syllables followed by finger and mouth movements without vocalization and finally the baseline condition in which neither vocal nor muscular activity was required. The findings of study 2 and 3 together highlight how strongly different types of movements interact.

4.2 ON THE COMPLEX LINK BETWEEN MOVEMENT AND COGNITION

Cognitive processes coincide with movements during natural behavior. When connecting our results to previous research, it becomes clear that the link between movement and cognition is not simple, but highly complex, since not only cognition influences movements, but also the other way around. Movement interactions further tie this link together. The following sections describe the relation of these aspects in more detail.

4.2.1 COGNITION INFLUENCES SPONTANEOUS BLINKS BEYOND VISION

When looking at influences on blinking, one can differentiate between a rate change that is temporally independent of events and a short-lived event based modulation of blink probability. Previous research is rather inconsistent in identifying a cognitively induced change in the overall blink rate (Holland & Tarlow, 1975; Oh, Han, et al., 2012; Tanaka & Yamaoka, 1993). However, more fine-grained temporal analyses showed consistently that blinks are primarily executed at sensory and cognitively defined breaks within visual information input and at the end of stimulus evaluation processes (Fukuda, 2001; Hoppe et al., 2018; Nakano et al., 2009; Wascher et al., 2015). Similar effects on blinks were shown in the auditory domain (Kobald et al., 2019; Oh, Jeong, et al., 2012). By systematically and directly comparing the influences across modalities, our findings support the idea that blinks are influenced by modality-independent cognitive mechanisms. First, the general attentional state increases the sensory induced blink modulation similarly in both domains. Second, cognitively defined differences in information input affects blinks, that is, the sensory input is processed, then interpreted as being standard, distractor or target and then blink behavior is influenced. This influence is domain general, too. Thus, cognition and spontaneous blinks are linked beyond the control of the visual consequences of a blink. Particularly the cognitively driven increase in blink rate suggests an active role of blinking. Blinks may help to improve processes under increased task demands, however, the presented research cannot define such underlying mechanisms. One possibility is that blinks consolidate previous information and/or facilitate up-coming processes. Our finding that modality-independent processes influence spontaneous blinks additionally suggests that blinks are not solely integrated into our system at the sensory level, but at a higher level of our perceptual system that is modulated by high cognitive processes. Such underlying processes that influence blinks, possibly expand to other sensory input domains such as the somatosensory one.

A mechanism that acts comparably across sensory domains is not unique to spontaneous blinks, but was also shown for microsaccades. Interestingly, while the modality-independent stimulus evaluation of target stimuli increase blink probalitiy, microsaccades are longer inhibited (Valsecchi et al., 2007; Valsecchi & Turatto, 2009). Thus, general top-down processes affect different eye (-related) movements, but not necessarily in the same way.

4.2.2 SPONTANEOUS BLINKS INFLUENCE COGNITION

Around the turn of the millennium, researchers started to suggest that spontaneous blinks also act on cognitive processes. Consider these quotes:

- "the process of disengagement, (...) is triggered by spontaneous eyeblinks" (Nakano, Kato, Morito, Itoi, & Kitazawa, 2013, p. 3)
- "The blink may assist with modulating the size of the visual information stream." (Fukuda et al., 2005, p. C84)
- "the 'reset' capacity of eyeblinks (...) reflecting milestones in cognitive processes or 'cognitive punctuation marks'." (Bonneh et al., 2016, p. 13)

Behavioral evidence for an influence of blinks on cognitive processes comes from studies investigating changes in performance measurements and perceptual switches during bistable stimulus presentation after blink execution. As described previously, a switch in bistable perception reflects changes in cognitive processing that are independent of the sensory input. Two phenomena were reported to be related to blink presence using bistable stimulation. First, blink presence decreased the probability of a percept-specific switch in a binocular rivalry paradigm (Van Opstal, De Loof, Verguts, & Cleeremans, 2016). Binocular rivalry is a specific form of bistable perception during which one stimulus is presented to the left eye and another stimulus to the right eye. Again, sensory input is not changed throughout the experiment, but perception switches from one to the other interpretation, which is said to reflect internal cognitive processes (for more details, see Tong, Meng, & Blake, 2006). Van Opstal et al. (2016) suggested that blinks stabilize a specific percept by modulating cognitive processes possibly by delaying visual information processing. Second, a percept-specific switch followed blink presence in other bistable perception paradigms (Kalisvaart & Goossens, 2013; Nakatani, Orlandi, & van Leeuwen, 2011; Otero-Millan, Macknik, & Martinez-Conde, 2012). Thus, blinks might act as a reset signal to perceptual processes resulting in a new evaluation of sensory input (Otero-Millan et al., 2012). The observation that blinks facilitated a specific switch is not necessarily contradictory to the above presented work by Van Opstal. In all cases, a specific switch, and not all perceptual switches, was reported to be either facilitated or suppressed by the presence of blinks. This speaks for a percept-specific influence of blinks that might be linked to stimulus characteristics or additional higher cognitive processes.

Apart from the influence of blinks on bistable perception, Ang and Maus (2020) investigated the effect of voluntary blinks on attention using two versions of a rapid serial visual presentation task. In both experiments, performance accuracy increased significantly shortly after a blink. In other words, blinking seemed to be beneficial in these attention demanding tasks. Moreover, the simulation of blinks yielded a much weaker improvement in accuracy suggesting that the effect goes beyond the perception of the reappearing stimulus. In line with these findings, other studies reported that the presence of a blink decreased reaction times in response to target stimuli implicating a blink-related improvement of stimulus evaluation and/or responsiveness (Pivik & Dykman, 2004; Sirevaag et al., 1999). Even over time, reaction times associated with blink occurrences remained constant in contrast to the otherwise observed increase in reaction times (Pivik & Dykman, 2004). Altogether, these studies suggest that blinks influence higher cognitive processes such as attention and/or stimulus evaluation and improve perceptual performance.

In addition to the above reviewed behavioral studies, few neurological studies further reinforce the claim of blink-induced brain processes that go beyond low-level motor or visual responses. Nakano et al. (2013) compared brain (de-)activations during spontaneous blinks and external blackouts during video watching using fMRI. On the one hand, the results revealed a deactivation of areas belonging to the dorsal attention network after each blink and on the other hand, an increased activation of the default mode network. This was not the case after blackouts. The former network modulates goal-directed attention (Corbetta & Shulman, 2002), the latter increases activity during settings with low external processing demands thereby facilitating internal processes such as the exploration of possible future events (Buckner, Andrews-Hanna, & Schacter, 2008). Nakano et al. (2013) concluded that spontaneous blinks might actively trigger the process of attentional disengagement by deactivating the dorsal attention network as well as activating the default mode network, which is a first step before attention can be shifted and reallocated. Other researchers used methods with a higher temporal resolution to investigate blink-related neural changes, that is electroencephalography (EEG) and magnetoencephalography (MEG). Especially in parieto-occipital brain regions, so-called blink-related oscillations were identified (Bonfiglio et al., 2009). During rest and in the absence of any task specific requirements, spontaneous blinks were found to especially modulate delta oscillations in the precuneus starting in an amplitude increase before and a phase-coherency after the blink (approx. ranging from -500ms to 1000ms) (Bonfiglio et al., 2009). Cognitive task demands (Liu et al., 2019) and passive visual stimulation (Liu et al., 2020) decreased blink-related delta oscillations in the precuneus. Taken together, blinks increased activity in the precuneus during moments of low external processing demands, but less so during high external processing demands. This relation is in line with the findings that the precuneus is part of the default-mode network (Hagmann et al., 2008), which is, as stated above, linked to self-relevant, internally focused tasks (Buckner et al., 2008). All in all, neurological studies provide strong evidence for a direct influence of blinks on neural processes outside motor related brain areas.

Finally, not only the presence of a blink has an influence on cognition, but also the instruction to suppress them. A comparison across our own studies with and without such an instruction using the same task revealed a considerable larger pupil size, a strong indicator of cognitive demands, when participants were asked to suppress blinks. Thus, blinks seem to be incorporated into normal behavior, and therefore the suppression introduces an additional task demand. More evidence comes from an electrophysiological study by Verleger (1991). Here, the instruction to suppress blinks yielded in a decreased P300 amplitude, a brain potential that is known to be enhanced after active attention allocation (Squires et al., 1975). The authors similarly concluded that the secondary task to suppress blinks intervenes with the attentional task demands (Verleger, 1991). Based on this finding, researchers suggested to overcome electrophysiological influences of blinks by using methodological approaches for artifact rejection instead of instructing participants to suppress blinks (Ochoa & Polich, 2000; Verleger, 1991).

To summarize, several influences of blinks on cognitive processes have been described. The functions range from stabilizing perception (Van Opstal et al., 2016) to resetting stimulus evaluation (Otero-Millan et al., 2012) and to refreshing visual attention (Ang & Maus, 2020). Neuroscientific findings add that blinks might trigger attentional disengagement (Nakano et al., 2013) as well as internally focused attention during low external stimulation (Liu et al., 2020). Consequently, blinks seem to have an active role in the human brain-body communication possibly explaining why we spontaneously blink so often. Nevertheless, behavioral and neurological findings are still scarce asking for further investigations on how spontaneous blinks contribute to cognitive processes.

4.2.3 BODY MOVEMENTS INFLUENCE COGNITION

The idea that movements in general act on cognitive processes is not entirely new. On the one hand, some movements change the sensory input, such as eye movements. Consequently, information before an eye movement needs to be linked to information after an eye movement and attention is reallocated along the focus of the eye (Ibbotson & Krekelberg, 2011). Such an influence of movements on cognition via a shift in sensory input goes beyond vision, since the movement of any sensory organ results in a modulation of sensory input: Head movements change ear position and thus, auditory information intake and likewise, the movement of certain body parts changes somatosensory, olfactory, gustatory and vestibular information intake. Interestingly, various movements were reported to have a sensory independent and rather direct influence on cognition similar to the previously presented influence of spontaneous blinks on cognition. For example, primate and human patient studies demonstrated that saccades introduce a phase shift in brain oscillations thereby synchronizing brain activity which in turn facilitates perceptual processing and memory formation (Bartlett, Ovaysikia, Logothetis, & Hoffman, 2011; Hoffman et al., 2013; Jutras, Fries, & Buffalo, 2013). In addition, also large movements have been shown to influence cognitive processes. Cycling reduced the reaction time in response to infrequent stimuli interleaved in a sequence of visual, repetitive stimuli. Moreover, the physical activity modulated neuronal components associated with early sensory processing and late stimulus categorization (Bullock, Cecotti, & Giesbrecht, 2015). Using a comparable auditory experimental design, Schmidt-Kassow, Heinemann, Abel, and Kaiser (2013) reported that cycling to an auditory rhythm enhances cognitive components related to attention allocation. Furthermore, our own lab showed that walking leads to increased sensory processing of peripheral visual input by decreasing alpha power which is known to inhibit sensory processing (Cao et al., 2020; Cao & Händel, 2019). Interestingly, newest research additionally revealed that activity of internal organs, e.g. heart, lung and gut, has an impact on cognition. Such bodily signals were suggested to activate, but also enhance mental processes including attention, perception, memory, decision-making and motor control (for a review, see Critchley & Garfinkel, 2018). For example, Park, Correia, Ducorps, and Tallon-Baudry (2014) showed that heartbeat-evoked brain responses shape conscious perception of faint visual gratings. Moreover, it was possible to predict participants perception based on this heart-to-brain communication. As a further example, breathing or rather the respiratory phases were suggested to have an influence on the readiness potential, a neural activity preceding the onset of voluntary movement (Park et al., 2020).

Taken together, many body movements including eye (-related) movements, limb movements and movements of internal organs affect higher cognitive processes. Thus, our findings in line with previous research suggest that cognition and movement interact in a bidirectional way. Consequently, the brain and the body should not be seen as two distinct parts, but as one elaborated system. Investigations of this complex system will reveal a more realistic and complete picture of our natural behavior.

4.2.4 MOVEMENT INTERACTIONS INCREASE THE COMPLEXITY

Cognitive processes influence movements and movements have an impact on cognitive processes. Thus, the link seems to be bidirectional. However, motor events rarely occur in isolation, but are executed in parallel and influence each other during natural behavior. Therefore, movement interactions are important to consider when studying the link between movement and cognition.

Speaking is an example of a natural behavior, during which several movements are executed in parallel. In order to produce sounds, movements including lip, jaw, tongue and respiratory movements need to be executed (Smith, 1992). In study 2 of this thesis, we showed that natural mouth movements as during speaking interact with blinks in contrast to simple or isolated mouth movements. Similarly, experiments on walking revealed that the modulation of saccade and blink rate is stronger during the more natural, normal walking condition compared to slow, deliberate walking (Cao et al., 2020). What is important here is that many movement interactions can only be seen if natural movement is allowed. Yet, also movements that are close to natural behavior show interactions, for example, in study 2 the interaction between speaking without vocalization and blink rate or in study 3 the interaction between pupil size and simple motor output. Consequently, if we want to understand natural behavior, it is crucial to allow movements and their interactions during experiments at least to a certain extent.

In addition, if one movement can be linked to other movements and each movement might be linked to cognitive processes as described in the previous sections, then movement interactions add a new level of complexity to the link between movement and cognition. Highly interesting interactions are body-eye interactions, because a bodily-induced change in eye movement might not only directly affect brain activity, for example, by introducing a phase shift of oscillatory activity (e.g., Jutras et al., 2013), but it also shifts our visual information input and thus, inevitably influences perception. For example, head movements and saccades are linked (Morasso et al., 1973; Stahl, 1999), hand movements and saccades influence each other's trajectories (Nissens & Fiehler, 2018) and walking increases blink/saccade rate (Cao et al., 2020). Importantly, eye movements are not randomly elicited in time during body movements, but seem to follow suppression and facilitation phases. For example, they are preferably executed during the stance phase of walking (Cao et al., 2020), during the early phase of the cardiac cycle (Galvez-Pol et al., 2020; Ohl et al., 2016) or in alternation with other eye movements (Brych et al., 2021; Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008). Thus, the temporal coupling between body and eye movement indicate that visual information is sampled in a specific way, which in turn needs to be evaluated and interpreted. Furthermore, such a bodily-induced shift in sensory information intake influencing perception is also plausible for other sensors. During walking, a temporal relationship between step length/frequency and head movements (including the ear) exists (Hirasaki, Moore, Raphan, & Cohen, 1999). Head movements in turn enhance the performance of auditory perception such as sound localization (Perrett & Noble, 1997). Consequently, the improvement in an auditory localization task during walking as compared to standing still might be due to the interaction between body and head movements (Brungart, Kruger, Kwiatkowski, Heil, & Cohen, 2019). Yet, further research is needed to determine the exact underlying mechanisms.

All in all, different movements can be linked to cognitive processes through complex interactions thereby increasing the complexity of the whole system. Therefore, movement interactions are an important phenomenon and a highly relevant part of natural behavior, which needs to be taken into account during experimental investigations.

4.3 OUTLOOK

4.3.1 BLINK-RELATED OSCILLATIONS DURING BOTTOM-UP AND TOP-DOWN PROCESSES

As reviewed above, cognitive processes and spontaneous blinks seem to be linked in a bidirectional way. Yet, influences of blinks on brain processes have not been studied extensively. To understand the mechanisms of this link, knowledge about the neural consequences outside motor-related brain areas is needed. One promising account to empirically investigate this link is the recording of blink-related oscillations. Few research groups presented power changes or phase (de-) synchronizations in a wide range of frequencies around blinks. Especially the increase in power in the delta-band (0.5 – 4 Hz) before a blink and the synchronization of delta-band oscillations after a blink have been reported several times when participants were at rest (Bonfiglio et al., 2009; Bonfiglio et al., 2011; Liu et al., 2017; Liu et al., 2019). This increased delta response possibly reflects attention allocation to task relevant sensory input (Bonfiglio et al., 2009; Händel, Lutzenberger, Thier, & Haarmeier, 2008). When these blink influences are weakened by either cognitive demands or sensory input, attention is possibly more directed towards internal processes (Liu et al., 2020; Liu et al., 2019). In addition, alpha oscillations (8 – 14 Hz) were shown to be synchronized for a short time after the blink followed by a desynchronization (Bonfiglio et al., 2011; Liu et al., 2019). Alpha likely reflects top-down processes in a way that alpha increases (e.g., via phase synchronization) when suppressing irrelevant information and decreases (e.g., via phase desynchronization) when focusing attention (e.g., Haegens, Händel, & Jensen, 2011). The blink-related alpha change therefore fits with the suggestion that blinks terminate focused attention followed by a reallocation of attention (Nakano et al., 2013).

The oddball paradigm used in study 1 of this work might be suited to add insights to the influence of blinks on brain oscillations. One might hypothesize that blink-related delta oscillations are strongest in the precuneus when no task and no sensory input is presented, followed by a decrease in delta during passive stimulation (no task condition) and an even stronger decrease during the same sensory input, but additional task demands. Therefore, one would need to compare oscillations around blinks following standard (frequent) stimuli. Apart from the blink modulation around standard (frequent and irrelevant), distractor (infrequent, but irrelevant) and target (infrequent and relevant) stimuli, one could also investigate the blink-related alpha change around these different stimuli. Given the tight relation of alpha to attentional processes, one might find a decrease in alpha around blinks after targets focusing attention and an increase in alpha around blinks after distractors suppressing irrelevant information compared to blink-related alpha changes after standards. In addition, also exploratory analyses of such data are of high interest given the few findings so far. With such work, blinks or movements in general and ongoing brain activity will be further related and consequently, we get a step closer to understand natural behavior.

4.3.2 FROM HEALTHY HUMANS TO PATHOLOGICAL STATES

The tight interplay of eye movements, body movements and cognitive processes during natural behavior could be transferred to cases where the mind or the body is restrained. In the following, I want to highlight some examples how this might be beneficial.

Pupil size changes, a measure of cognitive processing, has been used to improve brain computer interfaces for highly immobile patients (Rozado et al., 2015). Such systems might be further improved by not only using the information drawn from pupil size, but also from blinks and (micro-)saccades. (Micro-)Saccades might enhance the classification of directed attention, blinks in turn could be used as markers of end points of information processing.

Insights on the link between movement and cognition could also be used to understand diseases and improve treatments. For example, hampered body movements characterize Parkinson 's disease, but at the same time this disease often encompasses sensory impairments and cognitive deficits (Armstrong, 2011; Sveinbjornsdottir, 2016). Understanding the link between movement and cognition might lead to a prediction of cognitive symptoms based on motor impairments. Moreover, training of motor output could possibly re-establishes cognitive abilities. In addition, studying movement interactions could lead to improve the understanding and treatment of co-occurring motor symptoms. In line with this idea, an interesting approach for the improvement of gait dysfunctions during physical therapy has been described: The presentation of rhythmic sounds. They positively influence walking speed as well as step length (Lim et al., 2005). Interestingly, such gait training was not only shown to enhance motor performance of different movements, but also improved perceptual performance (Benoit et al., 2014).

Overall, understanding natural behavior including the bidirectional link between cognition and movement as well as movement interactions could open possibilities for research that develops new techniques and efficient trainings for clinical disorders.

4.4 GENERAL CONCLUSION

The work at hands was dedicated to describe the interaction between cognition and movements. The investigations focused on spontaneous blinks, and specifically how those small eye-related movements are linked to other motor output as well as to cognitive processes. Our experimental design allowed differentiating sensory-based from cognitive influences on blink rate as well as blink timing. In addition, by directly comparing effects between visual and auditory input, our results suggest that cognitive processes influence blinks independent of vision. Interestingly, related research provides evidence that spontaneous blinks, but also other body movements, act on cognitive processes. Consequently, the link between movement and cognition is likely bidirectional. Importantly, whenever movements interact with other movements and each movement might be linked to cognition, the system increases in complexity. The second set of experiments therefore investigated how spontaneous blinks, but also pupil size, are linked to different aspects of speaking. In line with previous research, our findings revealed that speech-related motor activity increases blink rate and pupil size as well as modulates blink timing. Such a temporal link additionally indicates that body movements have an influence on our sensory information intake via a change in eye movement and thus, on perception.

Overall, our findings show a tight link between movement and cognition via spontaneous blinks, while thoroughly considering sensory influences. Importantly, the research has helped to establish that the link is independent from the visual domain and that the cognitive influence on spontaneous blink is comparable between sensory domains. Nevertheless, further research is needed to understand the exact underlying neural mechanisms of this influence. To conclude, movements are strongly connected with cognitive processes and should therefore be seen as an integral part of our system. By allowing movements and taking the influence of movements into account during experimental research, we will get closer to reveal a more realistic and complete picture of our natural behavior. Finally, this knowledge could open new possibilities for developing efficient treatments of clinical disorders.

REFERENCES

Ahern, S., & Beatty, J. (1979). Pupillary responses during information processing vary with Scholastic Aptitude Test scores. *Science*, *205*(4412), 1289-1292. http://dx.doi.org/10.1126/science.472746

Al-Abdulmunem, M. (1999). Relation between tear breakup time and spontaneous blink rate. *International Contact Lens Clinic*, *26*(5), 117-120. http://dx.doi.org/10.1016/S0892-8967(00)00033-X

Ang, J. W. A., & Maus, G. W. (2020). Boosted visual performance after eye blinks. *Journal of Vision*, *20*(10), 1-9. https://doi.org/10.1167/jov.20.10.2

Armstrong, R. A. (2011). Visual symptoms in Parkinson's disease. *Parkinson's Disease*, *2011*, 1-9. http://dx.doi.org/10.4061/2011/908306

Bagley, J., & Manelis, L. (1979). Effect of awareness on an indicator of cognitive load. *Perceptual and Motor Skills*, *49*(2), 591-594. https://doi.org/10.2466/pms.1979.49.2.591

Bailly, G., Raidt, S., & Elisei, F. (2010). Gaze, conversational agents and face-to-face communication. *Speech Communication*, *52*(6), 598-612. https://doi.org/10.1016/j.specom.2010.02.015

Bartlett, A. M., Ovaysikia, S., Logothetis, N. K., & Hoffman, K. L. (2011). Saccades during object viewing modulate oscillatory phase in the superior temporal sulcus. *Journal of Neuroscience*, *31*(50), 18423-18432. https://doi.org/10.1523/JNEUROSCI.4102-11.2011

Basso, M. A., & Evinger, C. (1996). An explanation for reflex blink hyperexcitability in Parkinson’s disease. II. Nucleus raphe magnus. *Journal of Neuroscience*, *16*(22), 7318-7330. https://doi.org/10.1523/JNEUROSCI.16-22-07318.1996

Basso, M. A., Powers, A. S., & Evinger, C. (1996). An explanation for reflex blink hyperexcitability in Parkinson’s disease. I. Superior colliculus. *Journal of Neuroscience*, *16*(22), 7308-7317. https://doi.org/10.1523/JNEUROSCI.16-22-07308.1996

Baumstimler, Y., & Parrot, J. (1971). Stimulus generalization and spontaneous blinking in man involved in a voluntary activity. *Journal of Experimental Psychology*, *88*(1), 95-102. http://dx.doi.org/10.1037/h0030638

Beatty, J., & Kahneman, D. (1966). Pupillary changes in two memory tasks. *Psychonomic Science*, *5*(10), 371-372. https://doi.org/10.3758/BF03328444

Beatty, J., & Lucero-Wagoner, B. (2000). The pupillary system. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of Psychophysiology* (Vol. 2): Cambridge University Press.

Benedetto, S., Pedrotti, M., Minin, L., Baccino, T., Re, A., & Montanari, R. (2011). Driver workload and eye blink duration. *Transportation Research Part F: Traffic Psychology and Behaviour*, *14*(3), 199-208. http://dx.doi.org/10.1016/j.trf.2010.12.001

Benjamini, Y., & Yekutieli, D. (2001). The control of the false discovery rate in multiple testing under dependency. *Annals of Statistics*, *29*(4), 1165-1188. https://doi.org/10.1214/aos/1013699998

Benoit, C.-E., Dalla Bella, S., Farrugia, N., Obrig, H., Mainka, S., & Kotz, S. A. (2014). Musically cued gait-training improves both perceptual and motor timing in Parkinson's disease. *Frontiers in Human Neuroscience*, *8*(494). https://doi.org/10.3389/fnhum.2014.00494

Bentivoglio, A. R., Bressman, S. B., Cassetta, E., Carretta, D., Tonali, P., & Albanese, A. (1997). Analysis of blink rate patterns in normal subjects. *Movement Disorders*, *12*(6), 1028-1034. http://dx.doi.org/10.1002/mds.870120629

Binda, P., & Murray, S. O. (2015). Keeping a large-pupilled eye on high-level visual processing. *Trends in Cognitive Sciences*, *19*(1), 1-3. http://dx.doi.org/10.1016/j.tics.2014.11.002

Bizzi, E., Kalil, R. E., & Tagliasco, V. (1971). Eye-head coordination in monkeys: evidence for centrally patterned organization. *Science*, *173*(3995), 452-454. http://dx.doi.org/10.1126/science.173.3995.452

Boghen, D., Troost, B., Daroff, R., Dell'Osso, L., & Birkett, J. (1974). Velocity characteristics of normal human saccades. *Investigative Ophthalmology & Visual Science*, *13*(8), 619-623. Retrieved from https://iovs.arvojournals.org/article.aspx?articleid=2122623

Bonfiglio, L., Sello, S., Andre, P., Carboncini, M. C., Arrighi, P., & Rossi, B. (2009). Blink-related delta oscillations in the resting-state EEG: a wavelet analysis. *Neuroscience Letters*, *449*(1), 57-60. http://dx.doi.org/10.1016/j.neulet.2008.10.039

Bonfiglio, L., Sello, S., Carboncini, M. C., Arrighi, P., Andre, P., & Rossi, B. (2011). Reciprocal dynamics of EEG alpha and delta oscillations during spontaneous blinking at rest: a survey on a default mode-based visuo-spatial awareness. *International Journal of Psychophysiology*, *80*(1), 44-53. http://dx.doi.org/10.1016/j.ijpsycho.2011.01.002

Bonneh, Y. S., Adini, Y., & Polat, U. (2016). Contrast sensitivity revealed by spontaneous eyeblinks: Evidence for a common mechanism of oculomotor inhibition. *Journal of Vision*, *16*(7), 1-15. http://dx.doi.org/10.1167/16.7.1

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*(4), 433-436. http://dx.doi.org/10.1163/156856897X00357

Bristow, D., Frith, C., & Rees, G. (2005). Two distinct neural effects of blinking on human visual processing. *NeuroImage*, *27*(1), 136-145. http://dx.doi.org/10.1016/j.neuroimage.2005.03.037

Bristow, D., Haynes, J.-D., Sylvester, R., Frith, C. D., & Rees, G. (2005). Blinking suppresses the neural response to unchanging retinal stimulation. *Current Biology*, *15*(14), 1296-1300. http://dx.doi.org/10.1016/j.cub.2005.06.025

Brungart, D. S., Kruger, S. E., Kwiatkowski, T., Heil, T., & Cohen, J. (2019). The effect of walking on auditory localization, visual discrimination, and aurally aided visual search. *Human Factors*, *61*(6), 976-991. https://doi.org/10.1177/0018720819831092

Brych, M., & Händel, B. (2020). Disentangling top-down and bottom-up influences on blinks in the visual and auditory domain. *International Journal of Psychophysiology*, *158*, 400-410. http://dx.doi.org/10.1016/j.ijpsycho.2020.11.002

Brych, M., Murali, S., & Händel, B. (2021). The Role of Blinks, Microsaccades and their Retinal Consequences in Bistable Motion Perception. *Frontiers in Psychology*, *12*(647256). https://doi.org/10.3389/fpsyg.2021.647256

Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). *The brain's default network: Anatomy, function, and relevance to disease*. In A. Kingstone & M. B. Miller (Eds.), *The year in cognitive neuroscience 2008* (pp. 1-38). http://dx.doi.org/10.1196/annals.1440.011

Bullock, T., Cecotti, H., & Giesbrecht, B. (2015). Multiple stages of information processing are modulated during acute bouts of exercise. *Neuroscience*, *307*, 138-150. http://dx.doi.org/10.1016/j.neuroscience.2015.08.046

Cao, L., Chen, X., & Haendel, B. F. (2020). Overground Walking Decreases Alpha Activity and Entrains Eye Movements in Humans. *Frontiers in Human Neuroscience*, *14*(561755). https://doi.org/10.3389/fnhum.2020.561755

Cao, L., & Händel, B. (2019). Walking enhances peripheral visual processing in humans. *PLoS Biology*, *17*(10), e3000511. http://dx.doi.org/10.1371/journal.pbio.3000511

Cardona, G., García, C., Serés, C., Vilaseca, M., & Gispets, J. (2011). Blink rate, blink amplitude, and tear film integrity during dynamic visual display terminal tasks. *Current Eye Research*, *36*(3), 190-197. http://dx.doi.org/10.3109/02713683.2010.544442

Chatham, C. H., Frank, M. J., & Munakata, Y. (2009). Pupillometric and behavioral markers of a developmental shift in the temporal dynamics of cognitive control. *Proceedings of the National Academy of Sciences*, *106*(14), 5529-5533. http://dx.doi.org/10.1073/pnas.0810002106

Cho, P., Sheng, C., Chan, C., Lee, R., & Tam, J. (2000). Baseline blink rates and the effect of visual task difficulty and position of gaze. *Current Eye Research*, *20*(1), 64-70. http://dx.doi.org/10.1076/0271-3683(200001)2011-HFT064

Collewijn, H., & Kowler, E. (2008). The significance of microsaccades for vision and oculomotor control. *Journal of Vision*, *8*(14), 1-21. http://dx.doi.org/10.1167/8.14.20

Collewijn, H., Van Der Steen, J., & Steinman, R. (1985). Human eye movements associated with blinks and prolonged eyelid closure. *Journal of Neurophysiology*, *54*(1), 11-27. http://dx.doi.org/10.1152/jn.1985.54.1.11

Cong, D.-K., Sharikadze, M., Staude, G., Deubel, H., & Wolf, W. (2010). Spontaneous eye blinks are entrained by finger tapping. *Human Movement Science*, *29*(1), 1-18. http://dx.doi.org/10.1016/j.humov.2009.08.003

Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201-215. http://dx.doi.org/10.1038/nrn755

Critchley, H. D., & Garfinkel, S. N. (2018). The influence of physiological signals on cognition. *Current Opinion in Behavioral Sciences*, *19*, 13-18. http://dx.doi.org/10.1016/j.cobeha.2017.08.014

Dang, L. C., Samanez-Larkin, G. R., Castrellon, J. J., Perkins, S. F., Cowan, R. L., Newhouse, P. A., & Zald, D. H. (2017). Spontaneous eye blink rate (EBR) is uncorrelated with dopamine D2 receptor availability and unmodulated by dopamine agonism in healthy adults. *eNeuro*, *4*(5), 1-11. http://dx.doi.org/10.1523/ENEURO.0211-17.2017

Donchin, E., & Coles, M. G. (1988). Is the P300 component a manifestation of context updating? *Behavioral and Brain Sciences*, *11*(3), 357-374. http://dx.doi.org/10.1017/S0140525X00058027

Doughty, M. J. (2001). Consideration of three types of spontaneous eyeblink activity in normal humans: during reading and video display terminal use, in primary gaze, and while in conversation. *Optometry and Vision Science*, *78*(10), 712-725. http://dx.doi.org/10.1097/00006324-200110000-00011

Doughty, M. J. (2018). Influence of mouth and jaw movements on dynamics of spontaneous eye blink activity assessed during slitlamp biomicroscopy. *Clinical and Experimental Optometry*, *101*(3), 345-353. http://dx.doi.org/10.1111/cxo.12648

Drew, G. C. (1951). Variations in reflex blink-rate during visual-motor tasks. *Quarterly Journal of Experimental Psychology*, *3*(2), 73-88. http://dx.doi.org/10.1080/17470215108416776

Einhäuser, W., Stout, J., Koch, C., & Carter, O. (2008). Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *Proceedings of the National Academy of Sciences*, *105*(5), 1704-1709. http://dx.doi.org/10.1073/pnas.0707727105

Engbert, R. (2012). Computational modeling of collicular integration of perceptual responses and attention in microsaccades. *Journal of Neuroscience*, *32*(23), 8035-8039. http://dx.doi.org/10.1523/JNEUROSCI.0808-12.2012

Engbert, R., Longtin, A., & Kliegl, R. (2002). A dynamical model of saccade generation in reading based on spatially distributed lexical processing. *Vision Research*, *42*(5), 621-636. http://dx.doi.org/10.1016/S0042-6989(01)00301-7

Evinger, C. (2010). Eyelid anatomy and the pathophysiology of blinking. *Encyclopedia of the Eye*, *2*, 128-133. http://dx.doi.org/10.1016/B978-0-12-374203-2.00272-4

Evinger, C., Basso, M. A., Manning, K. A., Sibony, P. A., Pellegrini, J. J., & Horn, A. K. (1993). A role for the basal ganglia in nicotinic modulation of the blink reflex. *Experimental Brain Research*, *92*(3), 507-515. http://dx.doi.org/10.1007/BF00229040

Evinger, C., Manning, K. A., Pellegrini, J. J., Basso, M. A., Powers, A. S., & Sibony, P. A. (1994). Not looking while leaping: the linkage of blinking and saccadic gaze shifts. *Experimental Brain Research*, *100*(2), 337-344. http://dx.doi.org/10.1007/BF00227203

Fogarty, C., & Stern, J. A. (1989). Eye movements and blinks: their relationship to higher cognitive processes. *International Journal of Psychophysiology*, *8*(1), 35-42. http://dx.doi.org/10.1016/0167-8760(89)90017-2

Friedman, D., Hakerem, G., Sutton, S., & Fleiss, J. L. (1973). Effect of stimulus uncertainty on the pupillary dilation response and the vertex evoked potential. *Electroencephalography and Clinical Neurophysiology*, *34*(5), 475-484. http://dx.doi.org/10.1016/0013-4694(73)90065-5

Fukuda, K. (1994). Analysis of eyeblink activity during discriminative tasks. *Perceptual and motor skills*, *79*(3_suppl), 1599-1608. https://doi.org/10.2466/pms.1994.79.3f.1599

Fukuda, K. (2001). Eye blinks: new indices for the detection of deception. *International Journal of Psychophysiology*, *40*(3), 239-245. http://dx.doi.org/10.1016/S0167-8760(00)00192-6

Fukuda, K., & Matsunaga, K. (1983). Changes in blink rate during signal discrimination tasks. *Japanese Psychological Research*, *25*(3), 140-146. https://doi.org/10.4992/psycholres1954.25.140

Fukuda, K., Stern, J. A., Brown, T. B., & Russo, M. B. (2005). Cognition, blinks, eye-movements, and pupillary movements during performance of a running memory task. *Aviation, Space, and Environmental Medicine*, *76*(7), C75-C85. Retrieved from https://www.ingentaconnect.com/content/asma/asem/2005/00000076/a00107s1/art00014

Fukuda, M., Oishi, M., Takao, T., Saito, A., & Fujii, Y. (2008). Facial nerve motor-evoked potential monitoring during skull base surgery predicts facial nerve outcome. *Journal of Neurology, Neurosurgery & Psychiatry*, *79*(9), 1066-1070. http://dx.doi.org/10.1136/jnnp.2007.130500

Galvez-Pol, A., McConnell, R., & Kilner, J. M. (2020). Active sampling in visual search is coupled to the cardiac cycle. *Cognition*, *196*, 104149. https://doi.org/10.1016/j.cognition.2019.104149

Gawne, T. J., & Martin, J. M. (2000). Activity of primate V1 cortical neurons during blinks. *Journal of Neurophysiology*, *84*(5), 2691-2694. http://dx.doi.org/10.1152/jn.2000.84.5.2691

Gawne, T. J., & Martin, J. M. (2002). Responses of primate visual cortical neurons to stimuli presented by flash, saccade, blink, and external darkening. *Journal of Neurophysiology*, *88*(5), 2178-2186. http://dx.doi.org/10.1152/jn.00151.200

Gilden, D. H. (2004). Bell's palsy. *New England Journal of Medicine*, *351*(13), 1323-1331. http://dx.doi.org/10.1056/NEJMcp041120

Gregory, R. (1952). Variations in blink rate during non-visual tasks. *Quarterly Journal of Experimental Psychology*, *4*(4), 165-169. http://dx.doi.org/10.1080/17470215208416614

Gruart, A., & Delgado-Garcí, J. (1994). Discharge of identified deep cerebellar nuclei neurons related to eye blinks in the alert cat. *Neuroscience*, *61*(3), 665-681. https://doi.org/10.1016/0306-4522(94)90443-X

Haegens, S., Händel, B. F., & Jensen, O. (2011). Top-down controlled alpha band activity in somatosensory areas determines behavioral performance in a discrimination task. *Journal of Neuroscience*, *31*(14), 5197-5204. http://dx.doi.org/10.1523/JNEUROSCI.5199-10.2011

Hagmann, P., Cammoun, L., Gigandet, X., Meuli, R., Honey, C. J., Wedeen, V. J., & Sporns, O. (2008). Mapping the structural core of human cerebral cortex. *PLoS Biology*, *6*(7), e159. http://dx.doi.org/10.1371/journal.pbio.0060159

Hall, A. (1945). The origin and purposes of blinking. *The British Journal of Ophthalmology*, *29*(9), 445-467. http://dx.doi.org/10.1136/bjo.29.9.445

Händel, B., Lutzenberger, W., Thier, P., & Haarmeier, T. (2008). Selective attention increases the dependency of cortical responses on visual motion coherence in man. *Cerebral Cortex*, *18*(12), 2902-2908. http://dx.doi.org/10.1093/cercor/bhn049

Hari, R., Salmellin, H., Tissari, S., Kajola, M., & Virsu, V. (1994). Visual stability during eyeblinks. *Nature*, *367*, 121-122. https://doi.org/10.1038/367121b0

Hayashi, N., Someya, N., & Fukuba, Y. (2010). Effect of intensity of dynamic exercise on pupil diameter in humans. *Journal of Physiological Anthropology*, *29*(3), 119-122. http://dx.doi.org/10.2114/jpa2.29.119

Hess, E. H., & Polt, J. M. (1960). Pupil size as related to interest value of visual stimuli. *Science*, *132*(3423), 349-350. http://dx.doi.org/10.1126/science.132.3423.349

Hess, E. H., & Polt, J. M. (1964). Pupil size in relation to mental activity during simple problem-solving. *Science*, *143*(3611), 1190-1192. http://dx.doi.org/10.1126/science.143.3611.1190

Higgins, J. S., Irwin, D. E., Wang, R. F., & Thomas, L. E. (2009). Visual direction constancy across eyeblinks. *Attention, Perception, & Psychophysics*, *71*(7), 1607-1617. http://dx.doi.org/10.3758/APP.71.7.1607

Hirasaki, E., Moore, S. T., Raphan, T., & Cohen, B. (1999). Effects of walking velocity on vertical head and body movements during locomotion. *Experimental Brain Research*, *127*(2), 117-130. https://doi.org/10.1007/s002210050781

Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron*, *36*(5), 791-804. https://doi.org/10.1016/S0896-6273(02)01091-7

Hoffman, K. L., Dragan, M. C., Leonard, T. K., Micheli, C., Montefusco-Siegmund, R., & Valiante, T. A. (2013). Saccades during visual exploration align hippocampal 3–8 Hz rhythms in human and non-human primates. *Frontiers in Systems Neuroscience*, *7*(43). http://dx.doi.org/10.3389/fnsys.2013.00043

Holland, M. K., & Tarlow, G. (1972). Blinking and mental load. *Psychological Reports*, *31*(1), 119-127. http://dx.doi.org/10.2466/pr0.1972.31.1.119

Holland, M. K., & Tarlow, G. (1975). Blinking and thinking. *Perceptual and Motor Skills*, *41*(2), 403-406. http://dx.doi.org/10.2466/pms.1975.41.2.403

Hömke, P., Holler, J., & Levinson, S. C. (2017). Eye blinking as addressee feedback in face-to-face conversation. *Research on Language and Social Interaction*, *50*(1), 54-70. http://dx.doi.org/10.1080/08351813.2017.1262143

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The theory of event coding (TEC): A framework for perception and action planning. *Behavioral and Brain Sciences*, *24*(5), 849-878. http://dx.doi.org/10.1017/S0140525X01000103

Hoppe, D., Helfmann, S., & Rothkopf, C. A. (2018). Humans quickly learn to blink strategically in response to environmental task demands. *Proceedings of the National Academy of Sciences*, *115*(9), 2246-2251. http://dx.doi.org/10.1073/pnas.1714220115

Huestegge, L. (2011). The role of saccades in multitasking: towards an output-related view of eye movements. *Psychological Research*, *75*(6), 452-465. http://dx.doi.org/10.1007/s00426-011-0352-5

Huestegge, L., & Koch, I. (2013). Constraints in task-set control: Modality dominance patterns among effector systems. *Journal of Experimental Psychology: General*, *142*(3), 633-637. http://dx.doi.org/10.1037/a0030156

Huestegge, L., Pieczykolan, A., & Koch, I. (2014). Talking while looking: On the encapsulation of output system representations. *Cognitive Psychology*, *73*, 72-91. http://dx.doi.org/10.1016/j.cogpsych.2014.06.001

Ibbotson, M., & Krekelberg, B. (2011). Visual perception and saccadic eye movements. *Current opinion in neurobiology*, *21*(4), 553-558. https://doi.org/10.1016/j.conb.2011.05.012

Ito, J., Nikolaev, A. R., Luman, M., Aukes, M. F., Nakatani, C., & Van Leeuwen, C. (2003). Perceptual switching, eye movements, and the bus paradox. *Perception*, *32*(6), 681-698. http://dx.doi.org/10.1068/p5052

Iwasaki, M., Kellinghaus, C., Alexopoulos, A. V., Burgess, R. C., Kumar, A. N., Han, Y. H., . . . Leigh, R. J. (2005). Effects of eyelid closure, blinks, and eye movements on the electroencephalogram. *Clinical Neurophysiology*, *116*(4), 878-885. http://dx.doi.org/10.1016/j.clinph.2004.11.001

Jacobsen, T., & Schröger, E. (2001). Is there pre-attentive memory-based comparison of pitch? *Psychophysiology*, *38*(4), 723-727. http://dx.doi.org/10.1111/1469-8986.3840723

Jin, P., Zou, J., Zhou, T., & Ding, N. (2018). Eye activity tracks task-relevant structures during speech and auditory sequence perception. *Nature Communications*, *9*(1), 1-15. http://dx.doi.org/10.1038/s41467-018-07773-y

Jongkees, B. J., & Colzato, L. S. (2016). Spontaneous eye blink rate as predictor of dopamine-related cognitive function—A review. *Neuroscience & Biobehavioral Reviews*, *71*, 58-82. http://dx.doi.org/10.1016/j.neubiorev.2016.08.020

Jutras, M. J., Fries, P., & Buffalo, E. A. (2013). Oscillatory activity in the monkey hippocampus during visual exploration and memory formation. *Proceedings of the National Academy of Sciences*, *110*(32), 13144-13149. http://dx.doi.org/10.1073/pnas.1302351110

Kaas, J. H., Hackett, T. A., & Tramo, M. J. (1999). Auditory processing in primate cerebral cortex. *Current Opinion in Neurobiology*, *9*(2), 164-170. http://dx.doi.org/10.1016/S0959-4388(99)80022-1

Kalisvaart, J. P., & Goossens, J. (2013). Influence of retinal image shifts and extra-retinal eye movement signals on binocular rivalry alternations. *PLoS One*, *8*(4), e61702. http://dx.doi.org/10.1371/journal.pone.0061702

Kaminer, J., Powers, A. S., Horn, K. G., Hui, C., & Evinger, C. (2011). Characterizing the spontaneous blink generator: an animal model. *Journal of Neuroscience*, *31*(31), 11256-11267. http://dx.doi.org/10.1523/JNEUROSCI.6218-10.2011

Karatekin, C., Couperus, J. W., & Marcus, D. J. (2004). Attention allocation in the dual-task paradigm as measured through behavioral and psychophysiological responses. *Psychophysiology*, *41*(2), 175-185. http://dx.doi.org/10.1111/j.1469-8986.2004.00147.x

Karatekin, C., Marcus, D. J., & Couperus, J. W. (2007). Regulation of cognitive resources during sustained attention and working memory in 10-year-olds and adults. *Psychophysiology*, *44*(1), 128-144. http://dx.doi.org/10.1111/j.1469-8986.2006.00477.x

Karson, C. N., Berman, K. F., Donnelly, E. F., Mendelson, W. B., Kleinman, J. E., & Wyatt, R. J. (1981). Speaking, thinking, and blinking. *Psychiatry Research*, *5*(3), 243-246. http://dx.doi.org/10.1016/0165-1781(81)90070-6

Karson, C. N., Lewitt, P. A., Calne, D. B., & Wyatt, R. J. (1982). Blink rates in parkinsonism. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, *12*(6), 580-583. http://dx.doi.org/10.1002/ana.410120614

Katidioti, I., Borst, J. P., & Taatgen, N. A. (2014). What happens when we switch tasks: Pupil dilation in multitasking. *Journal of Experimental Psychology: Applied*, *20*(4), 380-396. http://dx.doi.org/10.1037/xap0000031

Katnani, H. A., Van Opstal, A., & Gandhi, N. J. (2012). Blink perturbation effects on saccades evoked by microstimulation of the superior colliculus. *PLoS One*, *7*(12), e51843. http://dx.doi.org/10.1371/journal.pone.0051843

Kleiner, M., Brainard, D., & Pelli, D. (2007). What's new in Psychtoolbox-3?

Kobald, S. O., Wascher, E., Heppner, H., & Getzmann, S. (2019). Eye blinks are related to auditory information processing: evidence from a complex speech perception task. *Psychological Research*, *83*(6), 1281-1291. http://dx.doi.org/10.1007/s00426-017-0952-9

Kowler, E. (1991). The stability of gaze and its implications for vision. In R. H. S. Carpenter (Ed.), *Eye Movements* (Vol. 9 of Vision and visual dysfunction, pp. 71-92): New York: Macmillan.

Ladefoged, P., & Maddieson, I. (1996). *The sounds of the world's languages*. Oxford, OX, UK: Blackwell Publishers.

Laeng, B., Ørbo, M., Holmlund, T., & Miozzo, M. (2011). Pupillary stroop effects. *Cognitive Processing*, *12*(1), 13-21. http://dx.doi.org/10.1007/s10339-010-0370-z

Laeng, B., Sirois, S., & Gredebäck, G. (2012). Pupillometry: A window to the preconscious? *Perspectives on Psychological Science*, *7*(1), 18-27. http://dx.doi.org/10.1177/1745691611427305

Lim, I., van Wegen, E., de Goede, C., Deutekom, M., Nieuwboer, A., Willems, A., . . . Kwakkel, G. (2005). Effects of external rhythmical cueing on gait in patients with Parkinson's disease: a systematic review. *Clinical Rehabilitation*, *19*(7), 695-713. http://dx.doi.org/10.1191/0269215505cr906oa

Liu, C. C., Ghosh Hajra, S., Cheung, T. P., Song, X., & D'Arcy, R. C. (2017). Spontaneous blinks activate the precuneus: characterizing blink-related oscillations using magnetoencephalography. *Frontiers in Human Neuroscience*, *11*(489). https://doi.org/10.3389/fnhum.2017.00489

Liu, C. C., Hajra, S. G., Pawlowski, G., Fickling, S. D., Song, X., & D’Arcy, R. C. (2020). Differential neural processing of spontaneous blinking under visual and auditory sensory environments: An EEG investigation of blink-related oscillations. *NeuroImage*, *218*, 116879. https://doi.org/10.1016/j.neuroimage.2020.116879

Liu, C. C., Hajra, S. G., Song, X., Doesburg, S. M., Cheung, T. P., & D'Arcy, R. C. (2019). Cognitive loading via mental arithmetic modulates effects of blink-related oscillations on precuneus and ventral attention network regions. *Human Brain Mapping*, *40*(2), 377-393. http://dx.doi.org/10.1002/hbm.24378

Lynn, R. (1966). *Attention, Arousal and the Orienting Reaction*. Oxford, UK: Pergamon Press.

Manning, K. A., Riggs, L. A., & Komenda, J. K. (1983). Reflex eyeblinks and visual suppression. *Perception & Psychophysics*, *34*(3), 250-256. http://dx.doi.org/10.3758/BF03202953

Mathôt, S. (2018). Pupillometry: Psychology, physiology, and function. *Journal of Cognition*, *1*(1), 1-16. http://dx.doi.org/10.5334/joc.18

Maus, G. W., Duyck, M., Lisi, M., Collins, T., Whitney, D., & Cavanagh, P. (2017). Target displacements during eye blinks trigger automatic recalibration of gaze direction. *Current Biology*, *27*(3), 445-450. http://dx.doi.org/10.1016/j.cub.2016.12.029

McAuley, J., Farmer, S., Rothwell, J., & Marsden, C. (1999). Common 3 and 10 Hz oscillations modulate human eye and finger movements while they simultaneously track a visual target. *The Journal of Physiology*, *515*(3), 905-917. http://dx.doi.org/10.1111/j.1469-7793.1999.905ab.x

McCullagh, J., Weihing, J., & Musiek, F. (2009). Comparisons of P300s from standard oddball and omitted paradigms: implications to exogenous/endogenous contributions. *Journal of the American Academy of Audiology*, *20*(3). http://dx.doi.org/10.3766/jaaa.20.3.5

Morasso, P., Bizzi, E., & Dichgans, J. (1973). Adjustment of saccade characteristics during head movements. *Experimental Brain Research*, *16*(5), 492-500. http://dx.doi.org/10.1007/BF00234475

Moresi, S., Adam, J. J., Rijcken, J., Van Gerven, P. W., Kuipers, H., & Jolles, J. (2008). Pupil dilation in response preparation. *International Journal of Psychophysiology*, *67*(2), 124-130. http://dx.doi.org/10.1016/j.ijpsycho.2007.10.011

Mulckhuyse, M., van Zoest, W., & Theeuwes, J. (2008). Capture of the eyes by relevant and irrelevant onsets. *Experimental Brain Research*, *186*(2), 225-235. http://dx.doi.org/10.1007/s00221-007-1226-3

Nakano, T., Kato, M., Morito, Y., Itoi, S., & Kitazawa, S. (2013). Blink-related momentary activation of the default mode network while viewing videos. *Proceedings of the National Academy of Sciences*, *110*(2), 702-706. http://dx.doi.org/10.1073/pnas.1214804110

Nakano, T., & Kitazawa, S. (2010). Eyeblink entrainment at breakpoints of speech. *Experimental Brain Research*, *205*(4), 577-581. http://dx.doi.org/10.1007/s00221-010-2387-z

Nakano, T., Yamamoto, Y., Kitajo, K., Takahashi, T., & Kitazawa, S. (2009). Synchronization of spontaneous eyeblinks while viewing video stories. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1673), 3635-3644. http://dx.doi.org/10.1098/rspb.2009.0828

Nakatani, H., Orlandi, N., & van Leeuwen, C. (2011). Precisely timed oculomotor and parietal EEG activity in perceptual switching. *Cognitive Neurodynamics*, *5*(4), 399-409. http://dx.doi.org/10.1007/s11571-011-9168-7

Necker, L. A. (1832). LXI. Observations on some remarkable optical phænomena seen in Switzerland; and on an optical phænomenon which occurs on viewing a figure of a crystal or geometrical solid. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, *1*(5), 329-337. http://dx.doi.org/10.1080/14786443208647909

Nissens, T., & Fiehler, K. (2018). Saccades and reaches curve away from the other effector's target in simultaneous eye and hand movements. *Journal of Neurophysiology*, *119*(1), 118-123. http://dx.doi.org/10.1152/jn.00618.2017

Norn, M. (1969). Desiccation of the precorneal film: I. Corneal Wetting-Time. *Acta Ophthalmologica*, *47*(4), 865-880. http://dx.doi.org/10.1111/j.1755-3768.1969.tb03711.x

O'Shea, H., & Moran, A. (2016). Chronometric and pupil-size measurements illuminate the relationship between motor execution and motor imagery in expert pianists. *Psychology of Music*, *44*(6), 1289-1303. http://dx.doi.org/10.1177/0305735615616286

Ochoa, C. J., & Polich, J. (2000). P300 and blink instructions. *Clinical Neurophysiology*, *111*(1), 93-98. http://dx.doi.org/10.1016/S1388-2457(99)00209-6

Oh, J., Han, M., Peterson, B. S., & Jeong, J. (2012). Spontaneous eyeblinks are correlated with responses during the Stroop task. *PLoS One*, *7*(4), e34871. http://dx.doi.org/10.1371/journal.pone.0034871

Oh, J., Jeong, S.-Y., & Jeong, J. (2012). The timing and temporal patterns of eye blinking are dynamically modulated by attention. *Human Movement Science*, *31*(6), 1353-1365. http://dx.doi.org/10.1016/j.humov.2012.06.003

Ohl, S., Wohltat, C., Kliegl, R., Pollatos, O., & Engbert, R. (2016). Microsaccades are coupled to heartbeat. *Journal of Neuroscience*, *36*(4), 1237-1241. http://dx.doi.org/10.1523/JNEUROSCI.2211-15.2016

Otero-Millan, J., Macknik, S. L., & Martinez-Conde, S. (2012). Microsaccades and blinks trigger illusory rotation in the "rotating snakes" illusion. *Journal of Neuroscience*, *32*(17), 6043-6051. http://dx.doi.org/10.1523/JNEUROSCI.5823-11.2012

Otero-Millan, J., Troncoso, X. G., Macknik, S. L., Serrano-Pedraza, I., & Martinez-Conde, S. (2008). Saccades and microsaccades during visual fixation, exploration, and search: foundations for a common saccadic generator. *Journal of Vision*, *8*(14), 1-18. https://doi.org/10.1167/8.14.21

Park, H.-D., Barnoud, C., Trang, H., Kannape, O. A., Schaller, K., & Blanke, O. (2020). Breathing is coupled with voluntary action and the cortical readiness potential. *Nature Communications*, *11*(1), 1-8. http://dx.doi.org/10.1038/s41467-019-13967-9

Park, H.-D., Correia, S., Ducorps, A., & Tallon-Baudry, C. (2014). Spontaneous fluctuations in neural responses to heartbeats predict visual detection. *Nature Neuroscience*, *17*(4), 612-618. http://dx.doi.org/10.1038/nn.3671

Pazo-Alvarez, P., Cadaveira, F., & Amenedo, E. (2003). MMN in the visual modality: a review. *Biological Psychology*, *63*(3), 199-236. http://dx.doi.org/10.1016/S0301-0511(03)00049-8

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*(4), 437-442. http://dx.doi.org/10.1163/156856897X00366

Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, *60*(4), 389-443. http://dx.doi.org/10.1093/brain/60.4.389

Perrett, S., & Noble, W. (1997). The effect of head rotations on vertical plane sound localization. *The Journal of the Acoustical Society of America*, *102*(4), 2325-2332. https://doi.org/10.1121/1.419642

Peterson, D. A., & Sejnowski, T. J. (2017). A dynamic circuit hypothesis for the pathogenesis of blepharospasm. *Frontiers in Computational Neuroscience*, *11*(11). http://dx.doi.org/10.3389/fncom.2017.00011

Pieczykolan, A., & Huestegge, L. (2014). Oculomotor dominance in multitasking: Mechanisms of conflict resolution in cross-modal action. *Journal of Vision*, *14*(13), 1-17. http://dx.doi.org/10.1167/14.13.18

Pivik, R., & Dykman, R. (2004). Endogenous eye blinks in preadolescents: relationship to information processing and performance. *Biological Psychology, 66*(3), 191-219. http://dx.doi.org/10.1016/j.biopsycho.2003.10.005

Ponder, E., & Kennedy, W. (1927). On the act of blinking. *Quarterly journal of experimental physiology: Translation and integration*, *18*(2), 89-110. http://dx.doi.org/10.1113/expphysiol.1927.sp000433

Privitera, C. M., Renninger, L. W., Carney, T., Klein, S., & Aguilar, M. (2008). *The pupil dilation response to visual detection.* Paper presented at the Human Vision and Electronic Imaging XIII. http://dx.doi.org/10.1117/12.772844

Rambold, H., El Baz, I., & Helmchen, C. (2005). Blink effects on ongoing smooth pursuit eye movements in humans. *Experimental Brain Research*, *161*(1), 11-26. http://dx.doi.org/10.1007/s00221-004-2040-9

Ramig, L. A. (1983). Effects of physiological aging on speaking and reading rates. *Journal of Communication Disorders*, *16*(3), 217-226. http://dx.doi.org/10.1016/0021-9924(83)90035-7

Recarte, M. Á., Pérez, E., Conchillo, Á., & Nunes, L. M. (2008). Mental workload and visual impairment: Differences between pupil, blink, and subjective rating. *The Spanish Journal of Psychology*, *11*(2), 374-385. http://dx.doi.org/10.1017/S1138741600004406

Richer, F., & Beatty, J. (1985). Pupillary dilations in movement preparation and execution. *Psychophysiology*, *22*(2), 204-207. http://dx.doi.org/10.1111/j.1469-8986.1985.tb01587.x

Ridder III, W. H., & Tomlinson, A. (1993). Suppression of contrast sensitivity during eyelid blinks. *Vision Research*, *33*(13), 1795-1802. http://dx.doi.org/10.1016/0042-6989(93)90170-2

Ridder III, W. H., & Tomlinson, A. (1997). A comparison of saccadic and blink suppression in normal observers. *Vision Research*, *37*(22), 3171-3179. https://doi.org/10.1016/S0042-6989(97)00110-7

Riggs, L. A., Volkmann, F. C., & Moore, R. K. (1981). Suppression of the blackout due to blinks. *Vision Research*, *21*(7), 1075-1079. http://dx.doi.org/10.1016/0042-6989(81)90012-2

Rolfs, M. (2009). Microsaccades: small steps on a long way. *Vision Research*, *49*(20), 2415-2441. http://dx.doi.org/10.1016/j.visres.2009.08.010

Rosenfield, M., Jahan, S., Nunez, K., & Chan, K. (2015). Cognitive demand, digital screens and blink rate. *Computers in Human Behavior*, *51*, 403-406. http://dx.doi.org/10.1016/j.chb.2015.04.073

Rozado, D., Duenser, A., & Howell, B. (2015). Improving the performance of an EEG-based motor imagery brain computer interface using task evoked changes in pupil diameter. *PloS one*, *10*(3), e0121262. http://dx.doi.org/10.1371/journal.pone.0121262

Sanders, R. D. (2010). The trigeminal (V) and facial (VII) cranial nerves: head and face sensation and movement. *Psychiatry (Edgmont)*, *7*(1), 13. Retrieved from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC2848459/

Schicatano, E. J., Peshori, K. R., Gopalaswamy, R., Sahay, E., & Evinger, C. (2000). Reflex excitability regulates prepulse inhibition. *Journal of Neuroscience*, *20*(11), 4240-4247. http://dx.doi.org/10.1523/JNEUROSCI.20-11-04240.2000

Schmidt-Kassow, M., Heinemann, L. V., Abel, C., & Kaiser, J. (2013). Auditory–motor synchronization facilitates attention allocation. *Neuroimage*, *82*, 101-106. http://dx.doi.org/10.1016/j.neuroimage.2013.05.111

Sescousse, G., Ligneul, R., van Holst, R. J., Janssen, L. K., de Boer, F., Janssen, M., . . . Cools, R. (2018). Spontaneous eye blink rate and dopamine synthesis capacity: preliminary evidence for an absence of positive correlation. *European Journal of Neuroscience*, *47*(9), 1081-1086. http://dx.doi.org/10.1111/ejn.13895

Siegle, G. J., Ichikawa, N., & Steinhauer, S. (2008). Blink before and after you think: Blinks occur prior to and following cognitive load indexed by pupillary responses. *Psychophysiology*, *45*(5), 679-687. http://dx.doi.org/10.1111/j.1469-8986.2008.00681.x

Simon, J. R., & Rudell, A. P. (1967). Auditory SR compatibility: the effect of an irrelevant cue on information processing. *Journal of Applied Psychology*, *51*(3), 300-304. https://doi.org/10.1037/h0020586

Sirevaag, E. J., Rohrbaugh, J. W., Stern, J. A., Vedeniapin, A. B., Packingham, K. D., & LaJonchere, C. M. (1999). Multi-dimensional characterizations of operator state: A validation of oculomotor metrics. (Publication No. DOT/FAA/AM-99/28. Washington, DC: Office of Aviation Medicine). Retrieved from https://rosap.ntl.bts.gov/view/dot/57915

Smit, A. E., Buisseret, P., Buisseret-Delmas, C., De Zeeuw, C. I., VanderWerf, F., & Zerari-Mailly, F. (2006). Reticulo-collicular and spino-collicular projections involved in eye and eyelid movements during the blink reflex. *Neuroscience Research*, *56*(4), 363-371. https://doi.org/10.1016/j.neures.2006.08.005

Smith, A. (1992). The control of orofacial movements in speech. *Critical Reviews in Oral Biology & Medicine*, *3*(3), 233-267. http://dx.doi.org/10.1177/10454411920030030401s

Sokolov, E. N. (1963). Higher nervous functions: The orienting reflex. *Annual Review of Physiology*, *25*(1), 545-580. http://dx.doi.org/10.1146/annurev.ph.25.030163.002553

Squires, N. K., Squires, K. C., & Hillyard, S. A. (1975). Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*, *38*(4), 387-401. http://dx.doi.org/10.1016/0013-4694(75)90263-1s

Stahl, J. S. (1999). Amplitude of human head movements associated with horizontal saccades. *Experimental Brain Research*, *126*(1), 41-54. http://dx.doi.org/10.1007/s002210050715

Stapleton, J., & Halgren, E. (1987). Endogenous potentials evoked in simple cognitive tasks: depth components and task correlates. *Electroencephalography and Clinical Neurophysiology*, *67*(1), 44-52. http://dx.doi.org/10.1016/0013-4694(87)90162-3

Stern, J. A., Boyer, D., & Schroeder, D. (1994). Blink rate: a possible measure of fatigue. *Human Factors*, *36*(2), 285-297. http://dx.doi.org/10.1177/001872089403600209

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*(6), 643-662. http://dx.doi.org/10.1037/h0054651s

Sun, W. S., Baker, R. S., Chuke, J. C., Rouholiman, B. R., Hasan, S. A., Gaza, W., . . . Porter, J. D. (1997). Age-related changes in human blinks. Passive and active changes in eyelid kinematics. *Investigative Ophthalmology & Visual Science*, *38*(1), 92-99. Retrieved from https://iovs.arvojournals.org/article.aspx?articleid=2161462

Sutton, S., Braren, M., Zubin, J., & John, E. (1965). Evoked-potential correlates of stimulus uncertainty. *Science*, *150*(3700), 1187-1188. http://dx.doi.org/10.1126/science.150.3700.1187

Sveinbjornsdottir, S. (2016). The clinical symptoms of Parkinson's disease. *Journal of Neurochemistry*, *139*, 318-324. http://dx.doi.org/10.1111/jnc.13691

Szabadi, E. (2012). Modulation of physiological reflexes by pain: role of the locus coeruleus. *Frontiers in Integrative Neuroscience*, *6*(94). http://dx.doi.org/10.3389/fnint.2012.00094

Tada, H., Omori, Y., Hirokawa, K., Ohira, H., & Tomonaga, M. (2013). Eye-blink behaviors in 71 species of primates. *PloS one*, *8*(5), e66018. http://dx.doi.org/10.1371/journal.pone.0066018

Tanaka, Y., & Yamaoka, K. (1993). Blink activity and task difficulty. *Perceptual and Motor Skills*, *77*(1), 55-66. http://dx.doi.org/10.2466/pms.1993.77.1.55

Tervaniemi, M., Saarinen, J., Paavilainen, P., Danilova, N., & Näätänen, R. (1994). Temporal integration of auditory information in sensory memory as reflected by the mismatch negativity. *Biological Psychology*, *38*(2-3), 157-167. http://dx.doi.org/10.1016/0301-0511(94)90036-1

Tong, F., Meng, M., & Blake, R. (2006). Neural bases of binocular rivalry. *Trends in Cognitive Sciences*, *10*(11), 502-511. https://doi.org/10.1016/j.tics.2006.09.003

Valsecchi, M., Betta, E., & Turatto, M. (2007). Visual oddballs induce prolonged microsaccadic inhibition. *Experimental Brain Research*, *177*(2), 196-208. http://dx.doi.org/10.1007/s00221-006-0665-6

Valsecchi, M., & Turatto, M. (2009). Microsaccadic responses in a bimodal oddball task. *Psychological Research*, *73*(1), 23-33. http://dx.doi.org/10.1007/s00426-008-0142-x

van Dam, L. C., & van Ee, R. (2005). The role of (micro) saccades and blinks in perceptual bi-stability from slant rivalry. *Vision Research*, *45*(18), 2417-2435. http://dx.doi.org/10.1016/j.visres.2005.03.013

Van Opstal, F., De Loof, E., Verguts, T., & Cleeremans, A. (2016). Spontaneous eyeblinks during breaking continuous flash suppression are associated with increased detection times. *Journal of Vision*, *16*(14), 1-10. http://dx.doi.org/10.1167/16.14.21

Van Zoest, W., & Donk, M. (2006). Saccadic target selection as a function of time. *Spatial Vision*, *19*(1), 61-76. http://dx.doi.org/10.1163/156856806775009205

VanderWerf, F., Brassinga, P., Reits, D., Aramideh, M., & Ongerboer de Visser, B. (2003). Eyelid movements: behavioral studies of blinking in humans under different stimulus conditions. *Journal of Neurophysiology*, *89*(5), 2784-2796. http://dx.doi.org/10.1152/jn.00557.2002

Verleger, R. (1991). The instruction to refrain from blinking affects auditory P3 and N1 amplitudes. *Electroencephalography and Clinical Neurophysiology*, *78*(3), 240-251. http://dx.doi.org/10.1016/0013-4694(91)90039-7

Volkmann, F. C. (1986). Human visual suppression. *Vision Research*, *26*(9), 1401-1416. http://dx.doi.org/10.1016/0042-6989(86)90164-1

Volkmann, F. C., Riggs, L. A., Ellicott, A. G., & Moore, R. K. (1982). Measurements of visual suppression during opening, closing and blinking of the eyes. *Vision Research*, *22*(8), 991-996. http://dx.doi.org/10.1016/0042-6989(82)90035-9

Volkmann, F. C., Riggs, L. A., & Moore, R. K. (1980). Eyeblinks and visual suppression. *Science*, *207*(4433), 900-902. http://dx.doi.org/10.1126/science.7355270

von Cramon, D., & Schuri, U. (1980). Blink frequency and speech motor activity. *Neuropsychologia*, *18*(4-5), 603-606. http://dx.doi.org/10.1016/0028-3932(80)90164-5

Von Cranach, M., Schmid, R., & Vogel, M. (1969). Über einige bedingungen des zusammenhanges von lidschlag und blickwendung. *Psychologische Forschung*, *33*(1), 68-78. http://dx.doi.org/10.1007/BF00424617

Wang, C.-A., & Munoz, D. P. (2015). A circuit for pupil orienting responses: implications for cognitive modulation of pupil size. *Current opinion in neurobiology, 33*, 134-140. http://dx.doi.org/10.1016/j.conb.2015.03.018

Wascher, E., Heppner, H., Möckel, T., Kobald, S. O., & Getzmann, S. (2015). Eye-blinks in choice response tasks uncover hidden aspects of information processing. *EXCLI journal, 14*, 1207-1218. http://dx.doi.org/10.17179/excli2015-696

Weiss, M. W., Trehub, S. E., Schellenberg, E. G., & Habashi, P. (2016). Pupils dilate for vocal or familiar music. *Journal of Experimental Psychology: Human Perception and Performance*, *42*(8), 1061-1065. http://dx.doi.org/10.1037/xhp0000226

Widmann, A., Engbert, R., & Schröger, E. (2014). Microsaccadic responses indicate fast categorization of sounds: a novel approach to study auditory cognition. *Journal of Neuroscience*, *34*(33), 11152-11158. http://dx.doi.org/10.1523/JNEUROSCI.1568-14.2014

Wood, J. G., & Hassett, J. (1983). Eyeblinking during problem solving: the effect of problem difficulty and internally vs externally directed attention. *Psychophysiology*, *20*(1), 18-20. http://dx.doi.org/10.1111/j.1469-8986.1983.tb00893.x

Zénon, A., Sidibé, M., & Olivier, E. (2014). Pupil size variations correlate with physical effort perception. *Frontiers in Behavioral Neuroscience*, *8*(286). https://doi.org/10.3389/fnbeh.2014.00286

APPENDIX

A. CURRICULUM VITAE

B. ACKNOWLEDGEMENTS

An dieser Stelle möchte ich mich zunächst herzlich bei meiner Erstbetreuerin Dr. Barbara Händel für die wissenschaftliche Unterstützung bedanken, ohne die diese Arbeit nicht möglich gewesen wäre. Ich bin sehr dankbar für ihr kompetentes Feedback, ihre Vorschläge und ihre Hilfe bei Fragen und Problemen während meiner gesamten Promotion. Auch eine globale Pandemie konnte uns nicht aufhalten Forschung auf hoher Qualität durchzuführen.

Daneben gilt mein Dank meinen weiteren Betreuern Prof. Dr. Wilfried Kunde und PD Dr. Robert Blum, sowie Prof. Dr. Lynn Huestegge, die mich mit Expertise und Ratschlägen durch die Zeit meiner Forschungsarbeit begleitet haben. Ich danke auch meiner Forschungsgruppe, besonders Supriya Murali, für die anregenden Diskussionen und den wissenschaftlichen Austausch. Ein riesiger Dank geht auch an meine Kolleginnen und Kollegen am Lehrstuhl III für den wissenschaftlichen Rat, ermutigende Worte, stärkende Mittagspausen und bereichernde Konferenzerfahrungen.

Schließlich möchte ich gerne meinen Eltern Birgit und Roland sowie meiner Schwester Annika danken, die mir den notwendigen Halt gegeben haben, immer an mich geglaubt haben und mich ermutigt haben Herausforderungen anzunehmen und meine Ziele zu erreichen.

C. STATEMENT OF INDIVIDUAL AUTHOR CONTRIBUTIONS

Publication (complete reference): Brych, M., & Händel, B. (2020). Disentangling top-down and bottom-up influences on blinks in the visual and auditory domain. *International Journal of Psychophysiology*, 158, 400-410. https://doi.org/10.1016/j.ijpsycho.2020.11.002

Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	MB	BH			
Data Collection	MB				
Data Analysis and Interpretation	MB	BH			
Manuscript Writing					
Writing of Introduction	MB	BH			
Writing of Materials & Methods	MB	BH			
Writing of Discussion	MB	BH			
Writing of First Draft	MB				

Publication (complete reference): Brych M., Murali S., & Händel B. (2021) How the motor aspect of speaking influences the blink rate. *PLoS ONE*, 16(10): e0258322. https://doi.org/10.1371/journal.pone.0258322

Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	MB SM BH				
Data Collection	MB	SM			
Data Analysis and Interpretation	MB	BH	SM		
Manuscript Writing					
Writing of Introduction	MB	BH	SM		
Writing of Materials & Methods	MB	BH			

Writing of Discussion	MB	BH			
Writing of First Draft	MB				

Publication (complete reference): Brych, M., Händel, B. F., Riechelmann, E., Pieczykolan, A., & Huestegge, L. (2020). Effects of vocal demands on pupil dilation. *Psychophysiology*, 58(2): e13729. https://doi.org/10.1111/psyp.13729

Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	MB ER LH BH	AP			
Data Collection	MB	ER	AP		
Data Analysis and Interpretation	MB	BH	LH	ER AP	
Manuscript Writing					
Writing of Introduction	LH	MB	BH		
Writing of Materials & Methods	MB	BH	LH		
Writing of Discussion	BH	MB	LH		
Writing of First Draft	MB	LH	BH		
Supplementary Material	MB	BH LH			

Publication (complete reference): Brych, M.*, Murali, S.*, & Haendel, B. (2021). The influence of eye movements and their retinal consequences on bistable motion perception. *Frontiers in Psychology, 12:*647256. https://doi.org/10.3389/fpsyg.2021.647256
*shared first authorship

Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	MB SM BH				
Data Collection	MB	SM			
Data Analysis and Interpretation	MB SM	BH			

Manuscript Writing					
Writing of Introduction	SM	BH			
Writing of Materials & Methods	MB	BH			
Writing of Discussion	SM	BH			
Writing of First Draft	MB SM	BH			

Explanations (if applicable): This publication is not included in its full form in this dissertation

The doctoral researcher confirms that she has obtained permission from both the publishers and the co-authors for legal second publication.

The doctoral researcher and the primary supervisor confirm the correctness of the above mentioned assessment.

Mareike Brych 12.10.2021 Würzburg

Doctoral Researcher’s Name Date Place Signature

Barbara Händel 12.10.2021 Würzburg

Primary Supervisor’s Name Date Place Signature

D. AFFIDAVIT (EIDESSTATTLICHE ERKLÄRUNG)

I hereby confirm that my thesis entitled

"HOW MOVEMENTS AND COGNITION INTERACT: AN INVESTIGATION OF SPONTANEOUS BLINKS"

is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

Place, Date

Signature

Hiermit erkläre ich an Eides statt, die Dissertation

„WIE BEWEGUNG UND KOGNITION INTERAGIEREN: EINE UNTERSUCHUNG SPONTANER LIDSCHLÄGE"

eigenständig, d.h. insbesondere selbstständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

Ich erkläre außerdem, dass die Dissertation weder in gleicher noch in ähnlicher Form bereits in einem anderen Prüfungsverfahren vorgelegen hat.

Ort, Datum

Unterschrift