Understanding the function of spontaneous blinks by investigating internally and externally directed processes

Eine Untersuchung zur Funktion spontaner Lidschläge durch die Differenzierung von extern und intern gerichteten Prozessen

Doctoral thesis for a doctoral degree

at the Graduate School of Life Sciences,

Julius-Maximilians-Universität Würzburg,

Section Neuroscience

submitted by

Supriya Murali

from

New Delhi, India

Würzburg, 2022

Submitted on: ……..

Office stamp

Members of the Thesis Committee

Chairperson: Prof. Dr. Thomas Dandekar

Primary Supervisor: Dr. Barbara Händel

Supervisor (Second): Prof. Dr. Wilfried Kunde

Supervisor (Third): Prof. Dr. Charlotte Förster

Date of Public Defence: ……

Date of Receipt of Certificates: ……..

List of publications

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

1) Murali, S., & Händel, B. (2021). The latency of spontaneous eye blinks marks relevant visual and auditory information processing. Journal of Vision, 21(6), 7-7.
2) Brych, M., Murali, S., & Händel, B. (2021). The role of blinks, microsaccades and their retinal consequences in bistable motion perception. Frontiers in psychology, 12.
3) Murali, S., & Händel, B. (2022). Motor restrictions impair divergent thinking during walking and during sitting. Psychological research, 1-14.

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

Parts of this thesis contain the following unpublished manuscripts:

4) Murali, S., & Händel, B. (in preparation) Spontaneous eye blinks modulate the probability of a perceptual reinterpretation during visual and auditory ambiguity *shared first authorship
5) Murali, S., Agayby B., Schmid, M., & Händel, B. (in preparation). Qualitative difference in blink related modulation of V1 activity for different processing states.

The publications listed above have been used with permission from the co-authors.

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

Summary

Humans spontaneously blink several times a minute. These blinks are strongly modulated during various cognitive task. However, the precise function of blinking and the reason for their modulation has not been fully understood. In the present work, I investigated the function of spontaneous blinks through various perceptual and cognitive tasks. Previous research has revealed that blinks rates decrease during some tasks but increase during others. When trying to understand these seemingly contradictory results, I observed that blink reduction occurs when one engages with an external input. For instance, a decrease has been observed due to the onset of a stimulus, sensory input processing and attention towards sensory input. However, for activities that do not involve such an engagement, e.g. imagination, daydreaming or creativity, the blink rate has been shown to increase. To follow up on the proposed hypothesis, I distinguished tasks that involve the processing of an external stimulus and tasks that involve disengagement.

In the first part of the project, I explored blinking during stimulus engagement. If the probability of blinking is low when engaging with the stimulus, then one should find a reduction in blinks specifically during the time period of processing but not during sensory input per se. To this end, in study 1, I tested the influence of task-relevant information duration on blink timing and additionally manipulated the overall sensory input using a visual and an auditory temporal simultaneity judgement task. The results showed that blinks were suppressed longer for longer periods of relevant information or in other words, blinks occurred at the end of relevant information processing for both the visual and the auditory modality. Since relevance is mediated through top-down processes, I argue that the reduction in blinks is a top-down driven suppression. In studies 2 and 3, I again investigated stimulus

processing, but in this case, processing was triggered internally and not based on specific changes in the external input. To this end, I used bistable stimuli, in which the actual physical stimulus remains constant but their perception switches between different interpretations. Studies on the involvement of attention in such bistable perceptual changes indicate that the sensory input is reprocessed before the perceptual switch. The results revealed a reduction in eye blink rates before the report of perceptual switches. Importantly, I was able to decipher that the decrease was not caused by the perceptual switch or the behavioral response but likely started before the internal switch. Additionally, periods between a blink and a switch were longer than interblink intervals, indicating that blinks were followed by a period of stable percept. To conclude, the first part of the project revealed that there is a top-down driven blink suppression during the processing of an external stimulus.

In the second part of the project, I extended the idea of blinks marking the disengagement from external processing and tested if blinking is associated with better performance during internally directed processes. Specifically, I investigated divergent thinking, an aspect of creativity, and the link between performance and blink rates as well as the effect of motor restriction. While I could show that motor restriction was the main factor influencing divergent thinking, the relationship between eye blink rates and creative output also depended on restriction. Results showed that higher blink rates were associated with better performance during free movement, but only between subjects. In other words, subjects who had overall higher blink rates scored better in the task, but when they were allowed to sit or walk freely. Within a single subject, trial with higher blink rates were not associated with better performance. Therefore, possibly, people who are able to disengage easily, as indicated by an overall high blink rate, perform better in divergent thinking tasks. However, the link between blink rate and internal tasks is not clear at this point. Indeed, a

more complex measurement of blink behavior might be necessary to understand the relationship.

In the final part of the project, I aimed to further understand the function of blinks through their neural correlates. I extracted the blink-related neural activity in the primary visual cortex (V1) of existing recordings of three rhesus monkeys during different sensory processing states. I analyzed spike related multi-unit responses, frequency dependent power changes, local field potentials and laminar distribution of activity while the animal watched a movie compared to when it was shown a blank screen. The results showed a difference in blink-related neural activity dependent on the processing state. This difference suggests a state dependent function of blinks.

Taken altogether, the work presented in this thesis suggests that eye blinks have an important function during cognitive and perceptual processes. Blinks seem to facilitate a disengagement from the external world and are therefore suppressed during intended processing of external stimuli.

Zusammenfassung

Menschen blinzeln spontan mehrmals pro Minute. Während verschiedener kognitiver Aufgaben ist die Häufigkeit dieser Lidschläge sehr unterschiedlich. Jedoch ist die genaue Funktion des spontanen Lidschlags und der Grund für deren Modulation noch nicht vollständig verstanden. In der vorliegenden Arbeit habe ich die Funktion des spontanen Lidschlags durch verschiedene Aufgaben im Bereich der Wahrnehmung und Kognition untersucht. Frühere Studien haben gezeigt, dass die Häufigkeit der Lidschläge bei einigen Aufgaben abnimmt, bei anderen jedoch zunimmt. Bei der Prüfung dieser scheinbar widersprüchlichen Ergebnisse beobachtete ich, dass die Reduzierung der Lidschlaghäufigkeit scheinbar immer bei der Beschäftigung mit externem Input auftritt. Zum Beispiel wurde eine Abnahme aufgrund des Beginns eines sensorischen Reizes, der Verarbeitung sensorischen Inputs und von Aufmerksamkeit auf sensorischen Input beschrieben. Für Aktivitäten ohne solch externes Engagement, z.B. Fantasie, Tagträume oder Kreativität, nimmt die Häufigkeit der Lidschläge zu. Um die vorgeschlagene Hypothese zu überprüfen, untersuchte ich explizit solche Aufgaben mit Verarbeitung eines externen Reizes und solchen mit einer Abgrenzung von externem Input.

Im ersten Teil des Projekts untersuchte ich die Lidschläge während der Präsentation von externen Reizen. Falls die Wahrscheinlichkeit der Lidschläge an eine Reizverarbeitung gekoppelt ist, sollte man eine Verringerung der Lidschläge während des Verarbeitungszeitraums feststellen aber nicht während sensorischen Inputs an sich. Zu diesem Zweck habe ich in Studie 1 den Einfluss der aufgabenrelevanten Informationsdauer unabhängig vom gesamten sensorischen Input auf den Zeitpunkt des Lidschlags getestet. Dies geschah mit einer visuellen und einer auditiven Aufgabe zur zeitlichen

Gleichzeitigkeitsbeurteilung. Die Ergebnisse zeigten, dass Lidschläge während Zeitfenster mit relevanten Informationen unterdrückt wurden, oder anders gesagt, Lidschläge traten am Ende der Informationsverarbeitung sowohl in der visuellen als auch auditorischen Modalität auf. Weil Relevanz durch Top-Down-Prozesse vermittelt wird, behaupte ich, dass die Verringerung der Lidschläge eine Top-Down-gesteuerte Unterdrückung ist. In den Studien 2 und 3 habe ich die Reizverarbeitung erneut untersucht, aber jetzt wurde die Verarbeitung intern ausgelöst und nicht auf Basis von spezifischen Änderungen im externen Input. Dazu habe ich bistabile Reize verwendet, bei denen der physikalische Reiz selber konstant bleibt, aber die Wahrnehmung zwischen verschiedenen Interpretationen wechselt. Studien über die Rolle der Aufmerksamkeit bei bistabilen Wahrnehmungsveränderungen zeigen, dass der sensorische Input vor dem Wahrnehmungswechsel erneut verarbeitet wird. Die Ergebnisse deckten eine Verringerung in der Häufigkeit der Lidschläge vor der Mitteilung über Wahrnehmungswechsel auf. Eine wichtige Erkenntnis hierbei war, dass diese Verringerung nicht durch den Wahrnehmungswechsel oder die Verhaltensreaktion verursacht wurde, sondern mit großer Wahrscheinlichkeit schon vor dem internen Wechsel anfing. Außerdem waren die Perioden zwischen einem Lidschlag und einem Wahrnehmungswechsel länger als die Intervalle zwischen den Lidschlägen, was darauf hinweist, dass einem Lidschlag eine Zeit stabiler Wahrnehmung folgt. Zusammenfassend zeigte der erste Teil des Projekts die Existenz einer Top-Down-gesteuerten Lidschlag-Unterdrückung während der Verarbeitung eines externen Stimulus.

Die Idee dass Lidschläge eine Abgrenzung von der Verarbeitung externer Signale markieren habe ich im zweiten Teil des Projekts erweitert und getestet, ob blinzeln mit einer besseren Leistung während intern gesteuerter Prozesse verbunden ist. Insbesondere untersuchte ich divergentes Denken, ein Aspekt der Kreativität, und den Zusammenhang

zwischen kreativer Leistung und Häufigkeit der Lidschläge sowie die Wirkung von motorischer Einschränkung. Ich konnte den Einfluss von motorischer Einschränkung auf divergentes Denken aufzeigen, jedoch auch dass die Beziehung zwischen Häufigkeit der Lidschläge und kreativem Output von der motorischen Einschränkung abhängig ist. Die Ergebnisse zeigten eine Verbindung zwischen höherer Lidschlaghäufigkeit und besseren Leistung bei freier Bewegung, jedoch nur innerhalb der Gruppe. Anders gesagt, Probanden mit insgesamt höherer Häufigkeit der Lidschläge erzielten bei der Aufgabe besser Resultate, aber nur wenn sie sich frei bewegen durften. Innerhalb eines Probanden waren Versuche mit höherer Häufigkeit der Lidschläge nicht mit einer besseren Leistung verbunden. Eine mögliche Interpretation ist, dass Menschen die sich insgesamt leichter von sensorischem Input abgrenzen, was möglicherweise durch eine insgesamt hohe Häufigkeit der Lidschläge angezeigt wird, bei divergenten Denkaufgaben besser abschneiden. Allerdings ist der Zusammenhang zwischen Häufigkeit der Lidschläge und internen Aufgaben an dieser Stelle noch nicht klar. Tatsächlich könnte eine komplexere Messung des Lidschlagverhaltens notwendig sein, um die Beziehung zu verstehen.

Im letzten Teil des Projekts wollte ich die Funktion von Lidschlägen über ihre neuronalen Korrelate besser verstehen. Ich habe die lidschlagbezogene neuronale Aktivität im primären visuellen Kortex (V1) aus bestehenden Aufzeichnungen von drei Rhesusaffen bei verschiedenen Aufmerksamkeitsverarbeitungszuständen extrahiert. Die lidschlagbezogene Rate der Aktionspotentiale, die Multi-Unit-Aktivität, frequenzabhängige Aktivität, lokale Feldpotentiale und laminare Aktivitätsverteilung habe ich während zwei Versuchsbedingungen analysiert, das Anschauen eines Films und einer Pause vor einem leeren Bildschirm. Die Ergebnisse zeigten einen Unterschied in der lidschlagbezogenen neuronalen

Aktivität in Abhängigkeit von der Versuchsbedingung und somit dem Verarbeitungszustand. Dieser Unterschied deutet eine zustandsabhängige Funktion der Lidschläge an.

Insgesamt legt die in dieser Dissertation vorgestellte Arbeit nahe, dass Lidschläge eine wichtige Funktion in Kognition und Wahrnehmungsprozessen hat. Lidschläge scheinen eine Abgrenzung von der Außenwelt zu erleichtern und werden daher bei beabsichtigter Verarbeitung externer Reize unterdrückt.

Table of contents

Summary ..... **VII**
Zusammenfassung ..... **X**
1 Introduction **16**
1.1 Types of blinks 16
1.2 The modulation of spontaneous blinking 18
1.2.1 During externally focused attention 19
1.2.2 During internally focussed attention 25
1.3 Neural correlates of blinks 28
1.3.1 Neural pathway of blinks 28
1.3.2 Neural activity during blinks 30
1.4 Overview of the presented work 34
2. Study 1: The Latency of Spontaneous Eye Blinks Marks Relevant Visual and Auditory Information Processing **37**
2.1 Introduction 38
2.2 Methods 40
2.3 Analysis 45
2.4 Results 46
2.5 Discussion (Study 1) 57
2.6 Supplementary material (Study 1) 62
3. Study 2: The role of blinks, microsaccades and their retinal consequences in bistable motion perception **71**
3.1 Introduction (Study 2) 73
3.2 Methods 75
3.3 Data analyses (Experiment 1 and 2) 79
3.4 Results 81
3.5 Discussion (Study 2) 90
3.6 Supplementary Material (Study 2) 102
4. Study 3: Spontaneous eye blinks modulate the probability of a perceptual reinterpretation during visual and auditory ambiguity **108**
4.1 Introduction (Study 3) 109
4.2 Methods 112
4.3 Analysis 117
4.4 Results 118
4.5 Discussion (Study 3) 131
4.6 Supplementary Material (Study 3) 137
5. Study 4: Motor restrictions impair divergent thinking during walking and during sitting **140**
5.1 Introduction (Study 4) 141
5.2 Experiment 1 146

5.3 Experiment 2 154
5.4 Experiment 3 159
5.5 Discussion (Study 4) 165
5.6 Supplementary material (Study 4) 172
6. Study 5: Qualitative difference in blink related modulation of V1 activity for different attentive and stimulation states **177**
6.1 Introduction (Study 5) 178
6.2 Methods 182
6.3 Analysis 186
6.4 Results 187
6.5 Discussion (Study 5) 198
6.6 Supplementary material (Study 5) 208
7. General discussion 230
7.1 Summary of the results 230
7.2 Blinks are suppressed during stimulus processing 233
7.3 Blinks denote the end of external engagement and a possible shift towards internal consolidation 239
7.4 Blink-related neural activity in the sensory cortex 242
7.5 Why do humans blink so much? 244
7.6 General conclusion 244
8. References 246
9. Appendix 260
A. Curriculum vitae 260
B. Acknowledgement 261
C. Statement of individual author contributions 262
D. Affidavit (Eidesstattliche Erklärung) 269

1. General Introduction

Eye blinks are an integral part of our everyday behavior and are known to have an important physiological function, namely to moisten and protect the eyes. However, research indicates that this might be a rather narrow perspective when it comes to the purpose of blinking, since humans tend to blink more than would be necessary for moisturizing the eyes. Moreover, blinks are influenced by cognitive processes and demands, as will be carefully reviewed below. Despite the vast evidence of the link between cognition on blinking, the general consensus seems to be that this link is due to a simple correlation between cognition and blinking. A purpose of blinking has not been established. In this project, I strive to uncover a function of blinks by analyzing their modulation during tasks involving an external (stimulus-driven) or internal (sensory independent) focus of attention.

1.1 Types of eye blinks

There are three types of blinks: reflex, voluntary and spontaneous. While the main focus of my research is on spontaneous blinking I want to give a short overview of the distinguishing features of the different blink types. In the following sections, I will briefly describe each type of blink.

Reflexive blinking, also known as the corneal blink reflex, is involuntary blinking that occurs as a response to direct external stimuli. It is observed in all mammals (Pearce, 2008) and is part of the startle reflex (Davis, 1984; Ladd et al., 2000). It is elicited, for instance, when the cornea is stimulated; but can also be a part of the startle response to other types of stimulation without direct contact of the cornea; examples of such stimuli include bright lights or sudden sounds (Sterling, 2013), somatosensory stimulation of the face (Miwa et al., 1998), and also fear inducing stimuli (Balaban & Taussig, 1994; Hamm et al., 1997; Miwa et al., 1998).

There seems to be an evolutionary aspect in the function of these blinks: since they are an integral part of the startle reflex, they might play a role in protection from potential external threats (Sterling, 2013).

The blink reflex was first observed by Overend (1896), who noted that there was a twitch on the lower eye lid of both eyes when the skin on the forehead is tapped. The first detailed description on the reflex blink introduced by corneal stimulation was given by Kugelberg (1952). The neural network behind such a reflex blink consists of a loop between the trigeminal nerve (5th cranial nerve or V) and the facial nerve (7th cranial nerve or VII). During a reflex blink, a stimulus makes contact with the cornea and activates the sensory receptors, the sensory information is then carried to the spinal trigeminal nuclei within the brain stem via the tegmental nerve. The signal from the brain stem then projects to the facial nerve, which activates the orbicularis oculi muscle, thereby eliciting a blink. Apart from stimuli that directly introduce a blink, secondary factors or stimuli can elicit a blink reflex through conditioning via the condition reflex circuit of the cerebellum (Kim & Thompson, 1997; Pearce, 2008; Sterling, 2013).

Voluntary blinks are blinks that occur under conscious control when the individual is explicitly asked to blink. These blinks differ from other blinks in some aspects. For instance, there is an upwards movement of the eyeball, which is referred to as the Bell's phenomenon (Bell & Davy, 1823). This upward movement is specific to these blinks and not observed during reflexive blinking (Collewijn et al., 1985a). Although the underlying neural network is similar to reflex blinks, there is some evidence that they involve a slightly different pathway (van Koningsbruggen et al., 2012). This was indicated by studies on patients with apraxia of the eye, who show an intact reflex blink response, but are usually unable to blink when explicitly asked to do so (Colombo et al., 1982; Miwa et al., 2001). These studies found lesions in the frontal

and/or parietal lobe of the right hemisphere (Colombo et al., 1982) and lesions in the right cerebral artery affecting the supplementary motor area (Miwa et al., 2001) in such patients.

The third type of blink, which is the focus of my work, are **spontaneous blinks**, also known as endogenous blinks. They constitute most of the blinks that we make in our everyday lives, and occur with little or no conscious effort. Even though they are the most common type of blinks that humans generate, their function is not fully understood. They occur about approximately 10 to 15 times a minute (Burr, 2005; Doughty, 2001; Kaminer et al., 2011) and one main function is to maintain the corneal tear film and protect the eyes (Craig, 2002). However, their frequency is much higher than what would be required for maintaining the tear film (Kaminer et al., 2011; Zametkin et al., 1979). The time for the tear film of the eye to break up is above 10s and about 27s on average (Sweeney et al., 2013) which means that approximately only 2 to 6 blinks are necessary to maintain the tear film (Norn, 1969).

If it is not only the physiological need to maintain the tear film, then why do humans blink so often? As early as the beginning of the 20th century, Ponder and Kennedy (1927), had observed that blinks were not just reflexive in nature and that quite a few of them were influenced by cognitive factors. Since then, quite a few studies have analyzed blink modulation during various cognitive tasks in order to understand the function of spontaneous blinks. Note that, blink modulation may refer to either changes in overall blink rate, time-resolved changes in blink rate or changes in the timing or latency of blinks

1.2 The modulation of spontaneous blinking

In the following section, I describe in detail the results of previous studies on the modulation of blinks during different cognitive and perceptual tasks. I have categorized the these studies into either a) tasks that involve an external attentional focus or b) tasks that

involve an internal attentional focus. An external focus occurs when there is an external stimulus or information that needs to be processed. An internal focus, as the term suggests, mainly involves processing that is internally directed and the individual disengages from the external world. Examples of internal focus include imagination, creativity and certain memory tasks. The concept of internal or external attentional focus in not new. In motor learning and sport psychology, this demarcation has been used to denote training that involves one's own body movements (internal) or objects in the environment (external) (Kal et al., 2015; Lawrence et al., 2011; Polskaia et al., 2015; Wulf et al., 2010; Wulf et al., 1998; Wulf et al., 1999). However, in my work, I use the terms external and internal in order to distinguish whether processing is directed towards a specific external stimulus or if takes place rather internally. The reason for this categorization was due to the fact that, as I will show in the following sub-sections, blinks decrease during tasks involving an external focus but increase during tasks involving an internal focus. To my knowledge, no previous research has explored the function of blinks by focusing on these different attentional states.

1.2.1 During externally focused attention

As mentioned above, humans refrain from blinking while processing and paying attention to external stimuli. Previous research has shown that this influence can be driven either by changes in the physical properties of the sensory input, or by internal factors that are independent of physical input changes. Please find a detailed description of these findings below.

Sensory input

Bonneh et al. (2016) described that blinks are suppressed during the processing of low-level changes of an external stimulus. Specifically, the length of blink suppression depended

on the stimulus parameters, i.e. the suppression was longer for higher contrast and lower spatial frequency. Supressing blinks during visual processing could be because we do not want to miss important information (J. Veltman & A. Gaillard, 1998), since the visual input is temporarily interrupted during a blink. This might explain why we refrain from blinking during reading (Karson et al., 1981) or during interesting scenes while watching a movie (Shin et al., 2015). Additionally, blinks during visual stimulus presentation tend to be shorter in duration than those occurring during rest (Bauer et al., 1987). Therefore, one could argue that there is a trade-off between the physiological need to blink and the task-related cost of missing information (Hoppe et al., 2018). Below, I will further argue that blink modulation goes beyond the need to not miss visual information.

Although the findings from visual studies allude to the idea that blinks are suppressed in order to not miss visual information, further evidence clearly indicates that there are other factors to consider. For instance, the ocular inhibitory mechanism described by Bonneh as involving a decrease/suppression-increase pattern during stimulus presentation, has also been observed during the presentation of auditory stimuli (Lance O Bauer et al., 1985; Goldstein et al., 1985; Gregory, 1952). Additionally, Gregory (1952) showed that the decrease during auditory task actually correlated with the performance. Specifically, they found that the more blinking decreased during stimulus presentation compared to baseline periods, the better the performance. Given that a blink does not interrupt auditory input, this finding clearly showed that, the modulation of blinks during tasks is at least not exclusively driven by the need to reduce visual information loss.

Processing of sensory input

An open question at this point is if the sensory input itself or rather the active processing of the sensory input leads to the suppression. For instance, Fogarty and Stern (1989) showed that blinks are suppressed longer for peripheral than centrally presented stimuli and Bonneh et al. (2016) reported that blink suppression was longer for visual input with lower contrast and higher spatial frequency. This influence might be based on the modulation of the visual input itself or on the changed processing introduced by it. However, further data revealed that the blink modulation is affected even if the stimulus input stays unchanged. Fogarty and Stern (1989) demonstrated that when the stimuli needed to be identified rather than merely detected this led to a longer blink suppression. On similar lines, a study by Siegle et al. (2008) found that when participants performed a digit sorting task and were given a cue before the stimulus onset as to how many digits would appear, the decrease was stronger for higher number of digits. Oh, Jeong, et al. (2012) also made similar observations that the degree of blink suppression depends on the difficulty of the task. That processing of the stimulus influences the blink modulation has also been shown by Brych and Händel (2020), who concluded that people tend to blink more after targets than distractors in an oddball task, independent of the physical properties of the stimulus. The idea that blink modulation goes beyond a simple reaction to sensory input and could represent the processing therefore has been suggested by previous research (Fogarty & Stern, 1989; Himebaugh et al., 2009; Oh, Han, et al., 2012; Oh, Jeong, et al., 2012; Hideki Ohdra, 1995; Ohira, 1996).

That the modulation of blinking is indeed independent of the actual sensory input is reaffirmed by the fact that blink suppression can occurs in preparation of stimulus onset (Brych & Händel, 2020; Fukuda et al., 2005; Hoppe et al., 2018; Poulton & Gregory, 1952;

Siegle et al., 2008). Such pre-stimulus decrease falls into line with the idea that the preparation of processing of the predicted stimulus input affects blink modulation. Furthermore, attention, which is known to influence the processing of sensory input, has shown to increase the blink modulation. For instance, Broadbent (1958) mentions that blinking decreases during increased demands of attention. In the study by Brych and Händel (2020), the authors also found that while unattended sensory (visual and auditory) input did not lead to a visible modulation of blink probability, once the input was attended, the modulation was clearly visible. Another study found that blink suppression is stronger during higher attention while watching a movie (Shin et al., 2015). The same study also found that participants were able to better recall portions of the movie wherein blinks were suppressed. Other studies have argued that decreased blinking could be a metric for the amount of attention directed towards an external stimulus while watching movies (Ranti et al., 2020; Shultz et al., 2011). Interestingly, Shultz et al. (2011) found the effect of attention on participants as young as two years of age.

To summarize, blinks are suppressed during the presentation of external stimuli both in the visual and the auditory domain. The length or degree of suppression depends on cognitive factors such as attention or the complexity of the information. This might be related to the extent of active processing needed to read out the sensory input. In order to understand if blink suppression is indeed driven by stimulus processing we asked if ***the length of blink suppression reflects the time of stimulus processing and if a blink marks the end of the processing period.*** To answer this questions, one needs to disassociate the time of the overall sensory input from the duration of the processing of relevant input. The aim of study 1 was, to analyse the modulation of blinks and test if the length of blink suppression actually reflected the time period when the stimulus was being actively processed independent of the overall

stimulus duration and motor response. Importantly, both the visual and auditory modalities were tested.

Perceptual interpretation of sensory input

In the previous sub-section, I had introduced the idea that blink suppression could reflect the active processing of external information and my study indeed confirmed that it is not the sensory input per se that drives the blink suppression but the processing of it. However, processing of sensory input and the perceptual interpretation based on such processing usually happens in parallel with the appearance or change of the input. This makes it hard to dissociate between sensory processing and more cognitive perceptual effects. In this sub-section, I put forth the idea that blink suppression is similarly engaged when we perceptually re-interpret external stimuli, independent of the stimulus appearance or changes. One way to test this is through bistable perception. Bistable perception occurs when a single unchanging stimulus can be interpreted in two or more ways (Leopold & Logothetis, 1999; Long & Toppino, 2004). Hence, while the sensory input stays the same, an internally triggered re-interpretation leads to switching between the different perceptions. Some examples of such stimuli are the Necker cube (Necker, 1832) which can be perceived in two different orientations, the apparent motion stimuli (Schiller, 1933), in which two dots appear moving either vertically or horizontally, or the ambiguous plaid (Hans Wallach, 1935; Wuerger et al., 1996), wherein gratings are perceived to move synchronously in one direction or in opposite directions.

Previous research has already found that blinks can be modulated during the presentation of bistable stimuli. Nakatani and Van Leeuwen (2005) showed that eye blink rates are generally lower for frequent switchers. Similar to the pattern of decrease-increase

caused by changes in the sensory input, a modulation in blinking also occurs around perceptual switches, or more precisely, around the report of a switch (Junji Ito et al., 2003; L. C. van Dam & R. van Ee, 2005). Junji Ito et al. (2003) showed that blinks decrease before the report of perceptual switches of the Attneave's triangle (Attneave, 1968) and increase during the report. Similar results were also shown by L. C. van Dam and R. van Ee (2005). According to Junji Ito et al. (2003), perceptual switching involves the reorganization and reinterpretation of the stimulus and cognitive effort to report it. They claim that blink suppression could be involved in that cognitive effort, but do not explain how it might be involved. L. C. van Dam and R. van Ee (2005), on the other hand, provide an even more general explanation and put forth that any relevant event such as external stimulus changes, attention, internal perceptual changes and even manual reports modulate blinking. In fact, they found that blinking was modulated even after random button presses.

Based on the idea that decreased blinking can be a marker of (increased) input processing as shown in study 1, I propose that blink modulation during bistable perception is also related to sensory processing. The blink decrease is therefore temporally linked to the re-interpretation of the stimulus. I therefore specifically asked the following questions: ***Could the reduction in blinks before a switch report reflect the period of active processing and subsequent re-interpretation of the bistable stimulus? And would a blink then occur when the re-interpretation is complete and the percept is stable?*** To this end, I conducted two studies (study 2 and 3) using both visual and auditory bistable stimuli and tested if blinks decrease during the re-interpretation of the stimuli and are generated after a stable perceptual interpretation was reached.

1.2.2 During internally focussed attention

While blinks are suppressed during sensory processing and therefore an external focus of attention, previous research has indicated that blinking increases during tasks that involve an internal focus. Salvi and Bowden (2016), for instance, argued that closing one's eyes is a way to disengage from the outside world and focus on internal thoughts. Smilek et al. (2010) observed increased blink rates during mind wandering and argued that it can be an indication as to what extent a person is engaging with internal thoughts. In another study, Salvi et al. (2015) put forth that increased blinking can help in problem solving through sudden insight. Indeed, when people engage in imagination and memory retrieval, they tend to make more saccades and blinks (Salvi & Bowden, 2016).

Creative processes and divergent thinking

A cognitive process that generally involves an internal attentional focus is creativity. There are several ways in which creativity can be defined, but the most widely accepted explanation of creativity is that it involves the balance between divergent and convergent thinking (Guilford, 1967). Divergent thinking is the process through which one comes up with several solutions or ideas to a specific problem. Brainstorming, for instance, is such an example of divergent thinking. Convergent thinking, on the other hand, is the ability to find a single solution or a commonality between ideas or concepts. The most widely used tests for divergent and convergent thinking are the Guilford's alternate uses test or AUT (Guilford, 1967) and Mednick's remote association test or RAT (Mednick, 1962), respectively. In the AUT, participants have to generate different alternate uses for everyday objects and in the RAT, they are given three words and asked to find a common word that links them all.

1 General Introduction

Studies have suggested that eye blinks particularly facilitate divergent thinking. Work by Akbari Chermahini and Hommel (2010) demonstrated that moderate eye blink rates (based on average blink rates of the group) were associated with the highest scores in the alternate uses task. Importantly, they looked at blinks during rest i.e. when the subjects were fixating on the screen and did not have to perform any task. The authors link their findings to dopamine. Eye blink rates and dopamine level have been shown to be associated (Blin et al., 1990; Bologna et al., 2012; Karson, 1983, 1988; Karson et al., 1984; Lawrence & Redmond Jr, 1991; Sax & Strakowski, 1998; Strakowski & Sax, 1998; Taylor et al., 1999). Since dopamine also plays a role during divergent thinking (Kulisevsky et al., 2009; Zabelina et al., 2016), the authors suggest that the correlation between resting eye blink rates and divergent thinking can possibly be explained by dopamine levels. While the aforementioned study looked at baseline blinking, a study by (Ueda et al., 2016), tested the relationship between task-related eye blink rates and performance in the AUT. These authors found that higher eye blink rates were related to higher scores.

One mechanism put forth through which eye blinks and divergent thinking might be related is through secondary processes that aid in divergent thinking. For instance, long term memory can play an important role when trying to come up with different ideas for an object and in fact, when people engage in imagination and memory retrieval, they make more blinks (Salvi & Bowden, 2016). Note that, this has not just been shown for blinks but also extensively shown for eye movements in general (Brandt & Stark, 1997; Damiano & Walther, 2019; De Jong & Merckelbach, 1990; Hebb, 1968; Johansson et al., 2012; Johansson & Johansson, 2014; Lenoble et al., 2019). Hebb (1968) suggested that eye-movement during imagery of an object are similar to while actually viewing that object. Brandt and Stark (1997) showed subjects an irregularly checkered grid and asked them to later imagine that grid. They found that subjects

made the same eye movements during imagery as during viewing the grid. In fact, apart from a mere correlation, other studies have come forth with evidence that eye movements may actually have a facilitatory role during memory by showing that not allowing any eye movements worsens performance in memory tasks (Damiano & Walther, 2019; Johansson & Johansson, 2014; Lenoble et al., 2019). In the study by Johansson & Johansson (2014), for instance, participants performed a visuospatial memory task and their performance deteriorated when they made eye movements that were incongruent with the position of the objects as opposed to when they made congruent movements. Lenoble et al. (2019) showed that eye movements increase when trying to retrieve autobiographical memories and importantly that memories retrieved while moving the eyes freely tended to be faster and more detailed. Another study by Damiano and Walther (2019) also proved that participants were better able to recall a visual scene when they were allowed to make eye movements freely as opposed to when they had to refrain from making any movement. Although many of these studies focussed on eye movements and not blinks, it is conceivable that blinks also have similar effects. In order to understand the role of blinking during tasks involving an internal attentional focus, I conducted experiments testing for the relationship between blinking and divergent thinking.

Previous work, showing a relationship between blinking and divergent thinking (Chermahini & Hommel, 2010; Ueda et al., 2016), tested the relationship of blinks and performance between subjects and not within a subject. Using a paradigm similar to Ueda, I tested if trials with higher blink rates was associated with better performance within a single subject. Additionally, studies had also shown that walking and more specifically free walking improves divergent thinking (Kuo & Yeh, 2016; Leung et al., 2012; Oppezzo & Schwartz, 2014; Zhou et al., 2017). Blinking has been shown to increase during various body movements, such

as walking (Cao et al. (2020b) and as mentioned earlier, speaking (Brych et al., 2020; von Cramon & Schuri, 1980). But how increased blinking and other body movements interact to facilitate divergent thinking is not known. The aim of the study 4 was to test ***if blinks facilitate divergent thinking and if movement restriction deteriorates performance in divergent thinking*** and importantly***, if the influence of blinks was mediated by the level of restriction***.

1.3 Neural correlates of blinks

While the link between blinking and behavioral measures can already shed some light on the function of blinks, in order to uncover the underlying mechanism it is crucial to understand the neural basis of blinking. Specifically, I explored the neural correlates of spontaneous eye blinks in the animal model. Importantly, since the results from the behavioral studies have shown that blinks are influenced by cognitive processes and attentional states, one could also assume that the underlying neural activity is dependent on the state itself. In the following paragraphs, I will explain the neural mechanism behind the generation of blinks and review studies regarding neural responses to a blink event.

1.3.1 Neural pathway of blinks

The neural pathway involved in blinking has been widely studied. However, the focus has generally been on reflex blinks. The generation of a reflex blink involves the basal ganglia circuitry (Basso et al., 1996; Berardelli et al., 1985; Evinger & Manning, 1993; Peterson & Sejnowski, 2017), which also happens to control other motor activity (Alexander et al., 1986; Bhatia & Marsden, 1994; Gerfen & Bolam, 2010). The circuitry involves a direct and indirect pathway, comprising of excitatory and inhibitory connections among the regions of the basal ganglia, leading to either an inhibitory or excitatory influence on the motor cortex. Basso et al. (1996) in their paper, describe the mechanism through which the basal ganglia influences

the blink reflex. It mainly involves an activation of the substantia nigra leading to an inhibition of the superior colliculus. This in turn leads to a decreased inhibition of the trigeminal nerve. As I mentioned earlier (when describing reflex blinks), a loop between the trigeminal nerve (5th cranial nerve or V) and the facial nerve (7th cranial nerve or VII) leads to the reflex blink. Although this pathway was specifically described for reflex blinks, it is fair to assume that spontaneous blinks could involve a similar pathway. For instance, (Kaminer et al., 2011) postulates that the activation of the trigeminal nerve via the basal ganglia circuitry and the superior colliculus is also involved in the generation of a spontaneous blinks. Also, since dopamine plays a central role in the basal ganglia pathway, unsurprisingly striatal dopamine levels seem to correlate with spontaneous blink rates (Blin et al., 1990; Bologna et al., 2012; Karson, 1983; Karson et al., 1984; Taylor et al., 1999). Additionally, blinking is also associated with increased activation of the default mode network (Nakano et al., 2013), which is linked to dopamine (Dang et al., 2012; Nagano-Saito et al., 2009). Strengthening the link between dopamine and blinking, blink rate has been shown to increase following the administration of dopamine agonists (Blin et al., 1990; Lawrence & Redmond Jr, 1991). Moreover, disorders with abnormal levels of dopamine also exhibit abnormal blinking; for instance schizophrenic patients exhibit high levels of dopamine and elevated blink rates (Freed et al., 1980), whereas patients with Parkinson's disease have lower levels if dopamine and lower blink rates (Deuschl & Goddemeier, 1998). Apart from the basal ganglia, other regions have also been shown to be involved in the generation of spontaneous blinks (Baker et al., 2001; Yoon et al., 2005). Yoon et al. (2005) concluded that the medial frontal gyrus facilitates spontaneous eye blink generation, whereas precentral gyrus might be involved in blink inhibition.

1.3.2 Neural activity during blinks

Changes in spiking activity and BOLD signal

The paragraph above has described the neural pathway involved in blink generation and suppression. Here, I will describe the findings regarding the neural activity associated with a blink event. This has been mostly studied in the light of blink-related suppression, whereby the visual system seems to ignore the transient interruption and darkening of the environment during a blink and maintains a constant visual percept (Volkmann, 1986; Volkmann et al., 1980). A study by Bristow, Frith, et al. (2005) tested the neural correlates of voluntary blinks using FMRI in humans distinguishing between blinks during and without visual stimulation. They found that blinking during visual stimulation led to a greater activation of the medial parieto-occipital sulcus compared with blinks in the absence of visual stimulation. The researchers concluded that this region might be involved in maintaining visual continuity across blinks. Specifically, they argue that there might exist a short-term mnemonic signal which maintains the previous percept of the input across the interruption caused by the blink.

Another study, on similar lines, tested reflex blinks in humans also using FMRI (Bristow, Haynes, et al., 2005). They looked at voluntary blinks with and without retinal illumination. In other words, the retina was directly illuminated through a fibre-optic light source placed in the mouth. Importantly, the participants in this study wore dark goggles so that opening or closing the eyes did not alter the input to the retina. The findings revealed a reduction in activation in visual area V3 when blinks were executed during retinal stimulation. On the other hand, when blinks occurred during no retinal stimulation, there was an increase in activity in the LGN and V1. The authors concluded that, while the decrease in V3 represents the neural correlates of blink-related suppression, the increase in LGN and V1 in the absence of retinal

illumination might be a purely motor signal. However, the reason why the increase does not occur during retinal stimulation, if indeed it is a motor signal, has not been discussed in detail. The authors merely point out that, during retinal stimulation, a lack of a decrease might explain the results.

In addition to the comparison between stimulation and no stimulation, a few studies have also compared blink and externally generated darkening. Golan et al. (2018a) in their study, distinguished voluntary and spontaneous blinks, as well as self-initiated darkening and external darkening. Using fMRI in humans, while participants performed an image discrimination task, they found that lower visual areas showed an increase in response for all events, whereas higher visual areas showed an increase during external darkening, but a decrease during blinks and self-initiated darkening.

Although the aforementioned FMRI studies provide valuable insights, they cannot unfold the time-resolved modulation in neural activity around blinks. Single-unit recordings and electrocorticography (ECoG) indeed have shown such a temporal modulation suggesting a suppression of neural response during a blink and a transient burst afterwards in various brain areas. This has been found in human (Golan et al., 2016) as well as animal studies (Buisseret & Maffei, 1983; Gawne & Martin, 2000). The decrease and transient burst also differs between blinks and external darkenings (Gawne & Martin, 2000; Golan et al., 2016). Gawne and Martin (2000) compared suppression of V1 activity in rhesus monkeys during reflex blinking. They compared blinks, darkening of the whole visual environment and also interruptions of the stimulus. Although both blinks and external interruptions showed a suppression in the firing rates of V1 neurons, the rate of decrease was faster and more pronounced during blinks. Importantly, there was a transient burst of activity after the suppression only for external changes which was observed in a sub-set of neurons (23 out of

64) that they recorded. The authors emphasize that it is the suppression of this transient burst that some neurons exhibit that distinguishes blinks from externally generated interruptions. They conclude that this facilitates visual constancy across blinks. Similar results were found for spontaneous blinks in a human ECoG study (Golan et al., 2016). These authors also found a decrease in activity during and a transient burst of activity after both blinks and external darkenings. However, they found that lower visual areas such as V1 did not differentiate between the types of input changes (blinks vs external), but in higher visual areas, the transient burst of activity was reduced for blinks. Note that, although the study by Gawne and Martin (2000) found that activity in V1 can depend on whether a blink or external interruption occurred, they only found this for a sub-set of neurons.

Power changes in various frequency bands during blinks

Apart from alterations in the spiking activity and BOLD responses, studies have also found changes in power in various frequency bands, especially during spontaneous blinks. This has been termed blink-related oscillations or BROs. Similar to the previous findings, the focus has not been on uncovering the function of blinks but rather on understanding blink-related suppression. Kern et al. (2021) found a broadband gamma (55-400Hz) power decrease during a spontaneous blink (starting before blink onset) and an increase after blink offset, while subjects completed a free-viewing task. The authors argued that the decrease in gamma power represents the suppression of visual processing during a blink and the increase could represent the recovery of visual perception and the resumption of visual processing. A number of studies by Bonfiglio and colleagues also have addressed blink-related oscillations. For instance, Bonfiglio et al. (2009) observed an increase in delta (0.5-3Hz) power during and after a blink during rest, specifically in a time period (300ms) which according to the authors could indicate the processing of environmental information. In another study, Bonfiglio et al. (2013)

discovered that this delta blink-related oscillation is localised to the precuneus particularly for healthy subjects. Similar findings have also been reported by Liu et al. (2017). Note that the precuneus has been hypothesized to be involved in information consolidation (Cavanna & Trimble, 2006; Goldman-Rakic, 1988; Kawashima et al., 1995; Lundstrom et al., 2003). Apart from delta oscillations, Bonfiglio and colleagues also demonstrated changes in alpha (8-12Hz) (Bonfiglio et al., 2011) and low beta (12-18Hz) power (Bonfiglio et al., 2014). Regarding alpha, they found three components: (i) an early blink-related synchronisation, which the authors speculate could be due to the short-term memory maintenance of the last perception before a blink, (ii) a blink-related desynchronization in the same time-window as the delta band changes (around 300 ms), which could be driven by the comparison of the older and newer visual input and (iii) a late blink-related synchronization, which according to the authors could represent neuronal recovery of the last perceived visual input before the blink. Regarding the low beta blink-related change, Bonfiglio et al. (2014) observed, similar to their previous study (Bonfiglio et al., 2013), that this change was present only for healthy subjects and not for subjects with disorders of consciousness.

In summary, studies have found blink-related changes in the neural response as well as blink-related power changes in different frequencies and various brain areas mainly related to visual processing. As I mentioned earlier, the focus of these studies was to understand blink-related suppression and not the actual functioning of blinks. But the results from the behavioural studies have indicated that blinks might have a specific role, which is the disengagement from external stimuli and a possible facilitation of internally directed processes. Given these findings, it becomes crucial to examine if the on-going activity around a blink is also dependent on the sensory processing state. But before one can answer this question, we would first need to test if the neural correlates of blinks differs between sensory

processing and no processing. Therefore, as a first step in the understanding of the function of blinks through their neural correlates, I tested if blink related neural activity in the primary visual cortex (V1) was dependent on the processing state i.e. on the presence and absence of actively processed visual stimuli. To this end, in study 5, I analysed blink-induced changes in V1 of three rhesus monkeys during active sensory processing vs. rest. The main research question here was: ***Would blink related activity in V1 be different while the monkey watches a visual stimulus as opposed to the presentation of a blank screen during rest?***

1.4 Overview of the presented work

Previous research had shown that blinks decrease around the presentation of a stimulus. However, the reason for this consistent modulation of blink probability was not fully understood. In **study 1,** the main aim was to test if the length of active blink suppression represents the timing of external stimulus processing in the visual and auditory modality or in other words, to test if mark the end of stimulus processing. To this end, participants were presented with bilateral stimuli and had to judge is they appeared simultaneously or not. The overall sensory input duration and the task-relevant sensory input duration were independently manipulated during a comparable auditory and visual simultaneity judgement task. I found that the length of blink suppression reflected the duration of the time required to process the task relevant stimulus in both modalities.

Given that study 1 showed that blinks are suppressed during sensory processing triggered by stimulus features, I wanted to test if blink reduction also occurs during the internally introduced processing. To this end, I analyzed bistable perception, in which the perceptual interpretation of the stimulus changes independent of any specific physical change to the stimulus. The reinterpretation is likely based on refocused processing of the ongoing

sensory input. Although previous studies have found that blinks decrease before switch reports of bistable percept (Junji Ito et al., 2003; L. C. van Dam & R. van Ee, 2005), it has not been established if the decrease represents the active processing of the stimulus. Therefore, in **study 2 and 3** I used bistable visual and auditory stimuli to test if blink decrease represents the internal perceptual reprocessing of the stimulus. Importantly, in study 3, the visual stimulus was conducted in normal light (Experiment 1) and complete darkness (Experiment 2) to test for effects of the visual consequences of blinks. Additionally, external blanks (mimicking blinks in terms of their rate and duration), which were either an external interruption of the stimulus alone or a darkening of the environment were also added. The main results showed a decrease in blinking before the switch report. Importantly, through the timing of the blank induced change in switch rate, I present evidence that the decrease in blinking most likely occurs during the internal re-interpretation. Notably, blinks were followed by a period of stable percept, indicating that they mark the end of the processing, possibly introducing a period of disengagement from sensory processing.

While blink reduction, which I will argue was based on a top-down driven suppression, occurred when engaging with an external stimulus, one could assume that increased blinking marks periods of sensory disengagement. Accordingly, I tested if blink rates correlate with performance during internally driven processes. While previous studies had found that blinks increase during tasks involving an internal focus (Salvi et al., 2015; Smilek et al., 2010) and also specifically during creativity (Ueda et al., 2016), such relationship was only shown between subjects. **Study 4** investigated blinking during divergent thinking using the Guilford's alternate uses test or AUT (Guilford, 1967). Importantly, I tested the correlation between blink rate and performance in a within subject design. A second factor tested was the influence of

unrestricted movement and its interaction with blinking. I found that subjects with higher blink rates performed better, but only during free movement.

The aim of **study 5** was to explore changes in blink related neural activity in the visual cortex depending on the processing state or particularly, during sensory processing vs rest. I analysed the effect of blinks on the on-going activity of the neurons in the primary visual cortex (V1) in three rhesus monkeys, while the animal was watching a movie compared to while it was resting during the presentation of a blank screen. The data was obtained as part of a collaboration with Beshoy Agayby of New Castle University and Dr. Michael Schmid from the University of Fribourg. Analysing spike related multi-unit activity, frequency dependent power changed, local field potentials and the laminar distribution of activity, I found a difference in blink-related neural activity dependent on the processing state. This difference suggests a state dependent function of blinks.

2 Study 1: The Latency of Spontaneous Eye Blinks Marks Relevant Visual and Auditory Information Processing

Eye blinks are influenced by external sensory and internal cognitive factors, as mainly shown in the visual domain. In previous studies, these factors corresponded to the time-period of task relevant sensory information and were often linked to a motor response. Our aim was to dissociate the influence of overall sensory input duration, task-relevant information duration and the motor response and further understand how the temporal modulation of blinks compares between sensory modalities. Using a visual and an auditory temporal judgement task, we found that blinks were suppressed during stimulus presentation in both domains and that the overall input length had a significant positive relationship with the length of this suppression i.e. with the latency of the first blink after stimulus onset. Importantly, excluding the influence of the overall sensory input duration we could show that the duration of task-relevant input had an additional influence on blink latency in the visual as well as the auditory domain. Our findings further suggest that this influence was not based on sensory input, but on top-down processes. We could exclude task difficulty and the timing of the motor response as driving factors in the blink modulation. Our results suggest a sensory domain independent modulation of blink latencies, introduced by changes in the length of the task-relevant, attended period. Therefore, blinks not only mark the timing of sensory input or the preparation of the motor output, but can also act as precise indicators of periods of cognitive processing.

2.1 Introduction (Study 1)

Humans spontaneously blink about 10-15 times a minute (Burr, 2005; Doughty, 2001; Kaminer et al., 2011). Although a main function of these blinks is to maintain the corneal tear film, their frequency is much higher than what would be required for that purpose (Kaminer et al., 2011; Zametkin et al., 1979). Importantly, these blinks do not occur randomly in time but show a specific modulation. Blink probability is reduced during the presentation of important sensory information and is increased after the offset of the sensory input (Bonneh et al., 2016; D.-K. Cong et al., 2010; Hoppe et al., 2018; Oh, Jeong, et al., 2012; Siegle et al., 2008; Edmund Wascher et al., 2015). This is also true for the auditory domain (Lance O Bauer et al., 1985; S. O. Kobald et al., 2019; Oh, Jeong, et al., 2012). In most of these studies, the sensory input was task-relevant and the effects of task-relevant factors and the sensory offset coincided with a task-related motor response. Therefore, while the pattern of blink modulation is well described, it is not clear if it is driven by a sensory input induced bottom-up process, by cognitively defined task-demands, or if it is linked to the motor response. We shortly review what is known about the influence of these processes on blink modulation.

Sensory input clearly affects blinking (Bonneh et al., 2016; Doughty, 2001). Bonneh et al. (2016) showed that the length of blink suppression during stimulus presentation is longer for stimuli with lower contrast and higher spatial frequency. Nevertheless, it has been suggested that the modulation of blinking is mediated by attentional mechanisms. The decrease of blinks has been discussed to reflect attention allocation and the subsequent increase to represent the point when all information processing has been completed (Edmund Wascher et al., 2015). Along the same lines, blinks have been shown to be influenced by task relevance as well as task difficulty. The increase in blink probability following stimulus presentation is lower if no task is involved and therefore no attention is needed to be directed

towards the sensory input (Brych & Händel, 2020). Accordingly, attention could be the driving factor in explaining why the suppression of blinks during sensory input is stronger for more difficult tasks (Oh, Jeong, et al., 2012). The literature clearly indicates that blinking can be modulated by top-down processes, but how much of this effect is related to the presence of sensory input itself is not known since the duration of sensory input usually coincided with the duration of task-relevant input.

Despite sensory input based effects, indication exists that blink modulation can also happen independent from sensory input. A study by Hoppe et al. (2018) showed that a mere expectation of a stimulus could already introduce a reduction in blink probability, meaning that the sensory input itself is not necessary to drive the modulation. Such a reduction, which is due to the expectation of the input, can also be modulated by attentional factors. The decrease preceding stimulus presentation has been shown to be stronger if attention is directed towards expected visual input compared to auditory input despite the fact that in both conditions identical audio-visual stimulation would follow (Brych & Händel, 2020). These findings indicate that blink modulation can be somewhat independent from the sensory input. However, it has not been tested how much the top-down modulation during stimulation depends on the sensory input itself.

Stimulus and task-relevant factors have not been disentangled within a single task. This is also true considering possible effects of the motor output. Although it has been found that tasks that do not require a motor response still lead to a modulation in blinks (Brych & Händel, 2020; S. O. Kobald et al., 2019; Edmund Wascher et al., 2015), other studies have found that blinks are in fact modulated around the motor response (Lance O Bauer et al., 1985; Oh, Jeong, et al., 2012). Additionally, blinks have been shown to be entrained by the motor response when participants engage in self-paced rhythmic finger tapping without external sensory cues

(D.-K. Cong et al., 2010). Considering both motor and task-related factors, Colzato et al. (2007) showed that blink rates reflect the strength of visuomotor binding between a task-relevant visual stimulus and a key press. The question remains if an executed task related motor response influences blink timing.

Our goal was to understand and disassociate the influence on blinking that stems from bottom-up sensory driven effects, the timing of the task related response and top-down influences, specifically focusing on the cognitively defined time of task-specific sensory information. To this end, we independently manipulated overall sensory input duration and the task-relevant sensory input duration during a comparable auditory and visual simultaneity judgement task. To secure comparable performance between the two modalities, smaller differences between the timing of the bilateral stimuli were used in the auditory task, since temporal processing has been shown to be better for the auditory domain (Kanabus et al., 2002). Additionally, since low level stimulus features have been shown to effect blinking (Bonneh et al., 2016), we conducted the experiments in complete darkness. Importantly, since there is a qualitative difference between bilateral simultaneous visual and bilateral simultaneous auditory stimuli due to binaural fusion, we analyzed and discuss the influence of this specific case separately. We hypothesized that blinks mark the active processing period of task relevant input, independent of the overall stimulation duration and independent of the timing of the planned or executed motor output and further predicted a comparable timing between modalities.

2.2 Methods

Eighteen subjects (4 males) between the ages of 18-35 years participated in the study. All participants gave their written informed consent and received either payment or study

credit for their participation. The study was approved by the local ethics committee and was in line with the European general data protection regulations (DSVGO).

The mobile SMI Eye tracker glasses (ETG 2W Analysis Pro- 120Hz) were used to record eye data. The responses were given via two buttons connected to a response box (model: K-RB1-4; The Black Box ToolKit Ltd, UK), which in turn was connected to a Dell Precision (M6700) laptop via a USB cable. The experiment and the analysis were coded in MATLAB 2012 and 2015a respectively, using the Psychtoolbox extensions (David H Brainard, 1997; M Kleiner et al., 2007b; Denis G Pelli, 1997). All data streams were recorded using the Lab Streaming Layer, LSL (https://github.com/sccn/labstreaminglayer) along with the LabRecorder (version 1.12b). Note that the visual condition was always tested first. The experimental room was completely dark as we used a light-tight EEG booth with internal ventilation. The infrared light of the eye tracker did not extend into the visible range, all internal light sources were turned off or carefully wrapped in light-tight material and no light could be detected even after staying 10 minutes inside the room.

2.2.1 Visual Condition

Participants

Of the 18 subjects, two were excluded for the visual condition because of an overall response accuracy of below 10% and a mean blink rate of below 1 blink per minute respectively.

Procedure

The visual stimulus was presented using three red light emitting diodes (LEDs) with a diameter of 4mm, placed at eye level using magnets on a horizontally mounted metal ruler at a distance of 50 cm from the participant. The central LED was only turned on at the start of

the experiment and switched off during the trials. It served to help subjects keep fixation in between the two lateral LEDs. The other two LEDs were placed on either hemifield, each at 11 degrees from the central fixation. During each trial, the two stimuli (LEDs) were turned on at the same or at different times with inter-stimulus intervals (ISI) ranging from 0 to 0.2s in steps of 0.02s. The 0 ISI indicates that both stimuli turn on simultaneously. In the non-simultaneous trials (ISI ≠ 0), the left stimulus appeared first in half of the trials. The order of the different trials (simultaneous and non-simultaneous, left first or right first) was randomized for each subject. After their onset, the two stimuli remained on for 0.4, 0.5 or 0.6s, which is referred to as the stimulus ON-time, until both were turned off simultaneously. The ON-time was randomly assigned for every trial and was added to the ISI here, but not in the auditory condition (see section 2.2). To further add to the unpredictability of the next trial, we jittered the next stimulus onset by randomly adding an inter-trial interval between 0.5 and 0.6s after the offset of the two stimuli in the current trial (see Figure 1).

The participants had to indicate whether the two lights appeared simultaneously or not, by pressing either a left or a right button (randomly assigned for each subject) with their dominant hand, as fast as possible at any time during the trial. There were a total of 1012 trials, presented in two sessions (11 ISIs*46 trials * 2 sessions). To avoid excessive fatigue, given the complete darkness of the environment, we included five mandatory breaks (two during each session and one between sessions) that were taken inside the dark chamber, wherein participants were allowed to relax and close their eyes if needed.

2.2.2 Auditory Condition

Participants

Of the 18 subjects tested, one subject was excluded for a low blink rate (<1 blink per minute). For the analysis regarding ON-time and ISI, six additional subjects were excluded due to missing information. Due to a programming error, the trigger information for the ON-time and ISI of was not recorded for these subjects.

Procedure

The auditory stimulus was presented using the Sennheiser PC3 headset along with the Steinberg UR22mk II external soundcard and consisted of two pure tones of 500 Hz, with no on/off ramps, presented to each ear. During each trial, the two stimuli turned on at the same or at different times with inter-stimulus intervals (ISI) ranging from 0 to 0.1s in steps of 0.01s. Similar to the visual condition, the 0 ISI indicated that both stimuli turn on simultaneously. In the non-simultaneous trials (ISI ≠ 0), the left stimulus (presented to the left ear) appeared first in one half of the trials. The order of the different trials (simultaneous and non-simultaneous, left ear first or right ear first) was randomized for each subject. The duration of the entire stimulation period (from onset of the first stimulus until the offset of both stimuli) was randomly assigned to the trials and lasted 0.4, 0.5 or 0.6s. This period was termed as ON-time. Unlike in the visual condition, the ON-time was not added to the ISI. After this period, both tones were turned off simultaneously. To further add to the unpredictability of the next trial, we jittered the next stimulus onset by randomly adding an inter-trial interval between 0.5 and 0.6s after the offset of the two stimuli in the current trial (see Figure 1).

The participants had to indicate whether the two sounds appeared simultaneously or not, by pressing either a left or a right button (randomly assigned for each subject) with their

dominant hand, as fast as possible at any time during the trial. There were a total of 506 trials (11 ISIs*46 trials * 1 session). To avoid excessive fatigue, we included two mandatory breaks that were taken within the dark chamber.

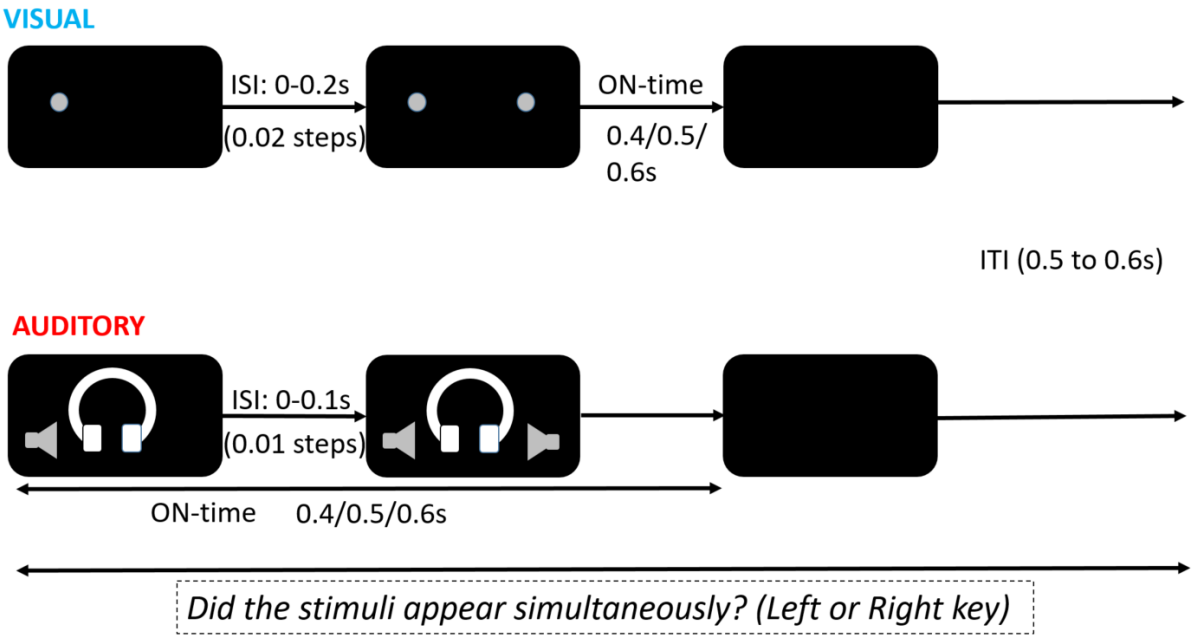


Figure 1. Stimulus and Task during the visual and the auditory condition. The ISIs (Inter-stimulus Interval) ranged from 0 to 0.2s in the visual and 0 to 0.1s in the auditory condition. Subjects had to judge whether the two stimuli appeared simultaneously or not. The ON-time was randomly assigned as 0.4, 0.5 or 0.6s, but was added to the ISI in the visual and not the auditory condition. Stimuli were turned off simultaneously. The ITI (Inter-trial Interval) ranged from 0.5 to 0.6s and was randomly assigned after the offset of the stimulus.

2.2.3 Stimulus Timing Test

Before we started the data collection, we tested our devices to make sure that the timing was precise. This was done using a photodiode for the visual stimulus and an audio output recorder that measured the audio output directly from the audio jack. The results of this test can be found in the supplementary material (Figure S12).

2.3 Analysis

2.3.1 Blink Detection

We computed a blink detection algorithm similar to previous studies (Brych & Händel, 2020; Brych et al., 2020, 2021), based on the pupil radius data. We first z transformed the radius data. After this a blink was detected if either 1) data from both eyes were missing or 2) if data from one of the eyes was missing and the other eye had a z-value below a certain threshold (-1, -2 or -3, set individually because of considerable difference in signal to noise ratio in the data). The onset and the offset of the blink were then extended until the pupil radii of either of the two eyes were higher than the set threshold. Blinks that were less than 100ms apart were combined. Lastly, blinks with durations longer than 0.5s were discarded.

2.3.2 Blink rates (time resolved)

To visualize the modulation of blinking during a task, we plotted the mean blink modulation against the trial onset i.e. the onset of the first stimulus (Figure 4). We calculated the normalized mean number of blinks in each time window (0.1s, non-overlapping) by first dividing the mean number of blinks in that time window by the mean number of blinks in all time windows for each subject. The global mean was then taken over all subjects for each time window.

2.3.3 Blink latency

To test which factor influenced blink latency, we calculated (as dependent variable) the latency of the first blink from the onset of the trial (i.e. onset of the first stimulus). The Kolmogorow-Smirnow-Test (KS-Test) revealed a non-normal distribution of blink latencies for both the visual (KS-stat = 0.64, $p<.0001$) and the auditory (KS-stat = 0.5506, $p<.0001$) condition. Therefore, a log-transformation was applied. Additionally, log transforming all

positive values has been recommended to improve the fit and predictive power of linear models (Gelman & Hill, 2006). We then conducted separate repeated-measures two-factor analysis of covariance (ANCOVA) for the visual and auditory condition to analyze the effect of the categorical variables ON-time (0.4, 0.5, 0.6s) and reaction time (Low and High, segregated for each subject according to the median RT of that subject) and the continuous predictor ISI (0.02 to 0.2s ISI for the visual and 0.01 to 0.1s ISI for the auditory) on the log-transformed blink latencies.

2.3.4 Reaction time

With regard to the influence on the motor output on blink latency, to test if there is a correlation on an individual level, we included a linear regression between blinks latency and reaction time for each individual subject. Additionally, to understand how stimulus and task features influence the reaction time, we conducted a one-factor analysis of covariance (ANCOVA) with the categorical variable ON-time (0.4, 0.5, 0.6 s) and the continuous predictor ISI (0.02 to 0.2s ISI for the visual and 0.01 to 0.1s ISI for the auditory) on the reaction time. Similar to the analysis on blink latency, we log transformed reaction time for both the individual regressions as well as the ANCOVA.

2.4 Results

2.4.1 Overall Performance (accuracy)

The overall mean accuracy and reaction time for the visual condition were 48.5% (*SD* = 15.4%) and 0.56s (*SD* = 0.22s) respectively; and for the auditory condition were 63.8% (*SD* = 22.5%) and 0.5s (*SD* = 0.14s) respectively. As predicted, for both the visual and the auditory condition, the accuracy was high for the 0 ISI. As further expected, the accuracy increased with increasing ISIs (for ISIs above 0) (Figure 2a and b). Regression analysis showed a significant

linear relationship between accuracy and ISI (calculated without the 0 ISI) for both the visual (R^2 = 0.98, b = 0.02, F (1,8) = 361.1, p < .001) and the auditory (R^2 = 0.90, b = 0.4, F (1,8) = 72.4, p < .001) condition.

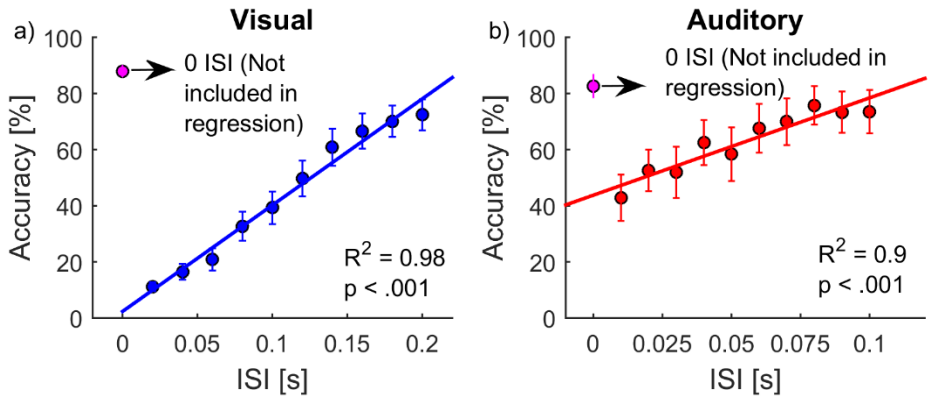


Figure 2. Accuracy plotted against the ISI. a) For the visual condition (N=16) b) For the auditory condition (N=11). Error bars represent standard errors.

2.4.2 General Blink Parameters (overall rate and duration)

The mean blink rate during the visual condition was 11.05 per minute (*SE* = 3.5) and during the auditory condition it was 14.7 per minute (*SE* = 3.7), as shown in Figure 3. A T-test showed a significant difference between the blink rates of the domains (t (14) = 2.3, p = .03).

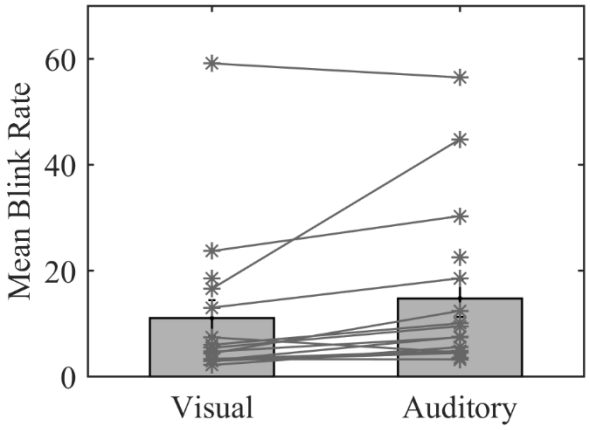


Figure 3. Mean blink rates (or blinks per minute) during the visual (N=16) and the auditory (N = 17) condition. Error bars represent standard errors. The asterisk symbols represent data of each subject.

2.4.3 Time Resolved Blink Rates

To visualize the modulation of blinking throughout the trial, we looked at the normalized mean number of blinks from 0.2s before the trial onset to 2s after the trial onset for both the modalities (Figure 4). Trial onset was defined by the onset of the first stimulus. The purpose was to see if we can replicate the previously described modulation in the visual domain and if it occurs similarly in the auditory domain. The graphs show a similar modulation in both modalities with an increase in blinks starting about 0.3s and lasting until 1.2s after the trial onset.

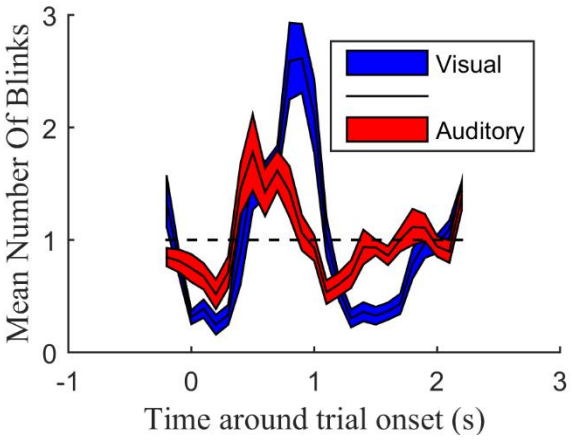


Figure 4. Normalized mean number of blinks during the visual and the auditory condition around trial onset (i.e. onset of the first stimulus of the pair). The x-axis represents timing with 0.1s non-overlapping windows. The y-axis represents the normalized mean number of blinks in each window over all subjects. The normalized mean was calculated by first taking the mean number of blinks in each 0.1s bin and dividing that by the mean number of blinks in all bins for each subject and finally taking the mean for each bin over all subjects. Therefore, a value of 1 would be the baseline number of blinks. The colored regions represent the standard error.

2.4.4 Blink Latency

To test which factors (overall stimulus i.e. ON-time, task-relevant period i.e. ISI, and motor output i.e. reaction time) have an influence on blink latency, we conducted a repeated-measures two-factor analysis of covariance (ANCOVA) for the visual and auditory modality separately.

Our results from the ANCOVA showed that there was a significant main effect of ON-time and ISI, but not for reaction time, in both the modalities. Specifically, for the visual condition, there were significant effects of ON-time (F (2,502) = 8.5, p = .0002) and ISI (F

(1,502) = 14.8, p = .0001), but not reaction time (F (1,502) = .02, p = .88). Similarly, for the auditory, there were significant effects of ON-time (F (2,357) = 3.13, p = .04) and ISI (F (1,357) = 5.38, p = .02), but not reaction time (F (2,357) = 5.8057e-04, p = .9). The individual influences and the corresponding post-hoc tests are presented in detail below.

Factor ON-time

Figure 5a and b show the mean blink latency (log-transformed) for both the visual and auditory condition. For the visual ON-times, post-hoc t-tests revealed significant differences between 0.4s and 0.6s (t (15) = 3.7, p = .002), 0.5s and 0.6s (t (15) = 3.4, p = .003), but not 0.4s and 0.5s (t (15) = 1.9, p = .07). For the auditory condition, there were significant differences between the 0.4s and 0.5s (t (10) = 3.4, p = .007) and 0.4s and 0.6s (t (10) = 2.7, p = .02), but not between the 0.5s and 0.6s (t (10) = .74, p = .5). Please see supplementary material, Figure S1, for individual data.

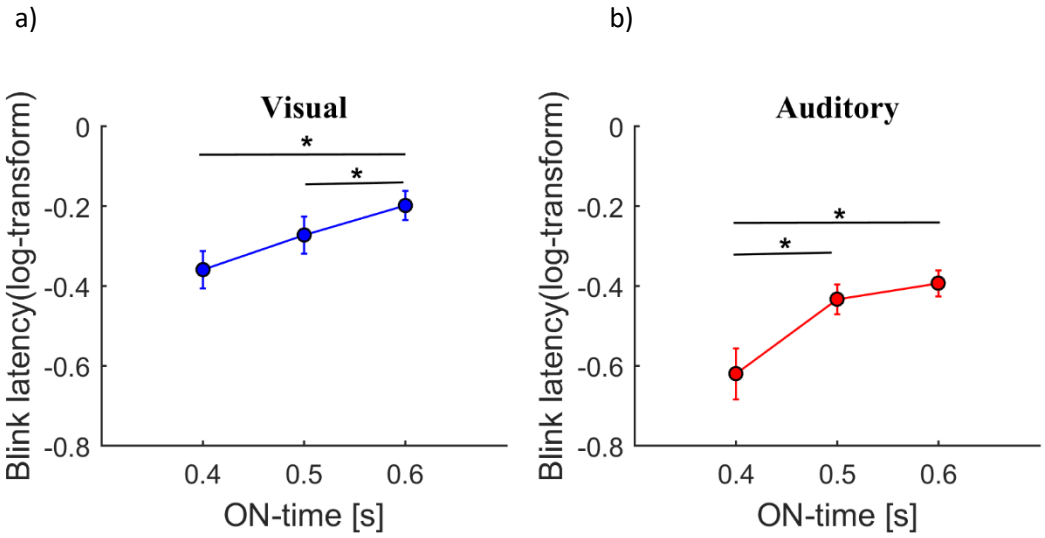


Figure 5. The effect of ON-time (overall stimulus duration) on blinks. Blink latency for the three ON-times in a) the visual (N=16) and b) the auditory (N =11) condition. The x-axis shows the ON-times and the y-axis shows the log transformed blink latency (onset of first blink after trial onset). Error bars represent standard errors. The ANCOVA revealed a significant influence in both the visual (F (2,502) = 8.5, p = .0002) and the auditory (F (2,357) = 3.13, p = .04) domain. Supplementary material Figure S1 shows individual data. The asterisks mark a significant post-hoc comparison.

Factor ISI

Figure 6 a and b show blink latency plotted against the ISI for both the visual and auditory modality. In the supplementary material, we show this relationship for each ON-time (Figure S7) and each RT (Figure S8). Based on the results from the ANCOVA, it is clear that blink latencies increase with increasing ISIs. Note that, all subjects did not contribute to all ISIs in the auditory condition, because no blink was executed for some of the trials and therefore, no latency could be calculated. Please see supplementary material (Figure S2) for individual data.

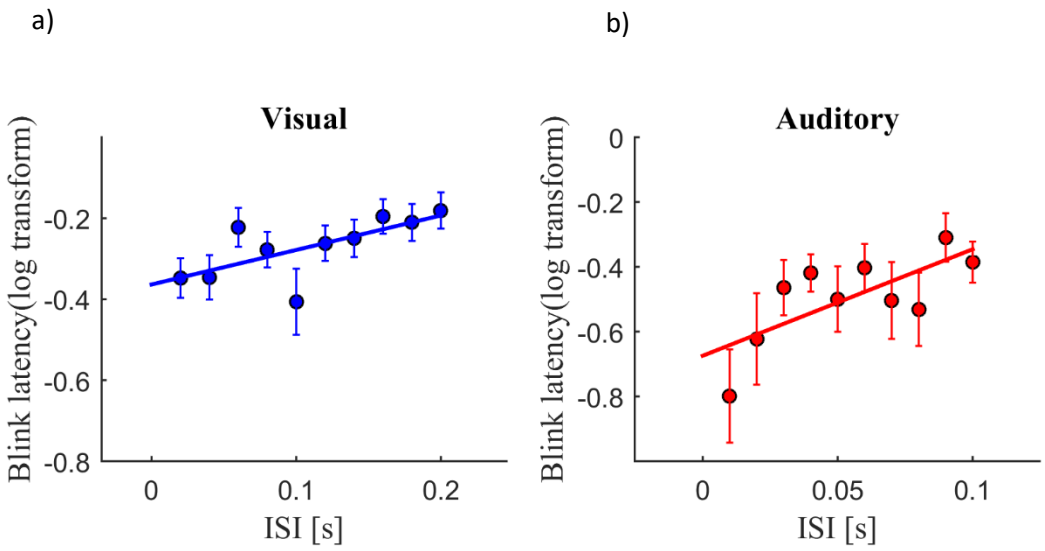


Figure 6. The effect of ISI (task-relevant input) on blinks. Blink latency plotted against the ISI in a) the visual (N=16) and b) the auditory (N =11) condition. The x-axis shows the ISIs and the y-axis shows the log transformed blink latency (onset of first blink after trial onset). Error bars represent standard errors. The ANCOVA revealed a significant effect in both the visual (F (1,502) = 14.8, p = .0001) and the auditory (F (1,357) = 5.38, p = .02) domain. Supplementary material Figure S2 shows individual data.

Since the ISI in the visual task was added to the ON-time, i.e. both factors defined the total stimulus duration, we wanted to see if the effect of the ISI on the blink latency was indeed due to increasing task-relevant information processing or merely due to its effect on the timing of the offset. Hence, we took only those trials wherein the first blink occurred before the end of the ON-time in the visual task (Figure 7). A linear regression model still showed a significant effect of ISI on blink latency (F(1,125) = 12.1, r^2 = .2, p = .0005). Note that, since only blinks before offset were taken into account, the number of usable data points is reduced as not all subjects contributed to all ISIs, since for some subjects no blink was executed at all

and therefore no latency could be calculated. Please see the supplementary material (Figure S3).

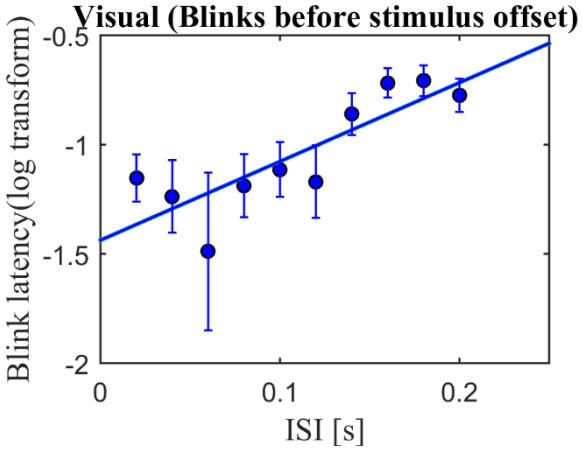


Figure 7. The effect of ISI (task-relevant input) on blinks occurring before the offset. Blink latency plotted against the ISI in the visual condition (N=16). The x-axis shows the ISIs and the y-axis shows the log transformed blink latency (onset of first blink after trial onset but only if this blink occurred before stimulus offset). Error bars represent standard errors. A linear regression model showed a significant effect (F (1,125) = 12.1, r^2 = .2, p = .0005). Please refer to supplementary material Figure S3 for individual data.

As motivated in the introduction, the 0 ISI was excluded from the ANCOVA and compared separately to the highest ISI. Note that it breaks from the pattern observed in Figure 8 in the auditory, but not in the visual condition. A T-test showed that there was a significant difference between the 0 and 0.2s ISI in the visual (t (15) = 5.8, p = 3.5989e-05), but not in the auditory (t (10) = .14, p = .9) condition.

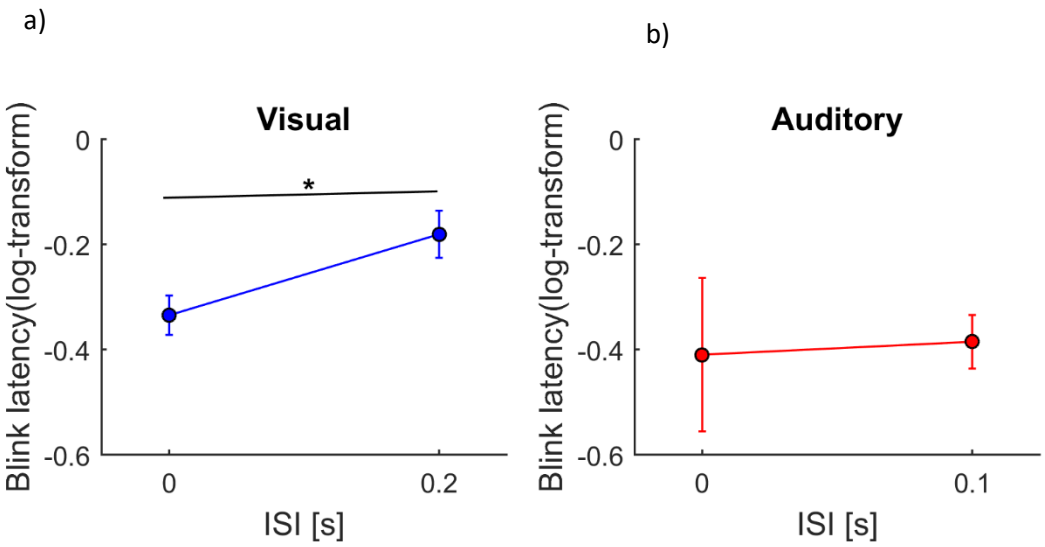


Figure 8. Blink latency plotted against the 0 vs. highest ISIs in a) the visual (N=16) and b) the auditory (N =11) condition. The x-axis shows the ISIs and the y-axis shows the log transformed blink latency (onset of first blink after trial onset). Error bars represent standard errors. T-tests revealed a significant difference in the visual (t (15) = 5.8, p = 3.5989e-05), but not in the auditory (t (10) = .14, p = .9) condition. Supplementary material Figure S4 shows individual data.

To see if the blink latency in the auditory domain was driven by the offset of the stimulus, we exclusively looked at the blinks that occurred after stimulus offset (Figure 9) and conducted a two-factor ANCOVA (excluding 0 ISI), which revealed no significant effect of ISI (F (1,305) = .9, p = .3). Therefore, we concluded that the ISI had no influence on the blink latency. However, the 0 ISI had a higher latency than the rest. A T-test between the 0 and 0.1s ISI revealed a p-value of .05 (t (9) = 2.2, p = .05). Note that we specifically looked at the auditory condition here because the visual ISI added to the offset time. Since only blinks after stimulus offset were taken into account, the number of usable data points was reduced because not all subjects contributed to all ISIs. Please see the supplementary material for the individual data (Figure S5)

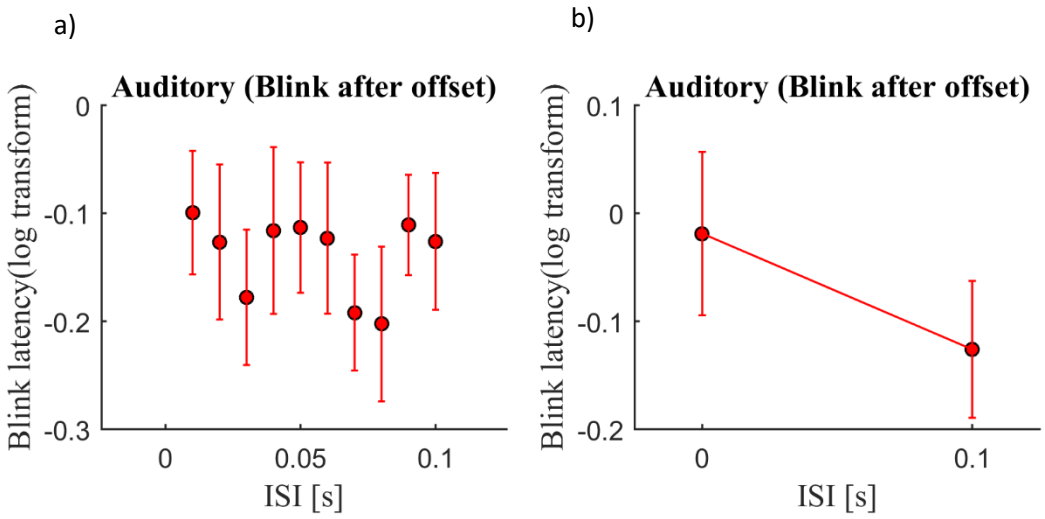


Figure 9. Blink latency plotted against the ISIs (a) and for the 0 and 0.1s ISI (b) in the auditory condition (N=10, one subject had no blinks after stimulus offset for the 0 ISI). Only those blinks that occur after stimulus offset were included. The x-axis shows the ISIs and the y-axis shows the log transformed blink latency (onset of first blink after trial onset but only if this blink occurred after stimulus offset). Error bars represent standard errors. A two-factor ANCOVA (excluding 0 ISI) revealed no significant effect of ISI ($F(1,305) = .9$, $p = .3$). A t-test between the 0 and the 0.1s ISI revealed a p-value of .05 ($t(9) = 2.2$, $p = .05$). Supplementary material Figure S5 shows individual data.

Factor RT

Figure 10 shows the blink latency (log-transformed) for the trials with high and low reaction times. Reaction times were divided for each subject based on the median reaction time of all trials for that specific subject. The ANCOVA showed no significant influence in either domain.

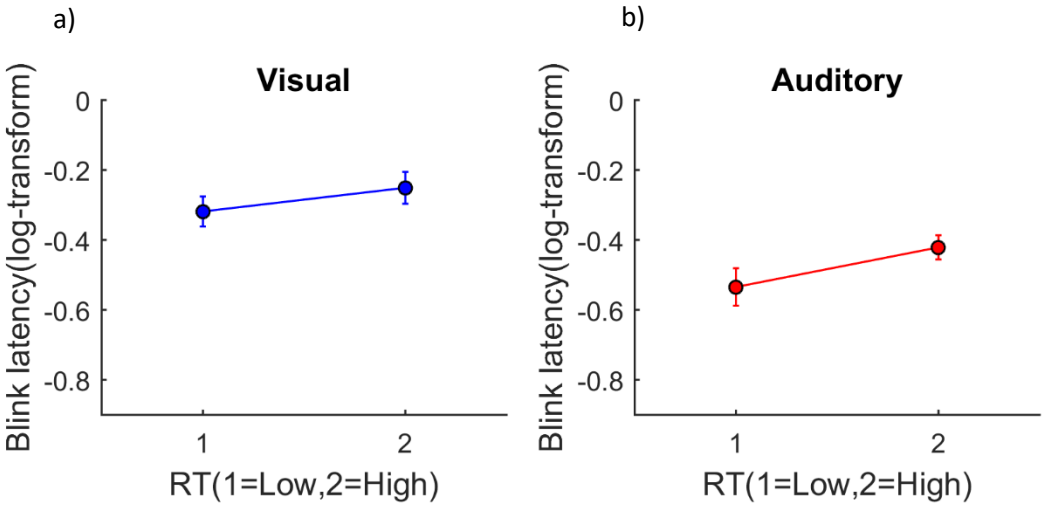


Figure 10. The effect of reaction time. Blink latency for the low and high reaction times in a) the visual (N=16) and b) the auditory (N =11) condition. The x-axis shows reaction times and the y-axis shows the log transformed blink latency (onset of first blink after trial onset). Error bars represent standard errors. The reaction times were segregated for each subject based on the median reaction time of all trials of that subject. Note that the ANCOVA showed no effect in both the visual (F (1,502) = .02, p = .88) and the auditory (F (2,357) = 5.8057e-04, p = .9) domain. Supplementary material Figure S3 shows individual data.

Although the reaction time (as divided in two categories, low and high) did not have a significant effect on the blink latency, there could still be a correlation on an individual level. We, therefore, conducted a two-sided linear regression between blinks latency and reaction time for each individual subject. Figure 11 shows the beta-values from the regression for each subjects, with stars representing subjects that showed a p-value above 0.05 for the regression analysis and circles representing those that did show a p-value below 0.05. Supplementary material (Table S1 and S2) show the beta-values, r2 values, F-values and the p-value for each individual subject for the visual and auditory condition.

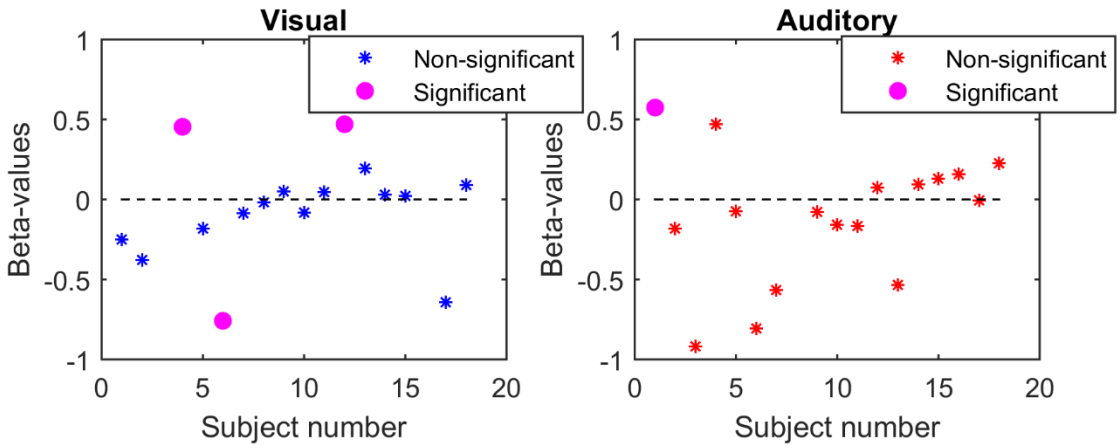


Figure 11. Beta-values from linear regressions conducted on blink latency vs reaction time for each subject separately (N=16 for visual and N=17 for auditory). Asterisk symbols represent subjects that showed a p-value above 0.05 for the regression analysis and circles represent subjects that showed a p-value below 0.05.

2.5 Discussion (Study 1)

Using an auditory and a visual simultaneity judgment task, our study shows a temporally precise modulation of blink latency, influenced by sensory as well as cognitive factors in both the auditory and visual domain. Specifically, periods of stimulus presentation were associated with a low blink rate, followed by an increase after the offset. Our aim was to understand what influences this modulation, by investigating the duration of this blink suppression. To this end, we specifically looked at the influence of the following factors on the blink latency: the duration of the overall sensory input, the time of the manual response (reaction time), the duration of the task specific sensory input (ISI), and indirectly at task difficulty. An understanding of whether these factors have similar influences across modalities, using comparable tasks, is missing to date.

The overall sensory input duration showed a robust effect since longer stimulus ON-times led to an increased blink latency (Figure 5). A modulation of blinking due to sensory input has been reported before in both, the visual (Oh, Jeong, et al., 2012; Siegle et al., 2008) as well as the auditory domain (Oh, Han, et al., 2012; Oh, Jeong, et al., 2012). The low blink rate during sensory input has been interpreted as an active suppression, which is then followed by a rebound (Bonneh et al., 2016; Hoppe et al., 2018; Oh, Jeong, et al., 2012). Our results further strengthen the domain generality of this sensory induced effect on blinking.

Importantly, our results show that the influence on blink latency goes beyond just the sensory input duration. We found that task-specific sensory input (ISI) was significantly associated with increasing blink latencies independent of the overall sensory input duration (auditory: Figure 6b, visual: Figure 7). There are several possibilities that might underlie the influence of the ISI: change in sensory input, task difficulty and the duration of task relevant input.

Any change of sensory input might modulate blinking. In our task, there are three changes in sensory input: the onset of stimulus one, the onset of stimulus two and the offset of both stimuli. That the offset modulates blink latency, we have discussed above. Further, since the onset of the first stimulus is identical for all ISIs it cannot explain the influence of ISI. We therefore can conclude that it is specifically the second stimulus shaping the mean latency of the first blink. However, data from the auditory domain suggests that the blink latency is not driven by the second bottom up sensory onset time that is defined by the ISI. For visual stimuli, two spatially non-overlapping but temporally overlapping signals can be perceived easily as two separate inputs. However, when two auditory signals are sufficiently temporally correlated between the ears they are fused and interpreted as a single auditory event. This is referred to as binaural fusion (Blauert, 1938; Broadbent, 1955; Leakey et al., 1958). The 0 ISI

in the auditory domain, therefore has a separate left and right ear input but results in a single perceived onset. If it were indeed the sensory input driving the blink latency for 0 ISI, we would expect a short blink latency after visual and auditory stimulus onset. However, the data suggest an increased blink latency for 0 ISI condition in the auditory domain (Figure 9), indicating that the influence of ISI is not based on a bottom-up effect of sensory offset but on the perception on the first and second stimulus in order to solve the task.

The specific case of 0 ISI further helps us to exclude effects related to task difficulty. Please note that in order to influence the blink latency within an ongoing trial, the difficulty must be perceived during this period. In our paradigm, the accuracy did not linearly correlate with the perception of task difficulty. For example, for short ISIs, the probability of indicating a simultaneous appearance was way above chance level. So subjects mostly perceived it wrongly, but as they did not receive feedback, they likely thought their response to be correct and therefore did not consider it as difficult. Additionally, as no feedback was provided, the perceived task difficulty could not be adapted. Therefore, it is rather response probability than the accuracy that marks the perceived task difficulty. The auditory 0 ISI has a similar task difficulty than visual 0 ISI (namely above 80 % response probability for simultaneous judgment). However, as the blink latency behaves differently for auditory and visual 0 ISIs, we conclude that task difficulty cannot be the driving factor. Additionally, the previously described influence of task difficulty (Drew, 1951; Goldstein et al., 1992; J. Veltman & A. Gaillard, 1998), always showed a positive correlation with blinking, i.e. the harder the task the later the blink. The visual 0 ISI condition clearly shows a different trend.

As we have reasoned above, our findings suggest that it is not task difficulty related effects, nor bottom-up sensory onset effects that underlie the ISI driven modulation of blink latency. However, our data is in line with the interpretation that the duration of task-relevant

input influences blink latency. While in the visual domain, the task-relevant input duration increases with ISI, this is also true for the auditory domain except for the 0 ISI. Synchronous auditory inputs would usually be fused and only after the assurance that no second stimulus was presented, the subject could conclude that the first input must have consisted of two stimuli. This increases the processing time required for auditory simultaneous input. An influence of the duration of task relevant input therefore can explain the observed pattern of blink latency as well as the prolonged latency following 0 ISI in the auditory domain. Of course, the timing needed to process the task-relevant information is closely related to attentional allocation towards this processing. Indeed, it has been argued that the suppression of blinks is associated with increased attention towards sensory input and the subsequent increase in blinks has been argued to mark the end of the attentional period i.e. when all information processing is completed (S. O. Kobald et al., 2019; Edmund Wascher et al., 2015). Our findings strengthen such interpretation by showing effects that are independent of the overall sensory input duration. Additionally, our data show that it is a domain general top-down effect on blink suppression.

Finally, our results showed that reaction time is largely independent from blink latency. As seen in Figure 11, only three out of 16 subjects in the visual and one out of 17 subjects in the auditory condition showed a significant relationship between reaction time and blink latency. Interestingly, some showed a negative relationship while others showed a positive one. This suggests that individual differences drives the relationship between blinks and motor responses. Studies have argued for a link between blinks and button presses since they involve overlapping brain regions (D.-K. Cong et al., 2010) and activate overlapping medial frontal structures (Hanakawa et al., 2008). Additionally, the supplementary motor area has been shown to be involved in different endogenous motor actions (Halsband et al., 1993) as well as

endogenous blinks (Jenkins et al., 2000). Hence, individual differences in the amount of activation and overlap between these different cortical areas might mediate the relationship between blinks and motor responses. Another relevant individual difference might be related to dopamine. Striatal dopamine level has been shown to be positively correlated with the blink rate (Karson, 1983; Taylor et al., 1999) while it shows a negative correlation with reaction time (Pullman et al., 1988; Rihet et al., 2002). An individually high or low dopamine level might therefore boost a specific relationship between blinking and other motor responses. Future studies are needed to identify the factors that lead to individual occurrences of a co-modulation between different motor outputs.

In summary, while a decrease in blinks was mainly associated with sensory input, our results show that minute changes of task relevant information length, independent of ongoing sensory stimulation, modulate blink behavior in the auditory as well as in the visual domain. Our study therefore, highlights domain general top-down influences that can precisely modulate the timing of blinking, mapping small temporal changes in sensory-attentional demands.

2.6 Supplementary material (Study 1)

Individual data

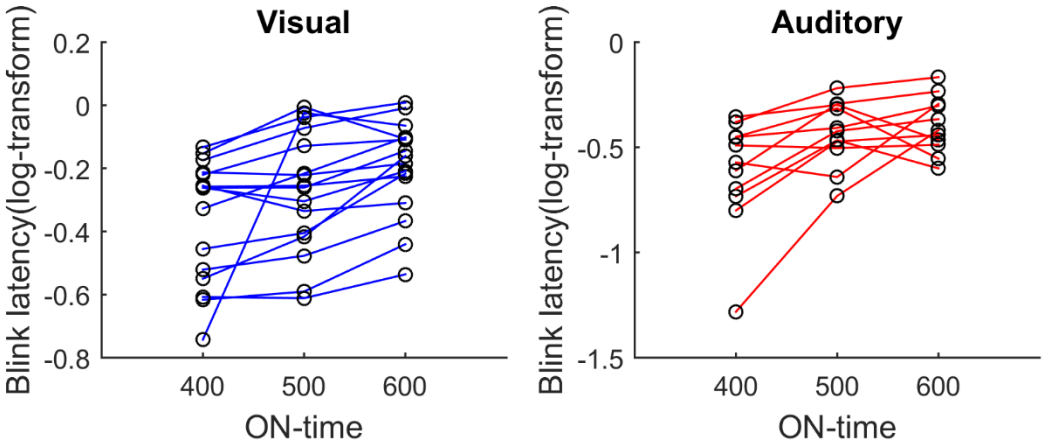


Figure S1 shows individual data for the blink latency (log transformed) for the 3 ON-times (400, 500 and 600ms) for both the visual and auditory task. Averaged data are shown in Figure 5 of the manuscript.

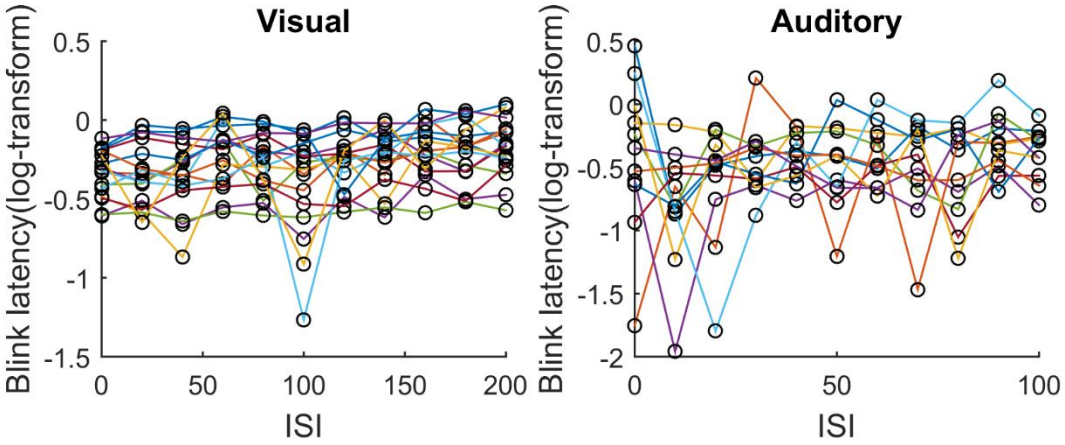


Figure S2 shows individual data for the blink latency (log transformed) for the different ISIs for both visual and auditory. Averaged data are shown in Figure 6 of the manuscript.

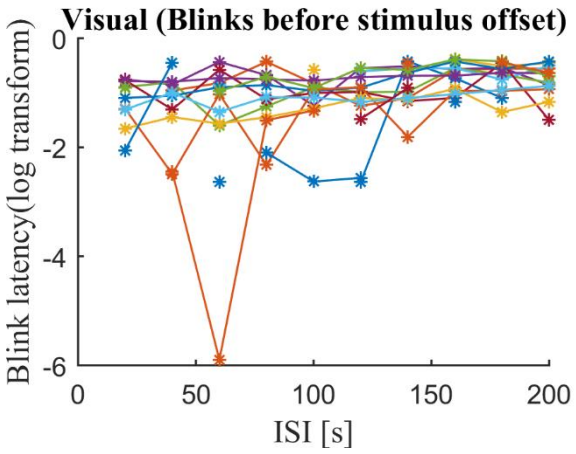


Figure S3 shows individual data for the blink latency (log transformed) plotted against the ISI in the visual task, the averaged data is shown in Figure 7 of the manuscript. Only those blinks that occur before the stimulus offset (after ISI plus ON-time) are taken into account.

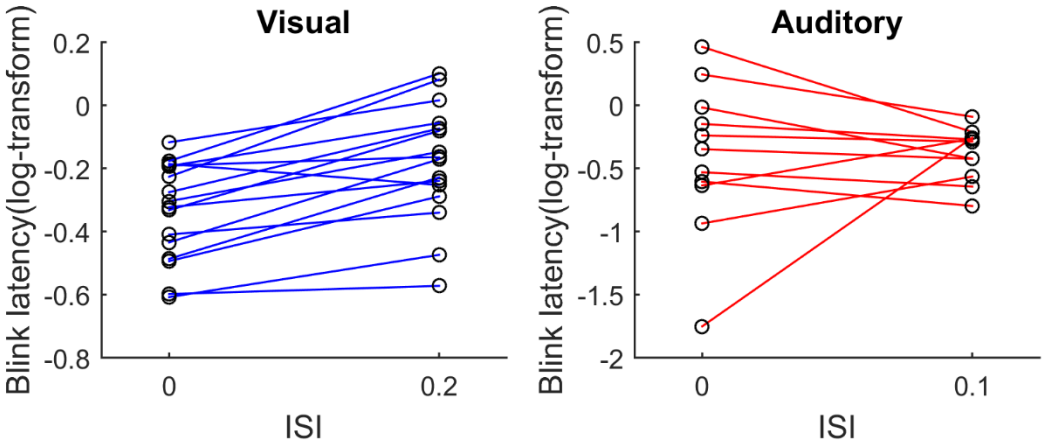


Figure S4 shows individual data for the blink latency (log transformed) for the 0 and highest ISI for both visual and auditory. Averaged data are shown in Figure 8 of the manuscript

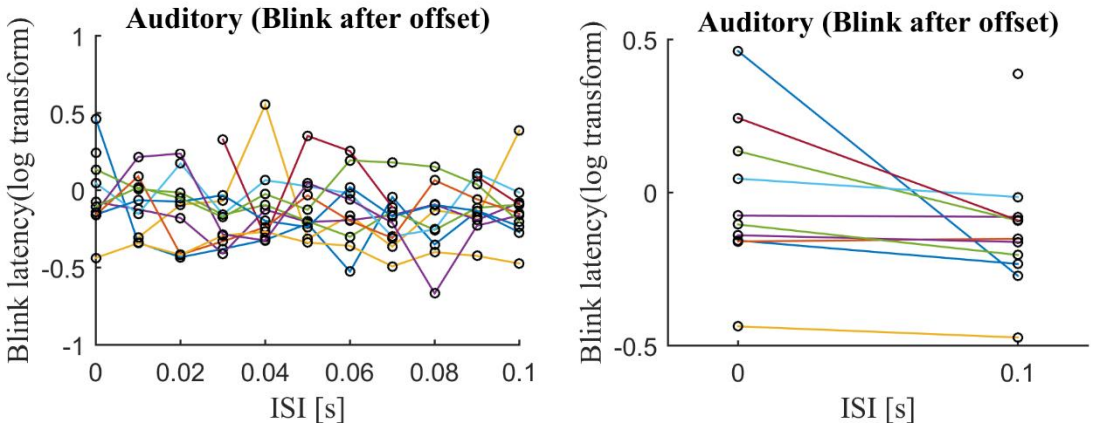


Figure S5 shows individual data for the blink latency (log transformed) plotted against the ISIs (left) and the 0 and 0.1s ISI for the auditory condition. Averaged data are shown in Figure 9 of the manuscript. Blinks that occur only after the offset are included.

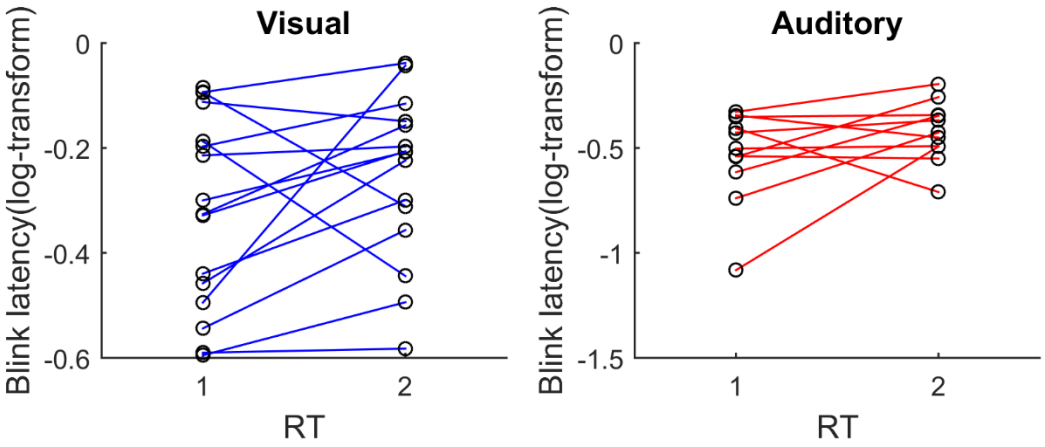


Figure S6 shows individual data for the blink latency (log transformed) for the low and high RTs (Based on median RT) for both visual and auditory conditions. 1 stands for low and 2 stands for high RT. Averaged data are shown in Figure 10 of the manuscript.

2. Study 1 (Supplementary)

Blink latency for each ISI and ON-time, and for each ISI and RT combinations

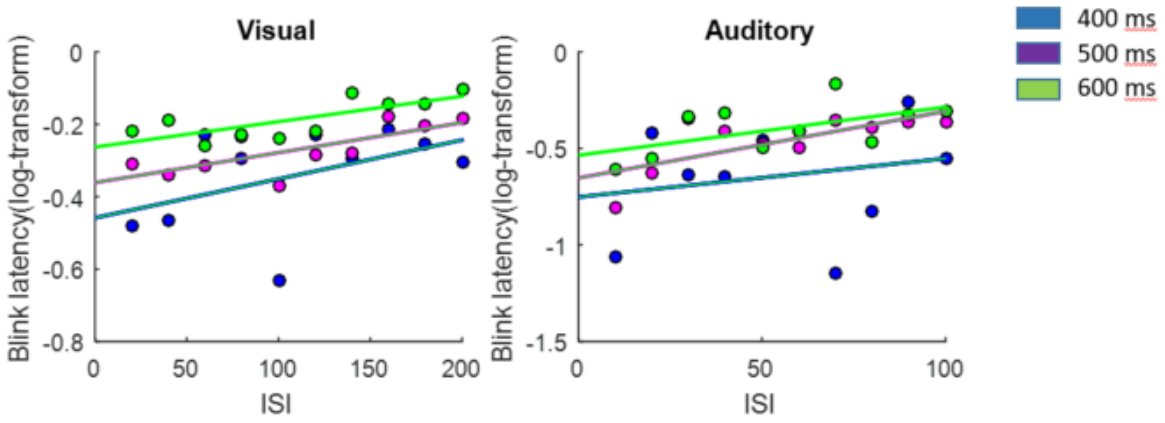


Figure S7 shows Blink latency vs ISI for each ON-time for both the visual and the auditory conditions.

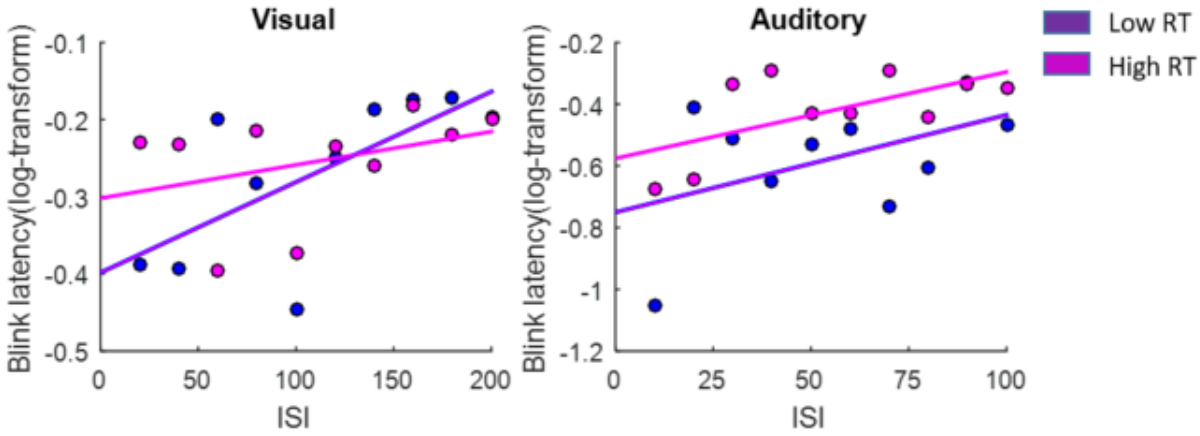


Figure S8 shows Blink latency vs ISI for the high and low reaction times (RT) for both the visual and the auditory conditions.

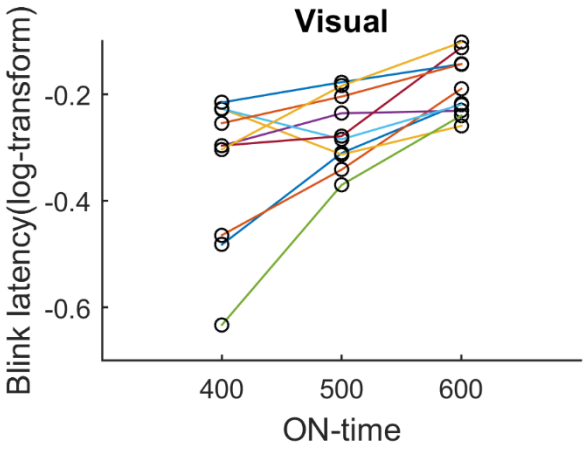


Figure S9 shows Blink latency vs ON-time for each ISI in the visual condition.

2. Study 1 (Supplementary)

Reaction time for the different ON-times and reaction times

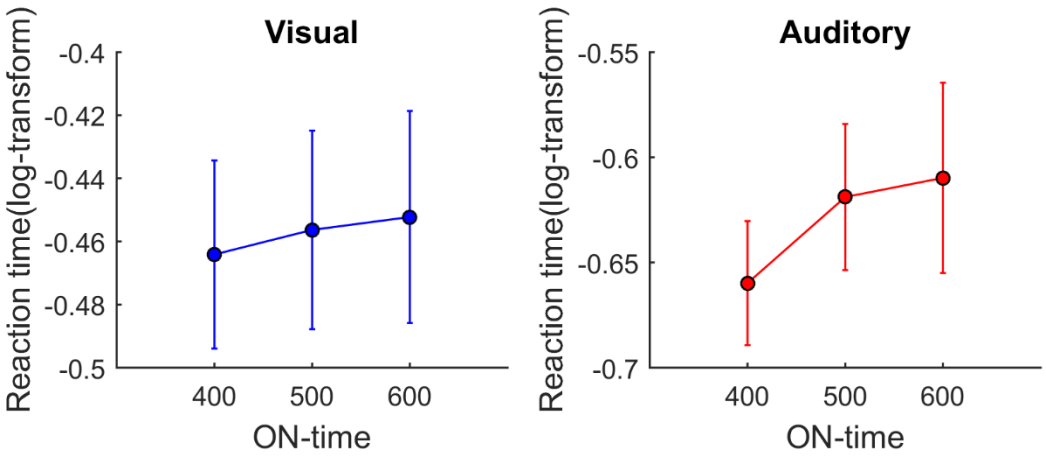


Figure S10 shows log-transformed reaction time for the different ON-times for both the visual and the auditory conditions.

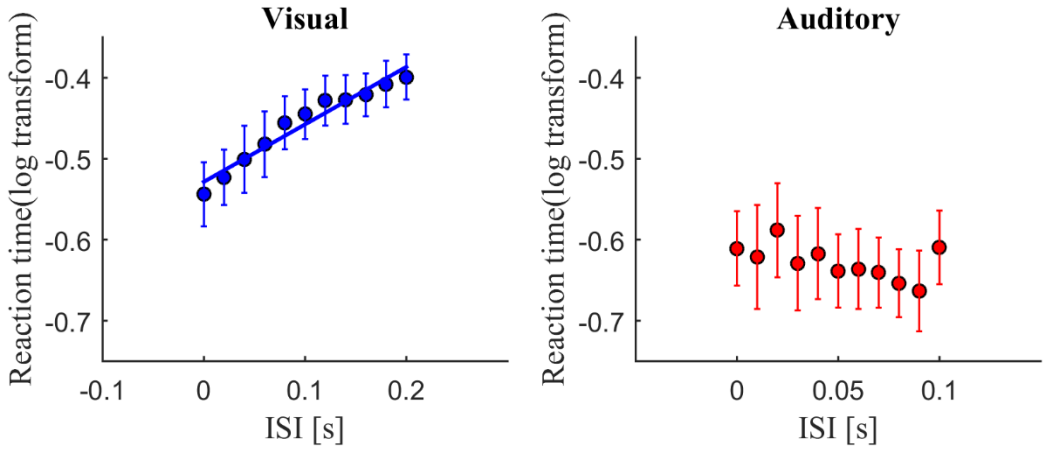


Figure S11 shows log-transformed reaction time for the different ISIs for both the visual and the auditory conditions.

2. Study 1 (Supplementary)

ANCOVA results:

1. For the visual, there is a significant effect of ISI ($F(1,527) = 26.8$, $p = .0001$) but not ON-time ($F(2,527) = 2.4$, $p = .09$) and no interaction ($F(2,527) = 0.92$, $p=.40$)

2. For the auditory there is no significant effect of ISI ($F(1,681) = 1.47$, $p = .25$), but significant effect of ON-time ($F(2,681) = 5.71$, $p = .004$) and no interaction ($F(2,681) = 2.8$, $p = .06$).

Stimulus timing test results

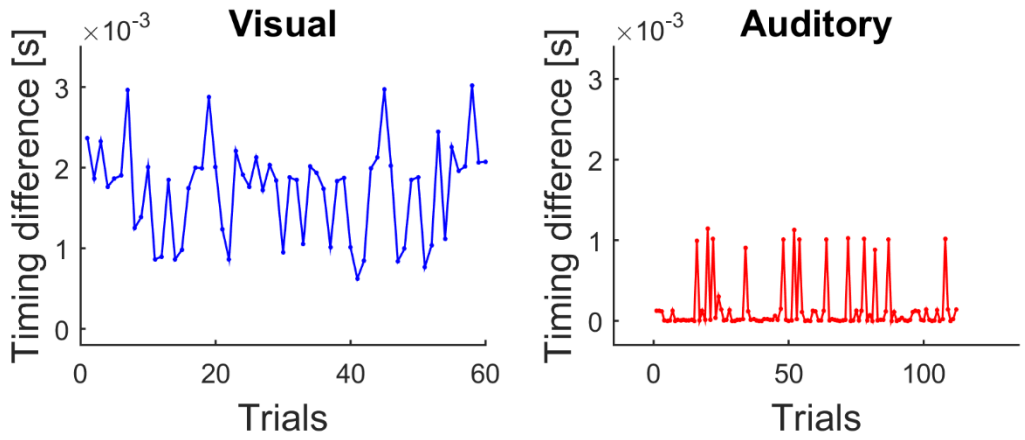


Figure S12 results from the stimulus timing test. The x-axis represents the trials. Each trial is defined by a different stimulus duration that we define in the experimental program. The y axis represents the difference between this predefined duration and the actual duration recorded by the photodiode or the audio-output recorders, respectively (i.e. Actual time – Time defined in experimental program) in seconds.

The results of the test revealed that the mean difference (over the trials) between the experimental input and the actual recording for the visual was 0.0017s (SD = 5.9265e-04s) and the auditory was 1.5364e-04s (SD = 3.1789e-04). Both domains therefore show an temporal accuracy of below 2 ms including stimulus on- and offset.

Table S1

Results from the individual regressions for blink latency vs response time for the visual condition. Note that two subjects had been excluded (see Methods).

Subject number	**Beta**	**R^2**	**F**	**p**
1	-0.25	0.01	1.2	0.26
2	-0.37	0.01	1.8	0.17
3	-	-	-	-
4	0.5	0.21	18.1	***6.59e-05****
5	-0.18	0.005	0.69	0.41
6	-0.75	0.06	6.4	***0.01****
7	-0.08	0.02	1.25	0.26
8	-0.02	0.0002	0.09	0.76
9	0.05	0.004	0.57	0.45
10	-0.08	0.006	0.404	0.53
11	0.04	9.25e-05	0.05	0.82
12	0.5	0.07	44.08	***7.3e-11****
13	0.2	0.01	0.46	0.5
14	0.03	0.0001	0.05	0.82
15	0.02	0.0004	0.02	0.873
16	-	-	-	-
17	-0.64	0.05	2.5	0.11
18	0.09	0.01	2.81	0.1

Table S2

Results from the individual regressions for blink latency vs response time for the auditory condition. Note that one subject had been excluded (see Methods).

Subject number	**Beta**	**R^2**	**F**	**p**
1	0.57	0.1	12.3	***0.001****
2	-0.2	0.001	0.13	0.71
3	-0.92	0.1	3.5	0.07
4	0.46	0.04	1.9	0.17
5	-0.07	0.03	3.14	0.08
6	-0.81	0.1	3.7	0.06
7	-0.56	0.04	2.1	0.1
8	--	-	-	-
9	-0.07	0.004	0.1	0.74
10	-0.15	0.01	0.76	0.38
11	-0.16	0.01	1.87	0.17
12	0.07	0.0002	0.07	0.77
13	-0.53	0.08	2.12	0.15
14	0.09	0.003	0.91	0.34
15	0.13	0.005	0.34	0.55
16	0.15	0.01	3.5	0.06
17	-0.005	1.5e-05	0.001	0.97
18	0.22	0.02	3.22	0.07

3 Study 2: The role of blinks, microsaccades and their retinal consequences in bistable motion perception

Eye related movements such as blinks and microsaccades are modulated during bistable perceptual tasks. However, if they play an active role during internal perceptual switches is not known. We conducted two experiments involving an ambiguous plaid stimulus, wherein participants were asked to continuously report their percept, which could consist of either uni-directional coherent or bi-directional component movement.

Our main results show that blinks and microsaccades did not facilitate perceptual switches. On the contrary, a reduction in eye movements preceded the perceptual switch. Blanks, on the other hand, thought to mimic the retinal consequences of a blink, consistently led to a switch. Through the timing of the blank-introduced perceptual change, we were able to estimate the delay between the internal switch and the response. This delay further allowed us to evaluate that the reduction in blink probability co-occurred with the internal perceptual switch. Additionally, our results indicate that distinct internal processes underlie the switch to coherent vs. component percept. Blanks exclusively facilitated a switch to the coherent percept, and only the switch to coherent percept was followed by an increase in blink rate. In a second study, we largely replicated the findings, and included a microsaccade analysis. Microsaccades only showed a weak relation with perceptual switches, but their direction was correlated with the perceived motion direction. Nevertheless, our data suggests an interaction between microsaccades and blinks by showing that microsaccades were differently modulated around blinks compared to blanks. This study shows that a reduction in eye movements precedes internal perceptual switches indicating that the rate of blinks can set the stage for a reinterpretation of sensory input. While a perceptual switch based on

changed sensory input usually leads to an increase in blink rate, such an increase was only present after the perceptual switch to coherent motion but absent after the switch to component percept. This provides evidence of different underlying mechanism or internal consequence of the two perceptual switches and suggests that blinks can uncover differences in internal percept related processes that are not evident from the percept itself.

3.1 Introduction (Study 2)

Spontaneous eye blinks are strongly influenced by sensory input (Bonneh et al., 2016). Additionally, they are closely linked to cognitive processes that influence the perceptual outcome (Brych & Händel, 2020; Grossman et.al., 2019; Ito, et. al., 2003; Maus et.al., 2020; Nakatani et al., 2011; Otero-Millan et al., 2012; van Dam & van Ee, 2005). Similarly, microsaccades are related to perceptual (Martinez-Conde et al., 2006; McFarland et. al., 2015; Intoy & Rucci, 2020, Ko et.al., 2010; Rolfs et al., 2008) and attentional processes (Gao et. al., 2015; Hicheur et al., 2013; Pastukhov & Braun, 2010; Pastukhov, et.al., 2013). The relationship between these eye movements and internal perceptual processes is still not clear. One way to study this is by looking at ambiguous stimuli, wherein a single unchanging stimulus can be interpreted in two or more ways. In such stimuli, any change in perception reflects an internal process and not an external change.

There have been attempts to understand the role of eye movements during internal perceptual switches using such ambiguous stimuli. Conducting a time-resolved analysis, some studies have found a reduction in microsaccade rate before and an increase after the perceptual switch report, using the apparent motion stimulus (Laubrock et al., 2008; L. C. J. van Dam & R. van Ee, 2006). According to these authors, this modulation was likely a consequence of the switch (van Dam & van Ee, 2006). Pertaining to the drop in microsaccade rate, Laubrock et al. (2008) discuss the possibility that the modulation could result from the switch itself and could be associated with the perceptual decision (Laubrock et al., 2008). The same authors (Laubrock et al., 2008) show that microsaccade directions causes a bias in the perceived motion direction. Others have also suggested such a causal role of microsaccades. For instance, Otero-Millan et al. (2012) reported that microsaccades increased before perceptual switches in the rotating snake illusion. Similarly, Troncoso et al. (2008) found that

higher microsaccade rates were associated with faster motion perception while viewing the Enigma illusion.

Concerning blinks, only a few studies have analyzed blink modulation around ambiguous perceptual switches in a time resolved manner. Junji Ito et al. (2003) for instance, using a version of the Attneave's (1968) triangles, found that blinks decreased before and increased after the perceptual switch report. A similar finding was reported in another study (L. C. J. van Dam & R. van Ee, 2005, 2006), using the slant-rivalry stimulus.

Our goal was to understand if eye movements are a cause or consequence of these transitions. On the one hand, these perceptual transitions could alter the ongoing eye movement rate for example due to attention diverted towards them. On the other hand, eye movements could also trigger switches. This effect could, of course, be due to the visual disruptions that accompany them. Therefore, to dissociate the effect of eye movements from their visual consequences, we added external disruptions to the stimulus that mimic the said eye movements. In experiment 1 we tested the role of blinks and dissociated influences mediated by their retinal consequences by adding short interruptions of the visual input. In experiment 2, we additionally analyzed the causal or consequential role of microsaccades and added small shifts.

Additionally, in both experiments, we accounted for the possible influence of the movement of eye ball during blinks and microsaccades by testing four different stimulus versions. For instance, during blinks, it has been reported that the eyeball moves mainly downward (Collewijn et al., 1985), whereas microsaccades during fixation are mainly executed in the horizontal direction. As these eye movements might preferably lead to a switch towards or away from the executed movement direction, we tested four different

stimulus rotations resulting in either the coherent or the component motion moving in a cardinal direction (see methods).

We used the ambiguous plaid stimulus, which consists of moving gratings superimposed over each other (Hupé & Rubin, 2004; H Wallach, 1935). The stimulus is seen either as one single grating (coherent percept) or as two separate gratings (component percept). The ambiguity arises due to the aperture problem (Binder et al., 2008).

Our main results showed that blinks and microsaccades did not facilitate perceptual switches. On the contrary, a reduction in eye related movements preceded the perceptual switch. Blanks, on the other hand, thought to mimic the retinal consequences of a blink, consistently facilitated a switch in percept. This allowed us to mark the time period in which the perceptual switch likely occurred, indicating that the reduction in blink probability was not a result of the perceptual switch but temporally co-occurring. We additionally found that blinks succeeding the switch were modulated in a percept specific manner showing a significant increase only for one type of perceptual switch. This deviation in blink behavior suggests a difference in the internal process associated with the two perceptual switches. Such an additional difference is not evident from the subjective perceptual experience.

3.2 Methods

The study consisted of two experiments using a very similar stimulus and setup. Experiment 2 was conducted as a replication study and additionally used an eye tracker that allowed us to analyze microsaccades in addition to blinks.

3.2.1 Stimulus

A moving grating displayed behind a fixed-size aperture is usually perceived as moving perpendicular to the parallel lines of the grating. Superimposing another grating with a different orientation creates the ambiguous plaid stimulus: The two gratings can either be

perceived on top of each other as two components with different directions or as a unified plaid pattern coherently moving in one direction. For the stimulus with 0° rotation, the coherent plaid pattern moved directly downward, the components moved in angles of ±67.5° to the coherent motion direction (Figure 12a). The lines of the grating were square-waved with a width of 0.5° and a spacing of 1.8° in experiment 1, and a width of 0.4° and a spacing of 1.4° in experiment 2. Line color was 180 on an 8-bit grayscale (0-black, 256-white), while the intercept color was 120. The overall size, speed and rotation of the moving grating is specified for each experiment, separately (please see below).

The experimental program was implemented in MATLAB, using the Psychophysics Toolbox extensions (D H Brainard, 1997; M Kleiner et al., 2007a; D. D. Pelli, 1997). Response buttons were stuck on the table being connected to a BBTK response box (model: K-RB1-4; The Black Box ToolKit Ltd, UK), which was connected to a laptop via USB. Participants indicated their prevalent percept by continuously pressing one of two buttons with their right index finger only. Lifting the button was the first indicator that the percept changed, which is why we present our results in relation to the button lift instead of the later happening button press.

3.2.2 Experiment 1

Participants

Fourteen psychology students of the University of Würzburg (age: 20.5 ± 2.18 years (mean ± SD)) took part in the first experiment. They received study credit for their participation. All participants had normal or corrected-to-normal vision. The study was approved by the local ethics committee and complied with the European data protection law (DSGVO). The participants gave their written informed consent before taking part in the study.

Procedure

Participants were seated in a dark room 40cm away from the screen with their heads kept in a fixed position using a chin rest. For stimulus presentation, we used a NEC MultiSync monitor (1280x1024 resolution, 60 Hz refresh rate), which was controlled by a Dell Precision (M6700) laptop running Windows 10. Binocular eye movements were recorded with 120 Hz using SMI eye tracking glasses (SensoMotoric Instruments GmbH, Berlin, Germany). Although we mentioned that eye gaze as well as blinks can be recorded with the eyetracker, participants were naïve to our intention to analyze blinks.

The stimulus was presented in an aperture of 7.2° in diameter, on a black background and the gratings moved with a speed of 0.9°/ sec. A red fixation spot of 0.3° in diameter was placed in the center of the stimulus (Figure 12a).

During a spontaneous eyeblink, the eyeball has been reported to slightly move downward and inward (Collewijn et al., 1985b). To test for a possible influence of the vertical movement of the eyeball during blinks on the percept, four different stimulus rotations were presented: 0°, 67.5°, 112.5° and 180°, with respect to the coherent motion. These specific rotations were chosen such that either the coherent motion of the gratings moved up (180°) or downwards (0°), or one of the gratings (components) moved up (112.5°) or downward (67.5°).

To control for the visual changes during a blink, the screen was blackened for a random duration between 116ms and 167ms randomly every three to six seconds (in steps of 0.5s) in half of the trials, which is similar to blink characteristics and will be referred to as “blanks”.

The first experiment consisted of eight trials with a duration of six minutes each. Each of the four stimulus rotations were presented twice, once with blanks once without. Trial

order was completely randomized. A 1-point calibration of the SMI eyetracker was performed prior to the start of the experiment.

3.2.3 Experiment 2

Participants

Twenty-two new participants (15 females, age: 27.4 ± 8.88 years (mean ± SD)) took part in the second experiment. They received payment or study credit for their participation. All participants had normal or corrected-to-normal vision. They gave their written informed consent prior to the participation. The study was approved by the local ethics committee and complied with the European data protection law (DSGVO).

Procedure

Participants were seated in a darkened room and placed their head on a chin rest 68cm away from the monitor. The stimulus was presented on a Mitsubishi Diamond Pro 2070SB monitor (1152x864 resolution, 60 Hz refresh rate). The experiment was controlled by a Tuxedo laptop running Ubuntu 16.04 LTS. To analyze very small eye movements, binocular eye movements were recorded at 500 Hz using an EyeLink 1000 eyetracker (SR Research, Ottawa, Ontario, Canada). Similar to experiment 1, we mentioned that the eyetracker is able to record various eye movements (blinks, (micro-)saccades, drift, …), but participants were naïve to our explicit analysis of blinks and microsaccades.

The stimulus had a diameter of 5.8° and the coherent pattern moved with a speed of 0.7°/ sec. The fixation spot was 0.25° in diameter.

Again, the influence of the vertical movement of the eyeball during a blink and the horizontal movement of the eyeball during a microsaccade were controlled with four stimulus rotations. We used again the stimulus rotations of 0° & 67.5° (blink related) and added rotations of 22.5° (coherent motion, i.e. one component moving horizontally to the left, the

other one to the bottom right) and 90° (coherent motion horizontally to the left) (microsaccade related). Our supplementary materials includes illustrations of the rotations.

In addition to the blanking trials, microshift trials were introduced to control for the visual changes during a microsaccade. During microshift trials, the stimulus randomly shifted every three to six seconds randomly towards the right or the left by 0.2°. While the size of the microshift was similar to a real microsaccade, we reduced the rate for two reasons. First, microshifts are clearly visible to the observer and if they are presented as often as microsaccades, they introduce a sort of jitter. This might interfere with the resulting percept possibly forming intermediate or additional perceptual interpretations. Second, to have a within condition control, we preferred to have periods with and without microshifts for data analysis. The fixation spot stayed at its position. The maximal deviation of the stimulus from the original position was 0.8°, i.e. the shift could maximally happen 4 times in the same direction.

The second experiment consisted of two blocks each having eight trials of three minute duration in random order. Before each block, a 5-point calibration and validation of the Eyelink eye tracker was performed. Each block consisted of four test trials (all four rotations described above), two blank trials to simulate blinks (rotations 0° and 67.5°) and two microshift trials to simulate microsaccades (rotations 22.5° and 90°).

3.3 Data analyses (Experiment 1 and 2)

For the first experiment, two participants were excluded because of a lower blink rate than 5 blinks/min, another one due to more than 39% of missing data. For the second experiment, one participant was excluded due to very high blink rate (>35 blinks/min) and two more due to a blink rate lower than 5 blinks/min during all trials without blanks or microshifts.

The identical trials of block one and two in the second experiment were concatenated before analysis. Event (blinks, blanks, microsaccades, microshifts) onsets were counted for bins every 100ms around the button lifts indicating perceptual switches. If such an event was detected around multiple switches, we divided the counts by the number of occurrences. To incorporate different switch rates, we averaged the time course over all switches. Furthermore, we controlled for different rates of eye movements by dividing the result by the number of eye movements during the trial. Finally, these time series were z-transformed and averaged over trials. These time series around a switch were compared to time series where no switch occurred, i.e. all possible non-overlapping 4sec time periods without a perceptual change starting two seconds after the last perceptual switch. Every second of these no switch periods was used for comparison with a switch to coherent motion, every other no switch period for comparison with a switch to component motion.

Cohen's d for paired samples t-tests was calculated as the mean of D divided by the standard deviation of D, where D is the differences of the paired samples values.

For statistical analysis, we implemented the nonparametric statistical test described by Maris and Oostenveld (2007) which is based on clustering of adjacent time samples that show a similar difference in sign and magnitude. The threshold for clustering was selected as the 97.5 quantile of a T-distribution. Critical t-values were approximated by a Monte Carlo estimate which was calculated on 1000 random partitions and a critical alpha-level of 0.05.

3.3.1 Blink detection (Experiment 1 and 2)

Whenever the eyelid covers the eye, rapid changes in pupil diameter are recorded by the eyetracker. Therefore, we developed a blink detection algorithm based on pupil diameter. Firstly, pupil diameter was z-transformed. By visual inspection, a manually set amount of standard deviations (between 1.9 and 4) of the z-transformed pupil diameter was chosen for

threshold. A blink was assumed when z-transformed pupil diameters of both eyes decreased below this threshold (pupil was partly covered by the eye lid during the start/end of a blink) or if the pupil was not detected at all (pupil was fully covered by the eye lid). The start and the end of the blink were then extended until the pupil diameter of both eyes were higher than half the threshold. Blinks less than 100ms apart from one another were concatenated and blinks shorter than 50ms or longer than 1000ms were discarded.

3.3.2 Microsaccade detection (Experiment 2)

We implemented an algorithm based on the description by Engbert and Kliegl (2003) where a transformation of fixation positions to two-dimensional velocity space is performed to detect (micro-)saccades using their high peak velocities. We assumed a minimal duration of four samples (8ms) and only considered binocular (micro-)saccades. In line with previous research, (micro-)saccades showed a linear relation of amplitude and peak velocity known as "main sequence" (Zuber et al., 1965). Microsaccades were defined by an amplitude of maximally 1°. Furthermore, we excluded microsaccades based on a velocity criterion (0.2% of all microsaccades) as well as around blinks (0.01% additional excluded). For more details, please refer to our supplementary materials.

3.4 Results

During the first experiment, participants perceived coherent motion for a longer total amount of time than component motion (21.03 ± 21.83 sec compared to 8.06 ± 8.03 sec (mean ± standard deviation); paired t-test: $t(10)=2.16$, $p = .056$, $d = 0.65$). Coherent motion was also dominant in the second experiment ($t(18) =4.61$, $p < .001$, $d = 1.06$), but percepts switched faster (percept durations of 14.77 ± 6.65 sec compared to 7.57 ± 4.41 sec (mean ± SD) for coherent and component motion respectively). The duration of percept was calculated

between a button press and the corresponding lift and revealed the typical unimodal and positively skewed distribution when plotted as histograms (not shown).

3.4.1 Blinks (Experiment 1 and 2)

During the first experiment, participants blinks on average 11.12 ± 5.39 (SD) times per minute with a mean duration of 136.80 ± 26.80 ms (SD). For the second experiment, the blink rate was 12.09 ± 8.83 (SD) blinks per minute with a mean blink duration of 171.32 ± 46.47 ms (SD). Furthermore, we calculated the blink rate separately for the different percepts taking into account the respective percept durations. During both experiments, participants blinked significantly more during coherent motion than during component motion (experiment1: $t(10) = 5.56$, $p < .001$, $d = 1.68$; experiment 2: $t(18) = 4.86$, $p < .001$, $d = 1.12$) (Fig. 1B,C). Blanks were slightly shorter than blinks in both experiments with a mean length of 125 ± 19 ms (SD) and 141 ± 19 ms (SD) respectively.

a) b) c)

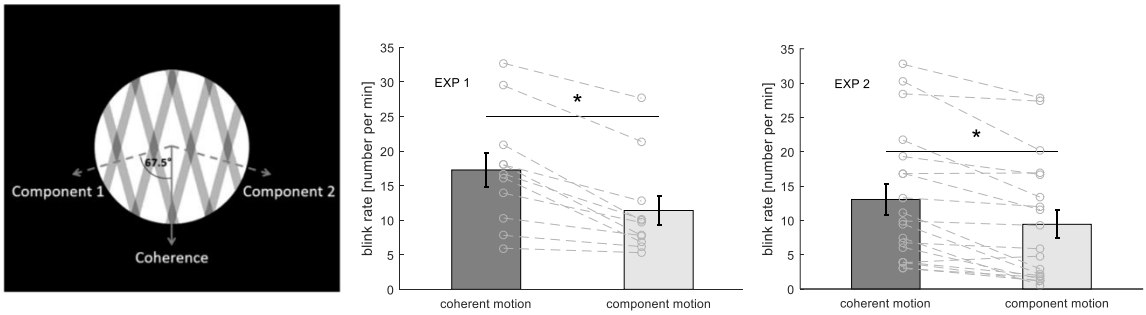


Figure 12. A. Stimulus representation B. Blink rate during the different percepts in experiment 1. C. Blink rate for the different percepts in experiment. Bars and error bars represent mean ± standard error of the mean (SEM). Gray lines represent data of individual participants. An asterisk marks a significant difference at $p < .001$.

To investigate if a change in perception is linked to a blink event, we looked at the normalized blink rate around perceptual switches, separately for switches to coherent and

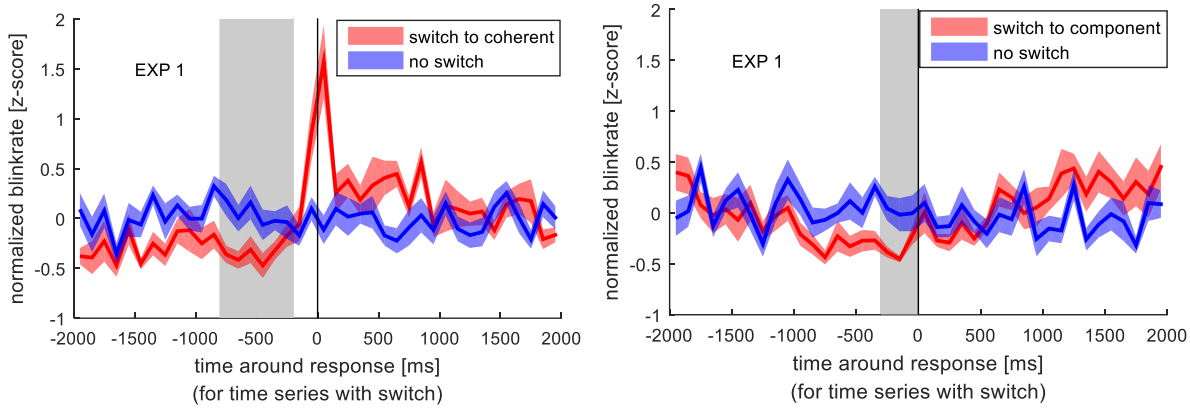
component motion and statistically compared it to the normalized blink rate when no switch occurred. The same was done for the normalized blank rate. This was done to assess if any influence was introduced by the visual consequences of the eye closure during a blink, as mimicked by the blank. Normalized blink rates were taken from trials without blanks or microshifts, but were combined over stimulus rotations. Please note that no p-values are reported due to the non-parametrical statistical testing that was applied (Maris and Oostenveld (2007).

When switching to coherent motion, there was a significant decrease in blink rate between -800 and -200 ms before the button lift (indicating a perceptual switch) in the first experiment compared to time periods with no switch. This decrease was replicated in the second experiment, where we found significant differences between -700 and -400 ms (Figure 13). When switching to component motion, such a decrease in blink rate was found in the first experiment (-300 to 0 ms before the switch), but did not reach significance in the second experiment, although a decrease before the switch is clearly visible. Interestingly, blink rate strongly increased around the time of a response indicating a switch to coherent motion, possibly at the time of the perceptual switch. This peak in blink rate is clearly visible in both experiments, but statistical comparison between blink rate around a switch and around no switch only reached significance in the second experiment between 300 and 600 ms after the response.

In contrast to the blink rate modulation, blanks, albeit again showing the strongest effect for switches to coherent motion, showed a different temporal pattern. As shown in Figure 14, the blank rate increased before the switch to coherent motion in experiment 1, which was even more pronounced in experiment 2. This increase in blank rate around the switch to coherent motion was significantly different from the blank rate around no switch

between -900 and -500 ms before the response in the second experiment. . This pattern was not visible when switching to component motion. When looking at the different stimulus rotations separately, all patterns were very similar which means that the effect of blanks and blinks are independent of the movement direction of the stimulus (see supplementary material).

a) b)



c) d)

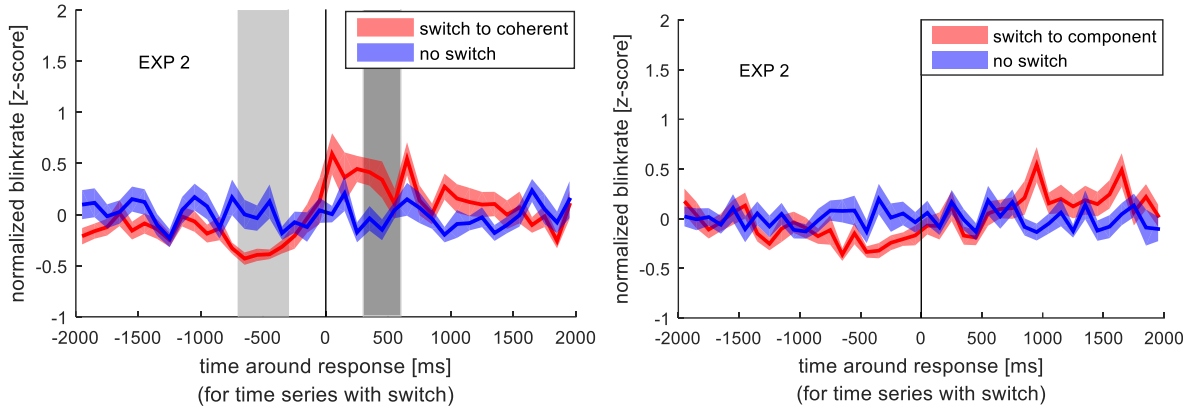


Figure 13. Normalized blink rate around the response indicating a perceptual switch (red) compared to the normalized blink rate during no switch (blue). Colored lines and ribbons represent mean ± standard error of the mean (SEM). Vertical shaded areas mark significant time points revealed by the non-parametrical statistical test procedure described by Maris & Oostenveld (2007). A. Switch to coherent motion in experiment 1. B. Switch to component

motion in experiment 1. C. Switch to coherent motion in experiment 2. D. Switch to component motion in experiment 2.

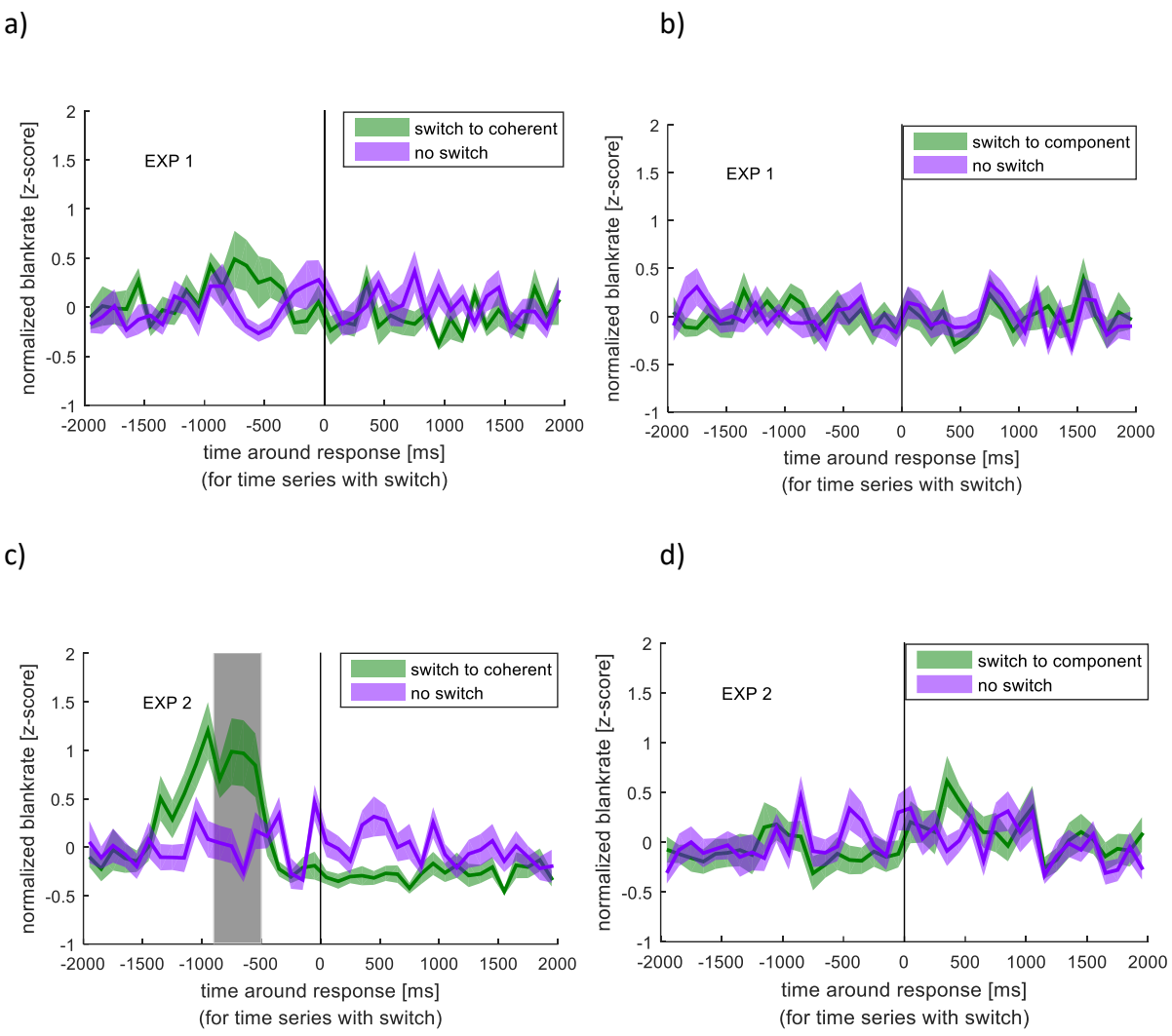


Figure 14. Normalized blank rate around the response indicating a perceptual switch (green) compared to the normalized blank rate during no switch (purple). Colored lines and ribbons represent mean ± standard error of the mean (SEM). Vertical shaded area marks significant time points revealed by the non-parametrical statistical test procedure described by Maris & Oostenveld (2007). A. Switch to coherent motion in experiment 1. B. Switch to component motion in experiment 1. C. Switch to coherent motion in experiment 2. D. Switch to component motion in experiment 2.

3.4.2 Microsaccades (Experiment 2)

Due to the low sampling frequency of the eyetracker used in experiment 1, we were only able to analyze microsaccades in the second experiment.

Over all trials and participants, we found a microsaccade rate of 1.39 ± 0.40 per second (mean ± SD). Looking at the different percepts, a paired t-test revealed that participants had a significantly higher microsaccade rate during coherent motion (1.42 ± 0.40 per second) than during component motion (1.29 ± 0.38 per second; $t(18) = 2.43$, $p = .026$, $d = 0.56$) taking into account the respective percept durations. Coherent percept is therefore associated with a higher microsaccade rate as well as with a higher blink rate as compared to the component percept.

Similar to the comparison of normalized blink rate around perceptual switches and no switches, we looked at the differences between normalized microsaccade rate around switches and no switches. To assess the specific influence of the visual shift accompanied by a microsaccade (as mimicked by the microshift), we compared microshift rate around switches and no switches (Figure 15).

Similar to the blink rate decrease before a switch, we found a significant decrease in microsaccade rate between -300 and 0 ms before the switch to component motion. However, such a decrease was not visible before a switch to coherent motion. Microshifts showed a different pattern, which resembles the blank rate pattern in respect to the increase before a switch to coherent motion, but the difference between normalized microshift rate before or after any switch compared to no switch was not significant.

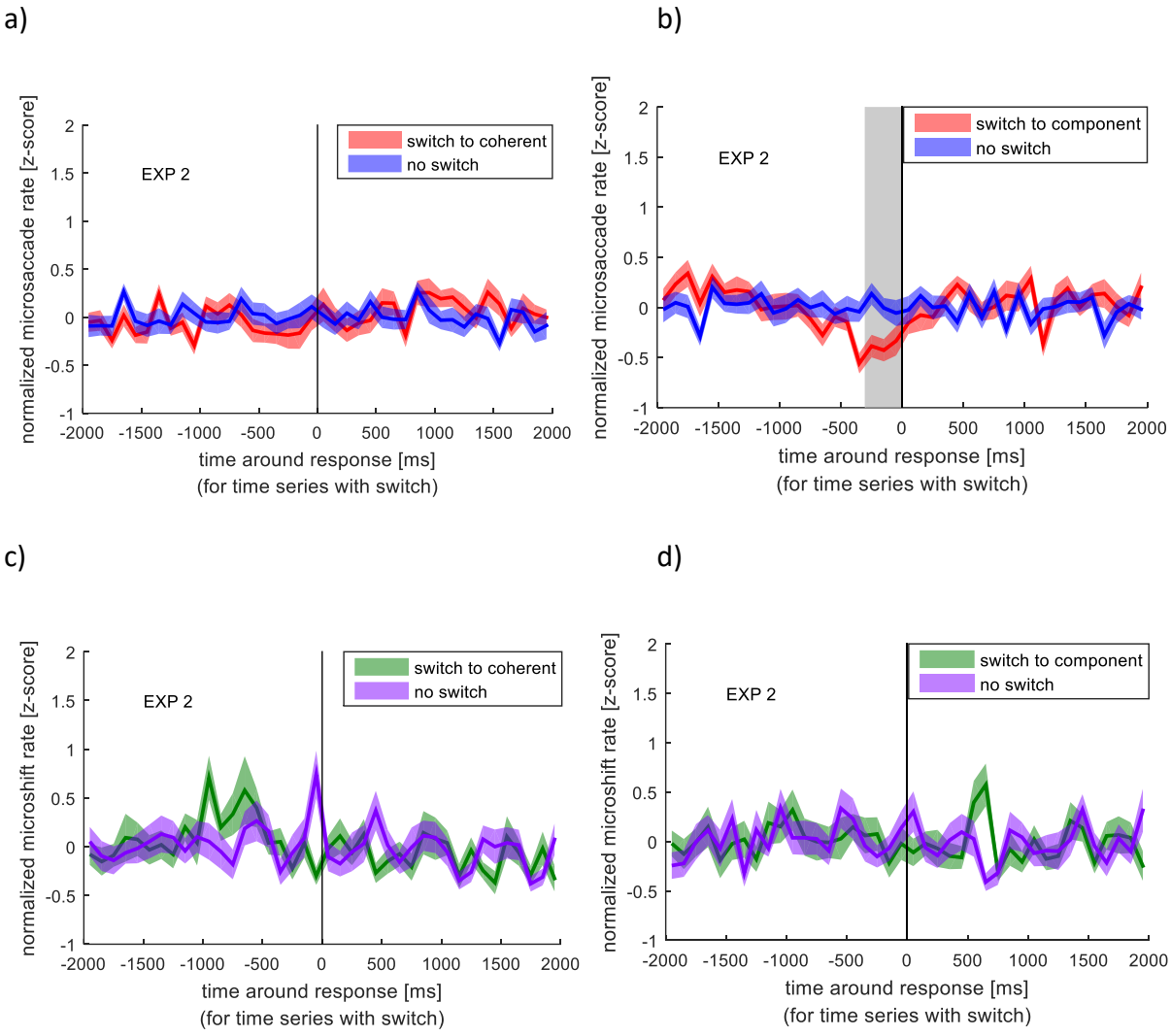


Figure 15. Normalized microsaccade/microshift rate around the response indicating a perceptual switch (red/green) compared to the normalized microsaccade/microshift rate during no switch (blue/ purple). Colored lines and ribbons represent mean ± SEM. Vertical shaded area marks significant time points revealed by the non-parametrical statistical test procedure described by Maris & Oostenveld (2007). A. Microsaccade rate around switch to coherent motion. B. Microsaccade rate around switch to component motion. C. Microshift rate around switch to coherent motion. D. Microshift rate around switch to component motion.

In addition to the analysis of microsaccade rate, we explored the direction of fast eye movements. During the perception of the stimulus, fast eye movements with typical

microsaccadic characteristics could be observed in the direction opposite to the stimulus motion. Independent of the percept, we found that the main direction of microsaccades was opposite to the coherent motion direction. After calculating the percentages of microsaccades for all directions in steps of 10° (Figure 16), we found 21.99 % of all microsaccades during coherent percept directed opposite to the physical movement of the coherent motion (180° ± 10°), but also 15.53 % during component percept share this direction.

Despite this clear dominance of the direction opposite to the coherent motion, there was an influence of the percept on the distribution of the microsaccade direction circumstantiated by the significantly higher percentage of microsaccades in this direction during coherent percept (mean ± SD: 21.99 ± 9.48%) than during component percept (15.53 ± 4.32%; $t(18) = 3.57$, $p = .002$, $d = 0.82$).

Accordingly, significantly more microsaccades were directed opposite to the component motions (112.5°±10° and 247.5°±10°) when component motion was perceived (12.70 ± 2.25%) compared to when coherent motion was perceived (8.63 ± 2.93%; $t(18) = -5.84$, $p < .001$, $d = 1.34$).

A B

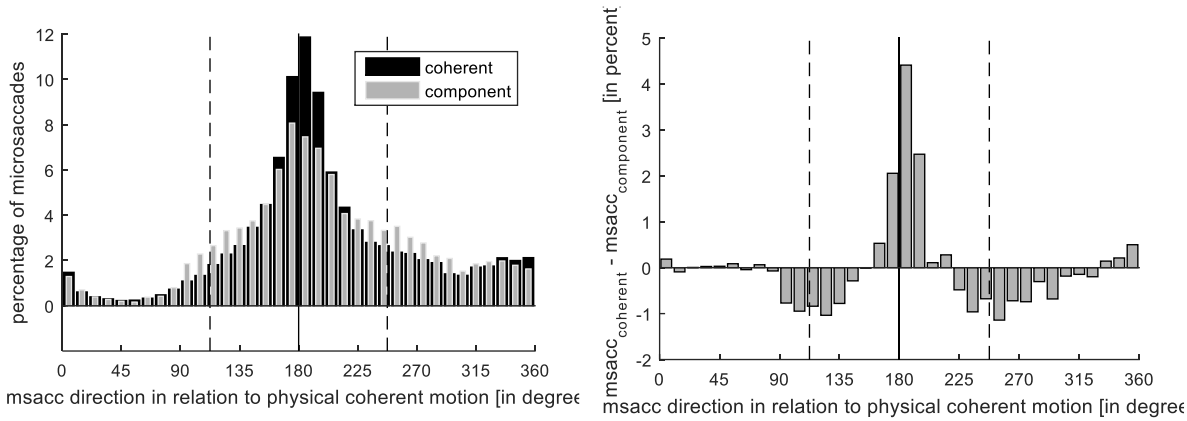


Figure 16. A. Microsaccade direction presented as microsaccade number in percent during coherent (black) and component motion (grey) perception, separately. The solid line marks the direction of the coherent motion, while dashed lines mark the directions of component motion. B. Microsaccade direction presented as the difference in microsaccade number during coherent motion and component motion perception in percent.

3.4.3 Relationship between eye blinks and microsaccades

Normalized microsaccade rate (within 50 ms bins) around external sensory changes (blanks and microshifts) and internally introduced sensory changes (blinks) is depicted in Figure 17 aligned to either blink or blank on- or offset. Microshifts consisted of a change between two frames, so the onset is equal to the offset. A pronounced reduction in microsaccade rate could be observed around all events. However, the microsaccade rate decrease started at different time points for external events (blank and microshift) compared to the internally introduced blinks. While the rate dropped immediately after the onset of the (unpredictable) blanks and microshifts, the decrease started already 200 ms before a blink. The quick closure and opening of the eye during a blinks can lead to the wrong detection of saccadic events. However, due to the observed long alteration in microsaccade rate around

blinks, our conservative exclusion of microsaccades 20 ms around a blink (see methods) is unlikely to have influenced this outcome.

Looking at the time after the onset of events, there was a clear peak in microsaccade rate at approx. 400 ms after blank onset, but not for microshifts or blinks. Note that the reduction before blink onset is a real rate modulation, while the low rate after blink onset is due to the fact that the eye is closed and therefore no microsaccades can be detected using a video-based eye tracker.

A B

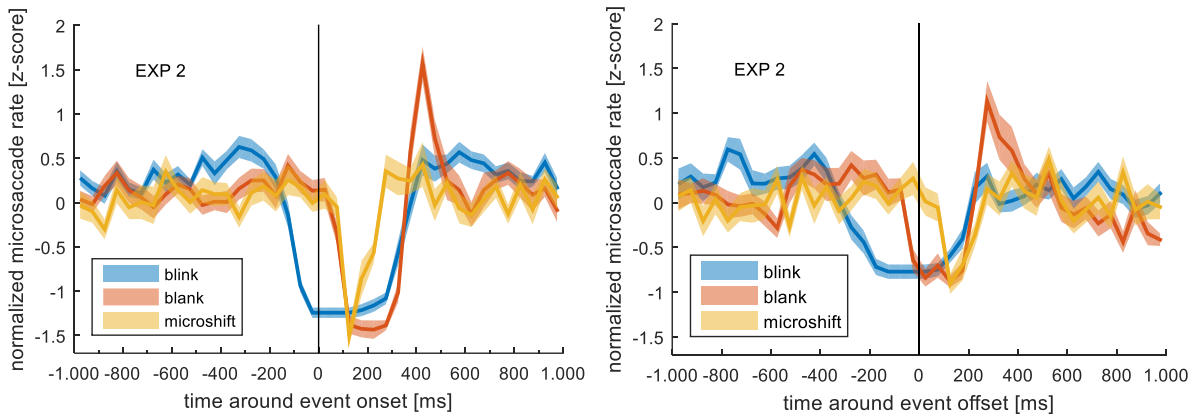


Figure 17. *A.* Normalized microsaccade rate around blink onset (blue), blank onset (red) and microshift (yellow). B. Normalized microsaccade rate around blink offset (blue), blank offset (red) and microshift (yellow). Colored lines and ribbons represent mean ± SEM.

3.5 Discussion (Study 2)

We examined the time-resolved rate of eye blinks and microsaccades during perceptual bistability of the ambiguous plaid stimulus. We found that eye blinks decrease before and increase after the reported perceptual switch depending on the percept. When examining the two types of perceptual switches (coherent vs component motion) separately, there was a difference in modulation, with only the switch to coherent motion being accompanied by an increase after the perceptual switch report. Microsaccades, also showed

a percept specific modulation in their rate, with a decrease specifically before the report of the switch to the component percept. Additionally, the distribution of microsaccade direction reflected the perceived motion direction. When mimicking the visual consequences of blinks and microsaccades, by introducing a transient visual interruption (blank) or a small shift of the stimulus (microshift), we found that a blank significantly facilitated a switch in percept, however, only towards coherent motion. Interestingly, a specific interaction between blinks, blanks and microshift was found with respect to the microsaccade rate. While all events led to a significant reduction in microsaccade rate, this reduction started notably before the onset of a blink. Additionally, a subsequent increase in microsaccade rate above the baseline was found only for the blank.

3.5.1 Overall rate changes

Independent of the fact that the length of the percept was significantly longer for coherent compared to component motion, we found a significantly higher overall rate of blinks and microsaccades for coherent motion. Our results further indicate that this difference might be explained by the modulation over time with respect to the switch event, as discussed below.

3.5.2 Temporal modulation of blinks dependent on the perceptual event

With regard to the time resolved modulation in blinks, the manual response indicating a switch was either preceded by a decrease or followed by an increase in eye blink rates depending on the type of percept subjects switched to. Previous studies have reported this modulation (Junji Ito et al., 2003; L. C. J. van Dam & R. van Ee, 2005, 2006) and have also found a percept specific influence of blinks (Nakatani et al., 2011; Otero-Millan et al., 2012)

Increase of blink rate after the indicated perceptual switch

An increase in blink rate occurred exclusively after the indicated switch to the coherent motion. The difference between the two percepts excludes several possible causes for the modulation of blink rate. Junji Ito et al. (2003) argue that blink modulation reflects response preparation. This has been further supported by, L. C. J. van Dam and R. van Ee (2005) who found that blinks increase, not just for the perceptual switch report, but also for random button presses. Similar results with regard to manual key presses, though in a different paradigm, were found by D. K. Cong et al. (2010), who showed that blinks are entrained by rhythmic finger tapping. The differences between the modulation of blinks around the two percepts in our study reveal that it is not a mere representation of the motor response and its preparation.

Another possible cause for the increase in blink rate is related to attentional processes. Many studies have found that at the end of an attentional period or at the end of task relevant information, there is an enhancement of blinking (Edmund Wascher et al., 2015). The reporting of the switch in our study could be considered the end of an attentional period or a task relevant perceptual event. In other words, to relate to the question of cause or consequence, it seems that blinks are a consequence of the coherent switch. However, this does not explain why the influence is specific to the coherent percept. It is, therefore, an interesting consideration that this difference in blinking reflects a difference in the internal process that underlies the two percepts. The two interpretations are not only quantitatively different (one motion direction vs two) but might also be qualitatively different, in the sense that, only the component motion might include an additional calculation of depth.

Another possible explanation could be related to the difference in perceptual dominance, which could bias attention towards one of the two precepts. However, previous findings do not support an interpretation based on perceptual dominance. Neither the

described idea that blinks lead to the preferred percept (Nakatani et al., 2011), nor the finding that a 'surprise' stimuli (which would correspond to the less likely non-preferred percept) causing a reduction in blinks (Bonneh et al., 2016) is consistent with our data. Nevertheless, the deviation in blink behaviour as revealed by our study suggests a difference in the internal process associated with the two perceptual switches. Many studies have shown that perceptual changes, based on a change in the sensory input, is associated with an increase in blink rate (Bonneh et al., 2016; Hoppe et al., 2018; Oh, Jeong, et al., 2012; Hideki Ohdra, 1995; Siegle et al., 2008). Such increase is further modulated by internal factors such as the interpretation of the sensory input as target or neutral stimulus (Brych & Händel, 2020). It is therefore an interesting observation, that the usually observed increase in blink rate is not present after a perceptual switch to component motion. It suggests a difference in the underlying mechanism or internal consequence of the two perceptual switches. While the subject is aware of the perceptual switch (and reports it), it seems not aware that the switch to coherent is resembling a real switch based on changing sensory input, whereas the switch to component motion does not. Therefore, blink behaviour is likely a marker to detect differences in percept related processes that are not necessarily evident from the subjective experience.

It is important to note that the exclusivity of the blink modulation for one specific percept was not due to differences in the physical direction of the perceived motion direction. We addressed this by changing the direction of the stimulus. This was done to understand 1) if the vertical movement of the eyes during a blink (Collewijn et al., 1985b) are linked to the perceived motion and 2) if the direction of the two motion percepts matters. It is known that the visual system is biased towards the cardinal directions, on a neuronal level and a perceptual one (Girshick et al., 2011; Schluppeck & Engel, 2010). If the coherent motion is

following a cardinal direction while the component one is not, this could cause the system to treat perceptual interpretations differently. However, we found that the direction of the perceived motion had no significant effect on the blinking pattern. Hence, the difference between the percepts is, most likely, not due to any preference of physical directions, but rather, due to some internal process.

Decrease of blink rate before the indicated perceptual switch

Our second main finding was a decrease in blink rate before the response indicating a switch. It is hard to tell if this decrease was percept specific, since it did not reach significance before the reported switch to component percept in the second experiment, albeit higher power. This could indicate a weaker or less stable effect compared to the switch to coherent motion.

In general, both perceptual changes are internal events in our task, which needed to be reported and therefore, should have drawn attention towards them. Studies have reported that people tend to suppress their blinks during moments of increased attention (Hoppe et al., 2018), and even before the onset of a task-relevant stimulus (Hoppe et al., 2018; J. A. Veltman & A. W. K. Gaillard, 1998). This suppression occurs even for stimuli outside the visual modality (Lance O Bauer et al., 1985), indicating the involvement of a more general, vision-independent attentional mechanism. The allocation of attentional resources caused by the switch in percept might have introduced the decrease in blink rate. This interpretation however would mean that the decrease happened as a consequence of the perceptual switch.

Another possibility is that the reduction in blinking is not only a result of the perceptual switch but also a likely cause. Indeed, increased fixation duration has been shown to lead to perceptual switching in other studies (Ellis & Stark, 1978) and since blinking interrupts fixation, the suppression of blinks might facilitate a perceptual switch. Unfortunately, it is

difficult to conclude with certainty as to which event, the switch or the reduced blinking, occurred first, simply because there was no objective measure of the internal perceptual switch itself. However, we have a strong indication as to when the perceptual switch happened by looking at the blank results (Figure 14). Here, it is clear that the blank must have introduced the switch and not the other way around. This allowed us to mark the period in which the perceptual switch likely occurred, namely between blank and response. Figure 13 clearly shows that the time of blink reduction before the perceptual switch overlaps with the time when the switch-introducing blank occurred. This indicates that the reduction in blink probability was not a result of the perceptual switch but temporally co-occurring. Interestingly, multi- second interruptions in ambiguous stimuli has been shown to stabilize percept (Leopold et al., 2002; Noest et al., 2007).

In summary, although one of our initial goals was to see if blinks act as a cause for perceptual switches due to their retinal consequences, we found that their role is different. Indeed, it is not the blink occurrence and the corresponding visual interruption that facilitates a switch, but rather the absence of a blink that does.

3.5.3 Modulation of microsaccades (rate and direction)

In experiment 2, we looked at the role of microsaccades in the ambiguous plaid stimulus and controlled for their retinal consequence by adding microshifts to the stimulus. We found that the overall microsaccade rate was higher for the coherent than the component percept. Additionally, we found a reduction in microsaccade rates specifically before the switch to the component percept. Please note that the discrepancy to other studies, reporting that an increase in microsaccades can introduce a perceptual switch, is most likely due to the different ambiguous stimuli used (Otero-Millan et al., 2012; Troncoso et al., 2008). These studies used the rotating snakes and the Enigma illusion, both of which alternate between

movement and stationary percepts. Hence, it is likely that microsaccades specifically facilitate a switch to a motion percept. The plaid stimulus, used in our experiments, does not have switches between movement and no movement percept, but involves switching between different types of motion. Using a more comparable ambiguous apparent motion stimulus a reduction before a perceptual switch has been reported before (Laubrock et al., 2008). These authors further argued that the microsaccade modulation might possibly precede the internal switch, indicating a possible causal role of microsaccades. As discussed above, we believe that our observed blank introduced perceptual switch is a strong indication as to when the perceptual switch happened with respect to the response, namely between -900 and -500 ms before the response (Figure 14). The timing of reduction in microsaccade rate as shown in Figure 15 (between -300 and 0 ms) therefore suggests that the effect happened between the perceptual switch and the response, given an average reaction time of about 500 ms to 700 ms to an actual external stimulus change (Baker & Graf, 2010; Laubrock et al., 2008; L. C. J. van Dam & R. van Ee, 2005, 2006). Although it is not possible to tell with absolute certainty if the decrease in microsaccade rate follows the internal switch, the decrease only before the response indicating a switch to component percept argues against a mere consequence of response preparation.

Interestingly, we found that the direction of microsaccades is linked to the direction of the ongoing percept. Specifically, as shown in figure 16, we found that while the overall direction was mainly opposite to the coherent motion, this proportion was reduced during component percept and at the same time, the proportion of microsaccades in the direction opposite to the two possible component motion directions was increased. Since the direction is opposite to the percept, it is likely that the percept draws the eyes in the direction of perceived motion and the detected microsaccade is a saccade back to the required position

of fixation. This could mean that the microsaccades we observe are some sort of small optokinetic nystagmus. (OKN), which is a well-known phenomenon that is triggered by moving background stimuli introducing optic flow. It consists of a slow phase in the direction of the optic flow and a short, fast jump back towards the center of the visual field. OKN is greatly reduced if visual fixation is demanded (Murphy et al., 1975). However, even during fixation of a stationary target, small eye movements, affected by a moving background, can be observed. For instance, Re et al. (2019) found that microsaccade directions are influenced by and correspond to the direction of moving dot clouds that are attended during fixation. While Laubrock calls them “OKN-like rudiments” (Laubrock et al., 2008), Pola and colleagues note that these residual movements have a rather complex relationship with the OKN (Pola et al., 1995). Further studies will need to clarify if the direction of microsaccades are a consequence of the percept or lead to the specific perceptual interpretation. What, however, is clear from our results is that, the microsaccade direction and the perceptual interpretation of sensory input are not independent from each other.

3.5.4 The effect of external events: blanks and microshifts

Blanks and microshifts are external events that were initially planned as controls for the visual consequences of blinks and microsaccades. Interestingly, they have a different effect on perceptual bistability compared to their corresponding eye movements. One main finding was that the blanks introduced a switch to the coherent motion in experiment 2. Please note that the effect is also visible in experiment 1 (Figure 14), but the lower power in experiment 1 might have prevented significance. Two questions arise through the finding: 1. Why do blanks but not blinks introduce a switch despite their similar visual consequences and 2. Why do blanks specifically introduce a switch to the coherent percept?

With regard to the first question, one should bear in mind that even though blinks and blanks have a similar consequence on the retinal image, they are intrinsically different (Deubel et al., 2004; Golan et al., 2018b; Higgins et al., 2009). Deubel et al. (2004) found that adding a blank after a saccade can counteract the reduced detection of target displacement due to saccadic suppression, but a blink after a saccade does not have the same effect. A similar finding was also reported for blink suppression, wherein introducing a blank period after a blink reduces the displacement suppression. The idea is that an external interruption due to a blank introduces a need to recompute the post-saccadic target location; whereas, if the interruption is due to a blink, no such need is generated (Higgins et al., 2009). In other words, interruptions or small changes during blinks are generally ignored (Maus et al., 2017). This means that the oculomotor system treats an internal event such as a blink, differently from a blank. A difference between the two is also found on a neural level. A higher activity in several visual areas have been reported for blanks, but not blinks (Gawne & Martin, 2000, 2002; Golan et al., 2018b) and blinks (both voluntary and spontaneous) along with self-initiated blanks are associated with a decrease in activity in higher visual areas; whereas unpredictable external darkening cause an increase in higher level areas (Golan et al., 2018b). A difference in perceptual consequence following a blink vs. a blank is, therefore, not surprising. Moreover, we must note that, in our experiments, there is also an additional difference between the two, namely that the blank causes interruptions in the stimulus, and not the entire visual scene like a blink.

However, the specificity of the perceptual change due to a blank, is somewhat surprising. Blanks often led to a switch to coherent percept. This was the preferred interpretation of the stimulus. This could indicate that if a certain interpretation of a sensory input is preferred, anything that causes one to reassess/ recompute the input will tend to

switch the perceptual interpretation to the preferred one. Once we reach this preferred perceptual interpretation we are more likely to blink, assuming that all relevant information has been assessed. It is important to point out that our findings might be specific for the ambiguous plaid stimulus where the two percepts are clearly based on different internal processes. While the component percept interprets the stripes separately due to different depth, the coherent percept is based on an integration over the two stripe stimuli. The investigation of other bistable stimuli can clarify this specificity.

With regard to microshifts, we did not find a significant modulation. This suggests that any possible effect of microsaccades is not due to the visual perturbation they introduce.

3.5.5 Modulation of microsaccade rate around internal and external events

We found that the microsaccade rate, albeit mostly constant around perceptual switches, was modulated around blanks, microshifts and blinks, but with a difference in temporal dynamics around the internal (blinks) versus the external (microshifts and blanks) events. Specifically, though there was a continued microsaccade reduction for approximately 250 ms after the event offset, this decrease started only after the onset of external events, but clearly before the onset of the internal event.

With regard to the blanks, the modulatory pattern introduced by the blank followed the typical microsaccade rate signature, characterized by a decrease, followed by an increase and a return to baseline (Bonneh et al., 2016). This modulation has been observed during other tasks and was suggested to be the reaction to sudden changes in visual input, such as display changes as well as to internal attention capturing processes (Betta & Turatto, 2006; Engbert & Kliegl, 2003; Gao et al., 2015; Pastukhov et al., 2013). Our blanks interrupted the visual information intake likely leading to a reassessment of visual input, which required the allocation of attention. However, microshifts and blinks did not show an increase in

microsaccade rate after the decrease. A possible explanation stems from the fact that during the shift, there still is visual input, whereas during the blank, there is no visual information at all, which might generate a stronger need for reevaluation. This again would not happen after a blink, since a blink is self-introduced and provides no reason to assume that the input has changed. With regard to the internal blink event, we found that the actual decrease started earlier than for the external events, namely around 200 ms before blink onset. It has been shown that microsaccades are suppressed when there is an expected visual stimulus followed by a response (Betta & Turatto, 2006). An expected change in sensory input due to a blink could trigger the same mechanism. However, it must be noted that the suppression reported by Betta and Turatto (2006) was specific to sensory information that should trigger a motor response and therefore, be linked to response preparation, as argued by the authors. The predicted sensory change caused by a blink is not task relevant and is, as mentioned earlier, ignored by the system. That no microsaccades were detected during a blink is a result of our video-based eye tracker, where it is not possible to detect microsaccades when the eyes are closed. We conclude that, although the reason for the suppression of microsaccades before blink onset is not certain, our findings clearly indicate an interaction between blinks and microsaccades.

3.5.6 Conclusion (Study 2)

Our study on blinks and microsaccades during a visual bistable task indicates that the execution of these eye related movements is related to internal perceptual processes, and that these movements influence each other's probability. The fact that different perceptual interpretations of the same sensory input are accompanied by a different eye movement pattern further suggests a difference in the internal process associated with the two perceptual switches. Such a difference is not evident from the subjective perceptual

experience. The analysis of eye movements can therefore differentiate between distinct cognitive processes that might otherwise go undetected. Additionally, our findings suggest that eye movements might play a role in stabilizing percept.

3.6 Supplementary Material (Study 2)

Details on microsaccade detection

We detected saccades based on an algorithm described by Engbert and Kliegl (2003). We further excluded all saccades which had a logarithmic peak velocity more than three absolute deviations away from the median (Leys et al., 2013a). As an example, Figure S13a shows the peak velocity plotted against the amplitude of all detected saccades in one trial of one participant. The excluded saccades based on peak velocity are marked by yellow stars. We further marked those events detected as saccades, which happened within 20 ms of a blink (Figure S13a, red crosses). These events show a much larger amplitude with higher peak velocity compared to other saccades. Additionally, they primarily show a downward direction when happening before the blink and an upward direction when happening afterwards (Figure S13b). This suggests, that these detected events are of different nature than saccades during undisturbed gaze and rather blink-induced. Importantly, our analysis regarding saccadic eye movements was confined to microsaccades, which were defined by a maximal amplitude of 1°. Only 0.2% of microsaccades were excluded by the velocity criterion and additional 0.01% were excluded around blinks (Figure S13c).

a) b) c)

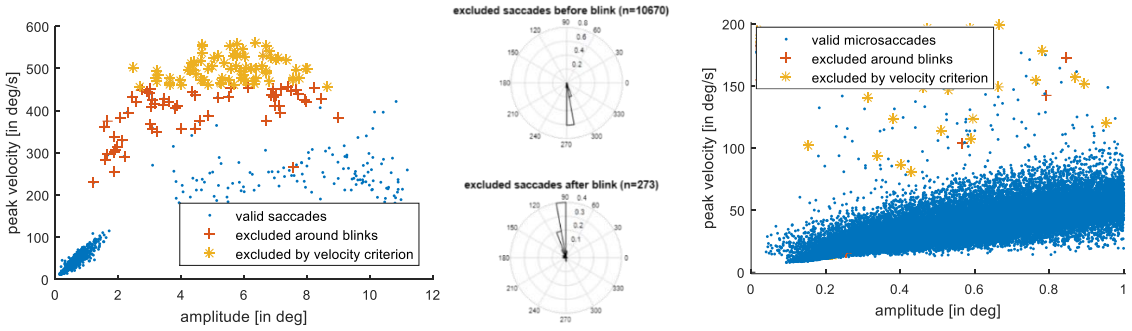


Figure S13. A. Example of saccade detection in one trial of one participant. Yellow dots mark saccades, which were marked based on the velocity criterion. Red crosses mark saccades, which were detected ± 20 ms around a blink. Blue dots represent valid saccades. B. Direction of detected saccades 20ms before or after a blink of all participants. C. Microsaccade detection of all trials and all participants.

Additional blink results

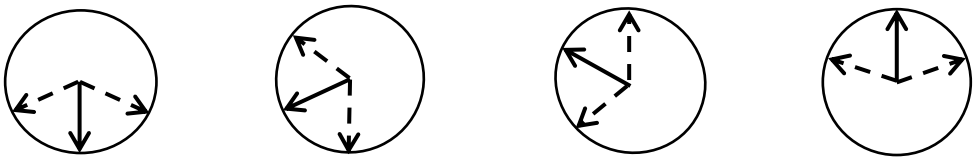
In addition to the analysis of the normalized blink/blank rate around perceptual switches averaged over stimulus rotations, we present the data for the four different stimulus rotations separately for experiment 1 (Figure S14) and 2 (Figure S15).

Following the significant effect of blink increase after the response indicating a perceptual switch to coherent motion, there is a clear increase for all four rotations. Similarly, all rotations show a decrease before the perceptual switch, however, as expected from the averaged results, this decrease is more pronounced for switches to component percept. We therefore assume that blink related effects are independent of the movement direction.

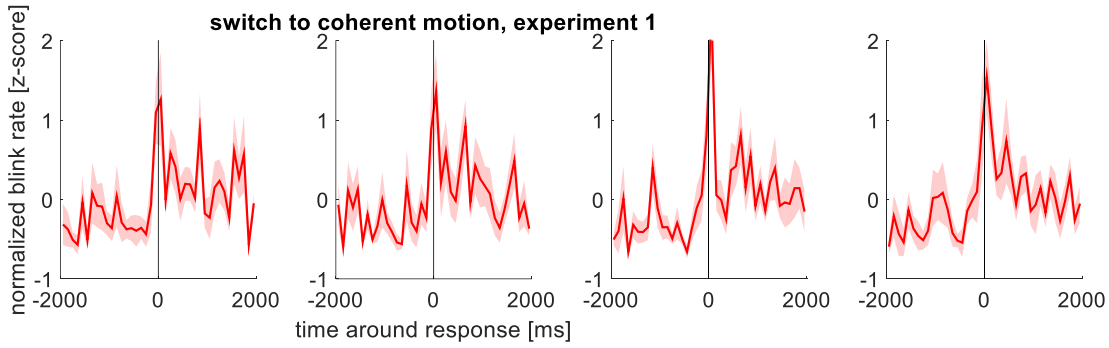
The effect of blanks on the perceptual switch is prevalent for switches to coherent motion only, as expected from the analysis of the averaged data, but the effect seems to be

mostly confined to downward motion of one component in experiment 1 (see second subplot of Figure S14d) . However, experiment 2 again shows a motion direction independent effect. Please note that rotations 22.5° and 90° (two right most rotations in Figure S15) were chosen because of the prevalence of microsaccades in the horizontal direction and therefore could include microshifts, but not blanks.

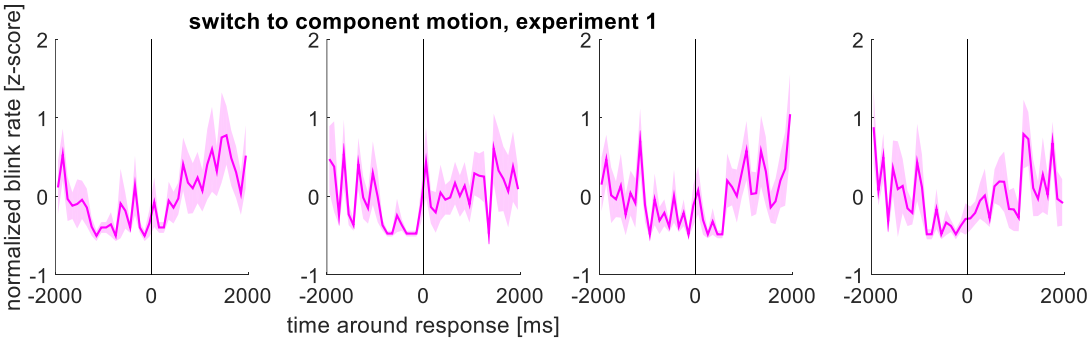
A



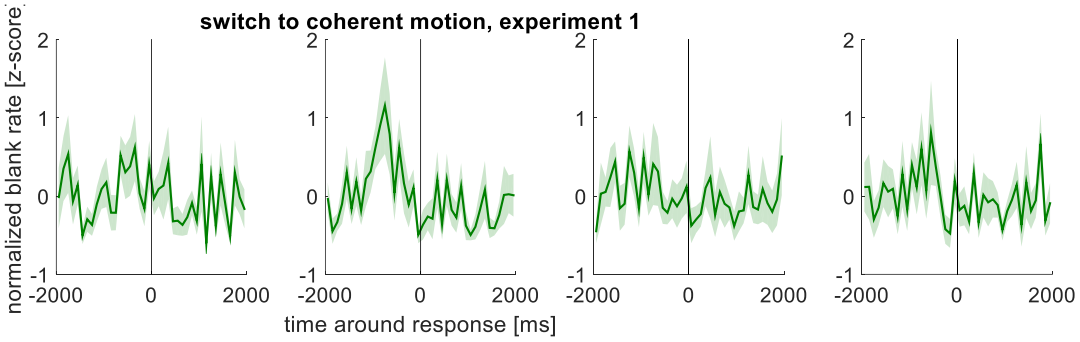
B



C



D



E

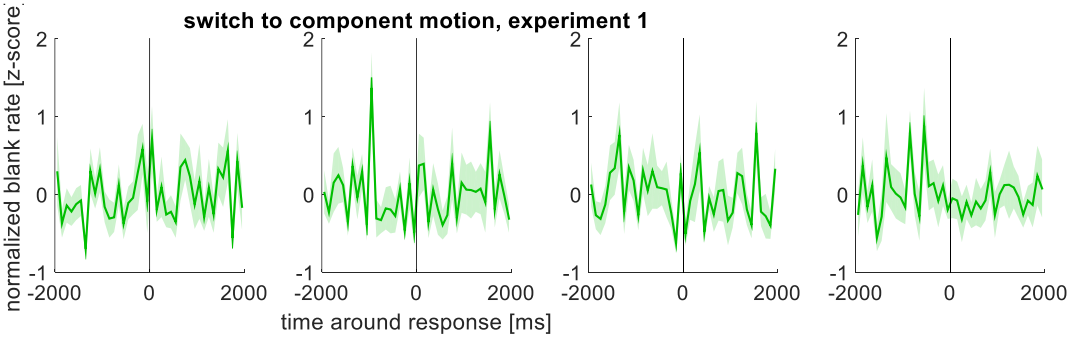
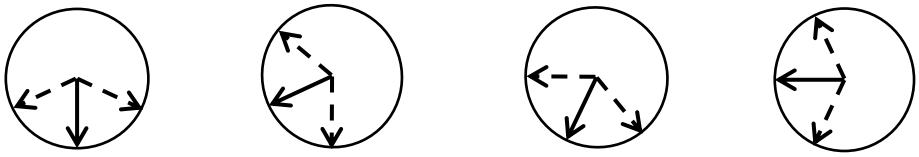


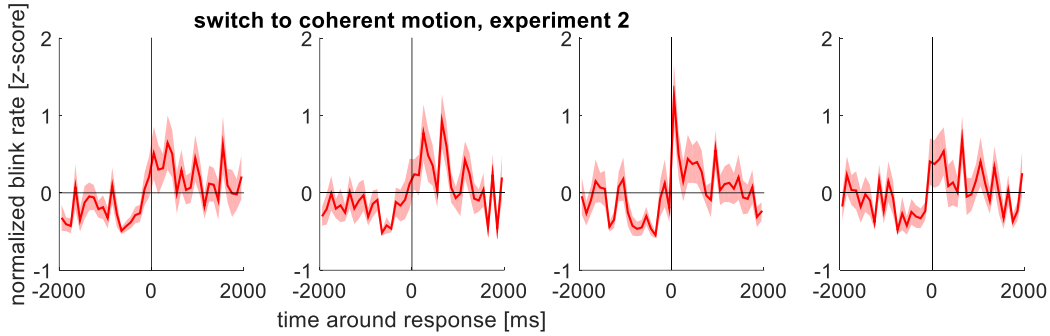
Figure S14. Normalized blink/blank rate separated for the four different stimulus rotations in *experiment 1*. A. Stimulus illustration for the rotations 0°, 67.5°, 112.5° and 180° (from left to right). Solid line represents direction of coherent motion, dashed lines represent direction of component motion. B. Normalized *blink* rate for the four rotations separately when a switch to coherent motion occurred. The mean is presented in the main manuscript in Figure 14a. C. Normalized *blink* rate for the four rotations separately when a switch to component motion occurred. The mean is presented in the main manuscript in Figure 14b. D. Normalized *blank* rate for the four rotations separately when a switch to coherent motion occurred. The mean is presented in the main manuscript in Figure 15a. E. Normalized *blank* rate for the four rotations separately when a switch to component motion occurred. The mean is presented in the main manuscript in Figure 15b.

3. Study 2 (Supplementary)

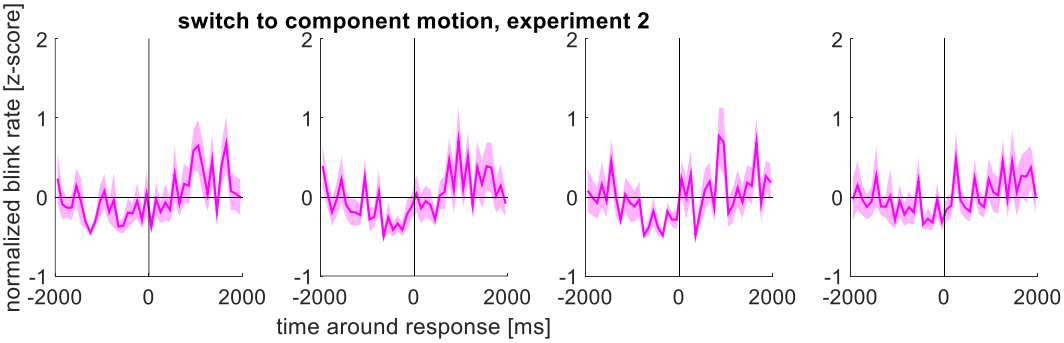
A



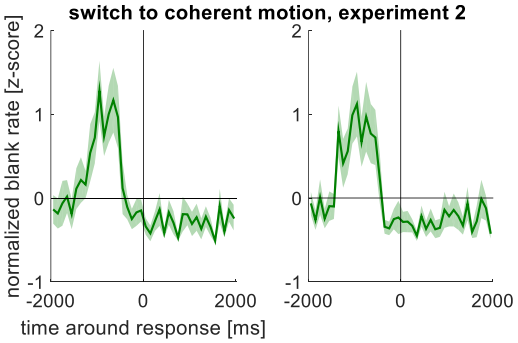
B



C



D



E

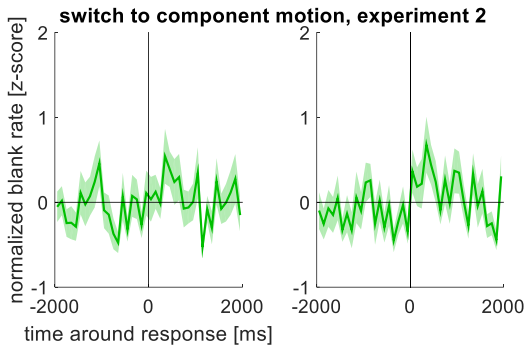


Figure S15. Normalized blink/blank rate separated for the four different stimulus rotations in *experiment 1*. A. (From left to right) Stimulus illustration for the rotations 0°, 67.5°(blank trials), 22.5° and 90° (microshift trials). Solid line represents direction of coherent motion, dashed lines represent direction of component motion. B. Normalized *blink* rate for the four rotations separately when a switch to coherent motion occurred. The mean is presented in the main manuscript in Figure 14c. C. Normalized *blink* rate for the four rotations separately when a switch to component motion occurred. The mean is presented in the main manuscript in Figure 14d. D. Normalized *blank* rate for the two rotations separately when a switch to coherent motion occurred. The mean is presented in the main manuscript in Figure 15c. E. Normalized *blank* rate for the two rotations separately when a switch to component motion occurred. The mean is presented in the main manuscript in Figure 15d.

4. Study 3: Spontaneous eye blinks modulate the probability of a perceptual reinterpretation during visual and auditory ambiguity

Spontaneous eye blinks are modulated around perceptual events. Our previous study, using the ambiguous plaid, indicated that blinks decrease before the reported switch. In the current study, we replicated these findings for the auditory domain and excluded an influence of the motor response and the visual consequences of blinking. Importantly, we tested our hypothesis whether an absence of blinks facilitates switches. Using three experiments involving the visual motion quartet (in light and darkness) and a bistable auditory streaming stimulus, we found a significant decrease in blink probability before the perceptual switch report in all three experiments. Through the timings of short interruptions in the visual stimulus that we introduced, termed blanks, which are accompanied by modulations in blinks and switches, we could estimate the time of the internally generated perceptual switch. We deduced that the decrease in blink rate possibly occurred before the internal switch. Importantly, by showing that the duration of switch to blink was significantly longer than the inter-blink interval, our study indicates that the absence of a blink facilitates a perceptual switch within and outside vision. Importantly, we discuss the role of attention during the reduction of blinking as an important influence and also propose that blinks might stabilize percept since they mark the end of the attentional period. Our study supports the idea that blinks can influence perceptual processes independent of the modality. From our work, we further derive the novel hypothesis that blinking stabilizes the perceptual interpretation of the sensory input.

4.1 Introduction (Study 3)

Spontaneous eye blinks are modulated around perceptual events introduced by visual and auditory input (Oh, Han, et al., 2012; Oh, Jeong, et al., 2012) or in expectancy or prediction of sensory input (Y. Bonneh et al., 2015; Brych & Händel, 2020; Hoppe et al., 2018). This modulation is further enhanced by internal processes like endogenous attention allocation towards visual (Hoppe et al., 2018; Hideki Ohdra, 1995; Siegle et al., 2008) and auditory (Lance O Bauer et al., 1985; O. S. Kobald et al., 2019) stimuli. A widely accepted explanation for the found pre-stimulus (if predictable) and stimulus induced decrease and the post-stimulus increase in blinking is that the system suppresses blinks during sensory input (and in preparation of it) and blink rate increases above baseline after this period. While this makes sense considering vision, as the closed eyes during a blink cannot receive input, it is rather puzzling for auditory input. Similarly, it is not obvious why a blink modulation is observed around perceptual switches of ambiguous stimuli where the perception is not based on external sensory changes (Brych et al., 2021; Junji Ito et al., 2003; L. C. van Dam & R. van Ee, 2005, 2006). The question if blinks, especially those modulated independent from sensory input serve a function is not known and subject of the present work.

Previous research that has observed a modulation of blinks around internally generated perceptual switches, have either argued that blinks are a consequence of the perceptual task (L. C. van Dam & R. van Ee, 2005) or that blinks facilitate perceptual switches (Junji Ito et al., 2003; Nakatani et al., 2011; Otero-Millan et al., 2012). Junji Ito et al. (2003), for instance, found that in a version of the Attneave's triangle blinks decrease before and increase after the response indicating a perceptual switch (Attneave, 1968). According to the authors, the decrease was a result of the effort required to complete the task, and the

increase was mediated by the relaxation after the response. Similar results were found by van Dam & van Ee (2005,2006) using a slant rivalry stimulus. After additionally finding increased blinking after random button presses, the authors concluded that blinks do not influence the percept but rather increase after a task relevant event.

Contrary to the aforementioned results, a study by Nakatani et al. (2011) indicated that blinks can trigger a perceptual switch to the preferred interpretation in the Necker cube. According to these authors, this could have been mediated by the visual interruptions brought about by blinks, leading to a detaching and reorganizing of attention. Similarly, Otero-Millan et al. (2012) reported that blinks facilitate switching to the rotating percept in the rotating snake illusion. They argued that the resetting of the retinal image after a blink triggers motion signals. In contrast to that, we previously found that a switch between two ambiguous motion states was rather preceded by a decrease in blinking (Brych et al., 2021). Overall, the findings concerning internal perceptual switches in ambiguous stimuli and the role of blinking are divergent. Additionally, motor responses were mostly not well differentiated from the perceptual event, the sensory consequence of blinking was not assessed and only the visual domain has been investigated so far.

In the current study, we set out to answer the following question:

1. Can we replicate our previous findings suggesting that a reduction in blinks precedes perceptual switches possibly facilitating them?
2. Is the influence of blinks linked to its visual consequence? In other words, would the role of blinks differ between different lighting conditions?
3. Can we find similar evidence for blink related perceptual switching for auditory bistability?

4. Is the modulation of blinks around perceptual changes mediated by the motor response?

To answer these questions, we compared the influence of blinks in complete darkness to normal light conditions and investigated a visual as well as auditory ambiguity paradigm. We used the ambiguous motion quartet in normal light or absolute darkness (Experiment 1 and 2) and the auditory ambiguous streaming stimulus (Experiment 3).

The motion quartet, also known as Stroboscopic alternative motion (von Schiller, 1933), is an ambiguous motion stimulus that consists of dots in opposing diagonals of an imaginary quartet that seem to be moving either horizontally or vertically. This specific stimulus allowed us to produce the ambiguous percept either conventionally, using a screen in a normally lit environment (Experiment 1), or with simple LED lights in an otherwise completely dark environment, minimizing the visual consequence of a blink (Experiment 2). To specify the timing of the motor response as well as the timing of the blink rate modulation with respect to a temporally unknown perceptual event, we added unpredictable short pauses to the visual input. In a previous experiment (Brych et al., 2021), we could show that such interruptions lead to perceptual switches thereby serving to estimate reaction times. To test if blink modulation is mediated by the motor response, we additionally analyzed blink rates around random key presses in complete darkness. Finally, to investigate the generalization of effects across modalities, we used an auditory streaming stimulus (Van Noorden, 1975), which is an ambiguous stimulus that can be interpreted as one rhythmic tone or two separate auditory streams (Experiment 3). To our knowledge, the only previous study that did look at auditory bistability and eye movements, focused on pupil dilation (Einhauser et al., 2008).

Our results showed that while blanks triggered switches, a refrainment from blinks likely facilitated switches in both modalities and independent from the lightning condition. Since other studies had found that blink reduction could be indicative of attentional processing, we discuss the role of attention in this influence and additionally propose that blinks could reflect the end of the attended period and stabilize percept.

4.2 Methods

We conducted three different experiments. Experiments 1 and 2 involved the visual ambiguous motion quartet in normal light and complete darkness respectively. Experiment 3 involved an auditory bistable streaming stimulus. Participants gave their written informed consent and either received study credits or payment for their participation in all experiments. The study was conducted according to the European data protection rules (DSGVO) and was approved by the local ethics committee (Ethik-Kommission des Instituts fuer Psychologie der Universität Würzburg). In the following sections, we describe the set up and procedure for each of the experiments.

4.2.1 Experiment 1: Motion Quartet in normal light

Participants and stimulus

Eighteen subjects participated in this experiment. The stimulus was displayed on a NEC MultiSync LCD1770NX monitor with a refresh rate of 60 Hz and a resolution of 1280*1024 pixels (33 * 27cm). The subject was seated 50 cm away from the screen with their head fixed using a chinrest, in a normally lit room. The stimulus consisted of 4 circles (diameter=30 pixels) that were presented alternatingly on opposing diagonal ends of an invisible rectangle of size 256*512 pixels or 7.6*15.4 degrees (width*height), and a central fixation circle (of 10 pixels).

We used a rectangular formation for the stimulus, since ambiguous motion quartets are usually biased towards the vertical percept (Boeykens et al., 2019; Genç et al., 2011; Gengerelli, 1948). One way to reduce this bias is to increase the distance between the vertical dots and decrease the distance between the horizontal ones.

Each diagonal pair was presented alternatively for 0.45s, with no pause between the alterations. The resulting perception was of two dots moving either horizontally or vertically (shown in Figure 18a).

Experimental design

There were a total of 10 trials of 5 minutes each. In five of these trials, transient interruptions in the stimulus referred to as 'blanks' were included, wherein we blackened the screen for a randomized duration between 0.1 to 0.2s and unpredictable onsets. The rate was about 10 per minute (leading to a blank between every 5 to 7 seconds). Duration and rate of these blanks was based on an averaged value of blink duration and rate as described in our previous study (Brych et al., 2021). Participants were not informed about the blanks. The trials (with or without blanks) were presented in a randomized manner for each subject. The task for the subjects was to continuously press one of two keys assigned to each percept, using one finger of the dominant hand, to indicate their percept. Indicating a perceptual change would require subjects to release one key first and then press the other.

4.2.2 Experiment 2: Motion Quartet in complete darkness

Participants and stimulus

Thirty-two subjects participated in this experiment. One subject was excluded because in the time-resolved analysis of blink rate around switches shown in Figure 19 and switch rate around blanks shown in Figure 24, there was data in only one of the time-windows.

The stimulus was created using 5 LED lights of diameter 4mm, placed on a metal frame with magnets. The participant sat at a distance of 50 cm from the stimulus with their heads resting on a chinrest. The central LED acted as the fixation cross and the remaining 4 LEDs were placed in the 4 corners of an imaginary rectangle of 5*10 cm (width*height). We again used a rectangular formation to reduce the vertical bias. Similar to Experiment 1, each diagonal pair of LEDs was alternatively switched on for a period of 0.45s (Figure 18a).

The experimental room was completely dark as we used a light-tight EEG booth with internal ventilation. Additionally, the infrared light of the eye tracker did not extend into the visible range, all internal light sources were turned off or carefully wrapped in light-tight material and no light could be detected even after staying 10 minutes inside the room.

Experimental design

Similar to experiment 1, we had 10 trials of 5 minutes, with five trials containing blanks and the other five containing an uninterrupted presentation of the stimulus. Trials were randomized for each subject. Blanks (wherein all 5 LEDs were shut of) were added the same way as for Experiment 1, with a randomized duration between 0.1 to 0.2s, an unpredictable onset and at a rate of 10 per minute (between every 5 to 7 seconds). Participants were not

informed about these blanks. The task, similar to experiment 1, was to continuously press one of two keys, using the one finger of the dominant hand, to indicate the percept.

4.2.3 Experiment 3: Auditory streaming

Participants and stimulus

Twenty-six subjects participated in this experiment. Two participants were excluded for having a very low switch rate (<1 per minute).

The auditory input was presented using a Sennheiser PC3 headset along with the Steinberg UR22mk II external soundcard for timing precision. The stimulus consisted of a high frequency pure tone of 500 Hz, alternated by another low frequency pure tone of 300 Hz as shown in Figure 18b. The duration of each tone was 0.12s. The parameters of the stimulus were similar to previous studies (Almonte et al., 2005; Kondo et al., 2012; Pressnitzer & Hupé, 2005). The only visual input that was presented was a fixation cross displayed on the NEC MultiSync LCD1770NX monitor. Participants sat at a distance of 50 cm distance from the screen with their heads fixed on a chinrest.

Experimental design

The experimental design was similar to experiment 1 and 2. There were five trials of uninterrupted presentation of the stimulus. Blanks were not included for this stimulus, since their purpose was to test the influence of external interruptions to a visual stimulus. The task was for the participant to press one of two keys, with one finger of the dominant hand, to indicate their percept.

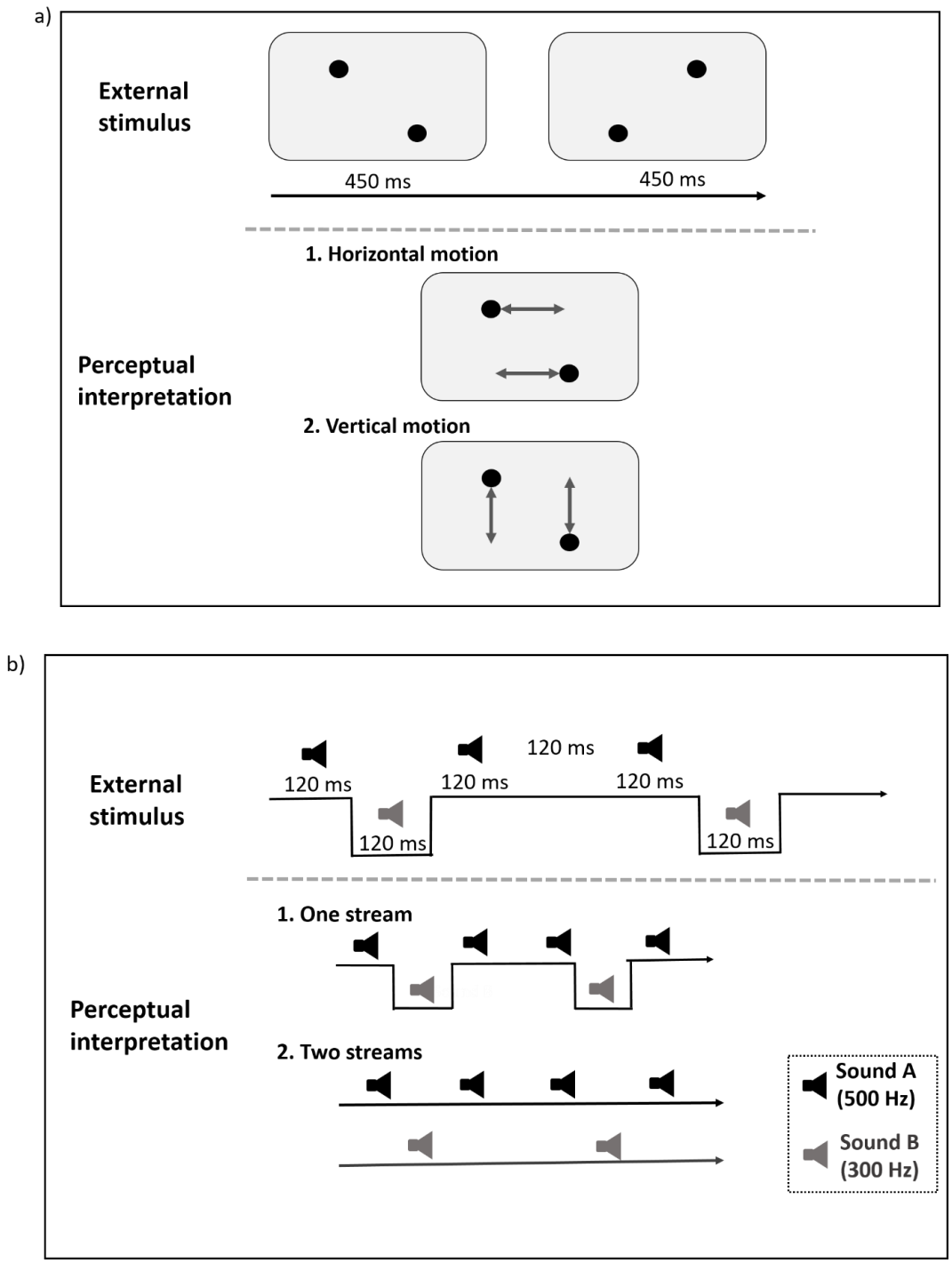


Figure 18. a) Visual motion quartet stimulus. The sensory input is depicted in the upper part and the most likely perceptual interpretation of horizontal or vertical motion are sketched below b) Auditory streaming stimulus. The auditory input is shown in the upper part. The two likely perceptual interpretations, namely of one single auditory stream or two separate streams is indicated below.

4.2.4 Data recording and equipment

In all 3 experiments, eye data was recorded using the mobile SMI Eye tracker glasses (ETG 2W Analysis Pro- 120Hz) and responses were recorded using the Black Box ToolKit K-RB1-4 response box. All devices were connected via a USB cable to a Dell Precision (M6700) laptop. The experiment and the analysis were coded in MATLAB 2012 and 2015a respectively, using the Psychtoolbox extensions (D H Brainard, 1997; Kleiner et al., 2007; D G Pelli, 1997). All data streams were recorded using Lab Streaming Layer (https://github.com/labstreaminglayer) along with LabRecorder (version 1.12b).

4.3 Analysis

4.3.1 Blink detection

We computed a blink detection algorithm based on the pupil radius data similar to the one described in previous studies (Brych & Händel, 2020; Brych et al., 2020, 2021). First, the z- score of the radius data was calculated (per trial, for each subject) and then a potential blink was considered if either 1) both radii values were missing or 2) if either the left or right eye data was missing and the other eye had a z-score below a threshold of -1 (Exception: Experiment 1: threshold set to -0.5 for one trial for one subject and two trials for another subject; Experiment 2: threshold set to -2 for 4 subjects). The onset and the offset of the blink was then extended until the pupil radius of either of the two eyes was higher than the set threshold. Blinks that were less than 16ms apart were combined. Lastly, blinks with durations longer than 0.5s were discarded.

4.3.2 Detection of the switch

As mentioned earlier, participants had to press a key continuously to indicate the percept. This would mean that when a perceptual switch occurs, he/she would have to release a specific key and press the second key. We take the moment of this release as the perceptual switch. This was done for two reasons: 1) The key release would be temporally closer to the actual perceptual switch than the press 2) A perceptual switch that is too short lived might consist of a release and press of the same button and in this case, the release could be informative.

4.3.3 Normalized blink and switch rates

Blink and switch rates were analyzed by taking into account a normalized rate, which was calculated by dividing the rate (or number of events in a minute), in a specific time window by the overall rate during the trial. Hence, a value above or below 1 would indicate an increase or decrease in rate during that time period compared to the mean rate during the trial.

4.3.4 Time resolved analysis

The time series consisted of 0.2s non-overlapping, sliding time windows. The normalized rate was calculated for each time-window as mentioned above with a value above or below 1 indicating an increase or decrease in the rate. Hence, we conducted one sample t-tests on each time window against 1 and tested it against a Bonferroni adjusted alpha. The adjusted alpha was calculated based on the number of time windows for which the one-sample test was applied.

4.4 Results

4.4.1 Overall blink and switch parameters (rate and duration)

Experiment 1

The mean blink rate was 19.3 (*SE* = 3.8) and the mean switch rate was 3.5 per minute (*SE* = .45). There was no dominant percept since a t-test between the mean switch durations revealed no significant difference (*t* (17) = 1.5, p= .2) between horizontal (*M* = 22.3s; *SE* = 2.5) and vertical (*M* = 30.1s; *SE* = 5.8) percepts.

Experiment 2

The mean blink rate was 16.3 (*SE* = 1.9) and the mean switch rate was 4.27 per minute (*SE* = .5812). T-tests again revealed no significant difference (*t* (30) = 1.7, p = .11) between the mean switch durations of the horizontal (*M* = 24.4s; *SE* = 3.8) and vertical (*M* = 28.4s; *SE* = 3.6) percepts.

Experiment 3

The mean blink rate was 22.4 (*SE* = 2.3) and the mean switch rate was 8.6 per minute (*SE* = 3.94). T-tests between the mean switch durations revealed no significant difference (*t* (23) = .32, p = .75) between the single (*M* = 19.8s; *SE* = 3.6) and two stream (*M* = 21.2s; *SE* = 4.2) percepts.

4.4.2 Blink rate modulation around perceptual switches

Time resolved analysis

To test if blink rates are significantly modulated around perceptual switches, we looked at the time-resolved evolution of normalized blink rates with respect to the baseline in a time period of 1.5s before and after the key release indicating a switch. This specific time period was chosen based on the results of a previous study (Junji Ito et al., 2003). We conducted a time-resolved analysis (moving time window of 0.2s, non-overlapping) with one-

sample t-tests against 1 (threshold for the normalized blink rate) and with a Bonferroni adjusted alpha of .0029 (based on the 17 0.2s windows between -1.5 and 1.5s). Results are shown in Figure 19, see supplementary Figure S16 for the t and p-values of each time window. Note that only trials without blanks were included.

Experiment 1

Time-resolved analysis showed significant decrease in the blink rate before the response at the consecutive time points of -0.6s ($p < .001$), -0.4s ($p < .001$) and -0.2s ($p < .001$)

Experiment 2

Time-resolved analysis showed significant decrease in the blink rate before the response during the time points of -0.8s ($p < .001$), -0.6s ($p < .001$) and -0.4s ($p < .001$).

Experiment 3

Time-resolved analysis showed significant decrease in the blink rate before the response during the time point -0.8 ($p < .001$).

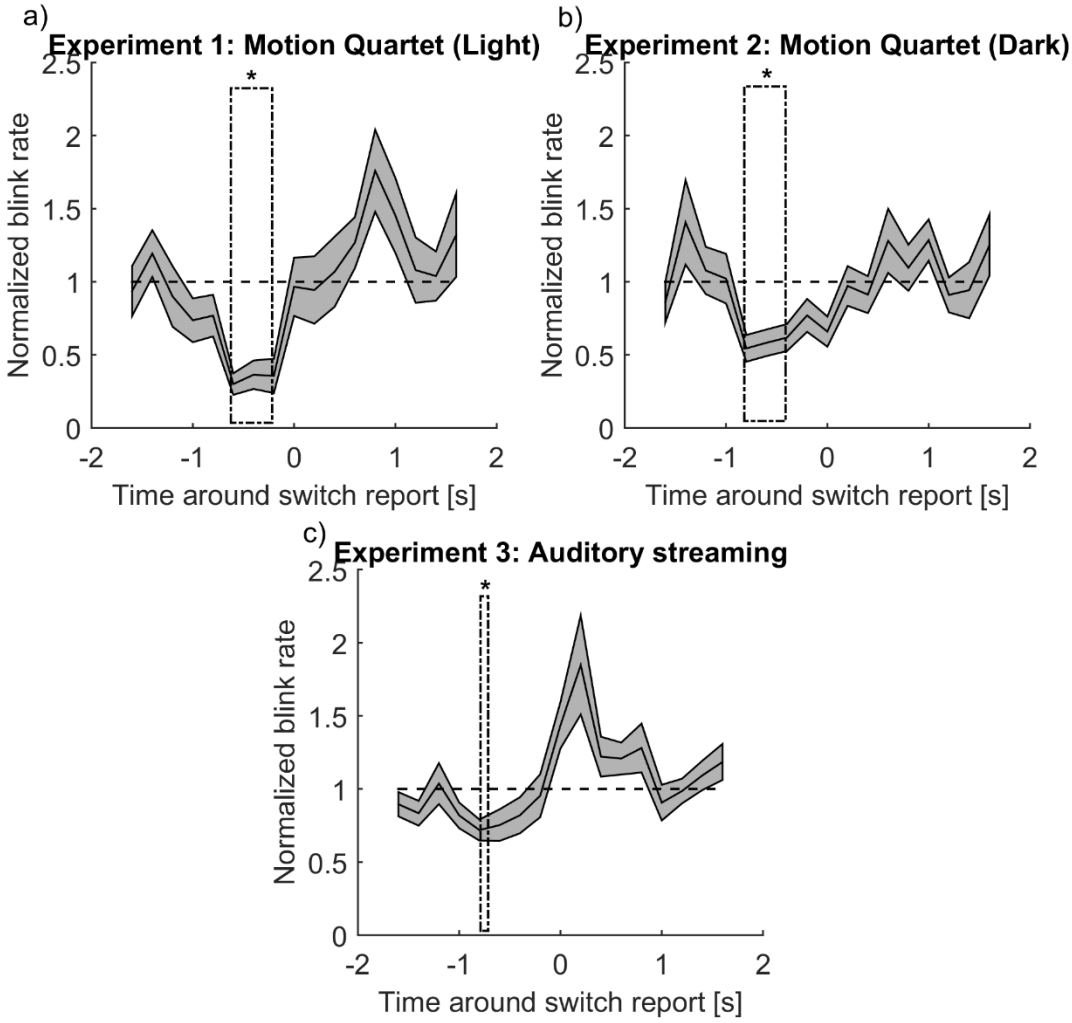


Figure 19. Normalized blink rates around the perceptual switch report during the Motion quartet-in light (a) in dark (b) and during auditory streaming (c). Only trials without blanks are included. The 0 on the x-axis represents the release of the key (see Methods) which is the first indication of a perceptual switch. The y-axis shows the normalized blink rate i.e. the blink rate in each time window divided by the blink rate for that trial; the mean over all trials is then calculated for each subject. The horizontal black dashed line indicates the baseline and the boxes mark time periods of significance (Bonferroni adjusted alpha = .0029). The grey colored regions in the graph show standard errors.

Percept specific modulation of blinks

To test if the modulation of blinks is specific for the switch to a particular percept, we took the mean of the entire 1.5s before and after the response and conducted a two-way ANOVA with factors Time (Before switch vs After switch) and Percept (Horizontal vs Vertical) as shown in Figure 20.

Experiment 1

The ANOVA (Figure 20a) revealed a significant effect of Time (F (1, 71) = 19.42, p < .01), but not of percept. Post-hoc t-tests showed a significant difference between before and after the percept for the vertical (t (17) = 3.8, p < .01), and horizontal (t (17) = 2.4, p = .02) switch.

Experiment 2

The ANOVA (Figure 20b) confirmed the significant effect of Time (F (1,123) = 9.94, p < .01). Post-hoc t-tests again revealed a significant difference between time periods for the vertical percept (t (30) = 2.14, p = .04), as well as the horizontal percept (t (30) = 2.5, p = .02)

Experiment 3

The ANOVA (Figure 20c) again revealed a significant effect of Time (F (1,95) = 9.2, p < .01) but not for percept. Post-hoc t-tests only showed a significant difference between pre- and post-switch time periods in the switch to the two-stream percept (t (23) = 4.23, p < .01), but not the single-stream percept (t (23) = 1.7, p = .12).

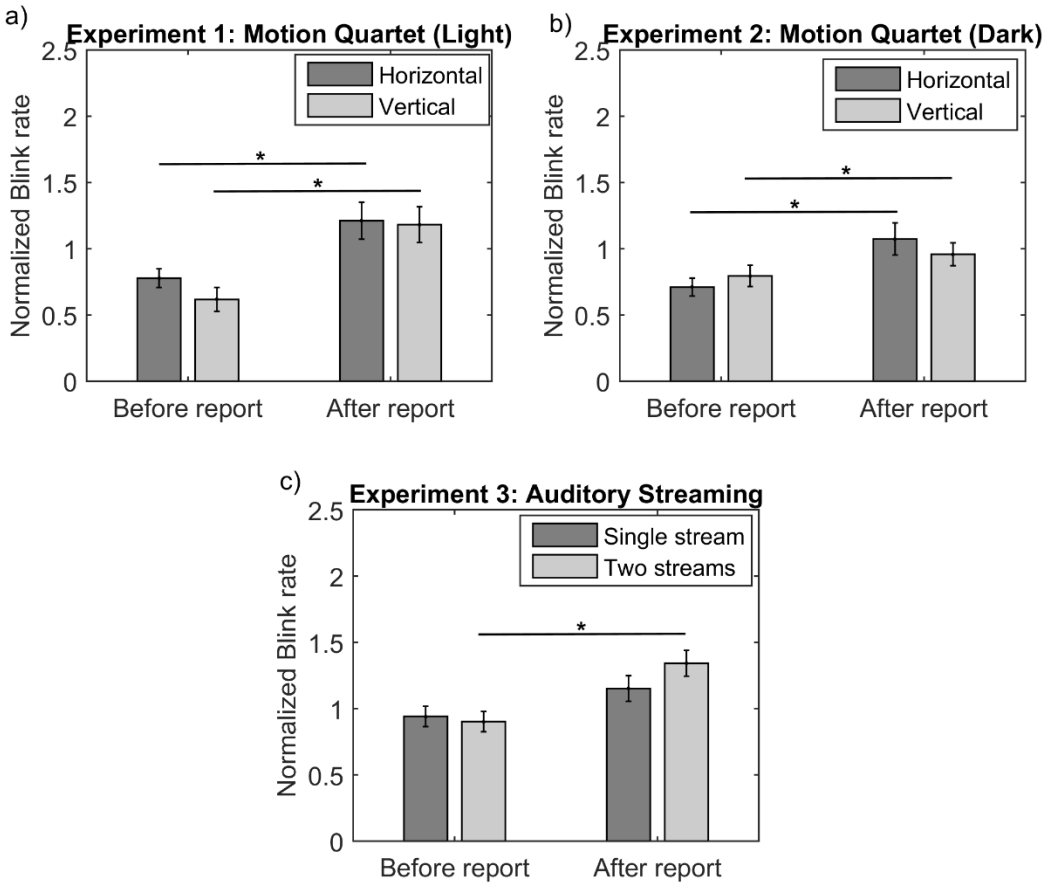


Figure 20. Normalized blink rates in the time period 1.5 s before and after the switch responses during the Motion quartet-in light (a) in dark (b) and during auditory streaming (c). Error bars represent standard errors. The normalized blink rate is calculated similar to Figure 19, but taking the whole 1.5 period before and after instead of a time-resolved approach.

4.4.3 Does blinking influence the switch probability?

The aforementioned results show that a blink does not lead to switching, however, that a significant blink reduction precedes the perceptual switch. To investigate if there is a causal relationship between blink reduction and perpetual switch, we compared the duration

between switches and the previous blink with the duration between blinks (i.e. inter-blink intervals or IBI) that do not have a switch in between them (Figure 21). We hypothesized that if the absence of a blink facilitates switching, the IBI would be significantly shorter than the blink-to-switch interval. A one-tailed paired t-test revealed significance in experiment 1 ($t(17) = 2.3$; $p = .02$), experiment 2 ($t(30) = 3.5$; $p < .001$ and experiment 3 ($t(23) = 1.8$; $p = .03$).

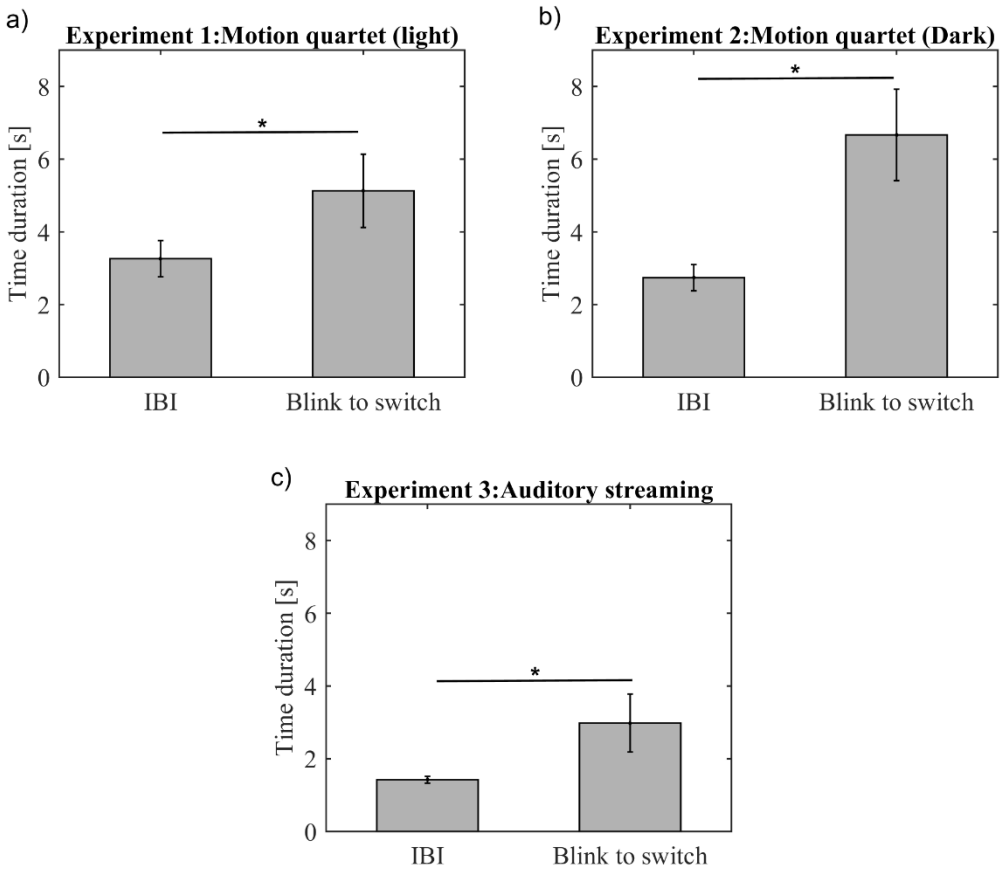


Figure 21. Inter-blink intervals (IBI) and the duration between a switch and previous blink (blink to switch) for experiment 1 (a), experiment 2 (b) and experiment 3 (c). Only those blinks that did not have any switches in between them have been included for the IBI. A one-tailed paired t-test revealed significance in experiment 1 ($t(17) = 2.3$; $p = .02$), experiment 2 ($t(30) = 3.5$; $p = 6.7006e-04$) and experiment 3 ($t(23) = 1.8$; $p = .03$).

In addition, we also related overall blink and switch rate between subjects. As a first step, we sorted participants into low or high blinkers (based on the median blink rate), and compared the mean switch rate between them (Figure 22). A one-tailed independent sample t-test revealed that low blinkers had a significantly higher switch rate than high blinkers for experiment 1 (t(16)=1.9; p=.03) and experiment 3 (t(19)=2.7; p=.006) but only marginally significant in experiment 2 (t(26)=1.4; p=.08).

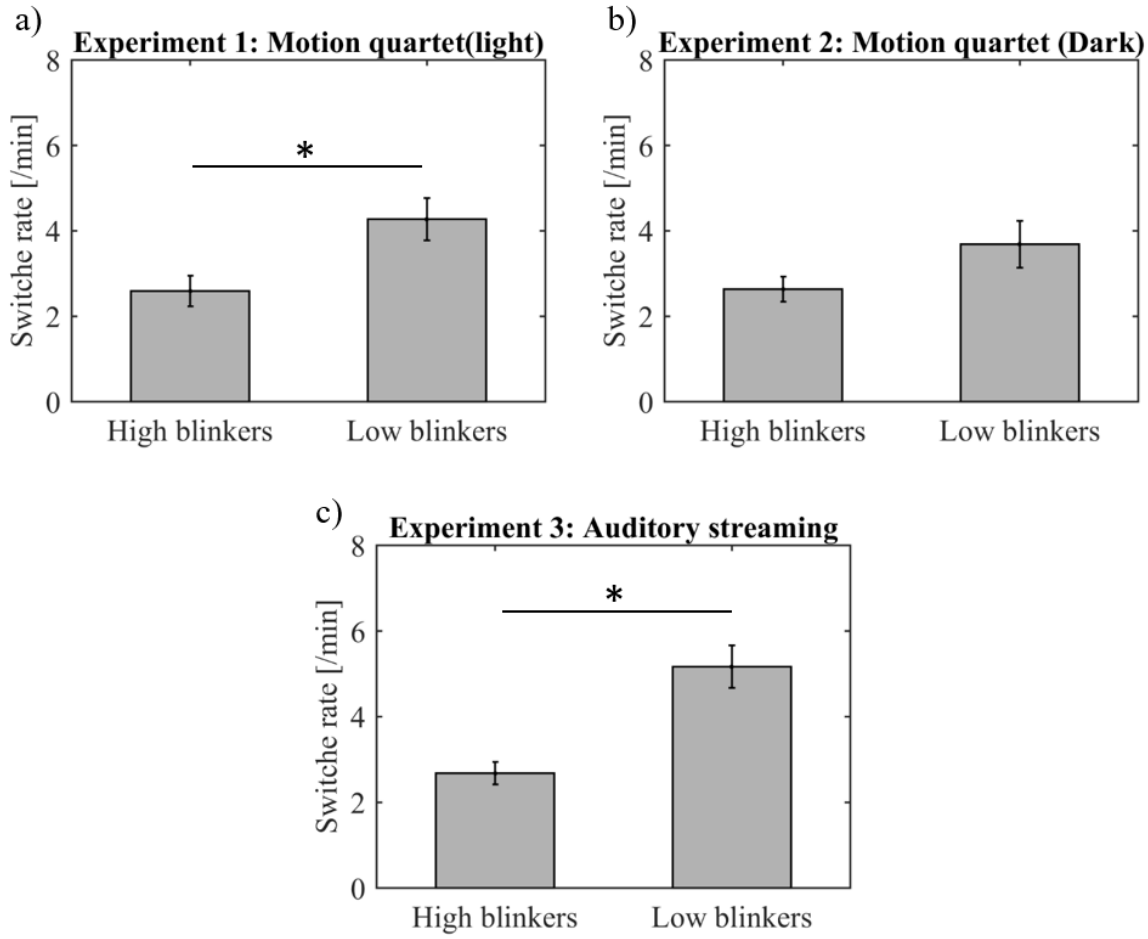


Figure 22. Switch rate (per minute) for low and high blinkers in experiment 1 (a), experiment 2 (b) and experiment 3 (c). A one-tailed independent sample t-test revealed that low blinkers had a significantly higher switch rate than high blinkers in experiment 1 (t(16)=1.9; p=.03) and experiment 3 (t(19)=2.7; p=.006), but only marginally significant in experiment 2 (t(26)=1.4; p=.08).

As a second step, we conducted a regression between the mean blink rate and mean switch rate over all the subjects (Figure 23). While there was a clear trend indicating a negative correlation, i.e. as the individual blink rate increased, the individual switch rate decreased, only for experiment 1 ($r^2=.3$; $p=.02$), but neither for experiment 2 ($r^2=.05$; $p=.2$) nor experiment 3 ($r^2=.1$; $p=.1$) this reached significance. Please note that we used an outlier rejection using the absolute deviation around the median (Leys et al., 2013b) for this analysis.

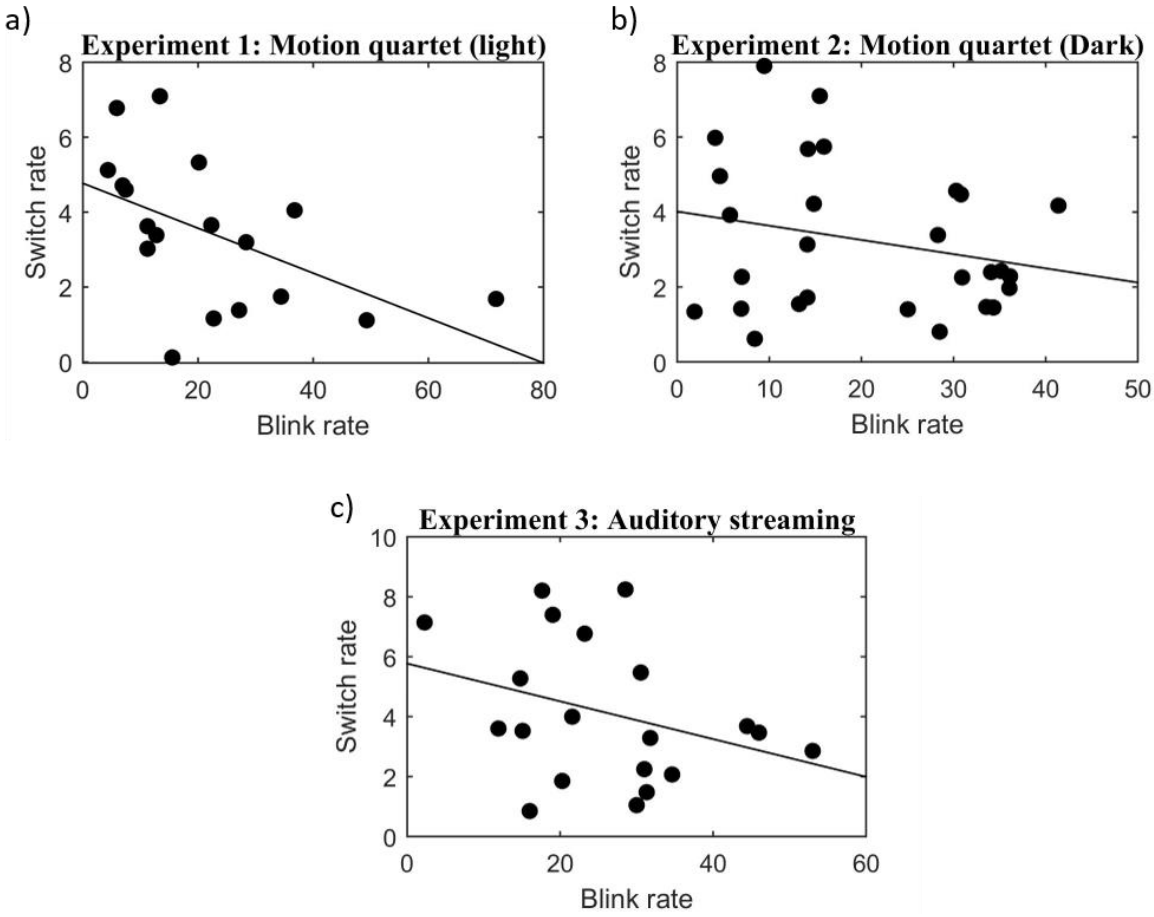


Figure 23. Mean switch rate vs mean blink rate with each data point representing an individual subject, for experiment 1 (a), experiment 2 (b) and experiment 3 (c). Regression showed significance only for experiment 1(r2=.3; p=.02), but not for experiment 2 (r2=.05; p=.2) or experiment 3 (r2=.1; p=.1).

4.4.4 The effect of Blanks on perceptual switches

To estimate the timing of the internally generated perceptual switch, we had included external interruptions called 'blanks' similar to our previous study (Brych et al., 2021). We looked at the time-resolved modulation of the normalized switch rates around the blank offsets (Figure 24a and b) for experiments 1 and 2 (experiment 3 did not have any blanks.) We specifically took the time windows from 0 to 1.5s after the blank offset for the analysis

and conducted time resolved one sample t-tests with a Bonferroni corrected alpha of .0056. The adjusted alpha was calculated based on the fact that there were 9 time windows (0.2s non-overlapping, from 0 to 1.5), and therefore, 9 one-sample t-tests conducted for each experiment. See supplementary Figure S17 for the t and p-values of each time window.

Experiment 1

Time resolved analysis revealed a significant decrease in switch rate during the 0 ($p = .002$) time point, marking that during a blank perceptual switches occurred less likely. Data shows a pronounced increase in switch rate between 0.8 to 1.2s after blank offset ($p < .05$), which however, after correcting for multiple comparisons, did not reach significance.

Experiment 2

Time resolved analysis revealed a significant decrease in switch rate at the 0 ($p < .001$) time point (during the offset of the blank) and a significant increase at 0.8s ($p = .0051$) and 1.2s ($p = .002$) after blank offset.

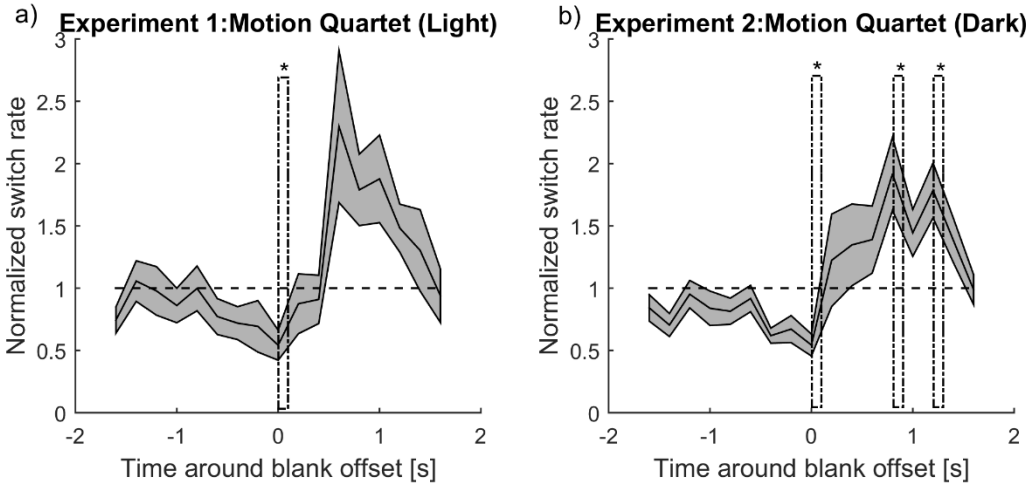


Figure 24. Normalized switch rates around the blank offset indicating switches during the Motion quartet-in light (a) and in dark (b). The 0 on the x-axis represents the offset of the blank. The y-axis shows the normalized switch rate i.e. the rate in each time window divided by the rate for that trial; the mean over all trials is then calculated for each subject. The horizontal black dashed line indicates the baseline and the dotted boxes mark the time period of significant deviation from 1 (Bonferroni adjusted alpha = .0056). Note that the time period from 0 to 1.5 s was taken for the analysis. The grey shaded regions in the graph show standard errors.

4.4.5 Modulation of blinks around blanks

We plotted blinks around blanks to disentangle the influence of the motor response on the blink modulation (Figure 25) as blanks are perceptual events that do not lead to a motor response. We considered only those blanks that were not followed by a switch report within 1.5s. One-sample t-tests with a Bonferroni adjusted alpha of 0.0029 was conducted. See supplementary Figure S18 for the t and p-values of each time window.

Experiment

The time-resolved analysis revealed a significant decrease in blink rate in the 0.2s ($p < .001$) time window after blank offset (Figure 25a).

Experiment 2

Similarly, the time-resolved analysis revealed a significant decrease in blink rate in the 0.6s ($p < .001$) time window after blank offset (Figure 25b).

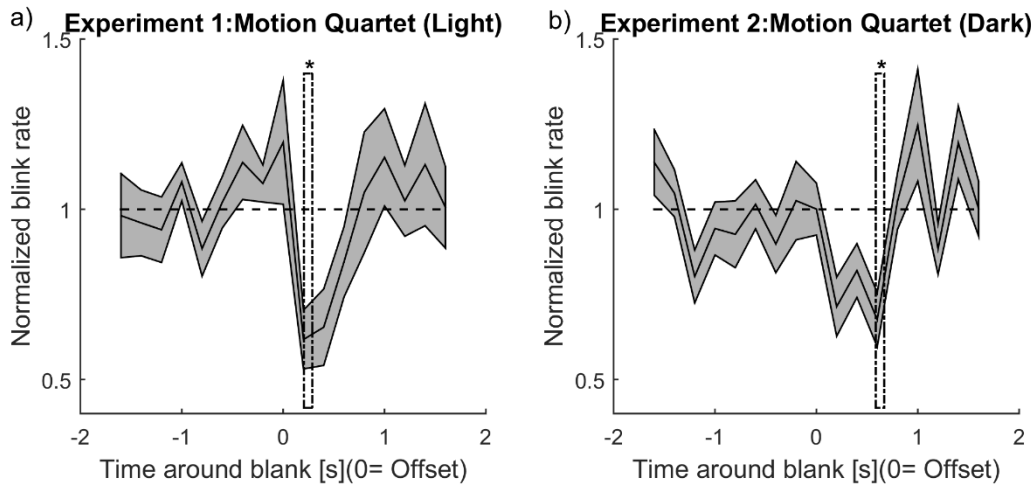


Figure 25. Normalized blink rates around the blanks during the Motion quartet-in light (a) and in dark (b). The 0 on the x-axis represents the offset of blanks. The horizontal black dashed line indicates the baseline and the dotted boxes mark the time period of significance (Bonferroni adjusted alpha = .0029). The grey colored regions in the graph show standard errors.

4.4.6 Modulation of blinks around random key presses

Lastly, to see if motor activity in the absence of an external stimulus could drive the blink modulation, we used 5 additional participants who were asked to press a key at random intervals in a completely dark room. We tested normalized blink rates around the key lifts as

shown in Figure 26. Our time resolved analysis did not reveal a significant change in any of the time windows. The adjusted alpha was again calculated based on the fact that there were 17 time windows (0.2s non-overlapping, from -1.5 to 1.5), and therefore, 17 one-sample t-tests in total. See supplementary Figure S19 for the t and p-values of each time window.

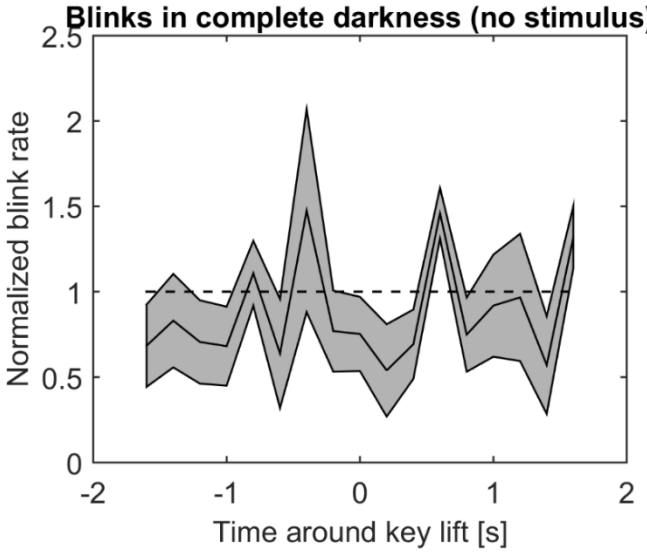


Figure 26. Normalized blink rate around key presses in complete darkness and in the absence of external stimuli. Time point 0 on the x-axis represents the onset of the key press. The horizontal black dashed line marks the baseline. One sample t-tests showed no significant change from the threshold (Bonferroni adjusted alpha = .0029).

4.5 Discussion (Study 3)

We studied the role of spontaneous eye blinks during visual and auditory ambiguity. In a previous study, we had found a decrease in blinks before visual perceptual switches (Brych et al., 2021). In the current study, we replicated these findings in the visual and auditory domain, showing a domain general link between blinking and internal perceptual switches. We could further demonstrate that neither motor responses nor the visual

consequences of blinks caused the observed blink modulation. Importantly, by showing that the time between switches and the previous blink were significantly longer than the inter-blink interval, our studies provide first evidence that a decrease in blink probability facilitates a perceptual switch. The corresponding conclusion, namely that blinking prevents a switch, was further supported by the finding that participants with a high blink rate showed a significantly lower rate of perceptual switches compare to participants who displayed a low blink rate.

4.5.1 The absence of a blink could facilitate switches in the visual and the auditory domain

A decrease in blinks was observed before the perceptual report in all three experiments. We thereby replicate previous findings within the visual domain (Brych et al., 2021), but add that the decrease in blinks is not mediated by the lighting condition and is therefore independent from the effect the blink has on the visual system. Further, we show that the decrease is not specific to the visual modality. Although others have also observed a switch related decrease in blink rate in the visual domain (Junji Ito et al., 2003; L. C. van Dam & R. van Ee, 2005), most have argued that attentional processes are likely the driving factor. For instance, according to Junji Ito et al. (2003), top-down processes such as attention and effort required to successfully complete a given task might lead to a decrease before the switch report. Similarly, L. C. van Dam and R. van Ee (2005) argued that a decrease in blinking might occur for relevant events such as perceptual switches due to attention directed towards them. Although attentional processes could very well be involved, it still does not rule out the possibility that the blink reduction occurred before the switch and likely caused it. We would first discuss evidence for why we believe the internal switch happened after blink reduction and then discuss the role of attention in this influence.

Our current results further support this interpretation by showing that the decrease in blinks starts before the perceptual switch (as deduced through the timing of the blank-induced perceptual switch) and that the length of this no-blink period exceeds the normal inter-blink interval. We could further show that subjects with a high blink rate have a lower switch rate. We will discuss each point in detail below.

Our blank results provide two important estimates: First, Figure 24b indicates that a blank increases the probability of a switch report after a period of around 0.8 to 1.2s. The actual switch therefore must have happened in between this period of blank and switch report. Additionally, since the blank introduced the perceptual switch likely after a certain lag, we can assume that the actual perceptual switch happened considerably after the blank. Therefore, the time taken from a switch to the report would, according to Figure 24b, be less than 0.8s. However, as seen in Figure 19b, the reduction in blinks is significant already 0.8s before the report of the switch which is before the estimated time of the switch. This indicates that the blink rate reduction is most likely not caused by the perceptual event. A second important result further shows that it is indeed unlikely that the internally introduced perceptual switch caused the blink decrease: Figure 25 indicates that a perceptual event (i.e. a blank) alters blinks after a period of 0.2 to 0.6 s. If we assume that the internally generated perceptual switch introduced the blink decrease, we need to assume this perceptual switch to happen 0.2 to 0.6s before the observed blink reduction (see Figure 19). However, as discussed above, this would assume the perceptual switch to happen even before the blank and we know that the blank precedes the switch. The two estimates therefore clearly argue against the interpretation that the perceptual switch caused the blink reduction but argue for the interpretation that the blink reduction started before the perceptual switch. Please note

that this estimate could only be done for the visual domain since no blanks were presented in the auditory domain.

To further show evidence that the decrease in blink probability is linked to the probability of switching, we compared the duration between a switch and a previous blink with the distribution of inter-blink intervals (IBI). We had theorized that, if the absence of a blink facilitates a perceptual switch, these no-blink intervals should be longer than the inter-blink intervals (in which no switch happened), which was confirmed by our results for both domains. This suggests that a period of no blinks sets the stage for a re-interpretation of the sensory input. Indeed, an early study by Ellis and Stark (1978) found that increased fixation durations were accompanied with increased switching. A decreased blink probability would increase the duration of a fixation period. The reduced blink rate during focused attention could therefore mark a stage of flexibility to allow a re-interpretation of sensory input. Conversely, we can deduce that blinks stabilize the perceptual interpretation. To test this hypothesis, we compared switch rates between participant with low and high blink rates and all experiments showed an increased switch rate for low blinkers (experiment 1 and 3 significant, experiment 2 marginally significant). We further conducted a regression between blink rate and switch rate, however, while again all experiments showed a clear trend, i.e. as the individual blink rate increased the individual switch rate decreased, the regression showed significance only for experiment 1.

4.5.2 The role of attention in the influence of blinks

The previous section provided evidence for the blink reduction preceding the internal switch. This would mean that a decrease or suppression of blinking could facilitate switching. But an important question is what the mechanism behind this influence is and if attention or

other top down processes could be involved. We and others have found that blink reduction is indicative of attentional processing. Importantly, in our previous work, we showed that a blink precisely represents the time point where all information processing has ended. Importantly, we showed that this is also the case for auditory information processing. Taking this idea, when a reduction of blinking occurs, we could assume that there is an increase in attention and therefore, processing of the stimulus. In this case, it would be a reprocessing to reinterpret the bistable stimulus. After the new percept is formed, a blink occurred, possibly indicating the end of the (re-)processing of the stimulus and therefore stabilizing the new current percept.

4.5.3 Blink modulation is not mediated by the motor response

We provide two results showing that the modulation of blinks preceding the switch response are not due to the preparation of the motor output. First, random key presses showed no influence on blinking which argues against it (Figure 26). Contrarily, L. C. van Dam and R. van Ee (2005) found that blinks were modulated even when subjects were asked to press keys at random. However, a key difference to our experiments is that we conducted the random key press task in complete darkness, whereas they continued to present the experimental stimulus. Hence, it is seems possible that the stimulus, albeit unintentionally, modulated key presses and blinks. Additionally, their low number of subjects did not allow a statistical test on a group level. A study by Cong et al. (2010) particularly showed a relationship between blinking and rhythmic tapping. As rhythmic motor outputs have been previously reported to show a temporal concurrence (Cao et al., 2020a), we speculate that such a process led to the co-modulation of tapping and blinking. The arrhythmic random motor output, as produced in our experiment, would not facilitate such temporal link via an internal

rhythm. Further findings from experiment 1 and 2 argue against the influence of motor output on blink rate. The decrease in blinks around blanks (Figure 25), despite not requiring any response, showed that sensory events can influence the blink rate without involving motor output. Blanks are unpredictable external events that likely lead to a re-computation of the sensory input (Deubel et al., 2004; Golan et al., 2018b; Higgins et al., 2009), and hence, suppress blinks. It is indeed interesting that these external events had an influence on blinks, despite not being of any relevance to the task itself. Overall, the absence of blink modulation around random key presses and the pronounced blink modulation despite the absence of motor output, suggests that the motor related processes did not triggered the blink modulation.

4.5.4 Conclusion (Study 4)

Our study showed that internally generated perceptual changes, as experienced during visual and auditory bistability, were preceded by a reduction in spontaneous blink rate. This reduction was independent of the visual consequences of a blink and not related to the motor response. As we further found that the time between switches and the previous blink were significantly longer than the inter-blink interval, we argue that an absence of blinks facilitates internally introduced perceptual switches within and outside vision. Importantly, we take the idea that blink reduction indicates increased attention and put forth that the reduction also indicates a re-processing of the bistable stimulus. Conversely, we propose that a blink represents the end of the re-processing and might stabilize percept.

4.6 Supplementary Material (Study 3)

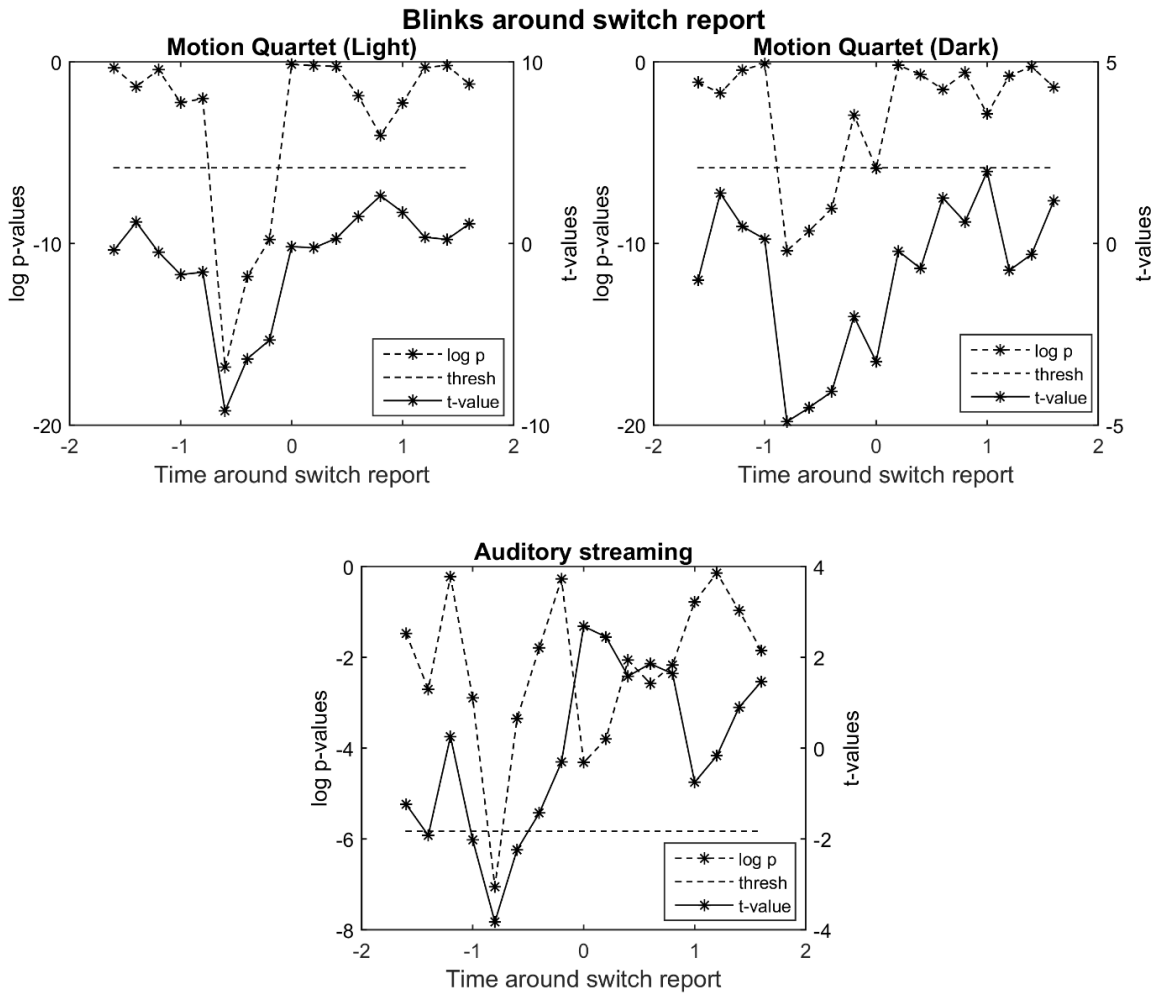


Figure S16 Shows the results of the time-resolved analysis of normalized blink rate around switch report (see Figure 19 in manuscript). The x-axis shows the time around the perceptual report in seconds, the y and z-axes show the log-p values and the t-values respectively. Note that a one-sample t-test against 1 was conducted for each time window and a Bonferroni correction was applied. The horizontal dashed line marks the threshold for the Bonferroni corrected p-value.

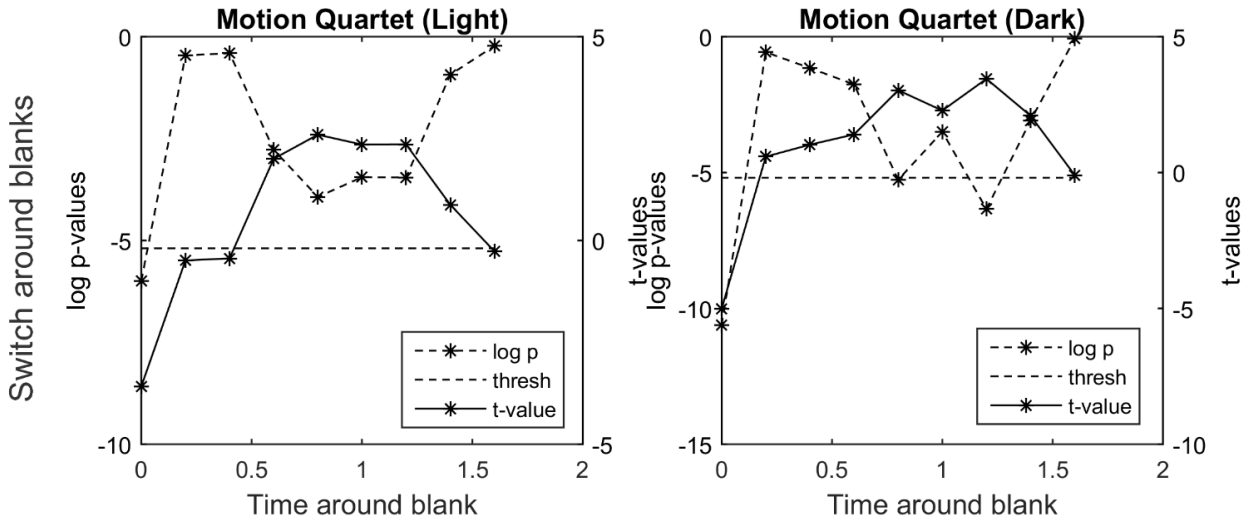


Figure S17 Shows the results of the time-resolved analysis of normalized switch rate around blanks (see Figure 24 in manuscript). The x-axis shows the time around the blank in seconds, the y and z-axes show the log-p values and the t-values respectively. Note that a one-sample t-test against 1 was conducted for each time window and a Bonferoni correction was applied. The horizontal dashed line marks the threshold for the Bonferoni corrected p-value.

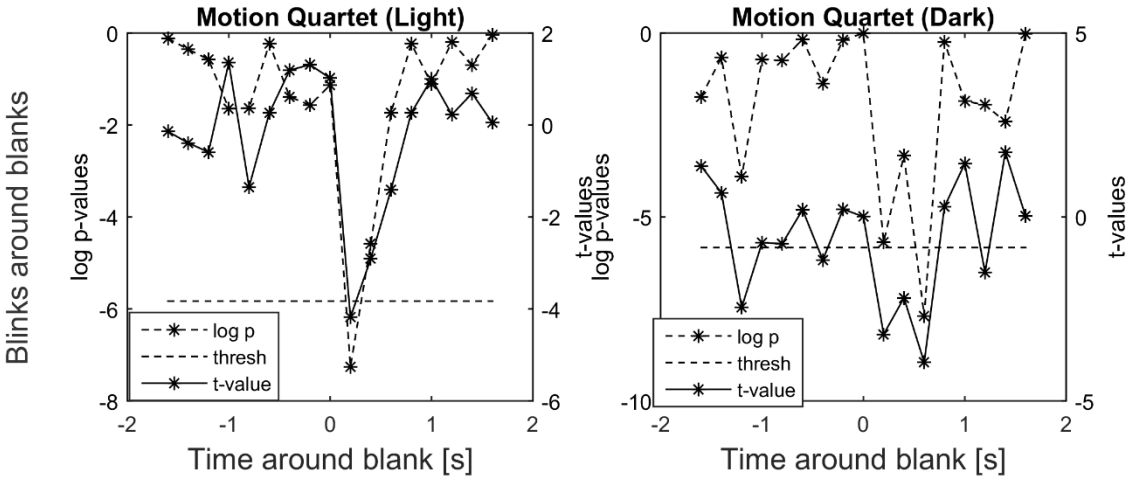


Figure S18 Shows the results of the time-resolved analysis of normalized blink rate around blanks (see Figure 25 in manuscript). The x-axis shows the time around the blank in seconds, the y and z-axes show the log-p values and the t-values respectively. Note that a one-sample

t-test against 1 was conducted for each time window and a Bonferoni correction was applied. The horizontal dashed line marks the threshold for the Bonferroni corrected p-value.

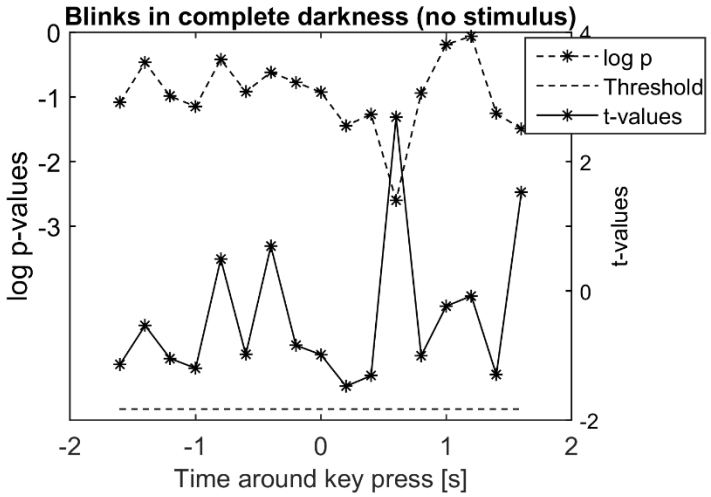


Figure S19 Shows the results of the time-resolved analysis of normalized blink rate around key lifts in complete darkness and no external stimulus (see Figure 26 in manuscript). The x-axis shows the time around the key lift in seconds, the y and z-axes show the log-p values and the t-values respectively. Note that a one-sample t-test against 1 was conducted for each time window and a Bonferoni correction was applied. The horizontal dashed line marks the threshold for the Bonferroni corrected p-value.

5. Study 4: Motor restrictions impair divergent thinking during walking and during sitting

Creativity, specifically divergent thinking, has been shown to benefit from unrestrained walking. Despite these findings, it is not clear if it is the lack of restriction that leads to the improvement. Our goal was to explore the effects of motor restrictions on divergent thinking for different movement states. Additionally, we assessed whether spontaneous eye blinks, which are linked to motor execution, also predict performance. In experiment 1, we compared the performance in Guilford's alternate uses task (AUT) during walking vs sitting, and analysed eye blink rates during both conditions. We found that AUT scores were higher during walking than sitting. Albeit eye blinks differed significantly between movement conditions (walking vs sitting) and task phase (baseline vs thinking vs responding), they did not correlate with task performance. In experiment 2 and 3, participants either walked freely or in a restricted path, or sat freely or fixated on a screen. When the factor restriction was explicitly modulated, the effect of walking was reduced, while restriction showed a significant influence on the fluency scores. Importantly, we found a significant correlation between the rate of eye blinks and creativity scores between subjects, depending on the restriction condition. Our study shows a movement state-independent effect of restriction on divergent thinking. In other words, similar to unrestrained walking, unrestrained sitting also improves divergent thinking. Importantly, we discuss a mechanistic explanation of the effect of restriction on divergent thinking based on the increased size of the focus of attention and the consequent bias towards flexibility.

5.1 Introduction (Study 4)

The notion that walking and thinking are linked goes back to the Peripatetic school of philosophy in ancient Greece and throughout history, there have been anecdotal claims that walking helps people think, solve problems and come up with creative ideas. Over the past couple of decades, some empirical evidence for these claims has been obtained.

Creativity has been proposed to involve two main processes: divergent and convergent thinking (Guilford, 1967). Divergent thinking, which is the focus of this study, is the ability to come up with new ideas or solutions to a single problem. Convergent thinking, on the other hand, involves the generation of a single novel solution by bringing together different concepts or problems. Two of the most commonly used tests are Guilford's alternate uses test or AUT (Guilford, 1967) for divergent thinking and Mednick's remote association test or RAT (Mednick, 1962) for convergent thinking. In the AUT, participants are asked to come up with alternate uses for everyday objects and in the RAT, they are required to find a commonality between three given words. Although these tests assess specific processes, they have been said to be good indicators for creative potential (Runco & Acar, 2012). With regard to the AUT, there are several sub-scores such as fluency, flexibility and originality. In this study we use fluency and flexibility sub-scores of the AUT, which is defined by the number of valid responses generated and the number of categories the responses can be assigned to, respectively to characterize divergent thinking.

Concerning large body movements, walking has been experimentally associated with better performance in divergent thinking (Kuo & Yeh, 2016; Leung et al., 2012; Oppezzo & Schwartz, 2014; Zhou et al., 2017). For instance, Oppezzo and Schwartz (2014) found that people performed better in a divergent thinking task while walking as opposed to sitting. The

same authors also found that there was a residual effect of walking by showing that performance continued to be enhanced when people performed the sitting condition after the walking condition.

Specifically, not just walking, but free walking has been shown to have the most benefit for divergent thinking. Kuo and Yeh (2016) showed that performance in the AUT improved during unrestrained or free walking as opposed to walking in a prescribed rectangular path. In the same study, the authors tested whether the effect was due to the path itself by including a condition where participants had to walk in a path which was generated during another participant's free walking condition. They found that performance improved only during the actual free walking and thus concluded that it is the freedom to move and not the characteristics of the path that has an influence.

Although unrestricted walking in particular seems to have an effect, to our knowledge, no study has tested if this effect pertains to motor restriction in general. However, studies have suggested that free walking as well as other fluid movements can form an association of bodily states and abstract concepts and thereby improve divergent thinking (Kuo & Yeh, 2016; Leung et al., 2012; Slepian & Ambady, 2012, 2014). Slepian and Ambady (2012), for instance, found that AUT fluency scores were higher when participants made fluid movement with the hand while drawing as opposed to when they made non-fluid movements (by drawing straight lines). The authors argue that fluid movements could be linked to fluid thought processes. A similar argument was made by Kuo and Yeh (2016) namely that walking/moving freely could activate the idea of mind wandering.

Albeit less, there also is evidence for a link between creativity and eye-related movements, namely blinks. Eye blinks are of three types: reflexive, spontaneous or voluntary.

Reflexive blinks occur as automatic responses to startling external stimuli such as an air puff. Voluntary blinks occur when someone is explicitly asked to make a blink. Spontaneous blinking, which is the focus of our study and has been found to be linked with divergent thinking (Akbari Chermahini & Hommel, 2010; Ueda et al., 2016), is blinking that occurs unconsciously and not as a reflexive response. These blinks occur about 10-15 times a minute (Burr, 2005; Doughty, 2001; Kaminer et al., 2011). Although they serve to moisten the eyes, their frequency is much higher than what is required just for that cause (Kaminer et al., 2011). The purpose of these surplus blinks is not completely decoded, but they have been shown to reflect cognitive processes (Brych & Händel, 2020; Brych et al., 2020, 2021; Fogarty & Stern, 1989; Goldstein et al., 1992). One study by Akbari Chermahini and Hommel (2010) found that participants who had a comparably moderate baseline eye blink rate, as identified as the centre of the distribution of blink rates for this specific study, had higher scores on the AUT compared to subjects showing blink rates at the left and right side of the distribution. Another study, specifically focussing on blinking during the task as opposed to during a baseline period, found a positive correlation between blink rate and AUT scores (Ueda et al., 2016).

Despite this sparse evidence from directly testing for creativity, there is rather strong experimental indication that cognitive aspects that might be applied during creative thinking are linked to eye movements. When people engage in imagination and memory retrieval, they tend to make more saccades and blinks (Salvi & Bowden, 2016). Although eye blinks are not specifically investigated, a number of studies have found a link between eye movements in general and memory retrieval (Damiano & Walther, 2019; Johansson et al., 2012; Johansson & Johansson, 2014; Lenoble et al., 2019). In fact, not allowing any eye movements worsens performance in these tasks (Damiano & Walther, 2019; Johansson & Johansson, 2014). Moreover, Johansson & Johanssonn (2014) also showed that asking participants to make eye

movements that were incongruent with the position of the objects during a visoospatial memory task, worsened performance as opposed to congruent movements. Apart from visual memory, a study by Lenoble et al. (2019) showed that eye movements could also aid in retrieving autobiographical memories. These authors found memories retrieved while making free eye movements were more detailed and faster than those retrieved during fixation. Moreover, Salvi and Bowden (2016) in their paper, mention how it has been anecdotally suggested that closing one's eyes is thought to reflect the process of disengaging from the outside world and concentrating on inner thoughts. Indeed, we recently showed that blinks could directly reflect cognitive processes independent of external sensory input (Brych & Händel, 2020; Brych et al., 2021; Murali & Händel, 2021).

So while there is strong evidence that eye movements are related to cognitive processes and some evidence that they are linked to creativity, it is not clear if eye movements play a role in cognition or if they are linked via a common process. Akbari Chermahini and Hommel (2010) suggested that the link between eye blinks and divergent thinking performance could be mediated by dopamine levels. Dopamine has been shown to play a role during divergent thinking (Kulisevsky et al., 2009; Zabelina et al., 2016) and at the same time is correlated with eye blink rates (Bologna et al., 2012; Karson, 1983; Taylor et al., 1999). Blink rate has been shown to increase following the administration of dopamine agonists (Karson et al., 1984) and decrease following dopamine antagonists (Blin et al., 1990; Strakowski & Sax, 1998; Strakowski et al., 1996). However, a few recent studies have found a lack of evidence for the positive relationship between dopamine and eye blinks in healthy human adults (Dang et al., 2017; Sescousse et al., 2018). Overall, when it comes to eye blinks, dopamine and creativity, the relationship is hard to interpret since there are several neuronal processes modulated by dopamine, which could influence blinking as well as creativity. For

example, a link might be realized via the default mode network. Blinks activate the default mode network (Nakano et al., 2013), which has been shown to play a role in creativity (Beaty et al., 2014; Kühn et al., 2014) as well as to be linked to dopamine (Dang et al., 2012; Nagano-Saito et al., 2009).

Using three experiments, we tested the influence of body movement and motor restriction on the AUT and additionally tested the relationship between blinks and performance during the different conditions and the interaction between blinks and other body movements. In experiment 1, we focused on the interaction between walking and blinking. When investigating specific movements, it is important to consider that many body movements interact. As shown by us and by others, spontaneous blink rate increases can be linked to movements of the mouth during speech (Brych et al., 2020; von Cramon & Schuri, 1980). Also walking goes hand in hand with an increased blink rate (Cao et al., 2020b). Importantly, this association is not dependent on the visual input, as it persists even during absolute darkness, suggesting a link deeply integrated into the system. We, therefore, set out to better understand the influence of different movement states on creativity, while additionally assessing the interactions between large movements and blinks. The purpose of experiment 1 was to a) replicate previous findings on walking and blinking on divergent thinking, b) to differentiate the effects for the different phases of the creativity task (baseline, thinking, responding), and c) to understand if effects of blinking and walking are additive or independent from each other.

The aim of experiment 2 was to understand if the mere execution of motor output is the relevant factor or if it rather is specific instruction/ body state, which introduces the effect. As detailed earlier, particularly walking without restriction to the path, has been

shown to improve divergent thinking. Free eye movements, although not been studied in the context of creativity, have been shown to benefit memory. We wanted to understand if the positive effect on cognition extends to other movement states and hence, compared performance in the AUT not only during free and restricted walking, but additionally during free and restricted sitting. The aim of experiment 3 was to replicate the findings of experiment 2 and importantly test if eye blinks show a link to fluency depending on the level of restriction.

5.2 Experiment 1

5.2.1 Participants

Twenty fluent German speakers (7 males) between the ages of 18 and 35, took part in the first experiment. All participants were bachelor's students from the Psychology department at the University of Wuerzburg and were recruited via the SONA-systems software. They gave their written informed consent and received study credit for their participation. The study complied with the European data protection law (DSGVO).

5.2.2 Procedure

Stimulus and equipment

We used 14 words (translated to German) from the Guilford's Alternate Uses Task: bandage, brick, chair, desk, frying pan, garbage bag, lipstick, pencil, newspaper, shoes, spoon, tile, toothbrush, and towel. These specific words were chosen based on two previous studies (Akbari Chermahini & Hommel, 2010; Ueda et al., 2016). In particular we used 13 words from Ueda et al. (2016) and additionally added the word "newspaper" from Akbari Chermahini and Hommel (2010) to get an even number of words to divide among the two conditions. A headset (Sennheiser PC3) was used to present the words and to record the verbally given

responses. The words as well as the instructions (more details in the next section) were presented via a text-to-audio function in MATLAB using an automated voice for audio output. The verbally given responses were saved as a raw audio (wav) format. A response key connected via a response box (model: K-RB1-4; The Black Box ToolKit Ltd, UK) was provided and used by the participant to begin the trials or conditions whenever they were ready (see next section for more information). The experimental program was implemented in MATLAB 2015a, with the Psychophysics Toolbox extensions (David H Brainard, 1997; Mario Kleiner et al., 2007; Denis G Pelli, 1997), using a Dell Precision (M6700) laptop running Windows 10. Binocular eye movements were recorded using the 120Hz SMI video-based eye tracking glasses (SensoMotoric Instruments GmbH, Berlin, Germany). The experiment was conducted in a normally lit room of size 9m * 2m and took approximately 90 minutes.

Experimental Design

A within-subject design was applied to test the effects of the two conditions: walking vs. sitting. The conditions were presented in two blocks, each consisting of 7 trials (words), with the order of the blocks randomized between subjects. Specifically, at the start of the experiment, a randomization was applied, such that a random order for the conditions and words was generated. Note that 7 subjects did the walking condition first and 13 subjects did the sitting condition first.

Before starting the experiment, subjects were prepared with the eye tracker, the headset and the laptop in a backpack. The experimenter then gave the initial instructions as to the task and the conditions. Participants were informed that they would have a minute to think after each word is presented. They were asked to give as many ideas as possible and told that they should not give non-uses such as ‘throw away’. After this, subjects could press

a key to receive further instructions and information regarding which condition they were going to start with, through an automated voice via the headphones.

Before starting each condition, the automated voice indicated that the baseline would begin and that an auditory beep would mark the start and end of the baseline period. Subjects were instructed to either walk or sit during this baseline, depending on the condition. No external stimulus or task was given during this period. In the walking condition, subjects were allowed to walk freely around the room. In the sitting condition, no specific instructions were given except that the subject had to comfortably sit in a chair. After the baseline, the audio instructions would again indicate that a trial was about to start and that a word would be presented followed by two auditory beeps to indicate the start and end of think time respectively. After the think time, participants were asked to give their responses after another beep. Lastly, participants were informed of the end of the (3 minutes) response time and that they could take a break and press a key for the next trial (or condition) to start. Note that the procedure for a trial with a separate think time and response time was similar to Ueda et al. (2016). The reason for this was because voluntary actions such as speaking is associated with an increase in blinking (Brych et al., 2020; von Cramon & Schuri, 1980). Participants were allowed breaks between trials and between conditions. However, there was no minimum or maximum time between conditions and all measurements were completed in a single session.

5.2.3 Scoring of the AUT

We scored the responses using the criteria from a previous study (Ottemiller et al., 2014). We first took all responses given by the subject and then filtered out responses that were 1) repetitive (a direct repetition of a previous use given); 2) implausible (given the

objects properties, e.g. pen used as a skirt) or 3) a non-use (e.g. throw in the garbage). For the repetition criteria, only direct repetitions were used. For example, for the object “towel”, responses such as “use as a skirt” and “use as a t-shirt” were considered separate ones. However, responses such as “used as shirt” and “used as a blouse”, were regarded as one idea, whether they were given consecutively or not. Responses that might belong to the same category (in the case of the first example: clothing) were not treated as repetitions. However, responses belonging to a specific subcategory (in the case of the second example: tops) were considered repetitions. This was done to avoid high fluency scores stemming from giving random repetitive ideas (Zhang et al., 2020).

Fluency was then defined as the total number of correct responses and flexibility was defined by the different categories in the responses.

5.2.4 Blink Detection

We used a blink detection algorithm based on the pupil radius data similar to our previous studies (Brych & Händel, 2020; Brych et al., 2021; Murali & Händel, 2021). Blinks were detected if the z-transformed radii data of either of the two eyes was missing or if the data from one of the eyes was missing and the other eye had a z-value below a certain threshold (-1,-2 or -3 set for each individual subject). These blinks were then extended until the radii data of either eye was higher than the set threshold. Blinks that were less than 100ms apart were combined and those longer than 0.5s were discarded.

5.2.5 Results

AUT fluency and flexibility score during walking vs sitting

The mean fluency score during walking was 14.1 (SD = 5.7) correct responses per trial and during sitting was 12.7 (SD = 5.3) correct responses per trial (see Figure 27). The mean flexibility score during walking was 7.3 (SD = 2.4) and during sitting was 6.5 (SD = 2.1). A T-test revealed a significant difference between the two conditions for fluency ($t(19) = 2.4$; $p = .03$) and for flexibility ($t(19) = 2.9$, $p = .008$). Additionally, supplementary figure S21 shows the mean fluency score over all subjects for each word. A within subject ANOVA revealed no significant effect of the words ($F(13,269) = 0.96$, $p = .5$).

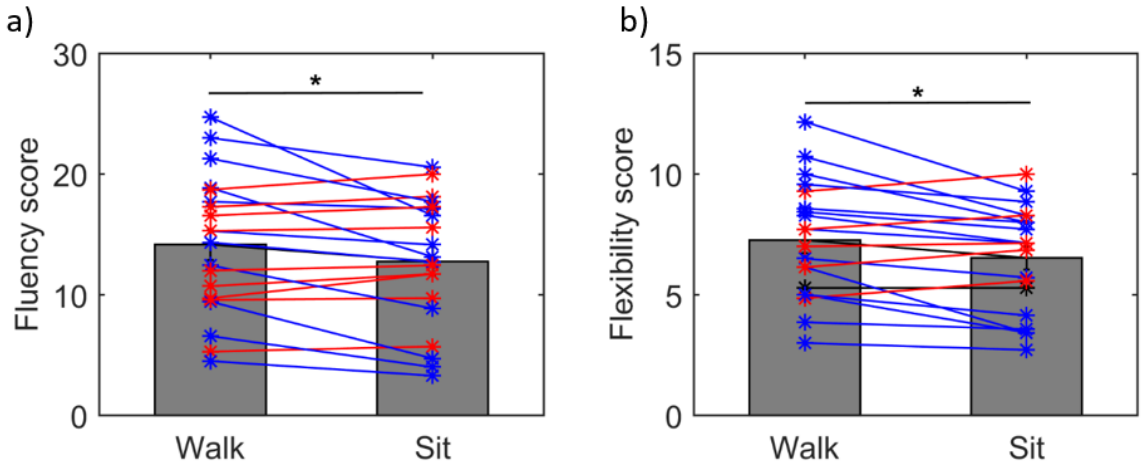


Figure 27. The mean fluency score (a) and the mean flexibility score (b) during walking and during sitting are shown. T-tests revealed a significant difference between walking and sitting for fluency ($t(19) = 2.4$; $p = .03$) and flexibility ($t(19) = 2.9$, $p = .008$). The asterisk symbols represent the data from each subject. The blue lines represent cases where the fluency score is higher for the walking condition and the red lines represent cases wherein it is higher for the sitting condition.

AUT fluency and flexibility score vs eye blink rate

The mean think-time eye blink rate (blinks per minute) during walking was 42.1 (SD = 22.9) and during sitting was 31.7 (SD = 13.2). A linear regression model was applied to see if eye blink rates (during the think time) predicted the fluency and flexibility scores (see Figure 28). For fluency, the analysis did not reveal any significance for either the walking (F (1,19) = .2, r2 = .01, p = .7) or the sitting (F (1,19) = 0.001, r2 = 4.49e-05, p = .7) condition. Also for flexibility, there was no significance either in the walking (F (1,19) = .2, r2 = .01, p = .6) or the sitting (F (1,19) = .07, r2 = .004, p = .7) condition.

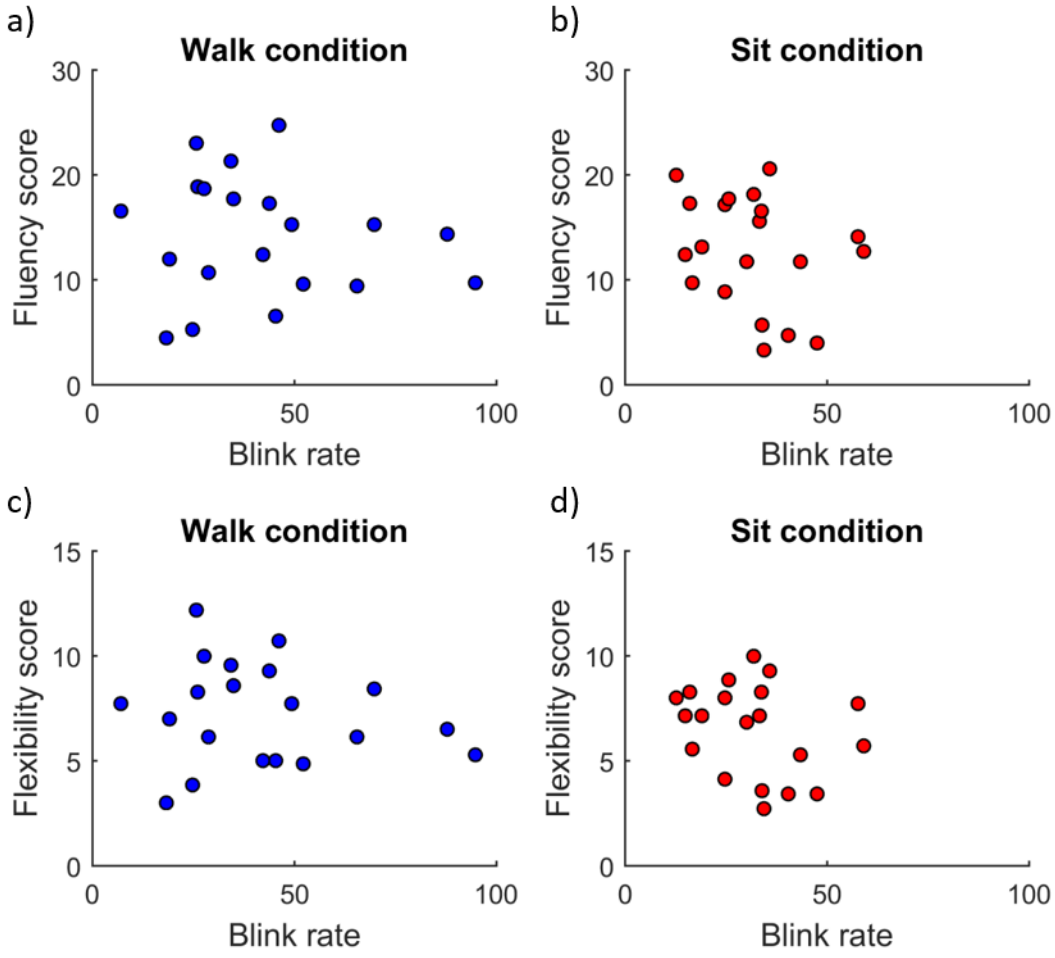


Figure 28. The mean fluency score (a, b) and flexibility score (c, d) is plotted against the blink rate for each subject during walking (a, c) and during sitting (b, d). Each coloured circle represents data from a single subject. Linear regression gave no indication that eye blinks predicted the fluency or flexibility scores during the think time.

Eye blink during walking vs. sitting and task vs. no task

To see if eye blink rates differed during the conditions and the different phases of the trial, we conducted a repeated measures two-factor ANOVA for the factors condition (Walk vs Sit) and task phase (Baseline vs Think time vs Response Time).

There was a significant effect of condition ($F(1,125) = 9.95$, $p = .005$). However, no significant effect of task phase ($F(1,125) = .86$, $p = .43$). From Figure 29, it is clear, that eye blink rates during walking were higher than during sitting. Additionally, it can be seen that task phase indeed has an effect on blink rate but only when sitting. This is confirmed by a significant interaction effect ($F(2,125) = 4.05$, $p=0.025$).

Post-hoc T-tests showed that eye blink rates were higher for baseline walking than baseline sitting ($t(20) = 2.5$, $p = .02$), as well as for think-time walking compared to the think-time sitting ($t(20) = 2.7$, $p = .01$), but not for response time walking compared to response time sitting ($t(20) = .3$, $p = .8$). In fact, eye blink rate during the sitting response time was higher than the sitting baseline ($t(20) = 2.7$, $p = .01$) and the sitting think time ($t(20) = 2.8$, $p = .01$).

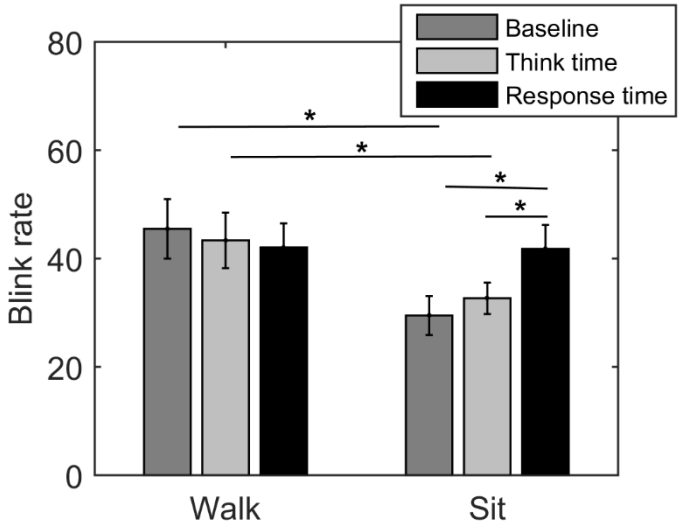


Figure 29. The mean blink rate during the different phases of the task, namely baseline, think time and response time, for the walking and sitting condition is shown. A two-factor ANOVA revealed a significant effect of condition ($F(1,125) = 9.95$, $p = .005$) and a significant interaction ($F(2,125) = 4.05$, $p = 0.025$), but no significant effect of the different phases of the task ($F(1,125) = .86$, $p = .43$).

5.2.6 Interim discussion

Experiment 1 showed that performance in the AUT is higher when walking than when sitting. However, as can be seen in figure 27 (a & b), 9 participants in the fluency score and 5 in the flexibility score showed the opposite trend. Interestingly, it seems that participants showing an improvement when walking do so rather pronounced, whereas those participants who are better for sitting, are only slightly better. It is important to point out that this is not caused by the order of conditions, as walking always showed a group-wise averaged improvement in fluency compared to sitting, independent if people walked or sat first (Figure S20). Nevertheless, in a supplementary analysis the improvement only reaches significance for those participants who sat first, which could be indicative of a residual effect of walking, as described in the literature (Oppezzo & Schwartz, 2014). However, as there is a power

difference between walking first (N=7) and sitting first (N=13), a larger sample size would have been necessary to draw conclusions as to such a residual effect.

As to the reason why not all subjects showed an improvement in AUT performance for walking compared to sitting, we speculate that the difference in movement restriction caused this division. As restriction was not explicitly instructed for experiment one, it is possible that some subjects interpreted the sitting condition as an unrestricted condition in which they moved freely (while sitting), whereas the other group of subjects interpreted the requirement of the sitting condition as moving as little as possible. This might explain why one group was very comparable in its performance (walking and sitting was equally unrestricted), whereas the other group showed gross difference in performance in the unrestricted walking condition as opposed to a very restricted baseline. In experiment 2 we directly tested if the effect of improved AUT performance is mediated by restriction, independent of walking.

5.3 Experiment 2

5.3.1 Participants

Seventeen new participants who were fluent German speakers (4 males) between 18 and 35 years, took part in the second experiment. They received monetary compensation for their participation. The study complied with the European data protection law (DSGVO) and was additionally approved for Hygiene regulations regarding COVID-19. All participants were recruited via the SONA-systems software.

5.3.2 Procedure

Stimulus and equipment

We used 12 words out of the 14 translated words that were used in experiment 1: bandage, brick, chair, desk, frying pan, garbage bag, lipstick, pencil, newspaper, shoes, spoon, tile. Similar to experiment 1, the experimental program was implemented in MATLAB 2015a, with the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997), using a Dell Precision (M6700) laptop running Windows 10. We also used the same response key connected to a response box (model: K-RB1-4; The Black Box ToolKit Ltd, UK). Restrictions due to the COVID-19 pandemic did not permit the use of an eye tracker or headset. All instructions and the words were instead presented directly using the in-built speakers of the laptop. This was again done similar to experiment 1, using a text-to-audio function in MATLAB. The responses were recorded via the in-built microphone and saved as a raw audio recording (.wav format). The experiment was conducted in a normally lit room of approximately 5*6m^2 and took approximately 60 minutes.

Experimental Design

Similar to experiment 1, a within subject design was conducted with 4 conditions and three words (trials) per condition. At the start of the experiment, a randomization was applied, such that a random order for the conditions and words was generated. The order of the conditions for each subject is presented in the supplementary table S3. Note that all subjects completed all condition and the recording was done in a single day. Similar to experiment 1, participants were allowed breaks in between conditions and trials, with no minimum or maximum length.

Before starting each experiment, subjects were informed by the experimenter as to the task and conditions. They were instructed that they would have one minute to think about the answers and three minutes to give their answers and that they could give as many responses as possible, but should not give non-use responses such as “throw away”. During this initial instruction phase, participant were also shown the restricted path that they had to take (details below).

Once the experiment began, the automated voice indicated the condition and that a trial was about to start. Note that unlike experiment 1, no baseline measurement was conducted since no eye tracker was used and the main purpose of the baseline in experiment 1 was to measure baseline eye blink rates. At the start of each trial, similar to experiment one, the audio instructions would indicate that a word would be presented followed by two beeps to indicate the start and end of the one minute think time. Following the end of the think time, participants were asked to start giving their responses after another beep. At the end of the (3 minutes) response time, participants were allowed to take a break and could press a key whenever they were ready to go to the next trial or condition. The experimenter kept a close watch on the participant, to detect obvious violations of the task requirements with regard to movement or restriction.

The 4 conditions were as follows:

1. Free walking: subjects could walk around a large room without any restriction as to the path.

2. Restricted walking: subjects had to walk back and forth in a straight path from wall to wall in the centre of the room. A horizontal mark depicted the width of the path.

3. Free sitting: subjects sat comfortably on a stationary non-rotating armchair with a solid non-moving back and no wheels. For all subjects the position of the chair was against one of the walls of the room such that the person would face the room and not the blank wall.

4. Restricted sitting: subjects sat at a distance of 50 cm from a computer screen with a fixation cross at the centre. The position of the chair and laptop was always the same for all subjects. As we did not track motor output, we cannot assess to what extent subjects were moving in the sitting condition.

5.3.3 Scoring of the AUT

We used the fluency and flexibility sub-scores as in experiment 1. The criteria were the same with the following responses considered as incorrect 1) repetitive (a direct repetition of a previous use given); 2) implausible (given the objects properties, e.g. pen used as a skirt) or 3) a non-use (e.g. throw in the garbage). For more details on the exclusion criteria, please see experiment 1.

5.3.4 Results

Effect of movement and restriction on fluency and flexibility

The mean fluency score during free walking was 10.5 (SD = 4.4), during restricted walking was 9.5 (SD = 4.9), during free sitting was 10.2 (SD = 4.4) and during restricted sitting was 9.3 (SD = 3.5). The mean flexibility score during free walking was 7.2 (SD = 3.2), during restricted walking was 3.6 (SD = 1.6), during free sitting was 7.1 (SD = 2.5) and during restricted sitting was 3.1 (SD = 1.2). Figure 30 shows the mean fluency and flexibility scores during all four conditions.

For fluency, a repeated-measures two-factor ANOVA was conducted between the factors movement (Walk vs Sit) and Restriction (Free movement vs. Restricted movement). The results showed a significant effect of restriction ($F(1,67) = 8$, $p = .01$), but not movement ($F(1,67) = .35$, $p = .56$), and also no significant interaction ($F(1,67) = .02$, $p = .8$). A post-hoc T-test for the factor Restriction (Free movement vs. Restricted movement) revealed that fluency scores were significantly higher during free movement ($t(33) = 2.8$, $p = .01$). Similarly, for flexibility, the two-factor ANOVA showed a significant effect of restriction ($F(1,67) = 39.4$, $p < .001$) but no significant effect of movement ($F(1,67)=1.07$, $p=.3$) and also no significant interaction ($F(1,67) = 1.6$, $p = .2$). A post-hoc T-test for the factor restriction (Free movement vs. Restricted movement) revealed that fluency scores were significantly higher during free movement ($t(33) = 8.7$, $p < .001$).

Supplementary figure S21 additionally shows the mean fluency score over all subjects for each word. Note that, just as in experiment 1, a within-subject ANOVA revealed no significant effect of the words ($F(11,203) = 0.3$, $p = .9$).

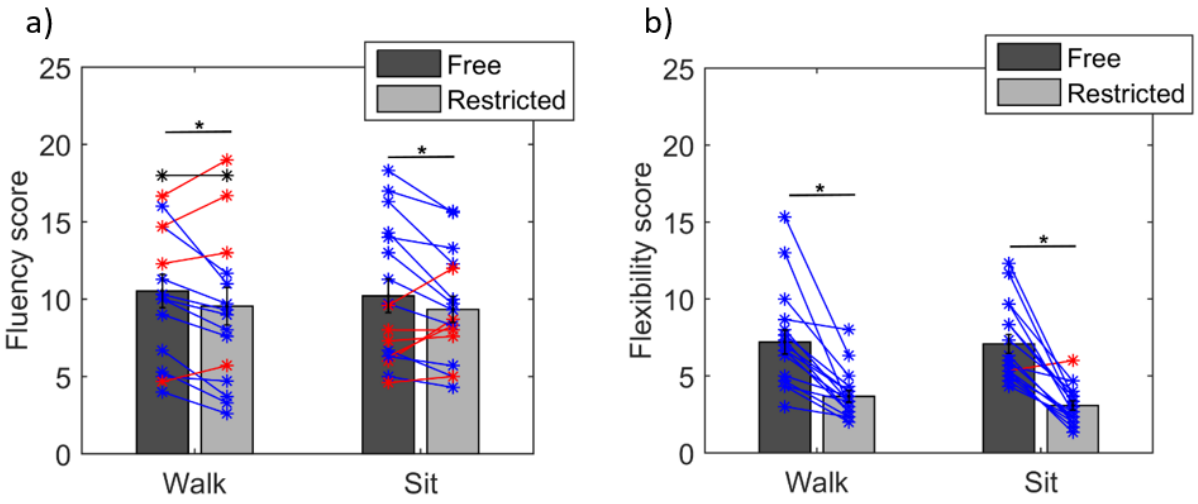


Figure 30. The mean fluency score (a) and the mean flexibility score (b) during free and restricted walking and sitting are shown. For the fluency, a two-factor ANOVA revealed a significant effect of restriction ($F(1,67) = 8$, $p = .01$), but not movement ($F(1,67) = .35$, $p = .56$), and no significant interaction ($F(1,67) = .02$, $p = .8$). Similarly, for flexibility, the two-factor ANOVA showed a significant effect of restriction ($F(1,67) = 39.4$, $p < .001$) but no significant effect of movement ($F(1,67)=1.07$, $p=.3$) and also no significant interaction ($F(1,67) = 1.6$, $p = .2$). The asterisks represent data from individual subjects. The blue lines represent cases with higher scores during free movement, the red lines represent higher scores during restriction and black lines represent equal scores.

5.3.5 Interim discussion

Experiment 2 showed that the absence of movement restriction rather than walking per se improves performance in the AUT. With this insight, we conducted a third study in order to i) replicate the importance of restriction and ii) to examine the relationship between blink rates and fluency or flexibility scores in dependence of restriction.

5.4 Experiment 3

5.4.1 Participants

Twenty-three new participants, who were fluent German speakers (4 males) between 18 and 35 years, took part in the third experiment. However, one subject had to be excluded for the eye blink analysis because the eye tracker had a technical problem during the recording. All participants received monetary compensation for their participation. The study complied with the European data protection law (DSGVO) and was additionally approved for Hygiene regulations regarding COVID-19. All participants were recruited via the SONA-systems software.

5.4.2 Procedure

Stimulus and equipment

We used 8 words in this experiment: bandage, brick, chair, desk, frying pan, garbage bag, lipstick, newspaper. For details regarding the experimental room and equipment, please refer to experiment 2. Binocular eye movements were recorded using Pupil Core mobile eye tracker developed by Pupil Labs (Kassner et al., 2014). The experiment took approximately 120 minutes.

Experimental Design

Similar to experiment 2, a within subject design was conducted with 4 conditions and two words (trials) per condition was conducted. For details regarding the procedure and the conditions, please refer to experiment 2. Supplementary table S4 shows the order of conditions for each subject. Note that, due to restrictions regarding the duration of the experiment in view of the COVID-19 pandemic, the think time was 45s instead of 1 minute.

5.4.3 Soring of the AUT

We used the fluency and flexibility sub-scores. The criteria to exclude incorrect responses was the same as experiment 1 and 2.

5.4.4 Blink Detection

The blink detection algorithm was the same as our previous studies (Brych & Händel, 2020; Brych et al., 2021; Murali & Händel, 2021) and same as in experiment 1.

5.4.5 Results

Effect of movement and restriction on Fluency

The mean fluency score during free walking was 10.6 (SD = 4.2), during restricted walking was 6.02 (SD = 2.9), during free sitting was 10.3 (SD = 4.01) and during restricted sitting was 5 (SD = 2.03). The mean flexibility score during free walking was 7.8 (SD = 2.6), during restricted walking was 3.1 (SD = 1.04), during free sitting was 7.5 (SD = 2.4) and during restricted sitting was 2.4 (SD = .92). Figure 31 shows the mean scores in all conditions.

For fluency, a repeated-measures two-factor ANOVA was conducted between the factors Movement (Walk vs Sit) and Restriction (Free movement vs. Restricted movement). The results showed a significant effect of restriction ($F(1,91) = 39.9$, $p < .001$), no significant effect of movement ($F(1,91) = 4.6$, $p = .0504$) and no significant interaction ($F(1,91) = 2.6$, $p = .4$). However, as one can see, the p-value for the factor movement is close to significance (.0504). A post-hoc T-test for the factor Restriction (Free movement vs. Restricted movement) revealed that fluency scores were significantly higher during free movement $t(45) = 7.8$, $p < .001$).

For flexibility, a repeated-measures two-factor ANOVA was conducted between the factors Movement (Walk vs Sit) and Restriction (Free movement vs. Restricted movement).

The results showed a significant effect of restriction (F (1,91) = 170.2, p < .001), but not for movement (F (1,91) = 4.6, p = .07) and no significant interaction (F (1,91) = .8, p = .4). A post-hoc T-test for the factor Restriction (Free movement vs. Restricted movement) revealed that flexibility scores were significantly higher during free movement (t (45) = 15.6, p < .001). Additionally, supplementary figure S21 shows the mean fluency score over all subjects for each word. A within subject ANOVA revealed no significant effect of the words (F (7,179) = 0.7, p = .6).

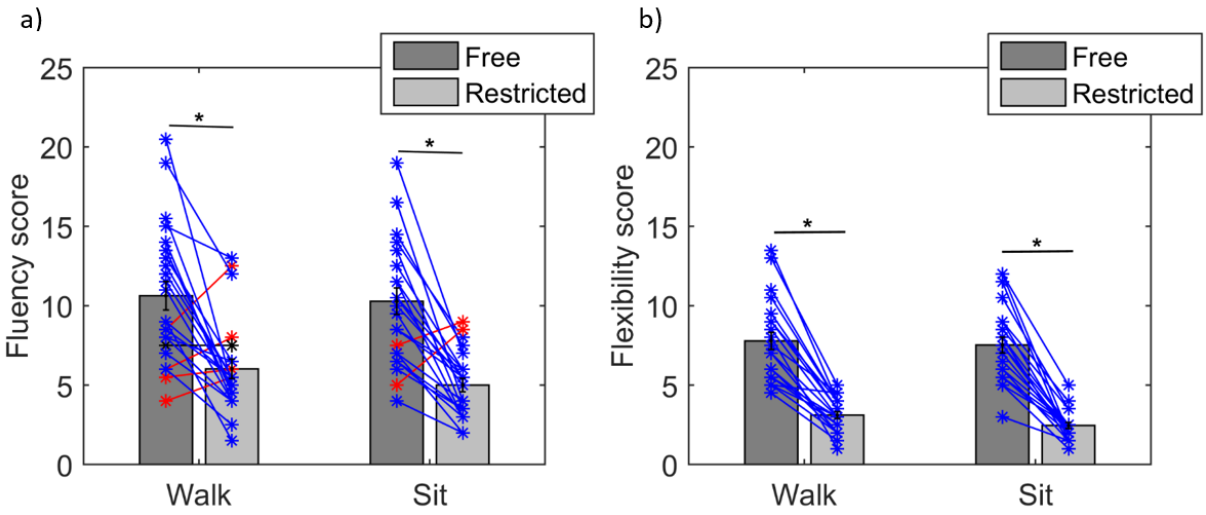


Figure 31. The mean fluency score (a) and flexibility score (b) during free and restricted walking and sitting in experiment 3 are shown. A two-factor ANOVA revealed a significant effect of restriction (F (1,91) = 39.9, p < .001), but no significant effect of movement (F (1,91) = 4.6, p = .0504). However, the p-value for the factor movement was close to significance (.0504). The asterisks represent data from individual subjects. The blue lines represent cases with higher scores during free movement, the red lines represent higher scores during restriction and black lines represent equal scores.

Eye blinks related to different motor states and AUT scores

The mean think time blink rate during free walking was 15.4 (SD = 13.1) and during restricted walking was 16.8 (SD = 13.4). A t-test showed no significant difference between the two conditions (t(21) =1.6 ,p = .1). The mean time blink rate during free sitting was 12.1 (SD = 7.8) and during restricted sitting was 10.9 (SD = 10.6). A t-test showed no significant difference between the two conditions (t(21) = .4,p = .6).

To test if eye blink rates are linked to the scores, we conducted a multiple regression model with eye blink rate as a predictor and movement (Walking or Sitting) and restriction (Free or Restricted) as categorical independent variables. For fluency, the model revealed a significant effect of blink rate ($F(2,182) = 19.1$, $p < .001$), no significant interaction between blink rate and restriction ($F(2,182) = 3.8$, $p = .054$) and also no significant interaction between blink rate and movement ($F(2,182) = .5$, $p = .4$). The p-value for the interaction between blink rate and restriction was close to significance (.054). For flexibility, the model showed a significant effect of blink rate ($F(1,182) = 18.4$, $p < .001$), a significant interaction between blink rate and restriction ($F(1,182) = 7.8$, $p = .01$), but no significant interaction between blink rate and movement ($F(1,182) = .3$, $p = .5$). Figure 32 shown the mean scores plotted against blink rate, for each subject.

A post-Hoc regression analysis conducted on fluency vs blink rate on the restricted and free conditions (taking the mean over the movement conditions) revealed no significance for free ($F(1,20)=3.5$,$r2=.2$,$p=.07$), or for the restricted ($F(1,20)=1.9$,$r2=.1$,$p=.2$) condition. A post-hoc regression test on flexibility revealed significance for the free ($F(1,20) = 4.6$, $r2 = .2$,$p = .04$) but not the restricted ($F(1,20) = 0.7$, $r2 = .03$, $p = .4$) condition.

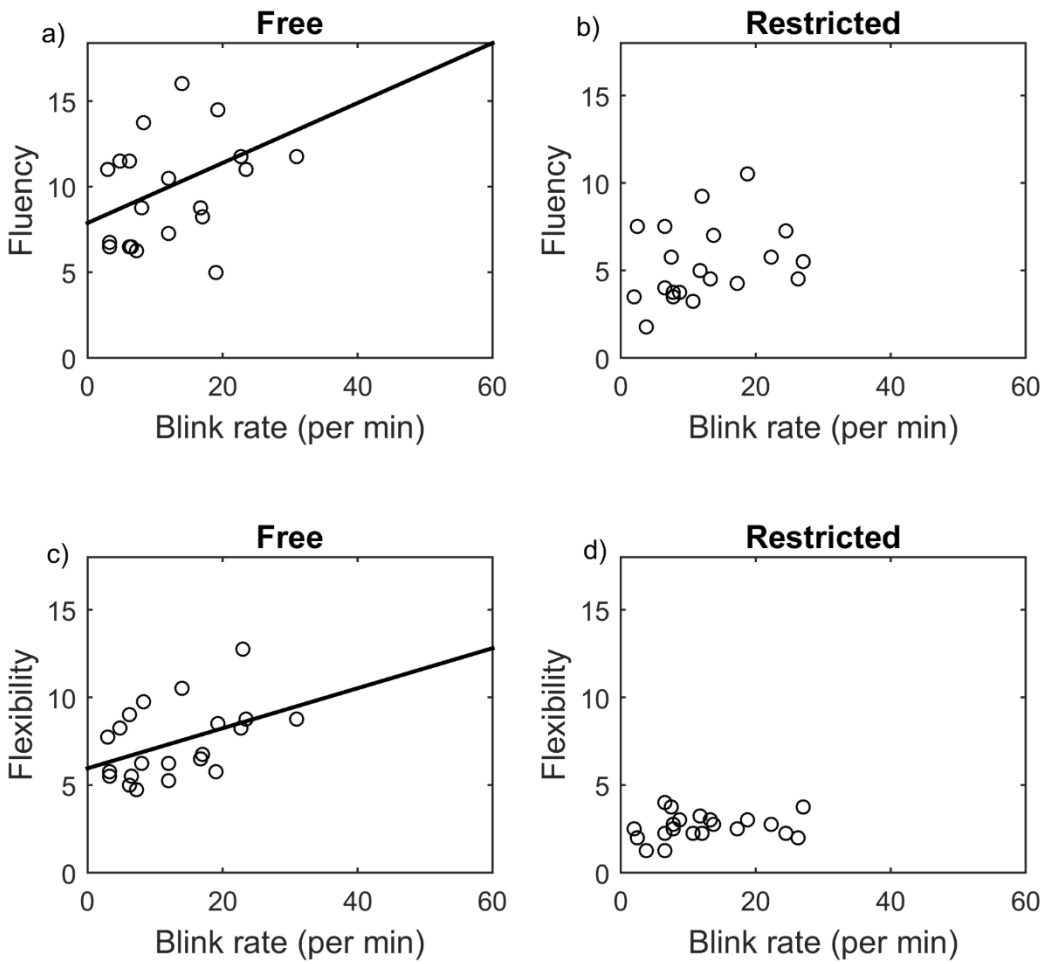


Figure 32. The mean fluency score (a, b) and flexibility scores (c, d) plotted against the blink rate for each subject during the free (a, c) and restricted (b, d) conditions are shown. Each circle represents data from a single subject. For fluency, a multiple regression model revealed a significant effect of blink rate ($F(2,182) = 19.1$, $p < .001$), no significant interaction between blink rate a restriction ($F(2,182) = 3.8$, $p = .054$) and no significant interaction between blink rate and movement ($F(2,182) = .5$, $p = .4$). The p-value for the interaction between blink rate and restriction was close to significance (.054). For flexibility, the model showed a significant effect of blink rate ($F(1,182) = 18.4$, $p < .001$), a significant interaction between blink rate a restriction ($F(1,182) = 7.8$, $p = .01$), but no significant interaction between blink rate and movement ($F(1,182) = .3$, $p = .5$).

Note that one outlier was excluded (due to blink rate > 3 standard deviations in the restricted sitting condition) in the above analysis (see figure 32).

Additionally , to test for a possible within-subject effect of eye blinks on performance, we included a within subject analysis sorting trials as to low and high AUT scores for each subject and tested for a difference in blink rates. There was no indication of a relationship between blink rate and flexibility/ fluency scores as can be seen in our supplementary material (see Figure S22).

5.5 Discussion (Study 4)

Our studies show that fluency and flexibility scores in a divergent thinking task are higher during unrestricted movement than during restricted movement. Although, previous work has already described a difference between free vs. restricted walking (Kuo & Yeh, 2016; Leung et al., 2012), we extend these findings by showing improved performance during free compared to restricted sitting, thereby identifying a movement state independent effect of restriction. We ascribe this effect to a broadening of the attentional focus, as will be discussed below. Additionally, our data suggests that while the overall rate of spontaneous blinking can correlate with the performance in the AUT, i.e. subjects with a higher blink rate tend to score higher, a change in the blink rate within subjects does not go hand in hand with a modulation in performance. Accordingly, while we found that blink rates increase during other motor output like walking and speaking, this blink rate increase is not related to divergent thinking but likely depicts movement interaction as part of natural behaviour.

5.5.1 The benefit of free movement during divergent thinking

The beneficial effect of free movement during divergent thinking seems surprising at first since performance normally suffers during dual tasks. Activity involving gait or balance, indeed binds cognitive resources as they interfere with certain cognitive tasks (Al-Yahya et al., 2011; Patel et al., 2014). This contradiction was explained by the idea that, for certain tasks like the AUT, depleting cognitive resources might actually be beneficial by reducing top-down control mechanisms (Zhou et al., 2017). In fact, a study by (Radel et al., 2015) showed that experimentally depleting cognitive resources through an additional task improved performance in the AUT. Both (Radel et al., 2015) and (Zhou et al., 2017) discuss the idea that a lack of top-down control leading to a decrease in attentional focus might benefit divergent thinking. This idea was applied to explain why participants performed better in a divergent thinking task while standing compared to while sitting or lying down (Zhou et al., 2017). Whereas in this case it is easily conceivable that sitting or lying down required less cognitive resources, in our study, it is not obvious that following instructions during restriction would involve fewer cognitive resources than unrestricted movement. In fact, one might expect the opposite. Our finding that restricting and thereby controlling motor output has a negative effect on divergent thinking, therefore rather supports an underlying mechanism of AUT improvement that is not based on the amount of cognitive or attentional resources but rather on the distribution of those resources. More specifically, we propose that the size of the attentional focus during free movement influences divergent thinking. Although, the influence of the size of attentional focus on creativity has been proposed before, as will be discussed in the next paragraph, the idea that the difference between free and restricted movement could stem from this attentional difference has not yet been put forward.

For quite some time, studies have shown that creative individuals tend to have a broader attentional focus than less creative individuals (Dykes & McGhie, 1976; Martindale, 1999; Mendelsohn & Griswold, 1964, 1966). More recent, studies have additionally revealed that manipulating attentional breadth can effect creative performance. For instance, Nijstad et al. (2010) conducted an experiment wherein attentional breadth was manipulated via a Navon task (Navon, 1977). They found that attending to the larger letter during the task, improved performance in a subsequent AUT task. Similar results were also shown by Friedman et al. (2003) where participants completed a visual search task in a narrow or broad visual area. Specifically, the visual stimuli were present either in a narrow area around the fovea or at a comparably large area including the periphery. The concluded that after broadening the focus of visual attention, participants gave more original ideas in a subsequent AUT. According to the authors, the narrowing or broadening of perceptual (or visual) attention could facilitate the narrowing or broadening of conceptual attention. The benefit of a broad attentional focus on divergent thinking has been replicated (Memmert, 2007; Moraru et al., 2016) and the longitudinal study by Memmert (2007) could show that attention broadening training improved creative performance.

However, studies have not linked the positive effect of a broad attentional focus to the benefit of walking or free walking for divergent thinking. Here we propose that a main difference between restricted and unrestricted movement lies in the size of the focus of attention. During our restricted sitting condition, subjects had to fixate a small dot on the screen. This means the task directly implied a focus of attention on a very small area. With regard to free and restricted walking, a similar effect is likely, as subjects had to monitor the visual markers that defined their walking path. Indeed, walking itself seems to broaden the attentional focus as it has been shown that compared to standing still, walking leads to a

stronger processing of peripheral visual input despite fixation (Cao & Händel, 2019). So even without explicit instruction, walking can broaden the attentional focus.

But how does a broad attentional focus facilitate divergent thinking? An explanation has been proposed by Nijastad in the dual pathway to creativity model (Nijstad et al., 2010). The dual pathway model proposes that two processes are involved in creative thinking, namely, cognitive flexibility and cognitive persistence. Flexibility involves switching between different ideas and concepts that are normally not associated with each other. On the other hand, persistence refers to the focused search for a specific solution. According to Nijstad et al. (2010) there could be a bias towards one or the other process, depending on the task. This idea has been extended to cognitive control by Hommel (2015) in the Metacontrol State Model (MSM). Both (Nijstad et al., 2010) and (Hommel, 2015) agree that a bias towards flexibility facilitates divergent thinking. Importantly, according to Nijstad et al. (2010), such a bias towards flexibility can be introduced by a broadening of attention.

To summarize, we propose that a broadening of the attentional focus during free compared to restricted movement biases the system towards flexibility and therefore improves divergent thinking. So rather than an activation of abstract concepts, such as voiced in the conceptual metaphor theory (Lakoff & Johnson, 1980) which was previously used to explain the positive effect of movement (Kuo & Yeh, 2016; Slepian & Ambady, 2012), we suggest that the attention based effect as previously described to influence divergent thinking can be extended to free movement.

5.5.2 The relationship between eye blinks and divergent thinking

Can blink behaviour help us to assess a difference in attentional state during the various conditions of our creative thinking task? It has been shown that there is an active

suppression of blinks during the processing of a visual stimulus (Bonneh et al., 2016; Murali & Händel, 2021; Edmund Wascher et al., 2015). This can be most prominently observed as blink rate reduction during the presentation of the sensory input and a subsequent blink rate increase (Brych & Händel, 2020; Oh, Jeong, et al., 2012; Siegle et al., 2008). The degree of blink rate modulation introduced by a stimulus is elevated if a perceptual task is included (Brych & Händel, 2020) and can further be suppressed by task difficulty (Oh, Jeong, et al., 2012). This could indicate that blinking is influenced by visual attentional load. When considering the difference between restricted and free conditions, subjects indeed needed to attend to the visual input that indicated the restriction (fixation point or marker for the walking path). However, the visual information was continuous whereas the blink rate modulation is mostly observed around stimulus on- and offset. Additionally, no task, such as a detection of temporal changes was required, which renders the suppression of blinks in order not to miss information unnecessary. It is therefore not surprising that we found no difference in blink rate between the restricted and free conditions (see Section 5.4.5). We conclude that the blink rate cannot shed further insights as to the attentional state during the two restriction conditions in our set up.

The comparably lower blink rate during sitting compared to walking (see Figure 29) is likely based on movement interaction as part of natural behaviour. Eye blinks, like other movements such as saccades and pupil size, are linked to other motor output such as walking and speaking. For instance, blink rates have been reported to be higher during walking compared to standing (Cao & Händel, 2019), corresponding to the present results (see Figure 29). Further, we corroborated the finding of increased blink rates due to speaking (Brych et al., 2020; von Cramon & Schuri, 1980) which was clearly associated with the motor activity during speech production (Brych et al., 2020). Interestingly, we could show that this increase

during speaking was specific to the sitting condition, while blink rates were similarly elevated during the walking condition for all three task phases (baseline, think time and response time). This suggests that blinking does not depict the quantitative motor output (as it is a non-cumulative effect) but rather marks a movement state. In other words, since walking and concurrent talking does not have a higher blink rate than walking or talking separately, the increase in eye blink rates goes hand in hand with a change in the state of movement, but more body parts moving would not lead to a stronger enhancement. Overall, our data clearly shows that an increase in blinking e.g. due to walking cannot be associated with an improvement in divergent thinking as restricted walking shows a clear blink rate increase but no behavioural improvement, while free sitting shows a low blink rate despite a behavioural improvement. Also within a movement condition, the blink rate does not indicate the ability for divergent thinking, as trials with high scores are not the ones with a high blink rate (Figure S22). This is true despite a quite sensitive within subject analysis.

However, we do find that subjects with a higher overall blink rate performed better in the AUT task during free movement. Previous studies have also shown such a between-subject correlation between eye blink rate and divergent thinking (Akbari Chermahini & Hommel, 2010; Ueda et al., 2016). While Akbari Chermahini and Hommel (2010) showed a quadratic relationship between baseline eye blink rates and AUT scores, Ueda et al. (2016) described a linear relationship when analysing eye blinks during the task. Baseline eye blink rates have been shown to reflect dopamine levels and therefore, as Akbari Chermahini and Hommel (2010) put forth, benefit divergent thinking when they exhibit moderate rates. However, Ueda et al. (2016) explain the linear effect of task-related eye blinks through the activation of the default mode network. As mentioned in the introduction, the default mode network has been proposed to be involved during creativity (Beaty et al., 2014; Kühn et al.,

2014). We can add, as the level of blink rate within a subject did not correlate with the scores (see Supplementary figure S22) a temporally fine-grained marker of dopamine is not likely. Our data further weakly indicates that blink rates mainly correlate during unrestricted behaviour. It is a possibility that only during unrestricted states the default mode network can exert its full influence. To our knowledge, studies have not tested the influence of restriction on the default mode network. However, as our study has a comparably low sample size compared to previous studies, future studies are required to test this specific effect.

5.5.3 Conclusion (Study 4)

Our studies showed a beneficial effect of unrestricted (or free) movement on divergent thinking independent if restriction was minimized during walking or during sitting. We propose that this effect is due to a broadening of the field of attention when no restriction is placed. The subsequent benefit in divergent thinking might be introduced by a bias towards flexibility due to the broadened focus of attention (Nijstad et al., 2010). Our results further provide evidence that an externally guided increase in motor output, walking or blinking, will not lead to improved creativity, because if subjects are forced to move in a controlled fashion, they will not profit from it. These findings have several important implications. Given the current situation of the COVID-19 pandemic and the resulting increase in online teaching, it is important to understand its effects on learning and creativity. Since most online teaching involves fixating on a computer screen, the amount of free body movements, including head and eye movements, are greatly reduced compared to a normal classroom set up. Considering our findings, simple and effective strategies such as introducing periods of free movements in between sessions of online teaching, even if during sitting, can improve the flow of ideas and aid in the learning process.

5.6 Supplementary material (Study 4)

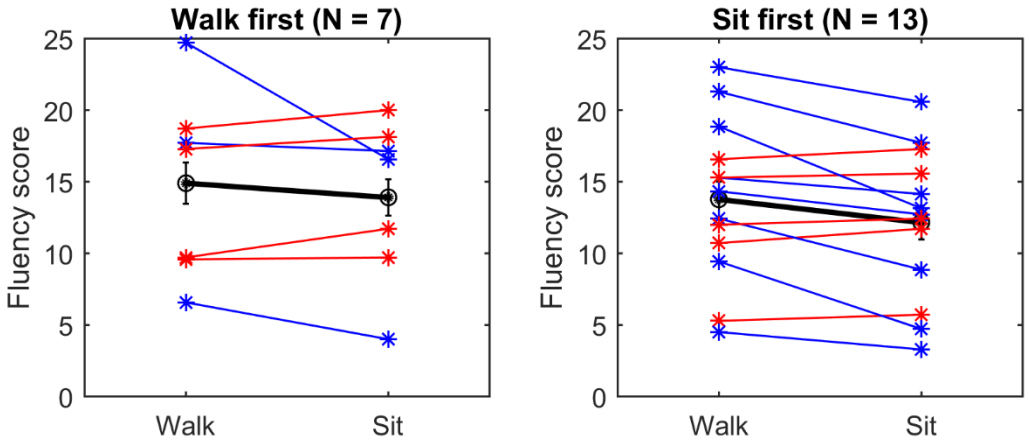


Figure S20 Shows the mean fluency scores for walking and sitting dependent on the order of the conditions in experiment 1; difference between the walk and sit condition for those who did the walk condition first (left) and those who did the sit condition first (right). The asterisks represent data from each subject. The blue lines represent cases where the fluency score is higher for the walking condition and the red lines represent cases wherein it is higher for the sitting condition. A t-test showed significance only for those who sat first ($t(12) = 2.6$, $p = .02$) and no significance for those who walked first ($t(6) = 0.7$, $p = .5$).

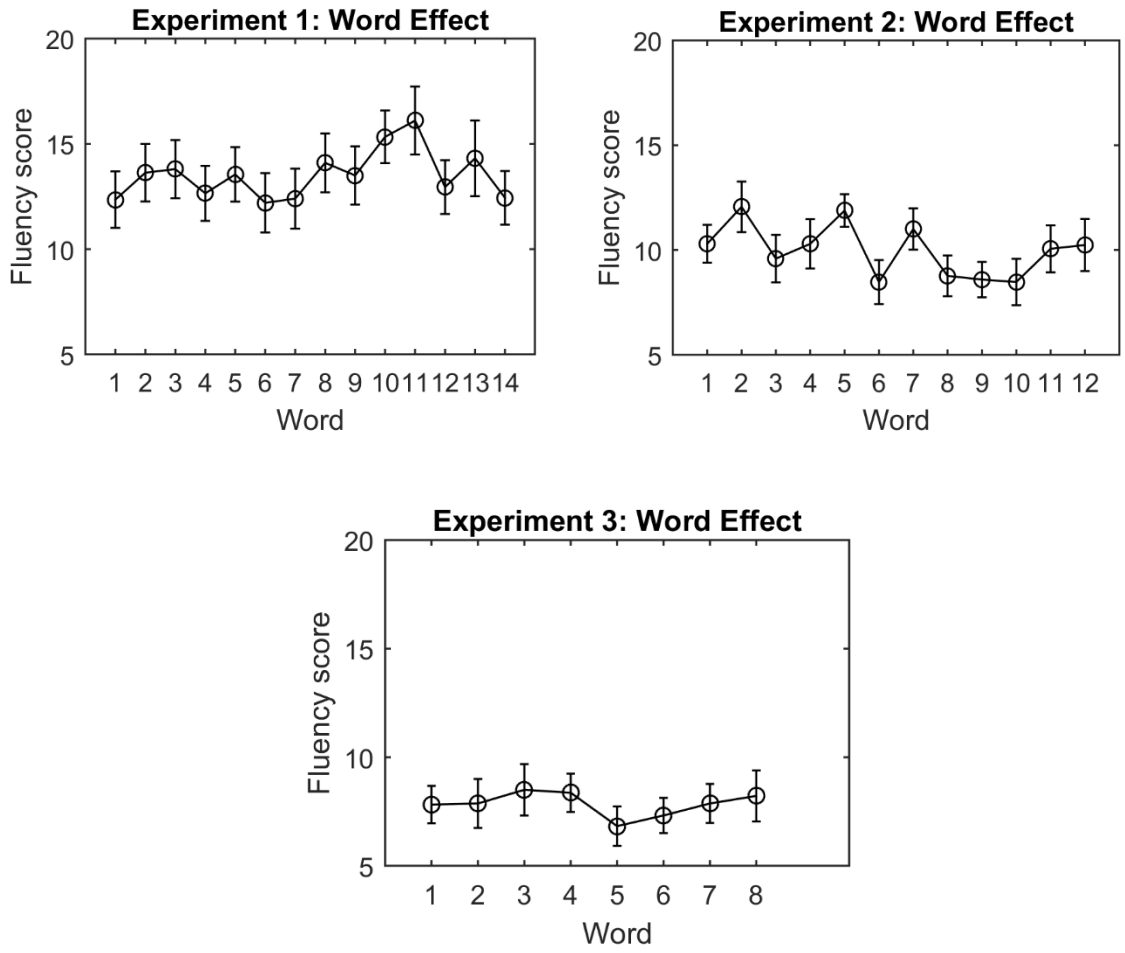


Figure S21 shows the mean fluency score over all subjects for each of the 14 words in experiment 1 and 12 words in experiment 2. An ANOVA revealed no effect of the words in experiment 1 ($F(13,269) = 0.96$, $p = .5$), experiment 2 ($F(11,203) = 0.3$, $p = .9$) and experiment 3 ($F(7,179) = 0.7$, $p = .6$)

Table S3

Shows the order of the conditions for each subject of experiment 2.

Subject	Condition sequence			
1	3	2	4	1
2	4	3	2	1
3	1	4	2	3
4	4	1	3	2
5	1	4	3	2
6	2	3	4	1
7	4	2	1	3
8	2	4	1	3
9	3	2	1	4
10	3	2	4	1
11	4	3	1	2
12	4	1	3	2
13	4	1	2	3
14	1	4	3	2
15	2	4	3	1
16	1	4	3	2
17	3	2	1	4

1= Free walking

2= Restricted walking

3 = Free sitting

4 = Restricted sitting

Table S4

Shows the order of the conditions for each subject of experiment 3.

Subject	Condition sequence			
1	3	2	4	1
2	2	1	4	3
3	4	2	3	1
4	4	3	1	2
5	4	1	2	3
6	1	3	4	2
7	2	1	3	4
8	4	3	1	2
9	1	3	2	4
10	3	1	2	4
11	1	2	4	3
12	2	4	1	3
13	2	4	1	3
14	2	4	1	3
15	4	1	2	3
16	2	4	1	3
17	4	2	1	3
20	4	3	1	2
21	1	2	3	4
22	1	3	4	2
23	4	3	1	2

1= Free walking

2= Restricted walking

3 = Free sitting

4 = Restricted sitting

To exclude any within subject influence, we took the difference between the blink rates of the trials with lowest and highest fluency for each subject in experiment 1 and 3 and conducted a one-sample T-test against 0 (see Figure 15). The T-test found no significant difference in walking (t(40) = .6, p = .5) or for sitting (t(40) = 1.5, p = .1). The same was done using the flexibility scores which also showed no significant difference during walking (t(40) = 1.5, p = .1) or during sitting (t(40) = 1.1, p = .2).

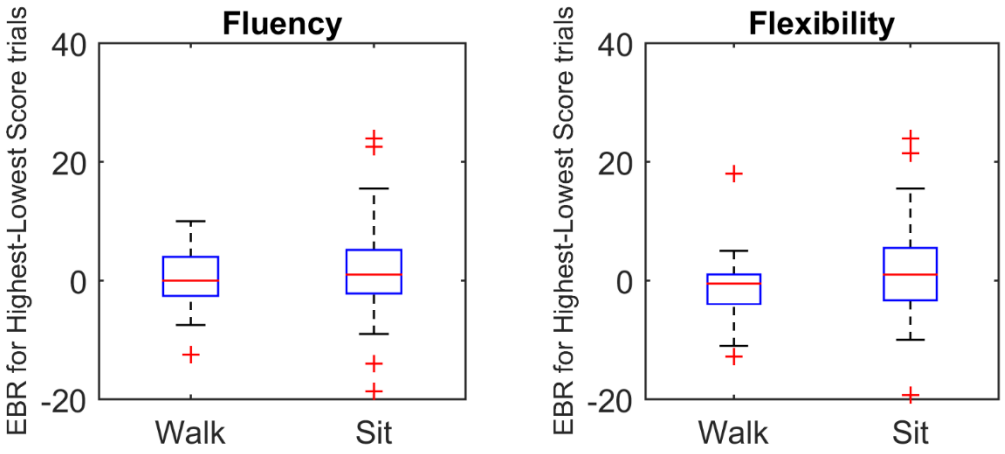


Figure S22. shows the difference in eye blink rate of the highest and lowest fluency (left) and flexibility (right) scores during walking and during sitting. The T-test found no significant difference from zero during walking (t(40) = .6, p = .5) or for sitting (t(40) = 1.5, p = .1) when taking fluency scores. Similarly, no significant difference was found during walking (t(40) = 1.5, p = .1) or during sitting (t(40) = 1.1, p = .2) when taking flexibility scores.

6. Study 5: Qualitative difference in blink related modulation of V1 activity for different processing states

Previous human behavioral studies have shown that spontaneous blinking decreases when engaging with an external stimulus. On the other hand, blinking possibly increases (or even facilitates) stimulus disengagement. However, whether the neural response to blinks differs between sensory processing states of the individual is not known. In order to understand this, we analyzed the neural activity, both spiking activity and changes in different frequency bands, in the primary visual cortex of three rhesus monkeys around a blink while the animal was watching a movie or shown a blank screen. The results revealed a difference in the neural activity between the two conditions/processing states. Specifically, we found that the multiunit activity envelope (MUAe) around blinks increased during the blank screen, decreased during the movie condition. With regard to frequency related modulations, there was an increase around blinks in three different frequency bands: theta (4-8 Hz), beta (16-30 Hz) and gamma (35-80 Hz) differed between conditions; however this increase was less pronounced and later in time during the movie condition. Additionally, the distribution over the channels in the laminar probe suggest a focus in the granular and infragranular layers. Overall the data suggests that blink related neural responses are dependent on the attentional state and that the main difference in the pattern between the states occurs in the deeper layers of V1.

6.1 Introduction (Study 5)

Blinking is an integral part of ongoing natural motor behavior. The most common type is spontaneous blinking, which consists of non-consciously executed blinks that are to a certain extent driven by the need to maintain the tear film of the eye. About 3-4 blinks a minute were calculate to be required for this purpose (Norn, 1969). However, the normal rate of occurrence is between 10 to 15 times a minute (Burr, 2005; Doughty, 2001; Kaminer et al., 2011; Zametkin et al., 1979), which means that approximately 70 to 80% of spontaneous blinking is not driven by such physiological needs. Despite quite a number of studies describing what factors modulate these excess spontaneous blinks, their role is not yet established.

Spontaneous eye blinks have been shown to be modulated by low-level stimulus features as well as cognitive processes that influence the processing or interpretation of such stimuli. The pattern that is generally found is that blinks decrease around stimulus onset and increase afterwards (Bonneh et al., 2016; Brych & Händel, 2020; Murali & Händel, 2021; Oh, Jeong, et al., 2012). Bonneh et al. (2016) found, using a passive-viewing task, that the degree of the reduction can depend on low-level stimulus features, such as contrast and spatial frequency. The pattern of blink decrease followed by an increase also occurs during active processing of the stimulus during a task (Brych & Händel, 2020; Oh, Jeong, et al., 2012; Siegle et al., 2008). Additionally, the decrease/ increase pattern can be independent from sensory input onset as it was found during continuous stimulation but temporally related to a perceptual change as shown using ambiguous stimuli (Plaid reference). For perceptual tasks, the decrease was shown to be/ interpreted to be an active suppression (Bonneh et al., 2016; Murali & Händel, 2021; Edmund Wascher et al., 2015). Indeed, the time taken to process the

important information embedded in the stimulation has been shown to be a relevant factor affecting the length of blink suppression (Murali & Händel, 2021). This clearly highlights a cognitive aspect as the relevance of the stimulus is not defined by sensory features but by cognition. Hence, the decrease or suppression does not merely occur in order to not miss any relevant visual information. This is also shown by the fact that it has also been observed in the auditory domain (Bauer et al., 1985; Goldstein et al., 1985; Gregory, 1952, Murali & Händel, 2021). The increase above baseline suggests an active process of blinking. Other cognitive factors such as task difficulty have further been shown to play a role in blink rate modulation (Brych et al., 2020; Oh, Jeong, et al., 2012).

An important observation we made in a previous study was the effect of attention on blink modulation. While unattended visual input led to a blink probability increase shortly after stimulus onset, this increase was enlarged if the visual input was attended. Even more interesting, while unattended auditory input did not lead to a visible modulation of blink probability, once the auditory input was attended, the modulation was clearly visible (Brych & Händel, 2020). Other studies have also found that attention and/or cognitive load would have an effect on the strength of the decrease or duration of blink suppression (Fogarty & Stern, 1989; Oh, Jeong, et al., 2012; Siegle et al., 2008). This would suggest that the role of blinks depends on the attentional state. Knowing the neural pattern related to blinks can help establishing and further understanding such this role.

Unfortunately, although the neural correlates of spontaneous blinks have been previously studied, researchers have not distinguished between the neural patterns introduced by blinks during different attentional states. In fact, most of the studies involved passive viewing (Bristow, Frith, et al., 2005; Bristow, Haynes, et al., 2005; Gawne & Martin,

2000, 2002). The reason is that the focus of previous research has been to understand visual constancy, which is the continuous perception of the surround despite the interruption by a blink. This visual constancy seems at least partly based on blink-related suppression, whereby the visual system seems to ignore the transient interruption and darkening of the environment during a blink (Volkmann, 1986; Volkmann et al., 1980). A study by (Bristow, Frith, et al., 2005), investigating voluntary blinks in humans, found a reduced fMRI BOLD signal in the bilateral temporo-occipital and parietal cortical loci when comparing periods of blinks with periods without blinks. They further described an increase in activation in the medial parieto-occipital cortex when comparing periods of blinking in the presence of a visual stimulus vs in the absence of a visual stimulus. They argued that the decrease in activity could be associated with blink-related suppression. The increased activity according to them, on the other hand, could indicate memory processes involved in visual constancy whereby the last visual image is maintained. In another study, the same authors (Bristow, Haynes, et al., 2005) analyzed blinks in the presence and absence retinal stimulation independent of the position of the eyelid. In their study, they directly stimulated the retina from the roof of the mouth while the actual closing and opening of the eyes did not generate any visual changes. They found that when blinks occurred during such retinal stimulation, there was a decrease in activity in area V3. However, when blinks occurred without retinal stimulation, there was an increase in activity in V1 and LGN. Similar to their previous paper, they concluded that a decrease in V3 might represent blink-related suppression since it occurs only during stimulation. The authors discuss that the increase in LGN and V1 could be a motor related signal. This however, would assume a rather complex process, as the motor act of blinking is executed independent if there is retinal stimulations during the blink or not. Comparing blinks, with external darkening and self-initiated external darkening while subjects performed

an image discrimination task, Golan et al. (2018a) found that lower visual areas showed an increase in response for all events, whereas higher visual areas showed an increase during external darkening. Overall these studies show that lower and higher visual areas respond differently dependent if the blink is leading to a change in visual input or not. They specifically suggest that V1 increases due to a blink if there is no retinal stimulation while it does not show any specific change in the absence of retinal stimulation.

The aforementioned studies were conducted on humans using fMRI and therefore could not show a temporal relationship between blink event and changes in BOLD signal but rather a temporally unspecific change dependent on task condition. ECoG recordings in humans (Bristow et al., 2005) and single unit recordings in animals (Buisseret & Maffei, 1983; Gawne & Martin, 2000) add such time resolved information on neural activity related to blink events. For instance, Buisseret and Maffei (1983) found that there was a decrease followed by an increase (sometimes) in the firing rate of neurons V1 of an anesthetized cat during a reflex blink, both during and without visual stimulation. Other studies have also found similar results, but most studies have focused on the blink related neural response during visual input. In a human ECoG study, probing areas beyond V1 one study compared blinks with external darkenings (Golan et al., 2016). These authors, using an image discrimination task, found a decrease in activity during and a transient burst of activity after both blinks and external darkenings. However, while the lower visual area (V1) did not differentiate between the types of input changes (blinks vs external), the transient burst was reduced for blinks in the higher visual areas (V3 and V4). A study by (Gawne & Martin, 2000), using single-unit recordings in rhesus monkey V1, compared blinks with external darkenings. They found that the rate of decrease was faster and more pronounced during blinks compared to external darkenings. Additionally, only a subset of neurons in V1 showed a transient burst and such

burst was only observed after the external darkening and not after a blink. The authors concluded that the suppression of this transient burst is the distinguishing factor between blinks and externally generated interruptions. In summary, these time resolved data indicate that blinks during visual input lead to decrease in V1 and that the corresponding transient burst differentiates external from blink related events.

These findings provide fascinating first insights about the neural activity related to blinking, however, these studies were conducted in order to explain the difference between blinking and externally introduced visual changes in order to explain why we do not perceive our blinks. Importantly, as reviewed above, if and when blinks are executed is highly affected by various external and internal factors. The suppression but particularly the increase of blink probability significantly above the normal rate suggests an active role of blinking during sensory and cognitive processes. Our aim was to understand if there is a neural difference in blinks dependent on the factor that influence blink execution. To this end, we analyzed the neural correlates of blinking during attended visual stimulation vs task irrelevant visual input in V1 laminar recordings in 3 rhesus monkeys. A distinct neural pattern might help to understand the function of spontaneous blinking.

6.2 Methods

6.2.1 Subjects

Three female rhesus monkeys (*Macaca mulatta*) were used to obtain the electrophysiological and eye movement data (DP, 6 years old, 9 kg; AL, five years old, 9 kg; FL, 4 years old, 6 kg). For the headpost and chamber implants, surgical and anaesthesia procedures, postoperative care, and implant methods were described in detail in a previous manuscript (Ortiz-Rios et al., 2018). All procedures were approved by the UK Home Office,

and they comply with the Animal Scientific Procedures Act (1986) on the care and use of animals in research and the European Directive on the protection of animals used in research (2010/63/EU).

6.2.2 Electrophysiological recordings and analysis

In all monkeys, the activity of all the cortical layers was recorded with laminar probes. A laminar Plexon S-probe (Plexon Inc., Texas, USA) was used with 24 or 32 contacts (100µm electrode spacing, 15µm electrode diameter) and a total length of 100mm and a probe diameter of 300 µm. Guide tubes were used to penetrate the granulation tissue on top of the dura and to stabilize the probe.

Raw electrophysiological signals were recorded using a Blackrock recording system (BlackRock Microsystems, Inc.) and sampled at 30kS/s. Data analysis was done in Matlab using the Fieldtrip toolbox (Oostenveld et al., 2011) and custom scripts. The CSDplotter toolbox (Pettersen et al., 2006) was used to calculate the CSD profiles of the visual responses using the standard CSD method. Local field potential (LFP) signals were obtained by downsampling the raw signal to 500Hz and then applying a notch filter at 50Hz to remove any line noise. Multiunit activity envelope (MUAe) signals were obtained by applying a high pass filter at 300 Hz to the raw signal, rectifying and then downsampling the signal to 500Hz (Supèr and Roelfsema, 2004).

6.2.3 Naturalistic viewing task

Animals were positioned at a distance of 84cm in front of a ViewPIXX computer screen (RR: 120Hz, VPIXX technologies), allowing for the presentation of stimuli on the screen at +/- 16° horizontally and +/- 9.5° vertically. Behavioural tasks were programmed and executed

using MWorks (MWorks) with custom scripts that used the MWorks Experiment Language (MWEL).

The animals passively viewed twenty video sequences in the experiment; each video sequence lasted 30 seconds (movie condition) and was followed by a blank grey screen for 30 seconds (blank screen condition). The video sequences consisted of four videos depicting a variety of activities and four edited versions of each video (such as tile scrambling and phase scrambling). The videos played in full screen and therefore occupying the visual field covered by the monitor. The video sequences were played sporadically across recording sessions with the animals so that they are not used to them and actively view them each time.

6.2.4 Eye movement recording

Eye position was recorded with Eyelink 1000 plus with a sampling rate of 1000 Hz; the raw signal was calibrated and converted to visual degrees by Mworks. The animals' eye movements were calibrated to the eye-tracking system such that we were able to infer their fixation location from a stimulus position on the screen and vice versa. During visual calibration, animals were performing saccades to visual stimuli that appeared at different locations (12 points) on the screen. The animals were trained to fixate on these stimuli for 500 ms with adequate precision (<2° visual angle). Upon successful fixation, the animals received a reward in the form of fruit juice or water.

Blinks were detected based on missing eye vector data. First, potential eye blinks were detected if data was missing for a minimum of 50ms and a maximum of 1000ms. Then, blinks that were less than 100ms apart were combined. The onset of the blink was defined by the first time point where the eye data was missing. The criteria was similar to previous studies (Brych & Händel, 2020; Brych et al., 2021b; Murali & Händel, 2021).

Two sessions have been used from monkey 1 and 3 and five sessions have been used from monkey 2. The table below (Table 1) shows how many trials were used per session. A trial refers to the presentation of a movie for 30 seconds (movie condition) and a subsequent 30 s period of blank screen (blank screen condition). The last column indicates for each session separately in which channel the first sink was observed following visual onset.

Table 1. The number of sessions and trials as well as the channel number at layer 4c (showing the first sink after visual onset) along with blink rate, is given for each monkey. Note that each trials consists of thirty seconds of a movie followed by thirty seconds of a blank screen.

Monkey	**Session**	**No. of trials**	**First sink channel**	**Blink rate (Blank, Movie)**
Monkey 1	Session 1	20	14	9.6; 7.7
	Session 2	20	15	10.9; 6
Monkey 2	Session 1	8	13	9.7; 12.2
	Session 2	10	12	7.8; 9.2
	Session 3	10	14	7.4; 8.8
	Session 4	5	15	6.8; 7.6

	Session 5	10	9	7.6; 9.2
Monkey 3	Session 1	15	14	4.5; 6.4
	Session 2	9	17	3.3; 4.1

6.3 Analysis

6.3.1 MUAe around blinks during a blank and during a movie

To analyze the time-resolved modulation of MUAe around a blink, we first combined the data from the different sessions for each monkey. As a second step, we low-pass filtered the MUAe data and cut out periods of 0.4 seconds around blink onset (0.2 s before and 0.2 s after) and averaged over the different channels for each blink separately. Lastly, we conducted a t-test for blank screen vs movie conditions on non-overlapping .002s time windows. A permutation-based approach by (Maris & Oostenveld, 2007) was applied to correct for multiple testing.

6.3.2 Frequency power changes around blinks

The spectral power was assessed by means of FFT (Hanning window). For the averaged time frequency representation (Figure 34), frequencies targeted were 2 to 100 Hz in steps of 2 Hz. The frequency analysis was done in shifting time windows (namely over 500ms in steps of 2ms) applied for a -0.5s to 0.5s period around blink onset. Power values were baseline corrected (relative baseline change, baseline from -0. 5 -0.3 s) All blinks irrespective of whether they occurred during a movie or a blank were used in order to visualize the changes

in the different frequencies with respect to a blink. The data from the different sessions were combined. For a consistent analysis in all three monkeys, we chose three frequency bands which we refer to as theta (4-8Hz), beta (16-30 Hz) and gamma (35-80 Hz). We then extracted the raw time resolved power over these different frequency ranges from the above frequency analysis (i.e. without baseline correction) separately for a one minute time period (-0.5s to 0.5s) around blinks occurring during a blank and during a movie. The time series consisted of 0.5s time windows with .002s overlap. Power values were averaged over sessions and channels. A t-test on each time window was conducted and a permutation-based (Maris & Oostenveld, 2007) was applied to obtain the significant time windows. In addition, we also tested the difference in the latency of peak power between the blank screen and movie.

6.3.3 Current source density (CSD)

The CSDplotter toolbox (Pettersen et al., 2006) was used to calculate the CSD profiles around blinks for the movie and the blank screen using the cubic spline iCSD method. Additionally, the average MUAe was taken over the channels of the supragranular (layers 2), granular (layers 4)and infragranular layers (layers 5-6) separately, using the position of the first-sink channel.

6.4 Results

6.4.1 MUAe around blinks during a blank and during a movie

Figure 33 shows the mean MUAe around blink onset plotted separately for the movie and the blank screen condition. Monkey 1 and 2 showed a similar pattern with an increase in activity during the blink onset for the blank screen condition and a decrease in activity for the movie condition. Note that the increase and decrease seem to start before the blink while the peak/ trough is reached after blink onset. For monkey 1 and 2 t-tests (on non-overlapping

.002s time windows) show a significant difference between blank screen vs movie condition (corrected for multiple testing using a permutation-based approach) before and after blink onset. The results of the non-parametric test including the T and p-values of each windows of the tested period (.202 s – 202 s) has been included as supplementary figure S46.

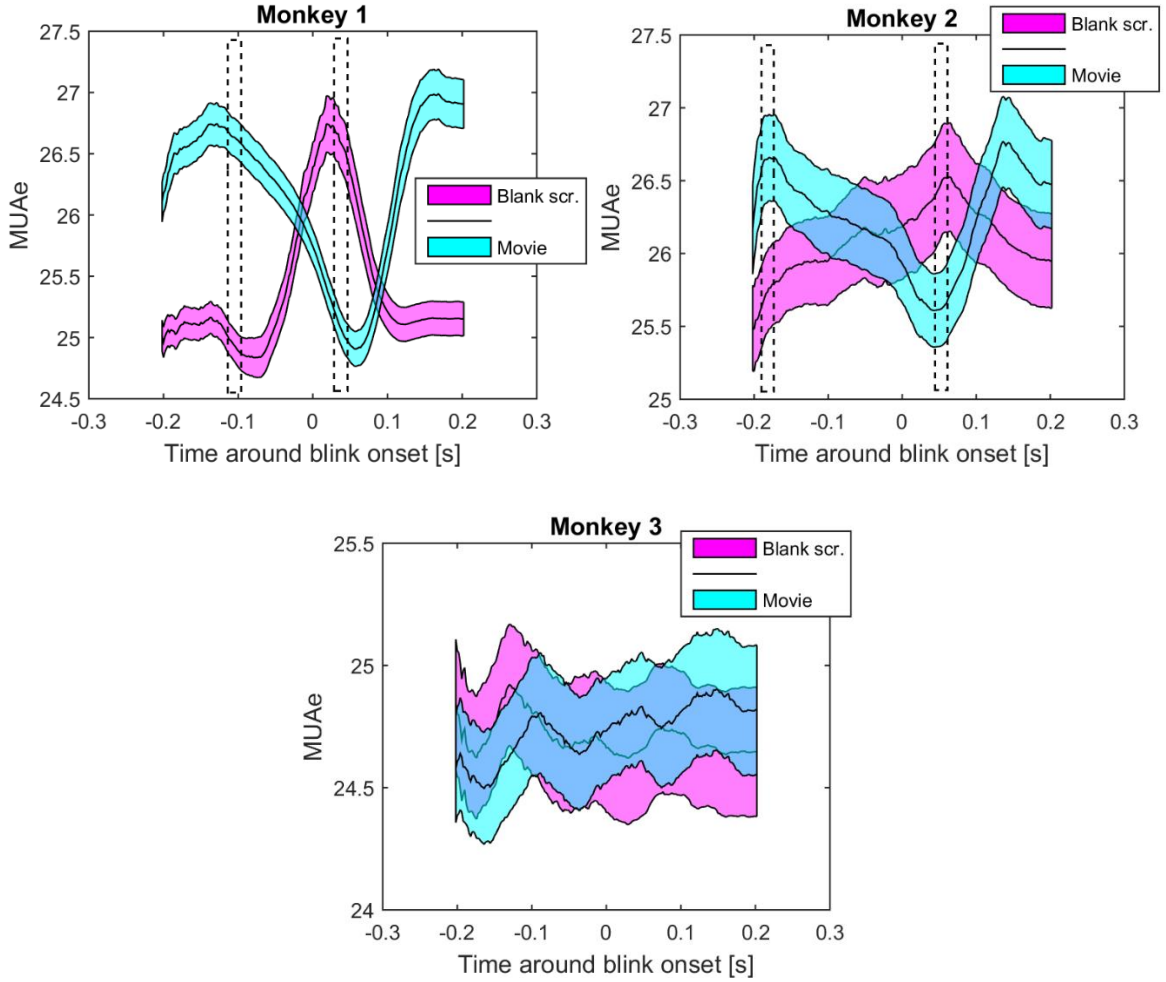


Figure 33. MUAe (averaged over channels) around blink onset for blank (pink) and movie (cyan) condition shown for monkey 1, 2 and 3. The x-axis marks the time around blink in seconds, with 0 indicating blink onset. The y-axis shows the MUAe averaged over channels and blinks. The shaded region marks the standard error. The dashed boxes show the time periods of significant difference between blank screen and movie condition as revealed by shifting t-tests and a permutation based correction.

Figure 34 shows the relative power plotted from -0.5 to 0.5 s in steps of .002 s around blink onset averaged over all blinks and sessions for each monkey separately. The plotted time refers to the center of the time window. Figure 34 shows an increase in relative power change in all three monkeys around blink onset. For monkey 1 and 2, we see a clear peak in power change in a low frequency band (around up to 8Hz), in a frequency range between 15-30 Hz and also at higher frequencies (>50 Hz). While monkey 3 showed a less clear pattern, the increase is still visible in however mainly above 60 Hz.

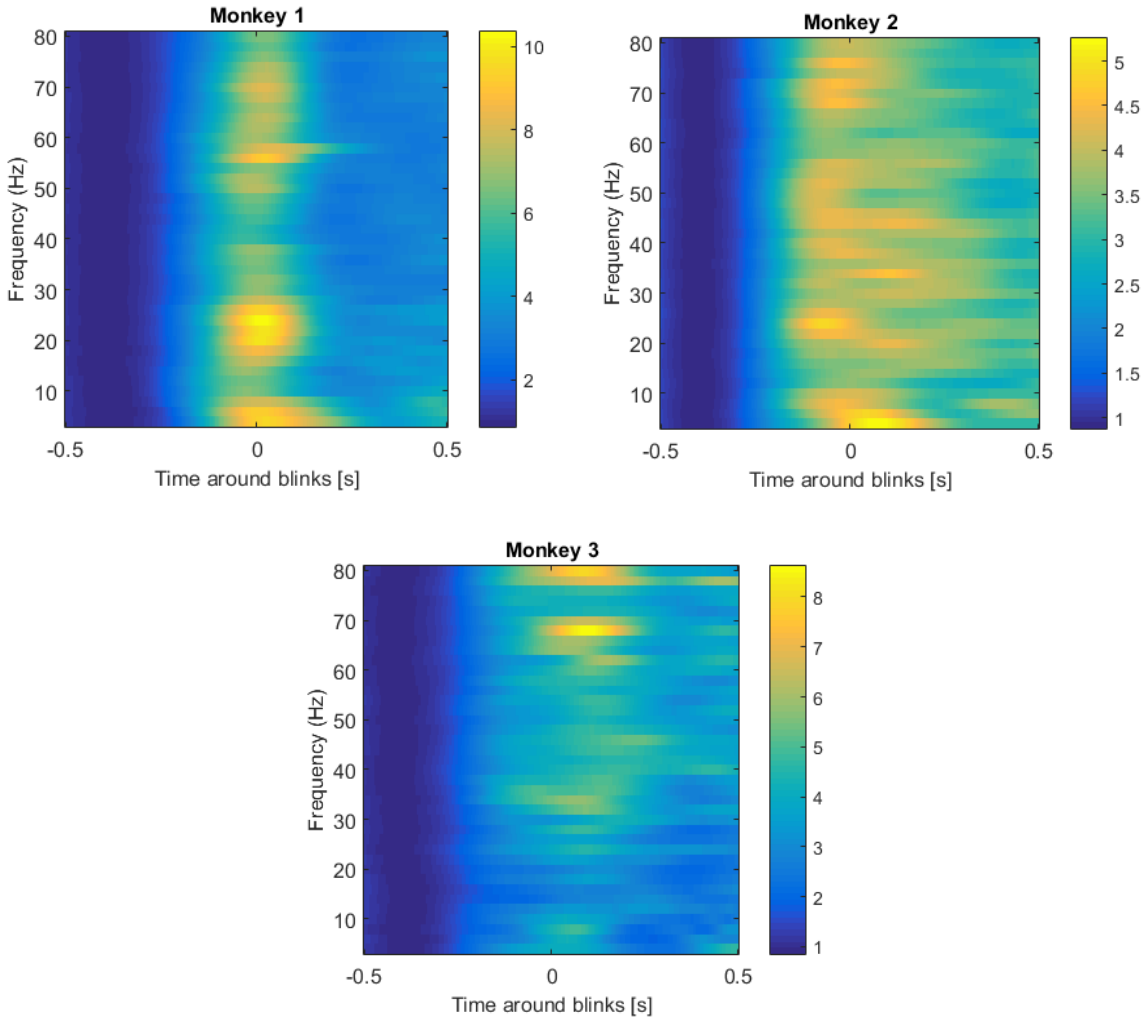


Figure 34. Relative power change around blink onset between 2 and 100 Hz shown for the three monkeys. All sessions, channels and blinks, regardless of movie or blank screen condition were included. The relative power change is plotted using -0.5 to -0.3 s as baseline. X-axis shows the different frequencies and the colour scale shows the relative power change.

condition (same for all three monkeys). Time windows that showed a significant difference (after T-test on each window as mentioned in the analysis) between movie and blank screen are marked with boxes (with dashed outlined). Please see supplementary figures S47-49 for the t and p-values for the whole period of .501 s – .501 s. In the theta and beta frequency bands, the raw power before the blink onset was significantly higher for blank screen condition compared to the movie condition. Power was significantly lower for blank screen condition compared to the movie condition after the onset. This pattern was consistent for monkey 1 and 2. Monkey 3 showed no significant effect in these two frequency ranges. In the gamma frequency band, there was a similar pattern and a significant effect for all three monkeys. In addition to these results, there was significant shift in peak latency the theta band ($t(340)=2.2, p=.02$) and a marginally significant shift in the beta band ($t(340)=1.9, p=.05$) only for monkey 1, but not for monkey 2 and 3 ($p > .1$). Note that the mean time window of the peak theta power is at -.02s (std=.2) for blank and .04s (std=.3) for movie for monkey 1. For the gamma band, however, there was no significant shift in peak power in any of the monkeys ($p > .1$).

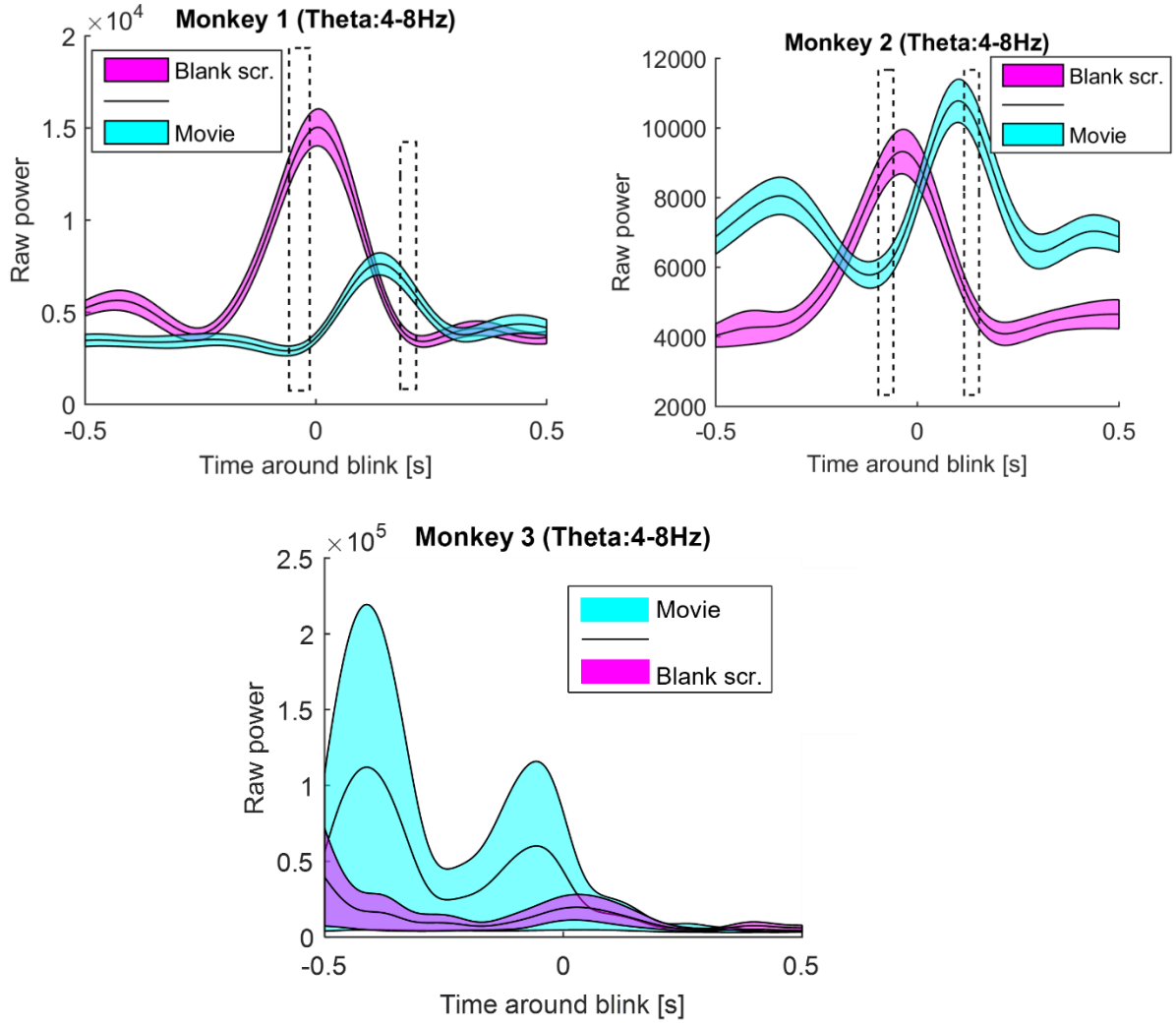


Figure 35. Raw theta power (4-8 Hz) around blink onset during blank screen (cyan) and movie (magenta) condition plotted separately for all three monkeys. The x-axis shows the time around blink onset in seconds. The y-axis shows raw change in power. Time of significant difference between blank screen and movie condition are marked with a box.

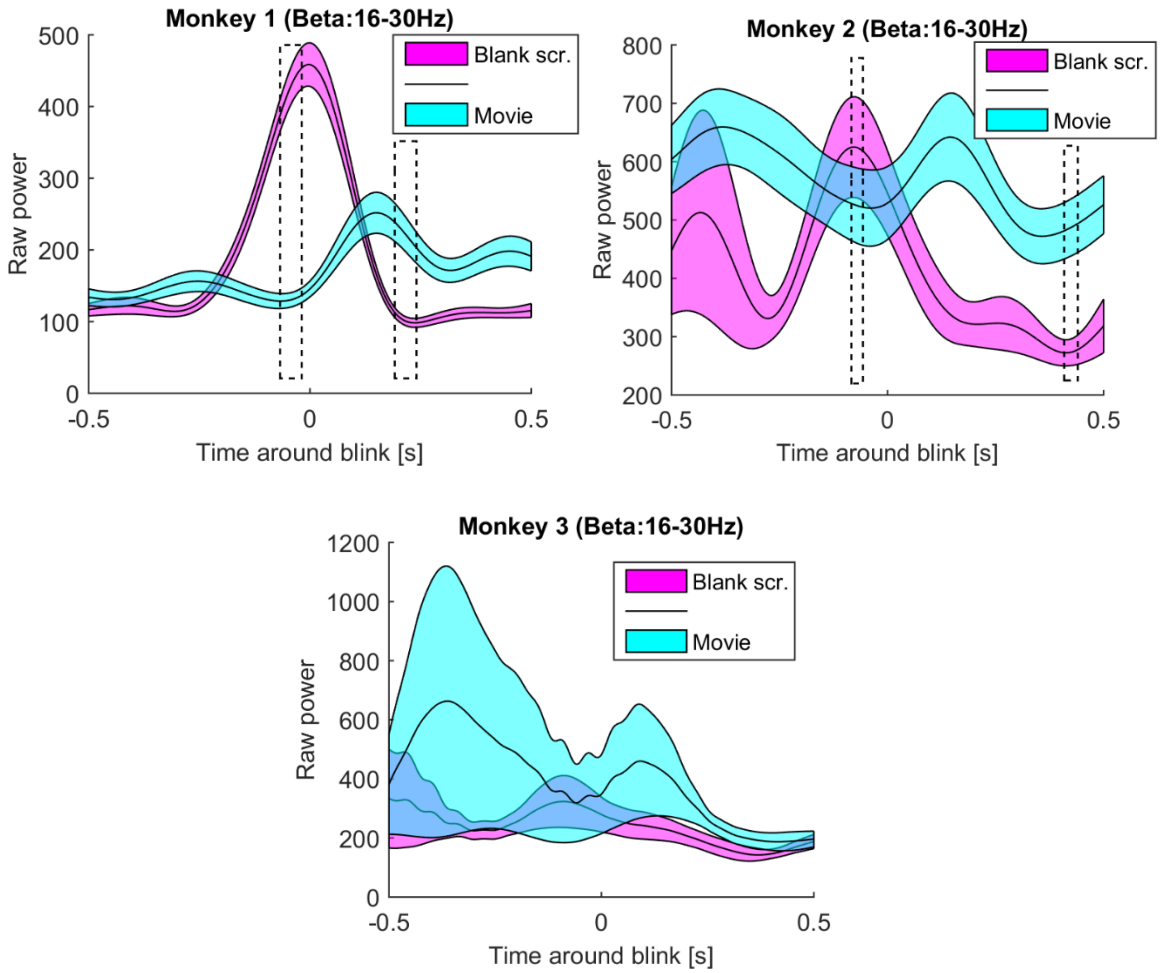


Figure 36. Raw beta power (16-30 Hz) around blink onset during blank screen (cyan) and movie (magenta) condition plotted separately for all three monkeys. The x-axis shows the time around blink onset in seconds. The y-axis shows raw change in power. Time of significant difference between blank screen and movie condition are marked with a box.

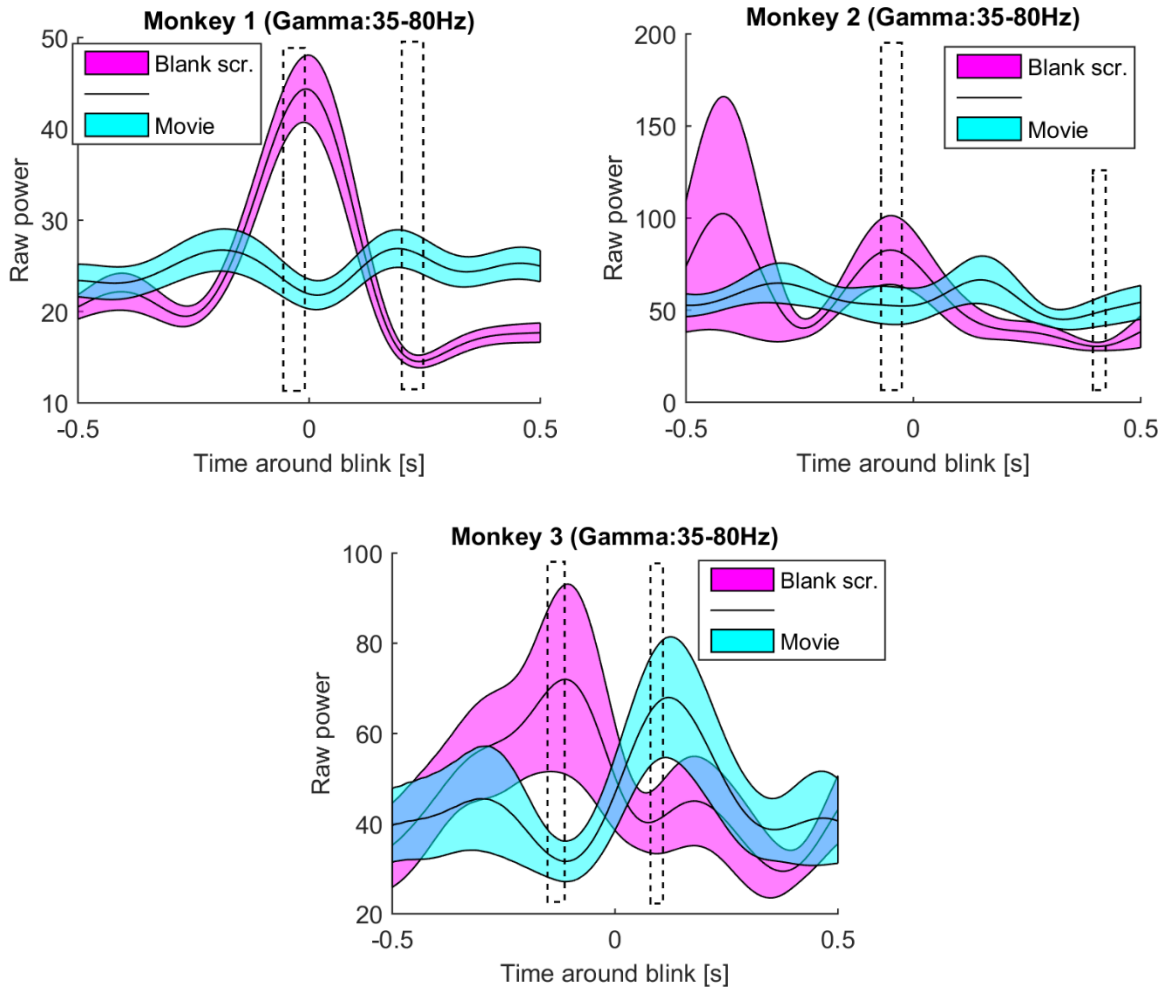


Figure 37. Raw gamma power (35-80 Hz) around blink onset during blank screen (cyan) and movie (magenta) condition plotted separately for all three monkeys. The x-axis shows the time around blink onset in seconds. The y-axis shows raw change in power. Time of significant difference between blank screen and movie condition are marked with a box.

6.4.3 Power in the different frequencies over the different V1 layers

To understand the distribution of power changes over the different layers, we plotted the raw power change around blink onset for each frequency range (theta, beta and gamma), separately for the different channels (Figure 38). We also plotted the difference in power between blank and movie (Figure 39). Figure 38 shows that, for the theta band, there is an increase around layer 4 and 5 for both the movie and the blank screen. The beta band shows

an ongoing increase in power below layer 4 for the movie condition (Figure 38) and a power increase around blink onset around layer 4 and 6. The gamma band also shows an ongoing activity for both the movie and the blank screen below layer 4. Figure 39 shows that this ongoing activity in the beta and gamma range is higher during the movie compared to blank screen condition in the time before and after blink onset. While there is a blink related gamma power increase around layer 4 and 5 during the blank screen condition, such an increase is if at all very week during the movie condition. Consistently over all frequency bands, the power increase seems to be earlier for the blank screen (starting even before the onset) but well after blink onset for the movie condition. Figure 39 shows that the change in power due to blinks is maximal around layers 4-5. For beta and gamma the maximal difference between blank screen and movie condition is in layer 4 (a/b) and possibly layer 6. Note that we show the results here for monkey 1, session 1. Session 2 and the corresponding figures for monkey 2 and 3 can be found as supplementary figures (S23 to S38). The pattern, is variable over sessions and monkeys, however overall one can observe that the maximum power difference seems to be around layers 4,5 or/and 6.

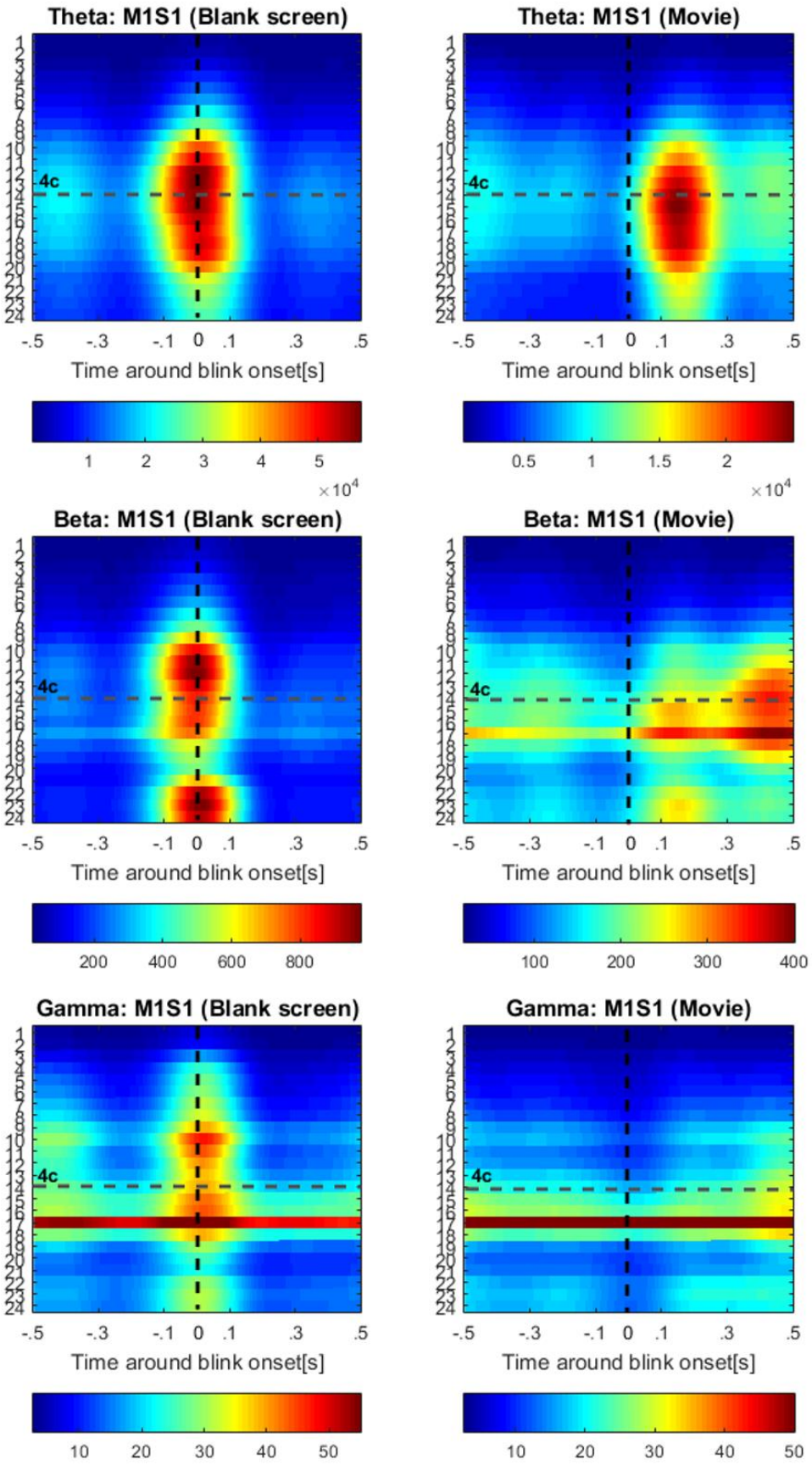


Figure 38. The raw power in the theta, beta and gamma frequencies with respect to blink onset for monkey 1, session 1. The x-axis shows the time period around blink onset in seconds and the y-axis shows the different electrodes (1:24). The vertical dashed line represents the blink onset and the horizontal line marks layer 4c. The colour scale shows raw power. The colour bar shows the raw power in each frequency band.

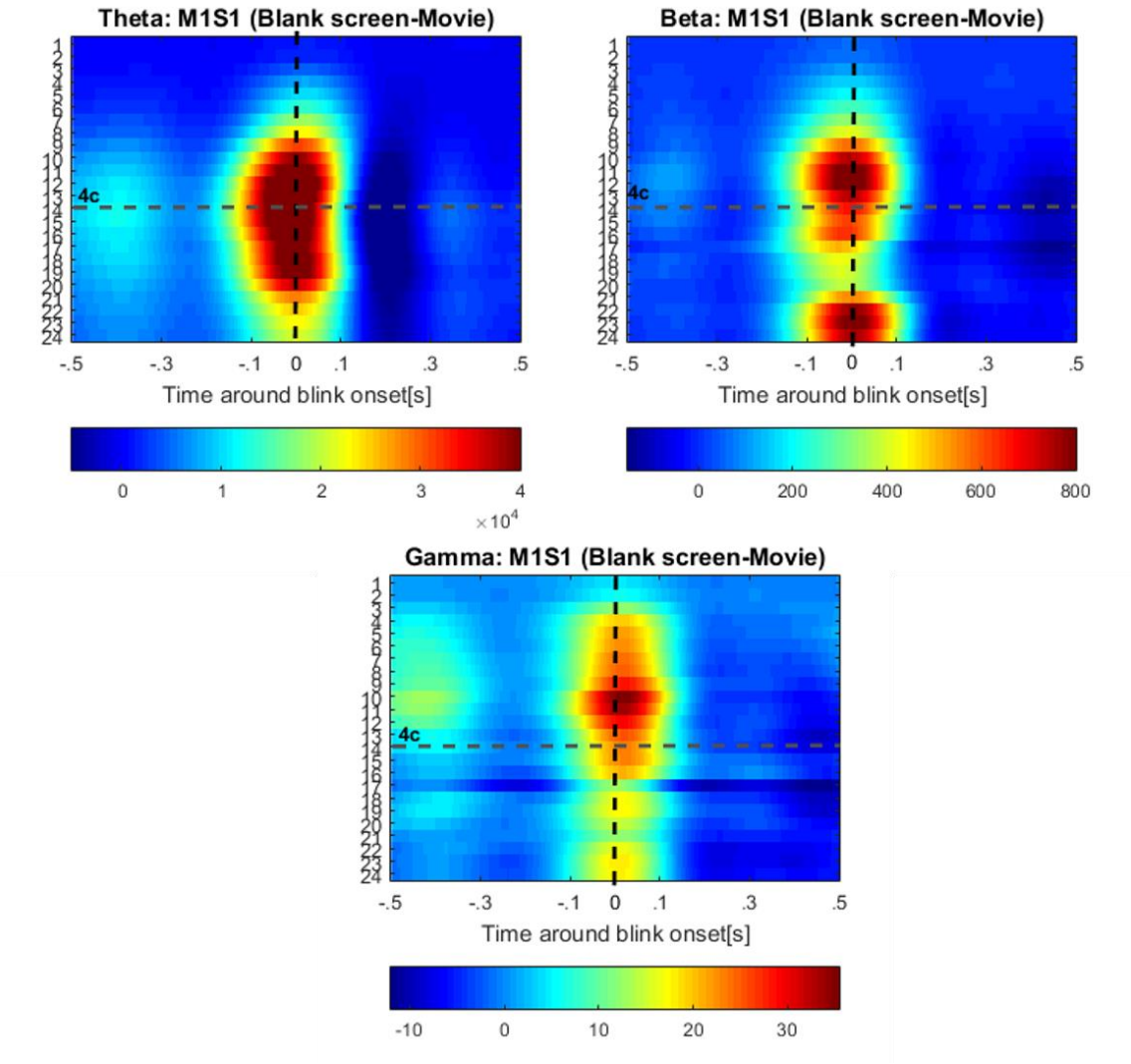


Figure 39. Power difference between blank screen and movie condition in the theta, beta and gamma frequencies with respect to blink onset for monkey 1, session 1. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power. The horizontal dashed line marks layer 4c and the vertical line shows the timing of blink onset. The colour bar shows the raw power in each frequency band.

6.4.4 Current source density (CSD)

As can be appreciated in Figure 40, there was a clear source-sink pattern at blink onset in the blank screen condition. For the movie condition, this pattern was less pronounced and

shifted in time so that the source only started after blink onset. While this pattern was mainly visible in the granular and infragranular layers for session 1, there was a shift to only the infragranular layers for session 2. The overlain MUAe pattern parallels this shift in latency of maximal deflection, and shows, as already shown in Figure 33, the opposite modulation for blank vs movie condition. The corresponding figures for monkey 2 and 3 can be found in the supplementary information as figures S39-45, but unfortunately do not show a clear pattern.

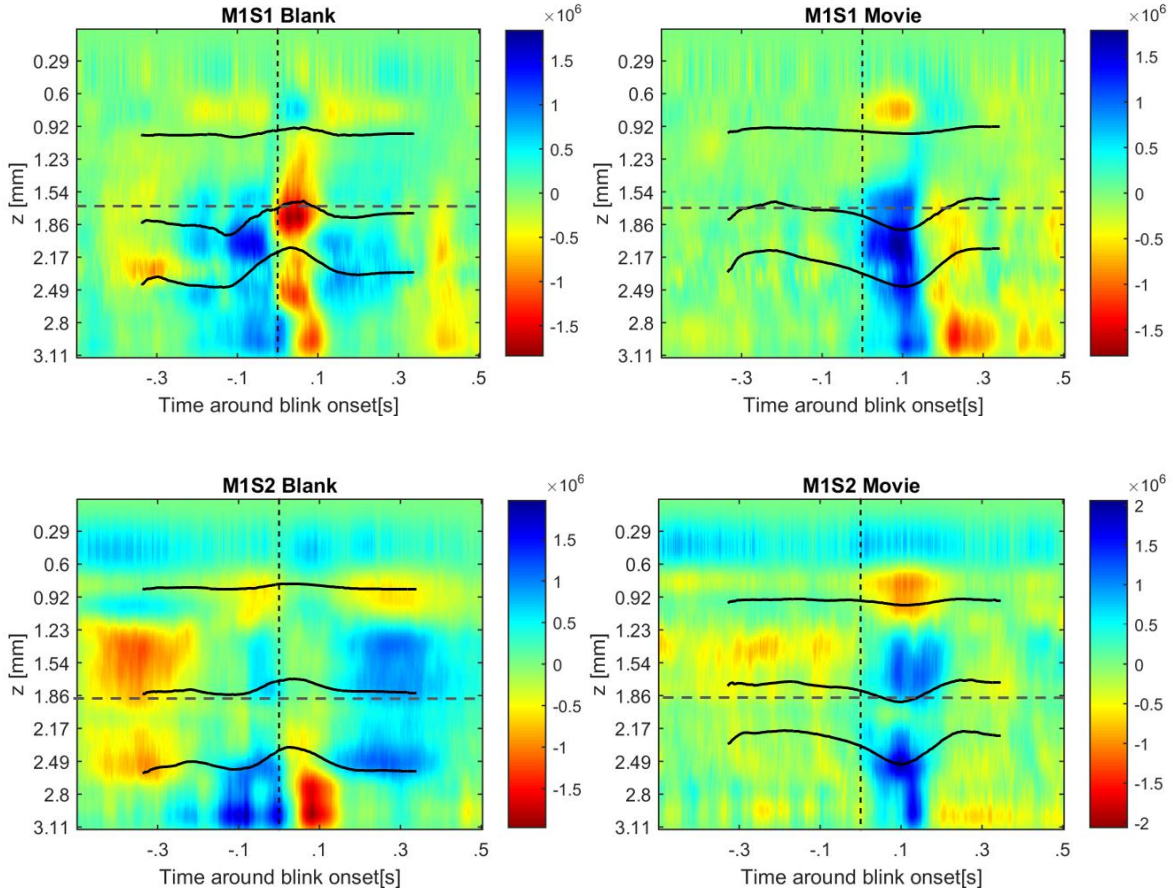


Figure 40. shows the CSD profiles around blinks for the blank screen and movie condition. The y-axis shows cortical distance in mm and the x-axis shows the time around blink onset in seconds. The vertical line shows the time of the blink onset and the horizontal line shows the layer 4c. The MUAe averaged over the supragranular, granular and infragranular layers has been superimposed.

6.5 Discussion (Study 5)

Comparing blink related V1 neural responses between two conditions which differed in attentional state and intensity of visual input revealed a pronounced difference in various measures. The MUAe showed a qualitative difference, i.e. an increase around blinks during blank screen, but an equally strong decrease in MUAe around blinks during the movie condition. When analyzing frequency specific effects, we found that the amplitude as well as the latency of the blink related power modulation in the theta (4-8 Hz), beta (16-30 Hz) and gamma (35-80 Hz) band also showed a significant difference between conditions; however, it was rather a quantitative one. Theta power, for example, increased more strongly around a blink during the blank screen condition, while this increase was less pronounced and later in time for blinks during the movie condition. The distribution over the channels in the laminar probe suggest a focus in the granular and infragranular layers (layers 4-6). A sink source pattern related to the blink along with a latency difference between conditions was found in the CSD, also mainly visible in the granular and infragranular layers. Overall the data suggests that blink related neural responses are dependent on the attentional state and that the main difference in the pattern between the states occurs in the deeper layers of V1.

6.5.1 MUAe around blinks decreases during movie and increases during blank

Our data shows a comparably low MUAe during the blank screen condition with a pronounced increase around blink onset. In contrast, MUAe is relatively high during the movie condition but shows a strong decrease around the blink. Previous studies, investigating blinking during visual stimulation, have already reported that activity in different areas of the visual cortex is reduced around blinks (Bristow, Haynes, et al., 2005; Gawne & Martin, 2000; Golan et al., 2016; Golan et al., 2018a). For instance, Gawne and Martin (2000) showed that

there is a decrease in firing rates in monkey V1 around 100 ms after blink onset. Similar results were also shown by Golan et al. (2016), reporting an activity minimum at blink offset across higher visual areas (V1-V4) in human ECoG recordings. The observed blink related decrease in MUAe during movie stimulation as described here is therefore well in line with previous studies (Bristow, Haynes, et al., 2005; Buisseret & Maffei, 1983), which have linked the reduction to the phenomenon of blink-related suppression. However, can this idea explain why the opposite blink related modulation of MUAe is found during the blank screen condition? There are two main differences between the blank screen and the movie condition, which is that visual input was reduced but still visible to the monkey and that the visual input was irrelevant and therefore no attended.

A few studies have investigated the influence of blinks with respect to variable visual input. Bristow, Frith, et al. (2005) looking at the interaction between blinking and visual input showed that BOLD activity in medial parieto-occipital sulcus increased during periods of voluntary blinking in the presence of a visual stimulus as opposed to blinking in the absence of a visual stimulus. Another study by the same authors Bristow, Haynes, et al. (2005), also analyzed BOLD activity related to blinking during retinal stimulation (by shining slight on the retina through the roof of the mouth) and blinking without retinal stimulation. They showed that activity in a number of visual areas, (including LGN, V1, V2 and V3) increased during the condition of blinking during no retinal stimulation, but did not show a significant change during the blinking during retinal stimulation condition. In contrast, they found that blinking during retinal stimulation was associated with a decrease in activity in V3. Our results could well explain these findings and link it to spiking activity in neurons as we show a MUAe decrease when blinks occur during retinal stimulation, and an increase if blinks occur without retinal stimulation. Despite this modulation, the MUAe shows the expected overall higher

level during extensive visual input in the movie condition vs an overall lower MUAe level during reduced visual input (blank screen condition). Further, our findings show that the modulation is specifically introduced by the blink event and not an overall in- or decreased during the time when blinks happen. As we find both increase and decrease in activity within V1 it is interesting to see if the laminar distribution would suggest that the decrease has a focus on layers of V1 that either forward information to V3 or receive input from V3. While there was no indication in the distribution on MUAe over the laminar profile, we find an effect in the frequency range which will be discussed below. As the BOLD signal is associated with spiking but also with power in various frequency bands (REF: Logothetis), we cannot be sure what neural signal caused the previously reported changes in BOLD signal.

Overall, our finding adds important insights to the role of blink related modulation in V1 activity. Previously, the increase in activity due to blinking in V1 and other early visual areas was ascribed to a motor signal. The reduction in activity in V3 found if visual stimulation was present, was linked to the phenomenon of blink-related suppression (Bristow, Haynes, et al., 2005). However, blinks are perceptually suppressed even if the visual input is weak and unattended and the motor aspect of spontaneous blinks is the same independent of visual input and attention. Our data therefore suggests that the MUAe modulation in V1 is neither due to a motor related signal nor is it the driving factor for blink-related suppression. We rather suggest that the blink induced MUAe modulation marks another process that is dependent on the attentional/ stimulation state of the observer. While a change in visual input usually leads to an increase in V1 MUAe, a decrease during ongoing stimulus presentation was reported based on the onset of an attentional cue indicating the direction of the relevant target position (Cox et al., 2019). In this study, the appearance of the visual cue introduced a pronounced but short lasting (~100ms) MUAe decrease with a latency of ~

100ms. Interestingly, this decrease was not observed in naïve and passively viewing monkeys but only in trained monkeys familiar with the task. This could suggest that blinks during active viewing are comparable to a cue to shift spatial attention. A possible attentional function of blinks will be discussed further below.

6.5.2 Power around blinks during movie and blank screen

Our frequency based results showed that there are relative power change around blinks in at least three frequency bands: theta, beta and gamma.

Theta

For the theta band, we found an increase in power temporally related to the blink. Previous research, analyzing power changes due to blinking, have described such an increase specifically in the delta (0.5 to 3/4 Hz) power (Bonfiglio et al., 2013; Bonfiglio et al., 2009; Bonfiglio et al., 2011; Liu et al., 2017; Liu et al., 2020; Liu et al., 2019) localized to the precuneus, during different attentional states (freely sitting, passive fixation with and without a visual stimulus, mental arithmetic task). As in our study, the theta frequency band (4-8 Hz) overlapped with the delta band in Bonfiglio's studies (0-4 Hz), the results are congruent. However, in our study the increase occurred earlier, i.e. about 100 – 200 ms after blink onset, compared to around 250 to 300 ms after the point of maximum blink amplitude observed in the EOG. Bonfiglio et al. (2009) compared the increase in delta power in their study with the P300 amplitude, which occurs after information processing. Interestingly, the P300 occurs specifically after targets in an oddball task and a previous study in our group showed that blinks increase after targets (Brych & Händel, 2020). This might link blinking to internal processes related to the consolidation of information. This is interesting as we found that

theta power modulation differed significantly between the movie (intended information processing) and the blank screen (reduced information intake) condition.

To further understand what the power modulation in the low frequencies could indicate, we looked how the power changes were represented in the different layers and how the latency changed with condition. The theta power increase was significantly earlier and more pronounced for blinks during the blank screen condition. The difference between movie and blank screen condition (Figure 39) showed that there was a positive power peak around blinks followed by a negative one as expected given the latency change of the modulation of the theta power. The maximum difference in power was mostly confined to layers (5-6) with some session showing an additional local increase in the difference in the supragranular layers. We further found that the maximum theta power was approximately in layer 5 and/or 6 for both the movie and the blank screen and only at some cases (mainly monkey 1) included part of layer 4. Visual input has shown to induce theta power in rat V1, generated through external input or by recurrent activity within cortical layers (Zold & Shuler, 2015). However, as the sensory input that reaches V1 via LGN has the same latency for blinks during blank screen and movie condition, we can assume that the theta power increase does not mark input from lower visual areas. The layer specificity could suggest that the blink related change in theta marks an output signal that is either sent back to the LGN or to the pulvinar or a top-down input from higher visual areas (Bastos et al., 2015). There is strong evidence that theta oscillations reflects feedforward sensory processing from V1 to V4 (Bastos et al., 2015; Bosman et al., 2012; Grothe et al., 2012; Spyropoulos et al., 2018; Van Kerkoerle et al., 2014), possibly even more than gamma (Kienitz et al., 2021). Our blink related theta power modulation therefore rather marks a feedforward signal. As to the difference between conditions, previous work has described lower theta V1 power if attention was directed

towards the visual stimulus compared to away from it (Spyropoulos et al., 2018). Indeed, this would fit to our observation, as attention was likely lower during the blank screen condition, which showed the stronger and earlier theta power modulation. However in our case, the theta modulation was linked to the blink event and possibly a corresponding change in visual input. Following the idea of attention induced effects, the different theta power modulation would indicate that blinks differ as to the attention associated with them. Taken together, our data shows evidence that theta power represents feedforward information linked to a blink event and that this information transfer is different, dependent on the attentional/ stimulation state of the observer. Meaning that activity in V1 is significantly affected by non-visual aspects as also shown by others (Fournier et al., 2020). Specifically, showed that, in the case of movement, the visual cortex is affected via hippocampal theta oscillations.

Gamma

With regard to gamma power, we repeatedly found ongoing high power approximately in layers 4 and 5. Gamma activity is strongest in superficial layers (Buffalo et al., 2011; Xing et al., 2012) suggesting that gamma might serve feedforward signaling (Fries, 2015). This was supported based on granger causality measures in human magnetoencephalography (Michalareas et al., 2016). The observed sustained gamma power in both conditions and independent of the blink event could mark input from LGN representing visual stimuli. Figure 39 shows that the ongoing gamma power is higher for the movie condition which would be in line with such an interpretation as the sensory input was more intense compared to the blank screen condition. However, the pattern is not consistently visible over sessions and monkeys.

The blink related change of gamma power shows a quite variable pattern over the channels. However, as we already know from Figure 37, gamma is such modulated around

blink onset that it shows a higher power around blink onset for the blank screen condition but a higher power approximately 250 ms after blink onset for the movie condition. This should be converted to a red-blue pattern when plotting the color coded power difference over the channels. Indeed when looking for such a pattern there is a relatively consistent one found in layer 5 and 6 as well as supragranually, but importantly, is not confined to the location where the ongoing gamma activity was found. This would suggest that the gamma difference is not caused by the sensory input sent from LGN. It might rather mark signals that are sent from V1 upstream the visual pathway. For the movie condition, there would be less signal related to a blink that additionally is forwarded with a delay compared to the blank screen condition.

While both theta and gamma power seem to represent a feedforward signal there is a fundamental difference. While theta follows the attentional state (i.e. lower for attended condition), the gamma power does not show the expected higher modulation due to attended sensory input.

Beta

When assessing the beta band, we unfortunately found that the variance over sessions and monkeys was very high. While for monkey 1, theta and beta seemed to be relatively similar, for monkey 2 it would be beta and gamma that were more alike. Additionally, monkey 3 showed a very high variance. Given that also the layer specific pattern were very variable, we would like to refrain from intending an interpretation. Overall, the laminar pattern as well as the latency change in the observed power modulation due to blinks in dependency of the condition suggests that the change in power, as well as the influence of the visual-attentional state is based on top-down information.

We want to add that while the power difference between blank and movie condition only reached significant shortly before and after blink onset, the MUAe difference already showed a difference well before blink onset. This, however, does not indicate a causal influence but might be only due to the fact that MUAe is overall increased during the movie condition, possibly reflecting the higher amount of processing of visual input. Interestingly, if we take the amount of raw MUAe as indicator of the level of sensory processing, we could interpret the pattern such that the processing drops to the blank screen level due to blink during the movie condition and processing increases to the movie level due to a blink during the blank screen condition.

6.5.3 CSD

Our CSD results showed that for monkey 1 there was a clear source-sink pattern at blink onset in the blank screen condition. For the movie condition, this pattern was less pronounced and shifted in time so that the source only started after blink onset. While this pattern was mainly visible in layer 4 to 6 for session 1, there was a shift of the maximal effect to layer 6 for session 2. The overlain MUAe pattern parallels this shift in latency of maximal deflection, which however, as already shown in Figure 33, is the opposite modulation for blank vs movie condition. This suggests that the MUAe and the CSD show independent blink related processes. Unfortunately, the CSD profiles of the other two monkeys show no clear pattern.

6.5.4 Role of blinking

The question remains as to why the neural blink related activity is different if there is no attended stimulus compared to when there is attended visual input? Behavioral studies show that a task will significantly change the timing and probability of blinking. In general,

blink probability is reduced during attentive sensory processing but increased above baseline after its completion or during internal processing. Accordingly, blinks executed during a task have a certain function, while blinks during passive viewing do not or have a different function. We suggest that the neural pattern observed in the condition including an attentional task (i.e. movie condition) is related to the task demand. Looking at the neural data, a blink during passive viewing leads to an increase in MUAe, gamma and theta power i.e. it rather follows a pattern as would be expected after a change in sensory input (as is the case due to the closing eyelid). The blink during the active task results in a decrease in MUAe and a shift in latency and amplitude in the theta and gamma range. As argued above, a decrease in theta power as well as a decrease in MUAe has been found in connection with changes in attention. Behavioral studies have associated the blink with attentional disengagement (Salvi et al., 2015; Smilek et al., 2010). We would like to put forward the idea that the decrease in MUAe and the reduction and latency change in theta power marks such an attentional disengagement from (visual) sensory input while attentively scanning the visual input of the movie. Such a mechanism could help observing the environment without over processing parts of increased spatial frequency, contrast, color or luminance, by helping to disengage and initiate an attentional shift.

6.5.5 Conclusion (Study 5)

Overall, while the qualitative and quantitative difference in neural modulation clearly suggest a difference in the consequence of blinks on the visual system, we connected this neural result to the well-known findings from behavioral studies, namely that blinks are suppressed during attentive visual processing but increased above baseline after its completion or during internal processing. While a suppression might only indicate that we do

not want to be disturbed by a blink during sensing, an active increase suggests an active role of blinks. This role of blinks could be, as argued above, be the disengagement from sensory input processing. The blink related decrease in V1 MUA and reduction and latency shift of theta power exclusively found during the attentive viewing condition might mark the disengagement from the processing of the sensory input. allowing to either shift the focus of attention or focus on internal processes. The blink related increase in MUA and increased theta power modulation during passive viewing is in line with a response to a change in visual input. Overall, our findings describe for the first time a qualitative difference in blink related V1 responses due to the attentional/ stimulation state. It further proposes that the function of blinks is to help disengaging attention which leads to a clear and testable prediction of blink modulation in experimental and natural settings. Additionally, our work confirms the complexity of the relationship between motor output, early sensory processing and attentional/visual input state.

6.6 Supplementary material (Study 5)

Power in the different frequencies over the different V1 layers for all sessions

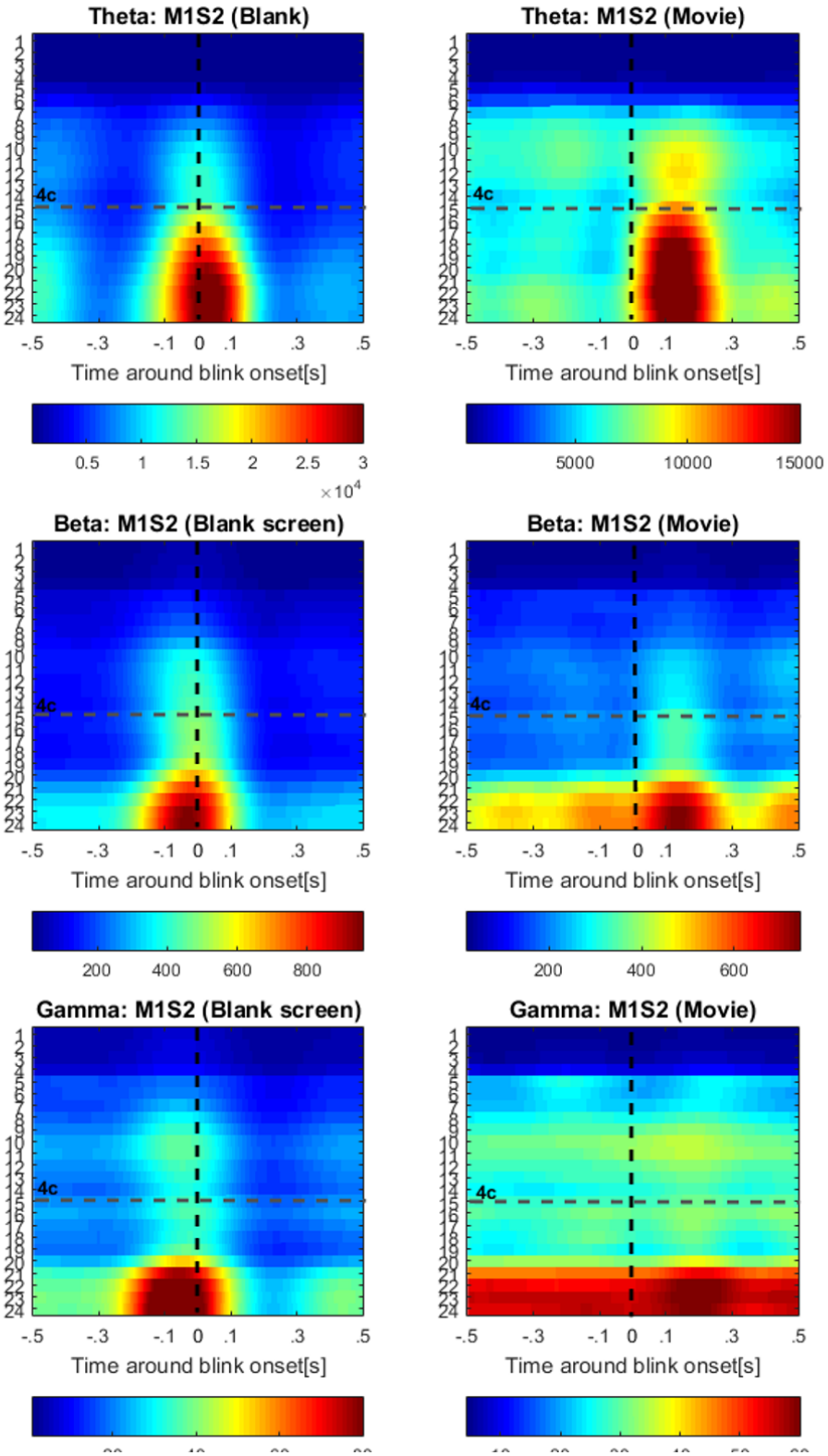


Figure S23. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 1, session 2**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

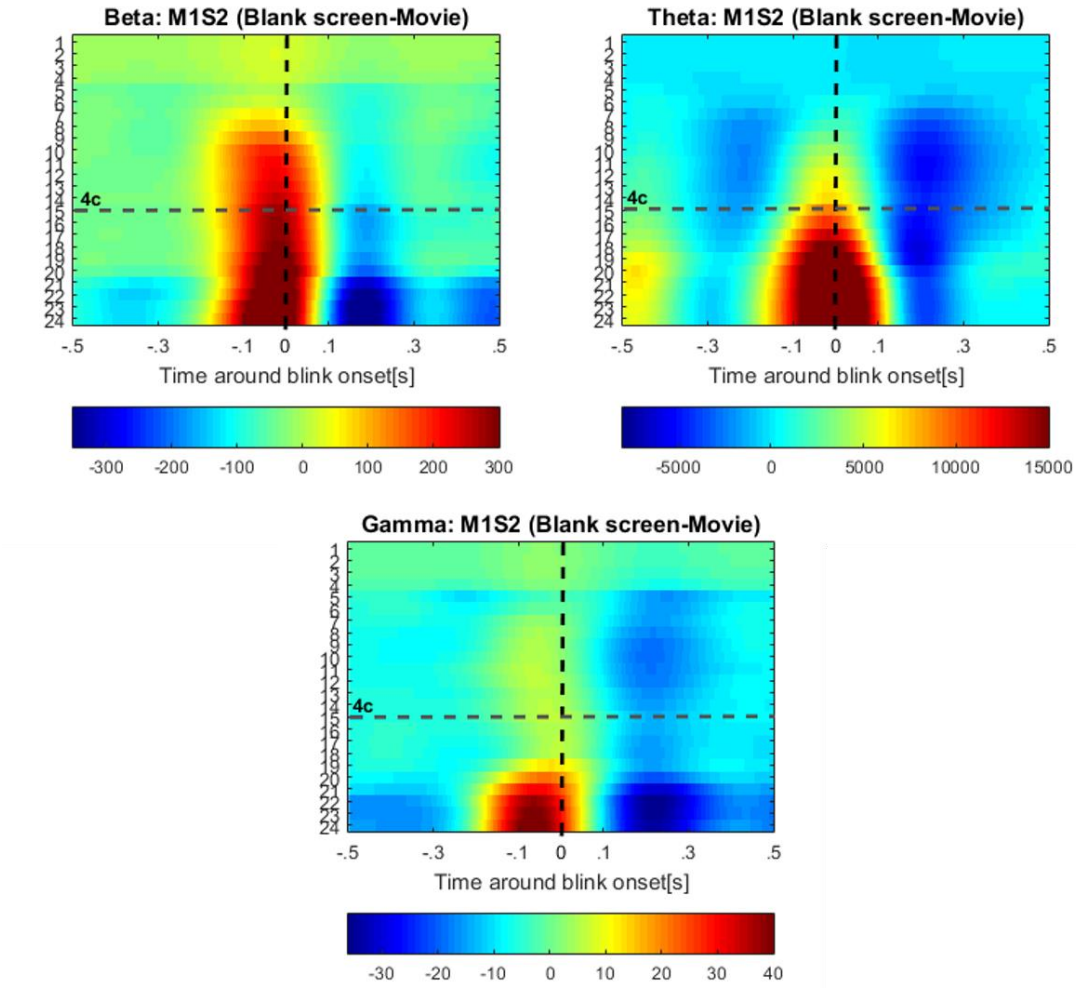


Figure S24. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 1, session 2**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

6. Study 5 (Supplementary)

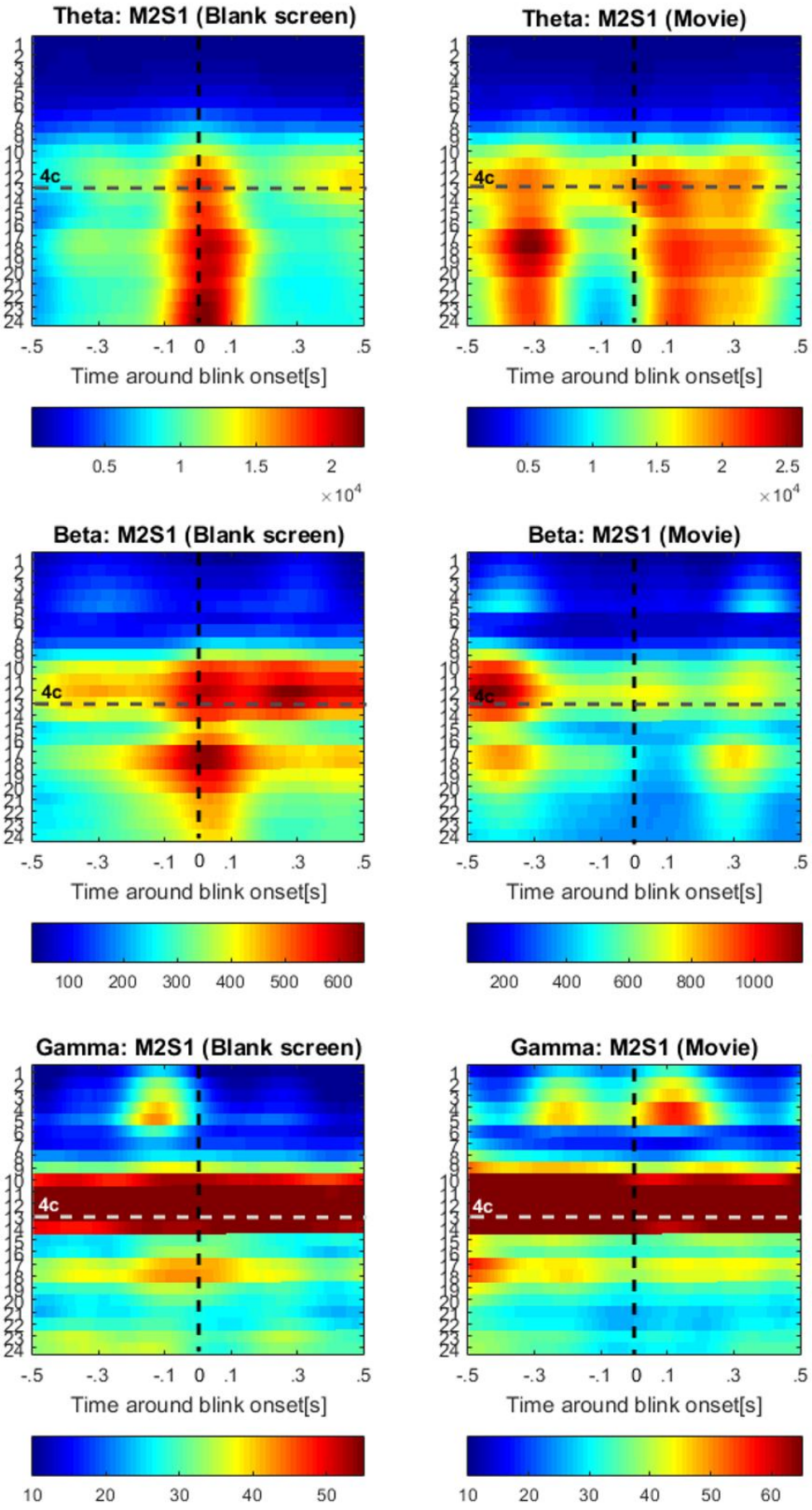


Figure S25. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 1**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

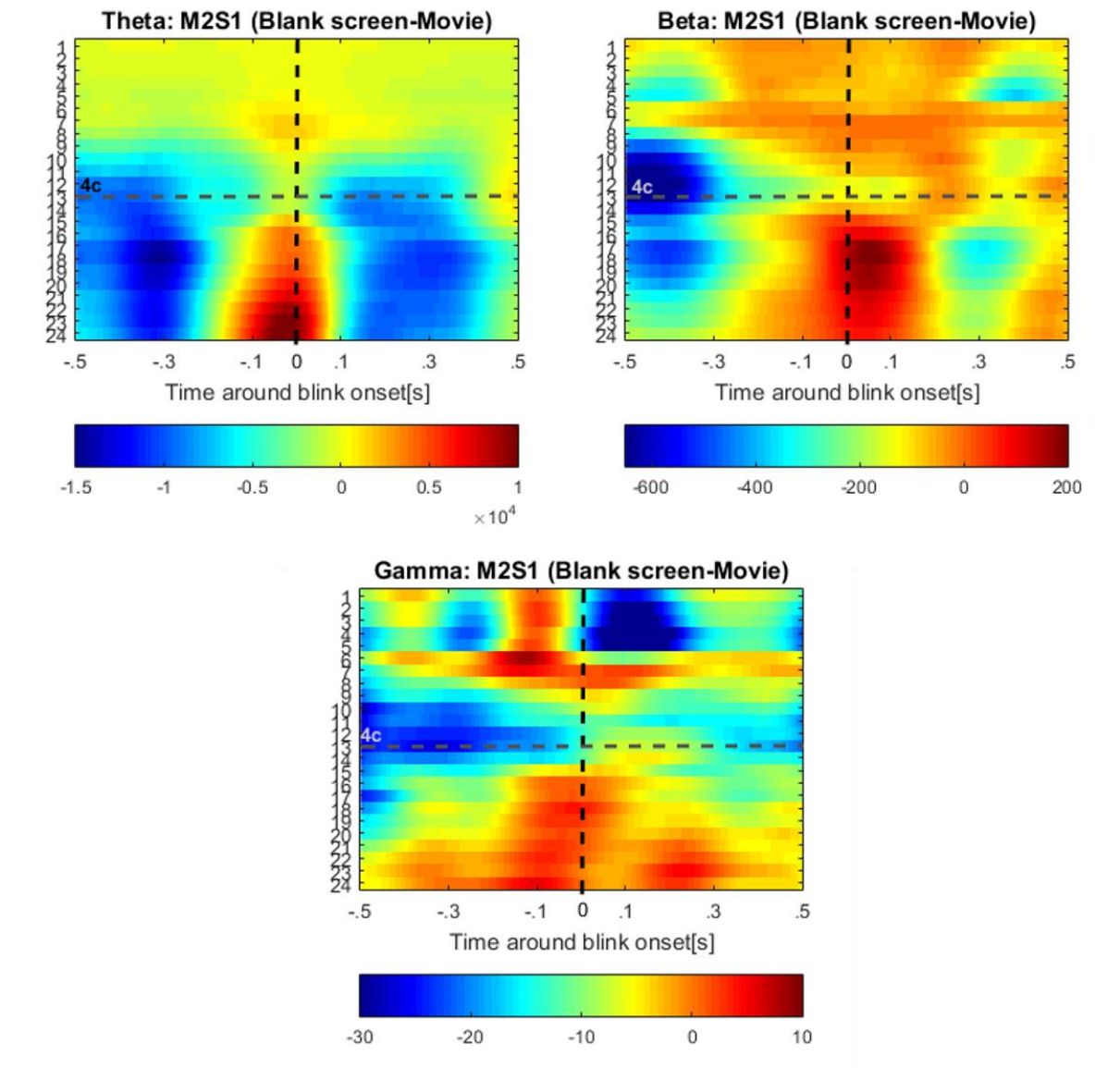


Figure S26. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 1**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

6. Study 5 (Supplementary)

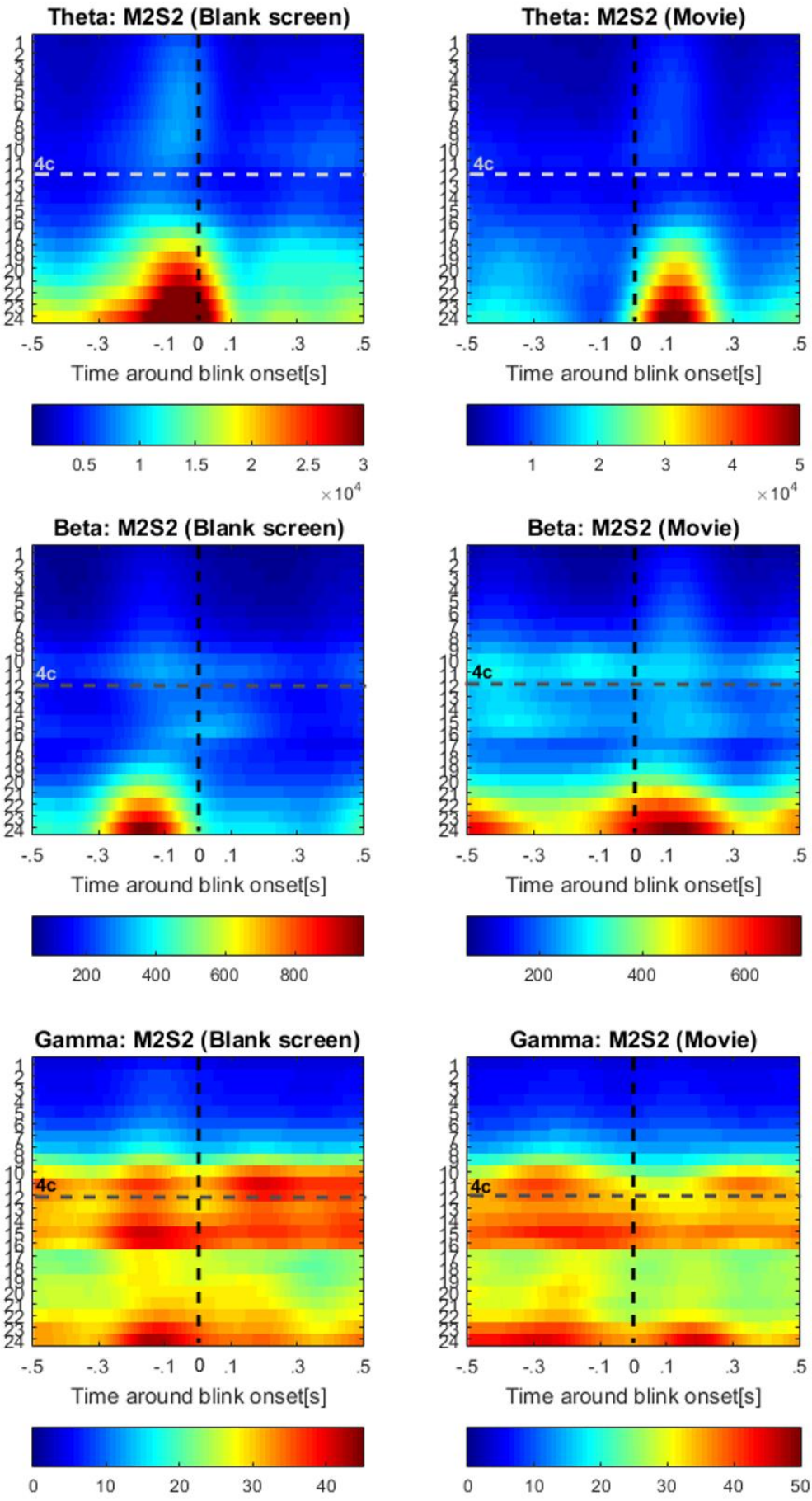


Figure S27. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 2**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

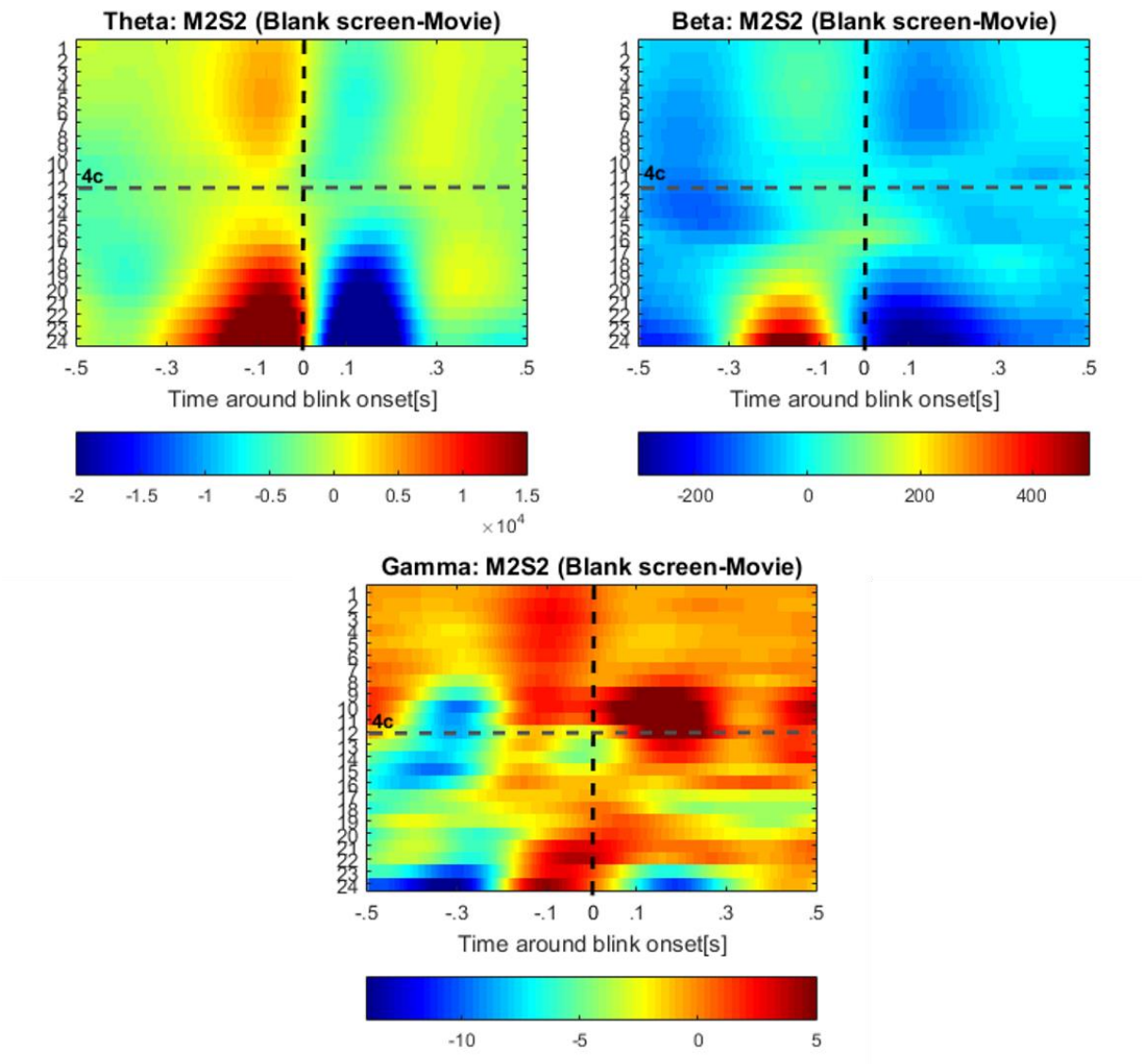


Figure S28. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 2**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

6. Study 5 (Supplementary)

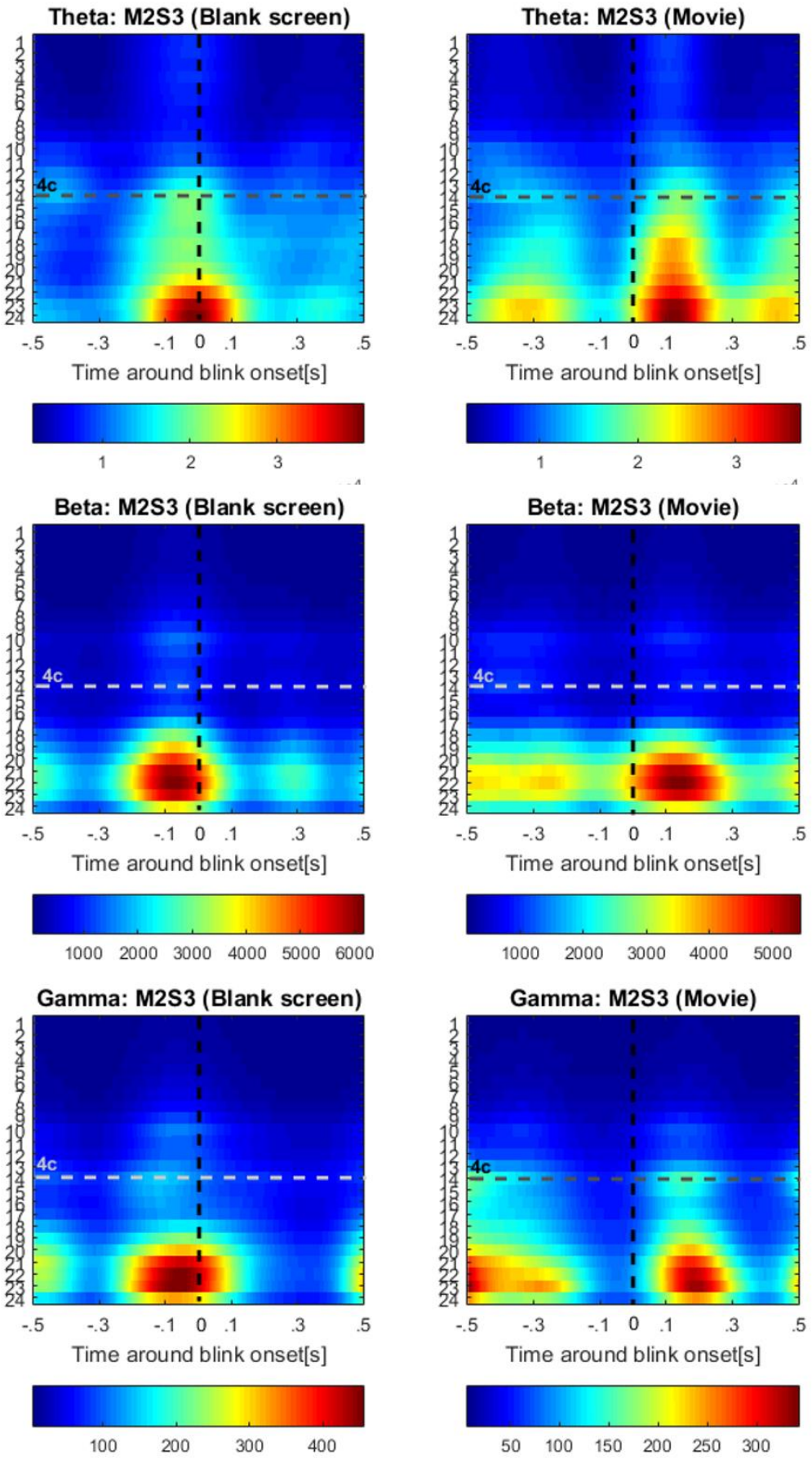


Figure S29. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 3**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

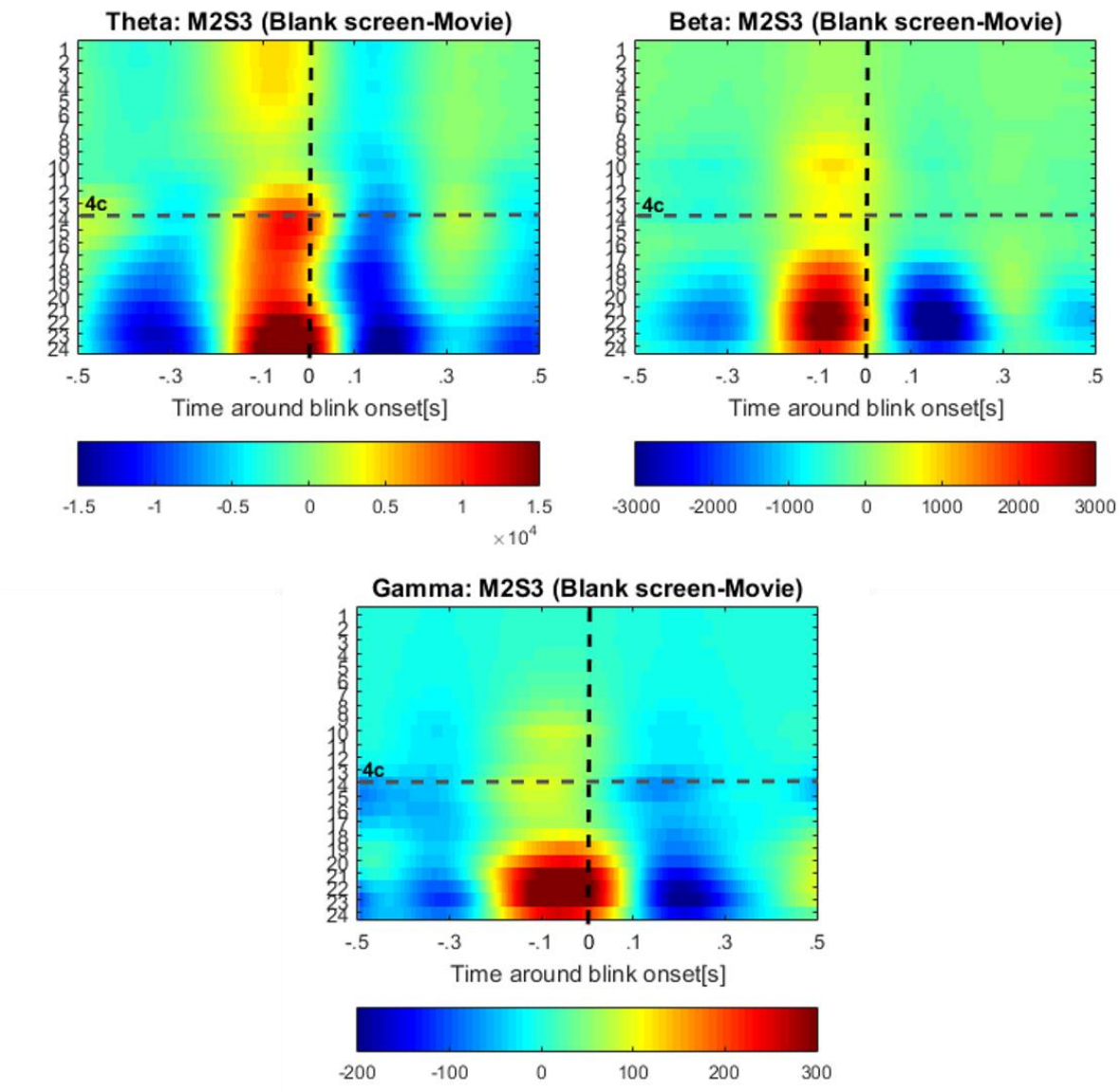


Figure S30. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 3**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

6. Study 5 (Supplementary)

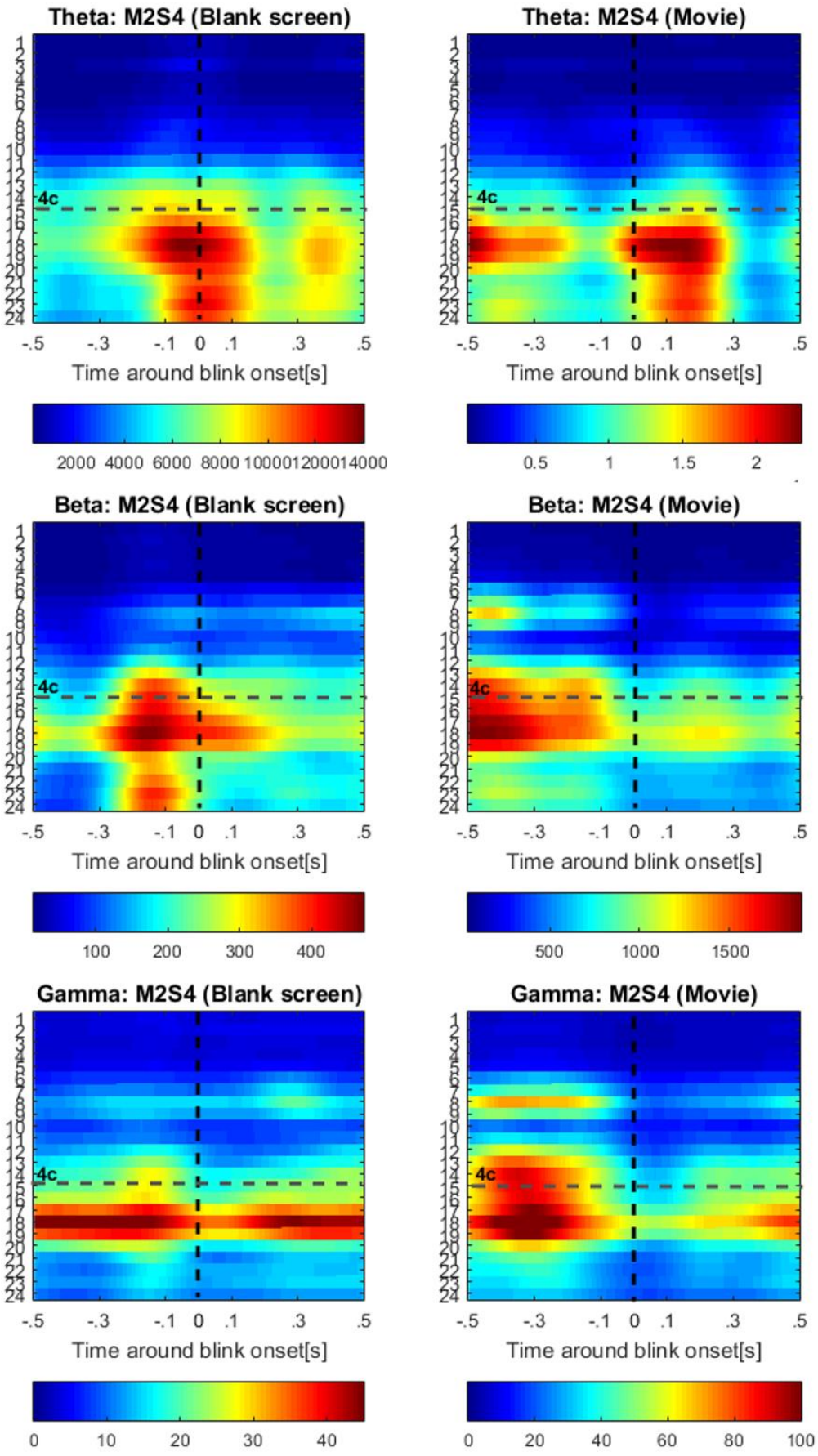


Figure S31. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 4**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

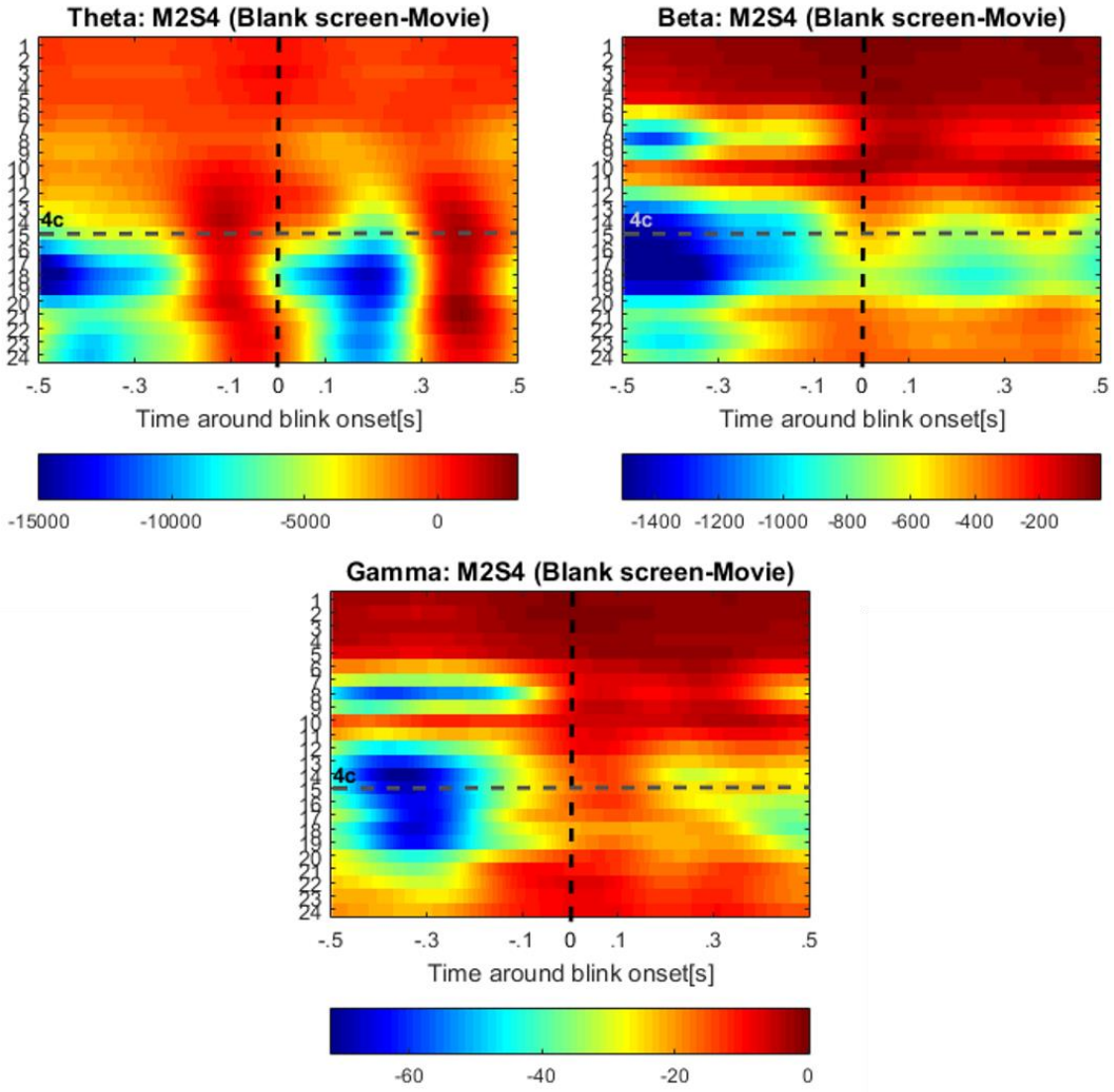


Figure S32. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 4**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

6. Study 5 (Supplementary)

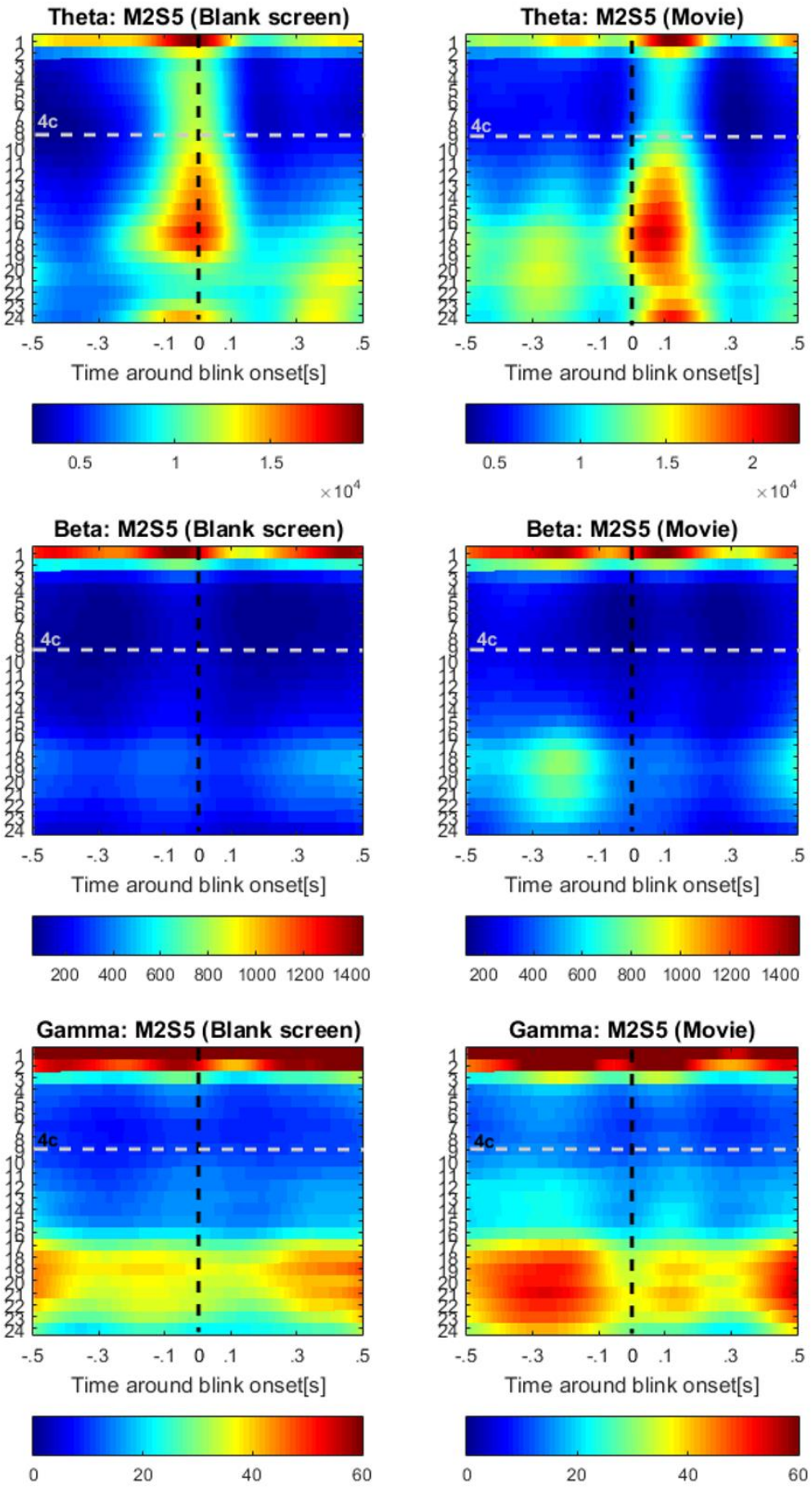


Figure S33. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 5**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

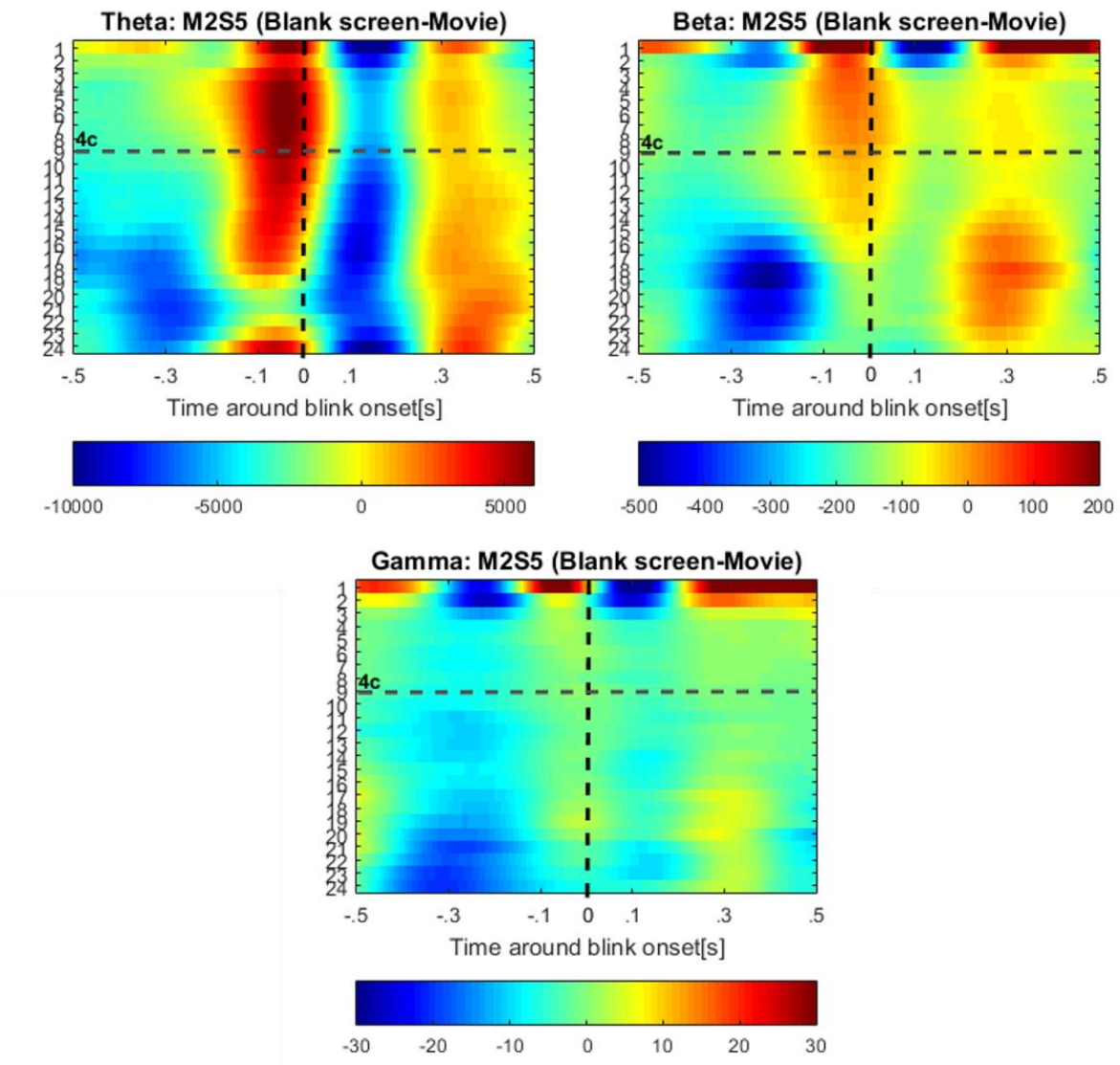


Figure S34. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 2, session 5**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

6. Study 5 (Supplementary)

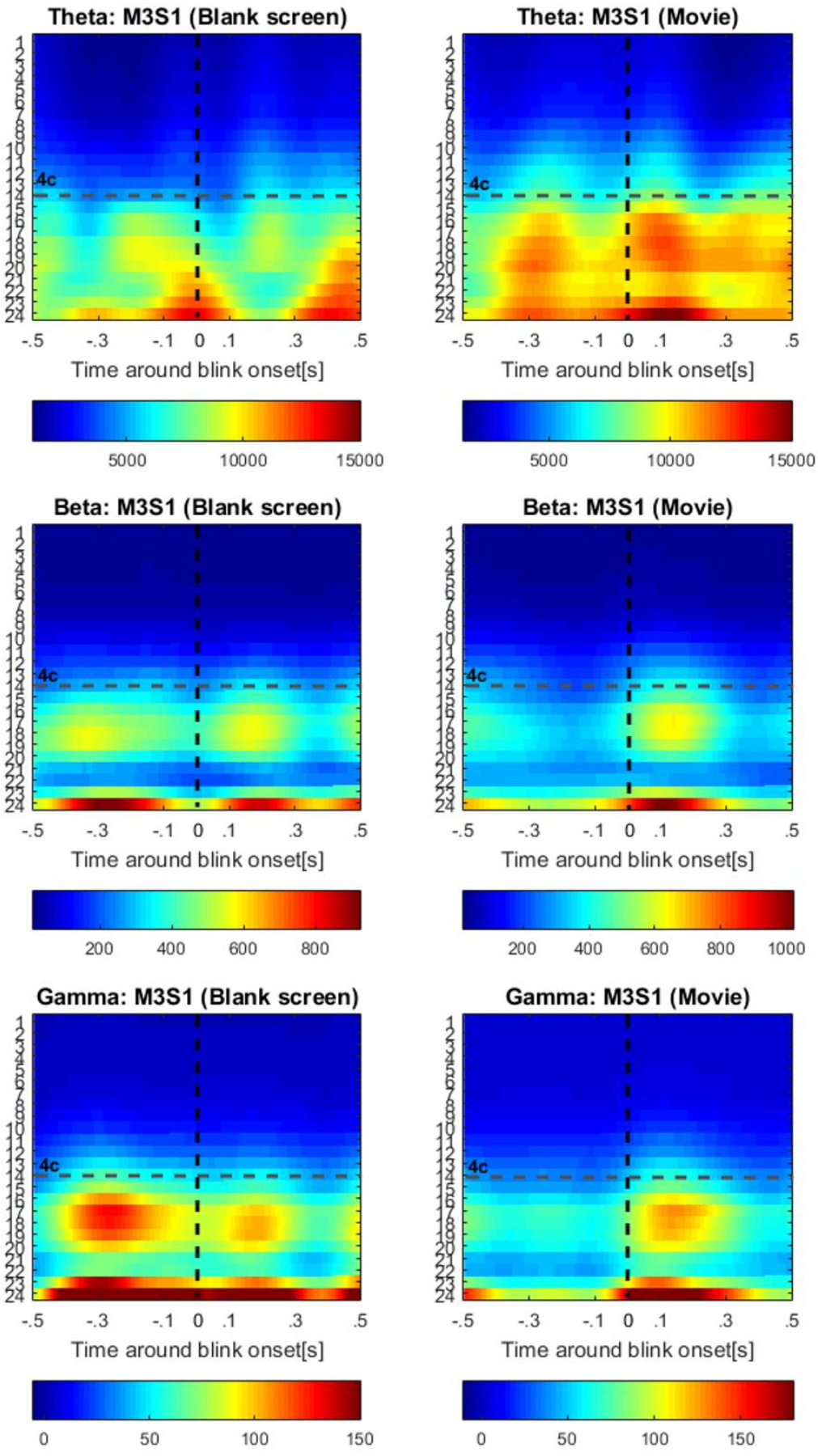


Figure S35. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 3, session 1**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

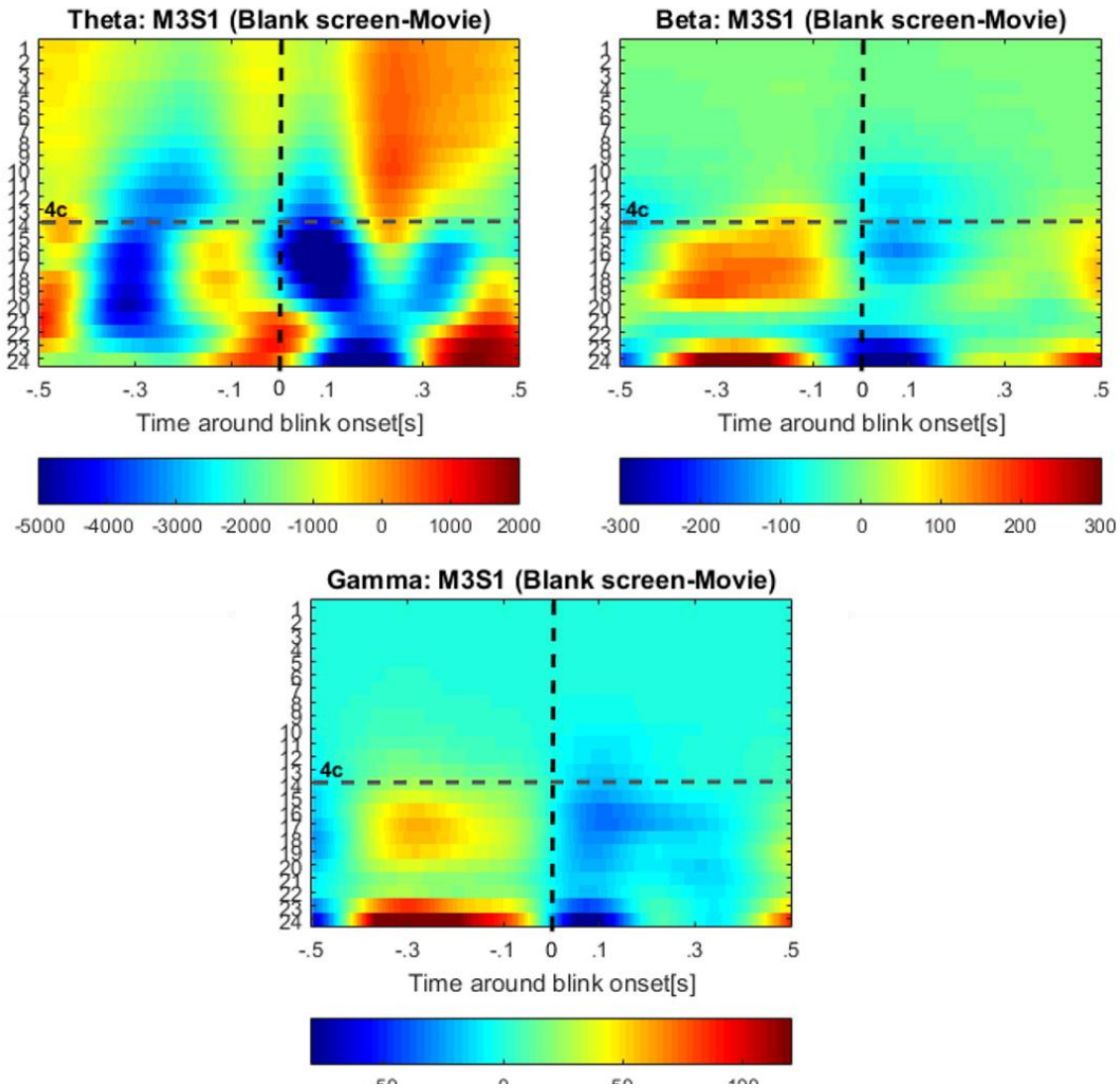


Figure S36. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 3, session 1**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

6. Study 5 (Supplementary)

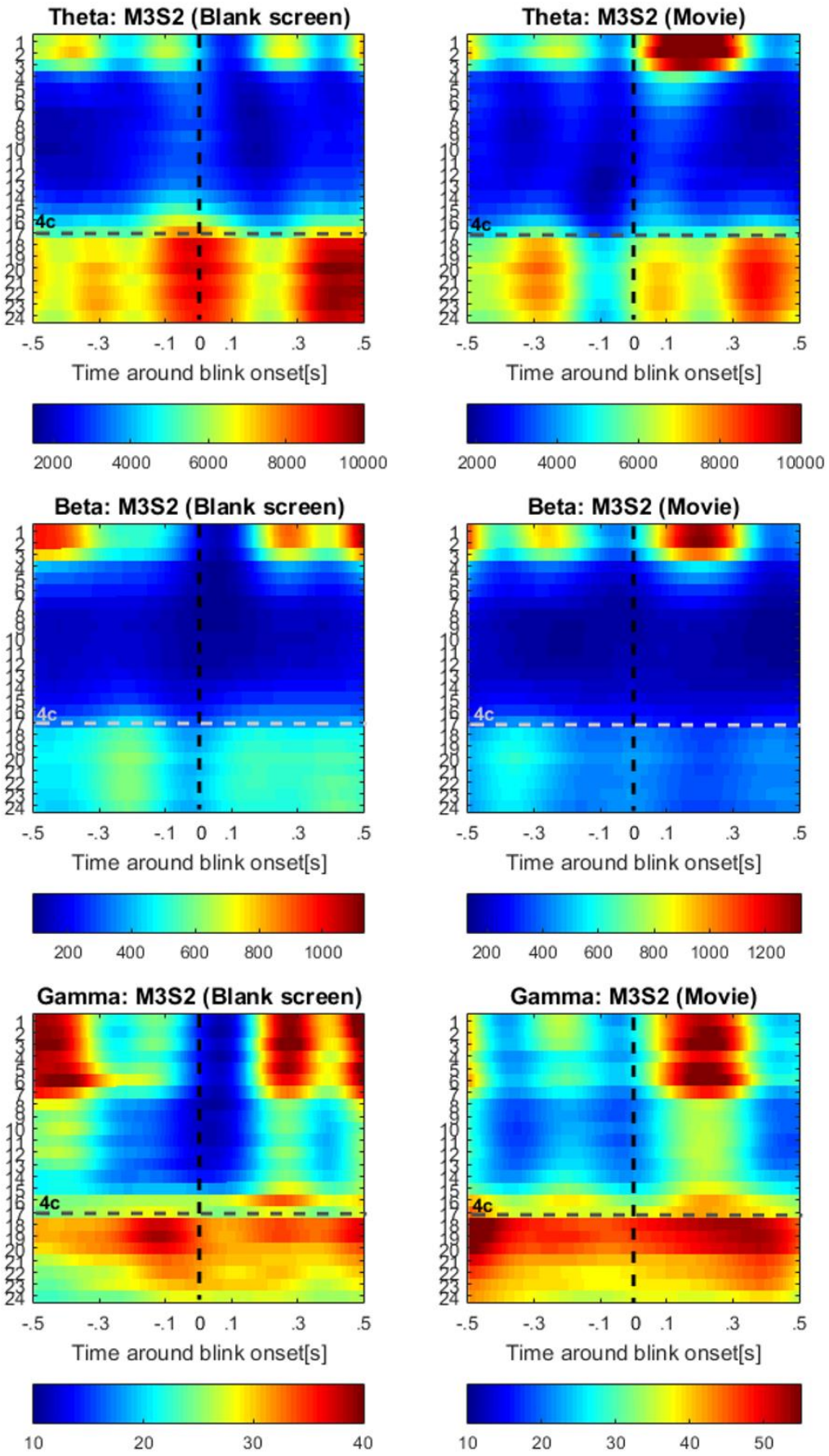


Figure S37. The power in the theta, beta and gamma frequencies over the different electrodes for **monkey 3, session 2**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). The colour scale represents the raw power.

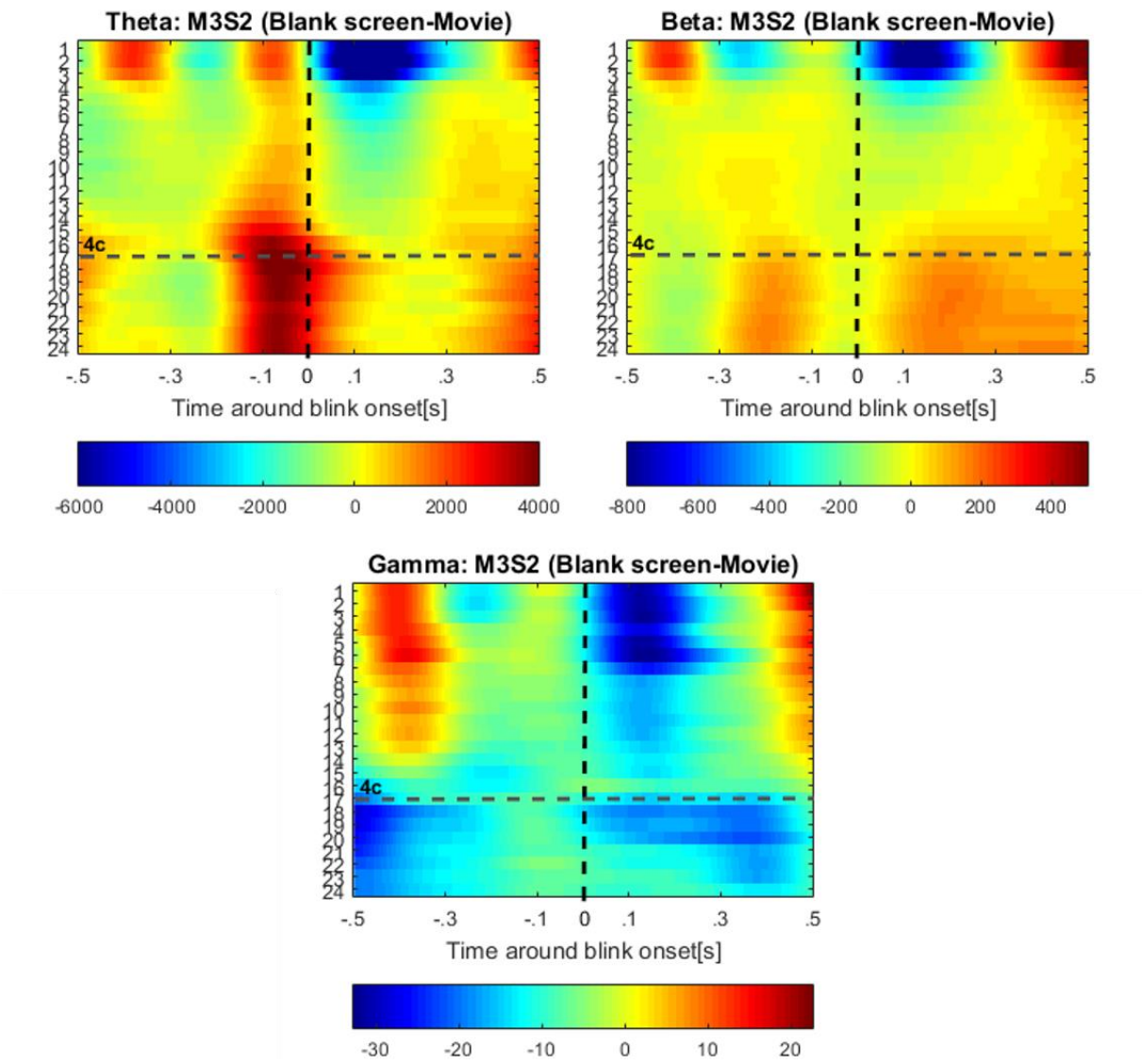


Figure S38. Power difference between blank and movie in the theta, beta and gamma frequencies over the different electrodes for **monkey 3, session 2**. The x-axis shows the time period around blinks in seconds and the y-axis shows the different electrodes (1:24). Power scale shows the raw power difference i.e. Blank power-Movie power.

The following figures show the CSD (using the cubic spline iCSD method) around blinks for the movie and the blank for each session for the three monkeys. The MUAe is the average over 5 channels above and below the first sink channel of each session.

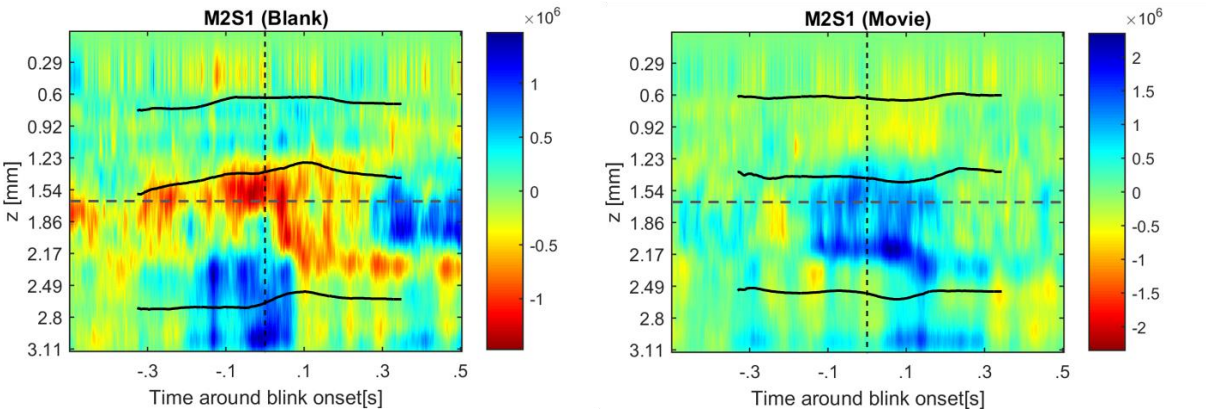


Figure S39. CSD using the cubic spline iCSD method for **monkey 2, session 1**. The x-axis shows the time period around blinks in seconds and the y-axis shows distance in mm. The colour scale represents the sinks (blue) and sources (red)

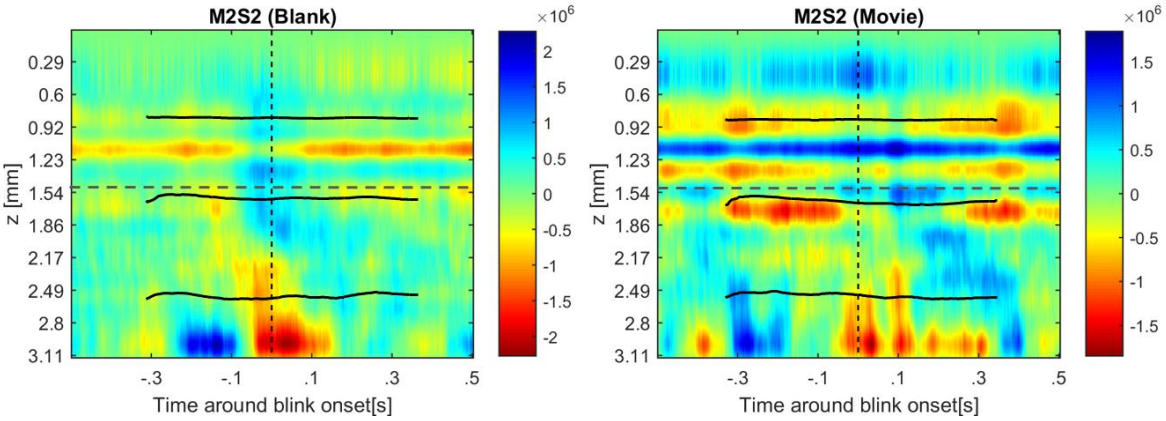


Figure S40. CSD using the cubic spline iCSD method for **monkey 2, session 2**. The x-axis shows the time period around blinks in seconds and the y-axis shows distance in mm. The colour scale represents the sinks (blue) and sources (red)

6. Study 5 (Supplementary)

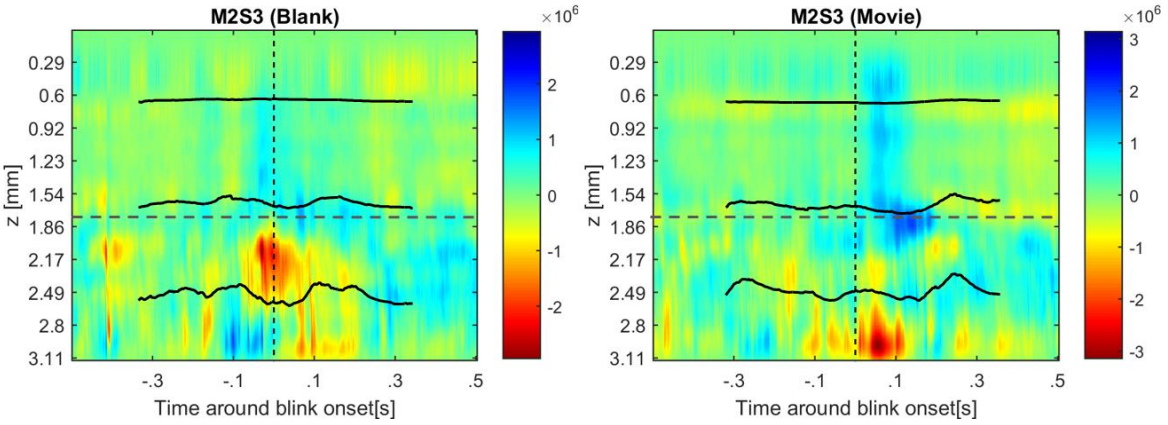


Figure S41. CSD using the cubic spline iCSD method for **monkey 2, session 3**. The x-axis shows the time period around blinks in seconds and the y-axis shows distance in mm. The colour scale represents the sinks (blue) and sources (red).

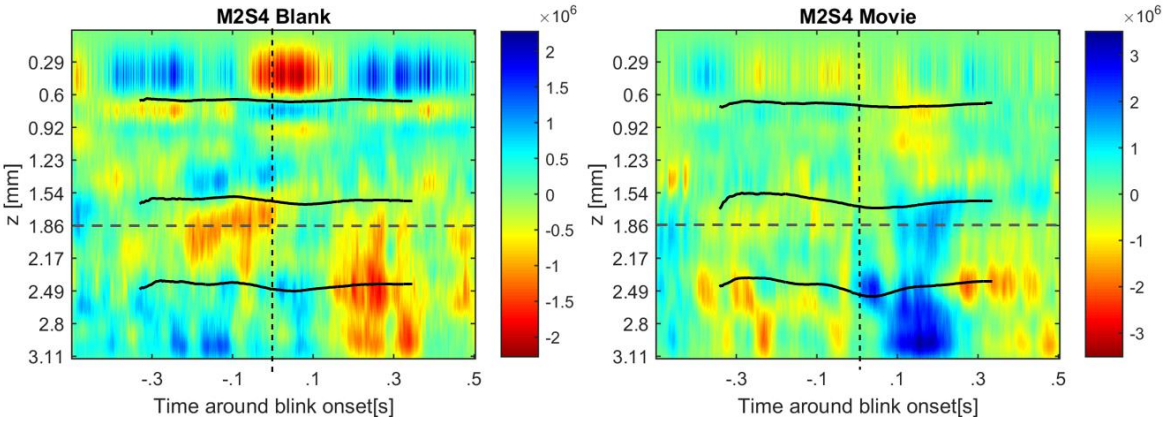


Figure S42. CSD using the cubic spline iCSD method for **monkey 2, session 4**. The x-axis shows the time period around blinks in seconds and the y-axis shows distance in mm. The colour scale represents the sinks (blue) and sources (red)

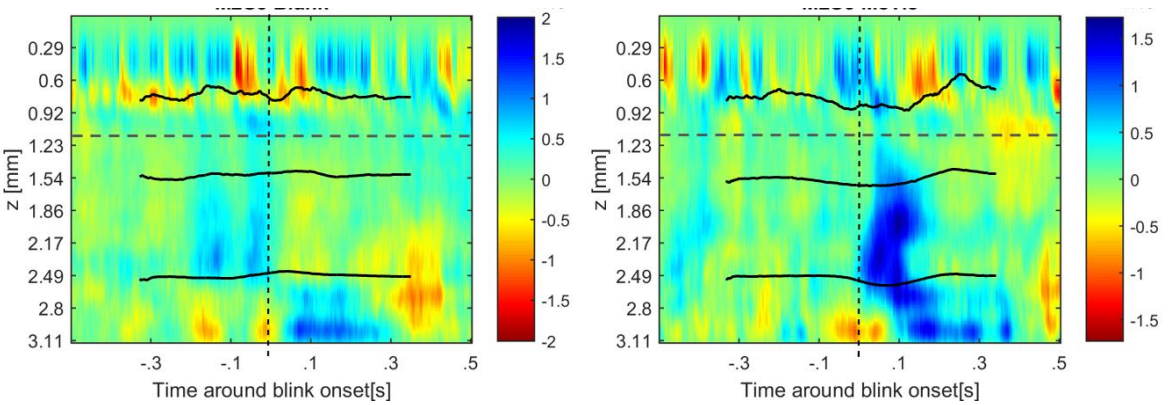


Figure S43. CSD using the cubic spline iCSD method for **monkey 2, session 5**. The x-axis shows the time period around blinks in seconds and the y-axis shows distance in mm. The colour scale represents the sinks (blue) and sources (red)

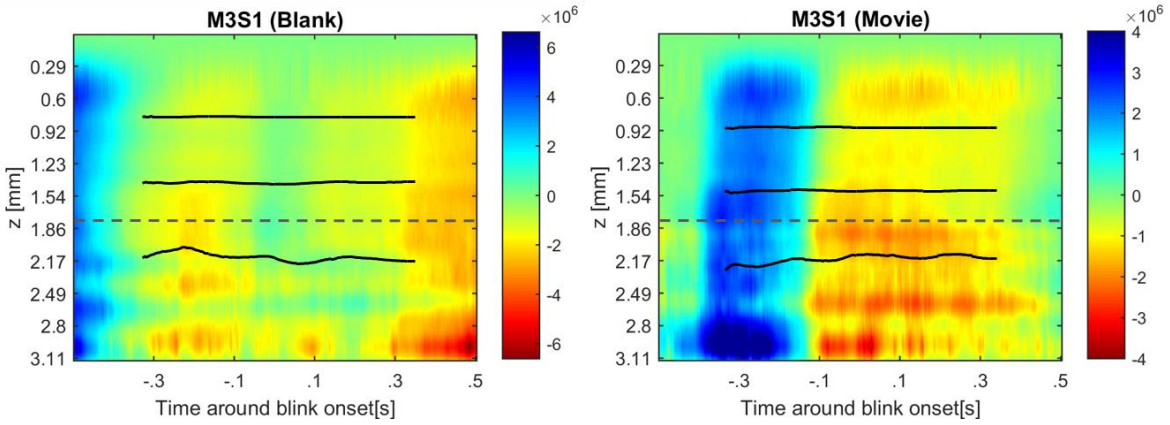


Figure S44. CSD using the cubic spline iCSD method for **monkey 3, session 1**. The x-axis shows the time period around blinks in seconds and the y-axis shows distance in mm. The colour scale represents the sinks (blue) and sources (red)

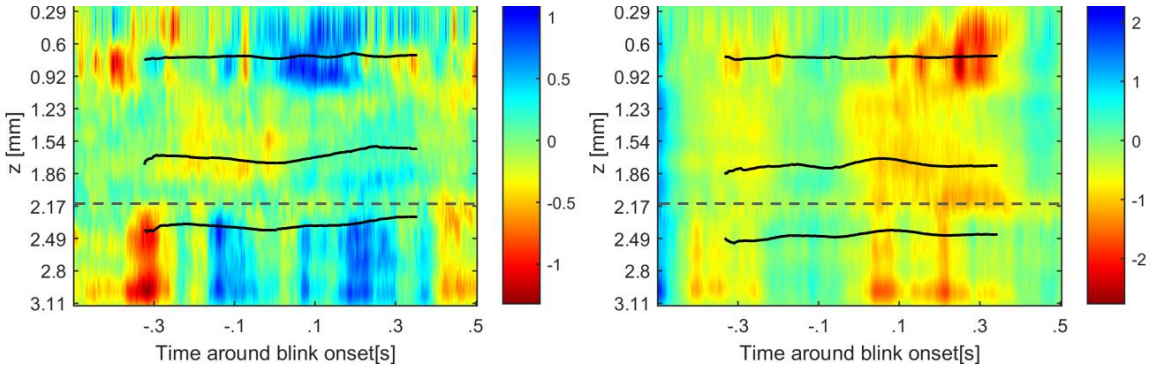


Figure S45. CSD using the cubic spline iCSD method for **monkey 3, session 1**. The x-axis shows the time period around blinks in seconds and the y-axis shows distance in mm. The colour scale represents the sinks (blue) and sources (red)

Results of the permutation-based approach

MUA results

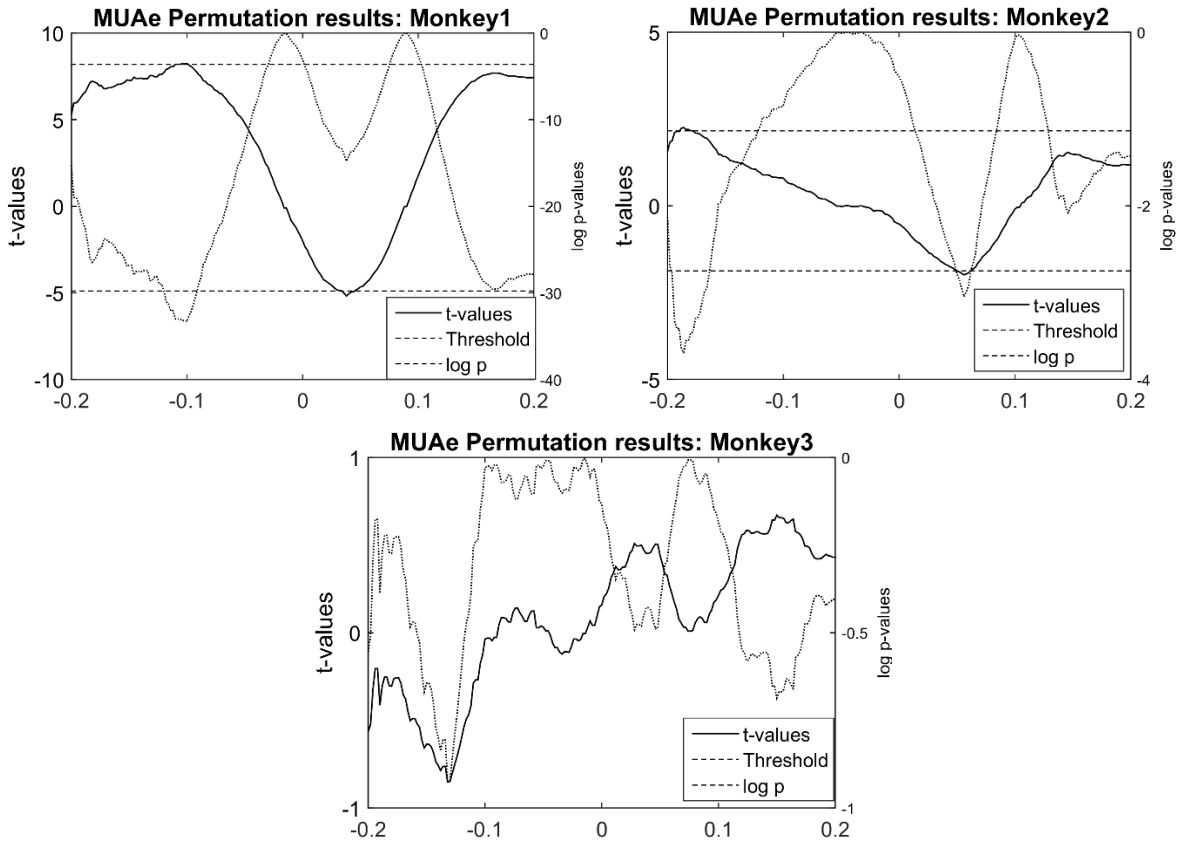


Figure S46. T-values and p-values of the independent sample t-test between the MUAe activity around blinks movie and blank screen.

6. Study 5 (Supplementary)

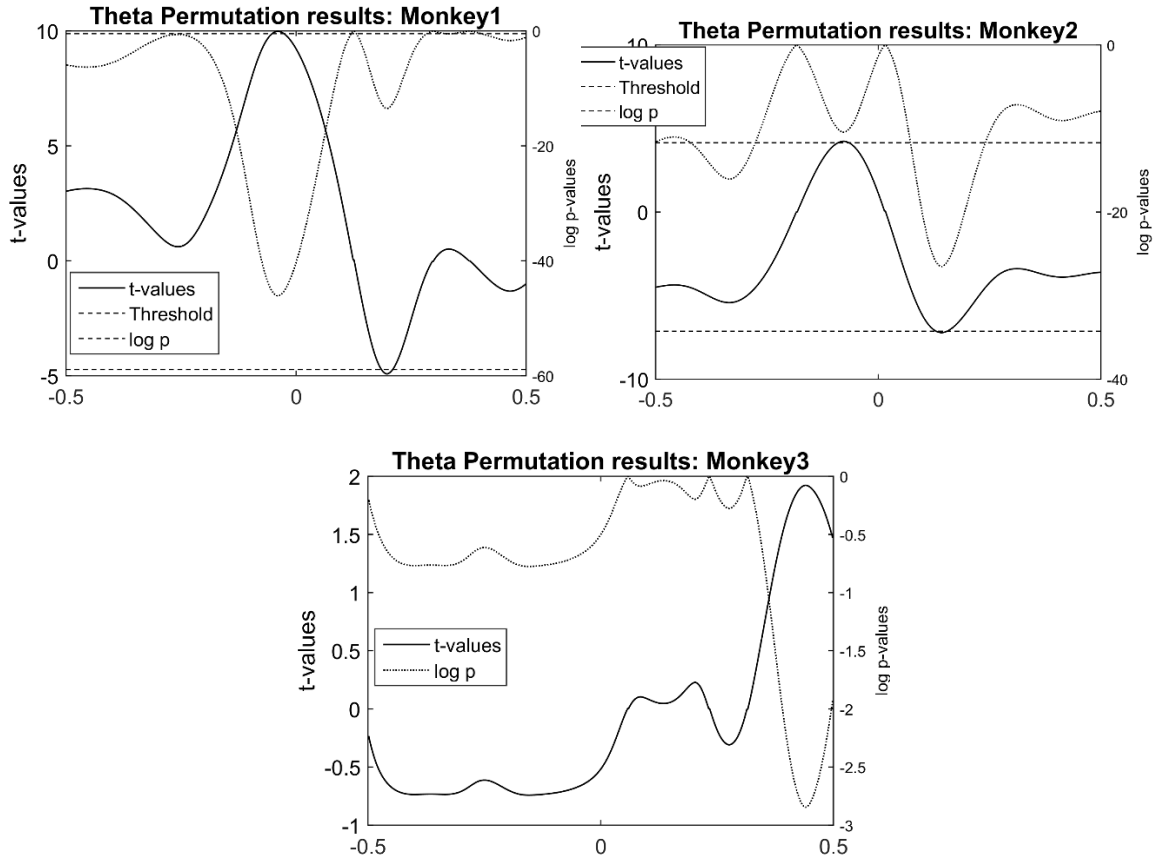


Figure S47. T-values and p-values of the independent sample t-test between the raw power in the theta range (4-8Hz) around blinks movie and blank screen.

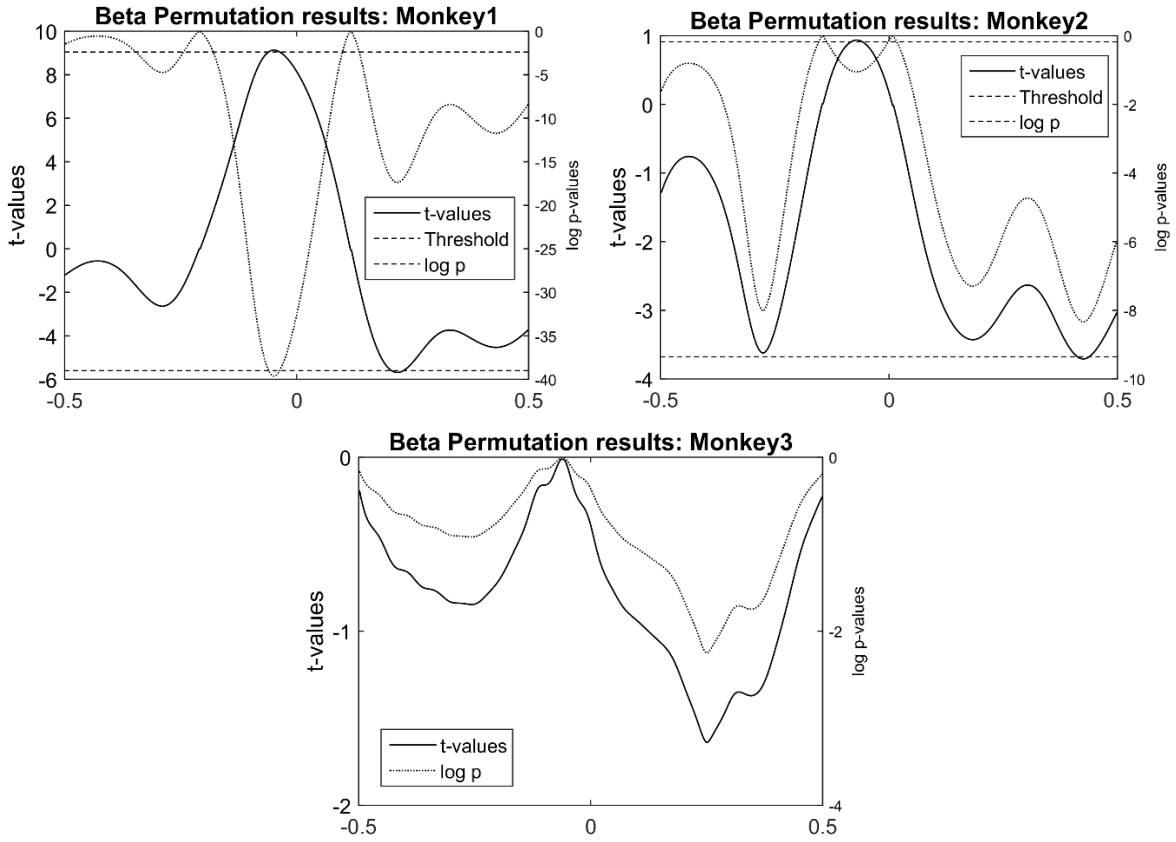


Figure S48. T-values and p-values of the independent sample t-test between the raw power in the beta range (16-30Hz) around blinks movie and blank screen.

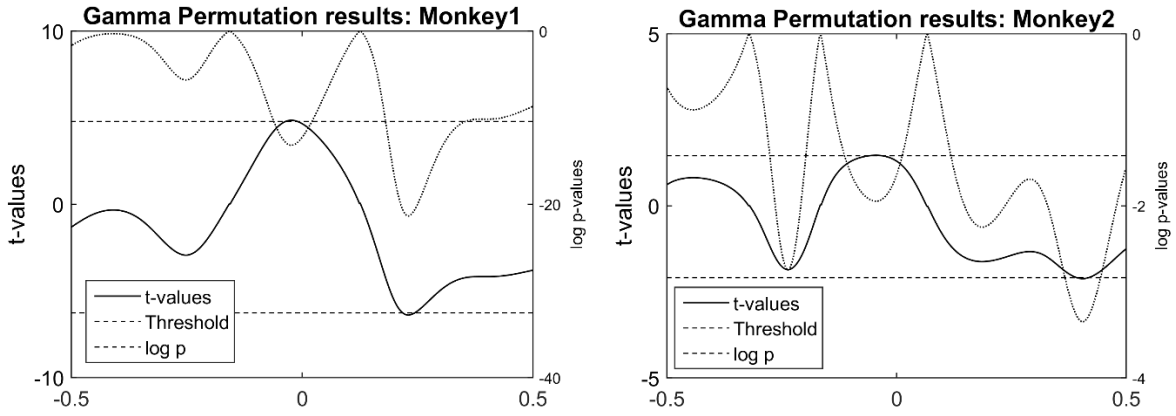


Figure S49. T-values and p-values of the independent sample t-test between the raw power in the gamma range (35-80Hz) around blinks movie and blank screen.

7. General discussion

Spontaneous blinking is one of the most frequently executed body movement in humans. Nevertheless, why we blink so often is not fully understood. The aim of this project was to understand the function of blinks through different tasks and attentional demands in the visual as well as the auditory domain and additionally by analysing the neural correlates of blinks. As reviewed in the introduction, previous research has suggested a relationship between blinking and cognition. To this end, in three studies, I investigated blinking during human behavioural tasks and analysed the neural correlates of blinks in rhesus monkeys. Specifically, the human behavioural tasks involved external processing using visual and auditory temporal judgement and bistable perception tasks, and internal cognitive processes using a divergent thinking task. The results have indicated that blinks are actively suppressed during external processing, independent from sensory onset and the visual domain. Extending this idea by taking into account that blinks are notable executed after the external processing resulting in a perceptual interpretation, we hypothesized that blinks might facilitate the disengagement from external input. Study 4 gave an indication (although a weak one) for a relationship between blinking and internally directed processing. Interestingly, study 5 revealed that the neural correlate of blinks differs depending between sensory processing and rest. In the following section, I will provide a short summary of the results from the different studies.

7.1 Summary of the results

In **study 1**, using one experiment, I tested whether the distribution of blinks reflects the timing of sensory input processing in the visual and auditory modality (Murali & Händel, 2021). To this end, a temporal judgement task was used wherein participants had to judge if

bilateral stimuli appeared simultaneously or not. The timing of the relevant information (inter-stimulus interval, i.e. time period between the onsets of the stimuli) and the duration of the entire stimulation was modulated independently. The results showed that blinks were shifted in latency, i.e. suppressed during a certain time period during sensory input. Importantly, this shift was predicted by the length of the relevant information (which was the ISI) and not mediated by the overall sensory input or the motor response. In other words, longer relevant information periods delayed a subsequent blink, indicating that blinks are supressed during processing of important sensory input. From an attentional point of view, blinking is suppressed when attention is directed towards an external stimulus.

While in study 1 the attentional and processing period was defined by changes in sensory input, **study 2 and 3** tested the modulation of blinks around purely internally generated events using bistable stimuli (Brych et al., 2021). In total, I conducted five experiments, using the visual plaid, the motion quartet and the auditory streaming paradigm. These stimuli are characterized by switching between two main perceptual interpretations, not mediated by any physical changes to the stimulus itself. The main results revealed that blinks decreased before the switch report and increased afterwards, and this modulation was found for both the visual as well as the auditory modality. The pattern was not driven by the motor response and was also present irrespective of lighting conditions, indicating that it was not based on the sensory change introduced by the closure of the eye during a blink. Importantly, when adding a condition with external darkenings (either of the stimulus or of the whole environment, both referred to as blanks) blinking decreased and switches increased after these interruptions. The timing of this blank-related blink and perceptual modulation allowed to decipher that the decrease in blinking before the switch report indeed occurred during the re-interpretation of the stimulus. In line with the suggested

interpretation from study 1, study 2 and 3 also indicate that blink reduction (which I will later argue is likely based on top-down driven blink suppression) marks the time period of productive processing (i.e. leading to conscious percept) of an external stimulus. Importantly, in study 3, I additionally found that inter-blink intervals were significantly shorter than intervals between a blink and a switch. In other words, a blink was most likely followed by a stable percept (as indicated by the longer duration between blink and switch). This finding is in line with the idea that blinks mark the end of the processing of sensory input, while periods of not blinking might stabilize percept.

In **study 4** I extended the idea that blinks mark the end of stimulus processing and therefore tested if they are associated with a possible shift towards internal processes (Murali & Händel, 2022). Specifically I analysed the association of blinking and divergent thinking, an important aspect of creative cognition using three experiments. I tested the influence of unrestricted walking and sitting on divergent thinking. Importantly, I assessed the relationship between eye blinks and performance in the task and if this relationship is dependent on the movement or restriction state. I had hypothesized that higher eye blinks would be associated with higher creativity scores within and between subjects. This is because, blinks might facilitate a disengagement from the external world, which would in turn benefit divergent thinking. The results revealed a modulation of eye blink rates by the movement condition and a significant correlation between the rate of eye blinks and creativity scores between subjects, i.e. subjects with higher blink rates showed higher scores; but only during free movement. There was no correlation between eye blinks and creativity scores within the subjects. Therefore, investigating blinking and internal cognitive processes, we did not find a simple relationship between blinking behaviour and creativity scores and therefore, increased blinking within a participant was not associated better performance. Nevertheless, although

dependent on motor restriction, there seems to some sort of correlation between eye blinks and internally directed processes between subjects. A more detailed analysis of blinking pattern might be necessary to understand such a relationship.

To further the understanding of the function of blinks, in **study 5** I explored the neural correlates of blinks during stimulus presentation vs rest. To this end, I analysed on-going neural activity in the primary visual cortex of three rhesus monkeys while they were shown a movie or a blank screen. The multi-unit activity envelope (MUAe), representing spiking activity, was reduced around blink onset during the movie, but increased during the blank screen condition. Additionally, there was also a blink-related change in power in the theta (4-8Hz), beta (16-30Hz) and gamma (35-80Hz) band, which was earlier and more pronounced for the blank screen as compared to the movie condition. This finding clearly indicates that blinks not only differ in rate and latency for various processing conditions but also that a blink has a different neural characteristic dependent on if it is executed during heightened sensory processing or rest. These findings, not only show for the first time that the neural response in V1 during a blink event is highly variable, but also show that it is dependent on the state of the subject.

7.2 Blinks are suppressed during stimulus processing

A total of six experiments (in studies 1-3) described in this thesis showed that blink probability decreases when attention is directed towards an external auditory or visual stimulus. Furthermore, the results revealed that a blink often marks the time point when task defined sensory processing has been completed and a perceptual interpretation has be reached.

7.2.1 Timing of suppression reflects the processing period

The experiments in this thesis have revealed that blinks probability is reduced during the processing of external stimuli in the visual and auditory domain. Specifically, when the processing is governed by changes to the stimulus itself (such as in the case of the temporal judgement task of study 1), the length of the reduction is predicted by the duration the relevant input. It is important to consider that the decision on what is relevant is a top-down driven process. When it comes to internal reinterpretation of unchanging bistable stimuli (in the case of ambiguous perception in studies 2-3), the timing of the reduction in blinking represent the time period of processing of the input that leads to a perceptual reinterpretation; however, this is not triggered by external events. Earlier studies have observed a modulation of blinking around stimulus presentation. Specifically, it has been reported by quite a few studies that blinking is reduced around the presentation of a stimulus (Baumstimler & Parrot, 1971; Y. Bonneh et al., 2015; Bonneh et al., 2016; Brych & Händel, 2020; Goldstein et al., 1992; Oh, Jeong, et al., 2012; Poulton & Gregory, 1952; Siegle et al., 2008; Edmund Wascher et al., 2015) and is increased after a certain time period (Y. Bonneh et al., 2015; Bonneh et al., 2016; Brych & Händel, 2020; Oh, Jeong, et al., 2012; Poulton & Gregory, 1952; Siegle et al., 2008). This pattern of decrease-increase has been termed as an oculomotor inhibitory mechanism by Bonneh et al. (2016). Importantly, because the decrease in blinks was found to occur even before the stimulus onset itself (Brych & Händel, 2020; Fukuda et al., 2005; Hoppe et al., 2018; Poulton & Gregory, 1952; Siegle et al., 2008), one can conclude that it is, to a certain extent, independent from sensory input. Hoppe et al. (2018), for instance, found that blinks decrease during, what they term as "high event probability" which is the high probability that a stimulus would occur. Similarly, Fukuda et al. (2005) observed that participants tended to blink only during non-stimulus periods. Some studies have postulated the decrease to be an active suppression of blinks (Y. Bonneh et al., 2015;

Bonneh et al., 2016; Brych & Händel, 2020; Goldstein et al., 1985; Oh, Jeong, et al., 2012). I would also argue that the reduction in blinks is in fact a top-down suppression. In study 1, I had analysed blink latency, which was the time period from the onset of the first stimulus to the onset of a first blink. This time period had a positively correlated with the relevant information period, which was defined by the inter-stimulus interval (ISI). As I mentioned earlier, relevance is defined by top-down processes. Therefore, the period of reduced blink probability could be taken as a period of top-down driven blink suppression.

Studies have further shown that stimulus complexity can modulate blink suppression. For example, Bonneh et al. (2016) demonstrated that the suppression was longer for lower contrast and higher spatial frequency and postulated that this increase was likely due to the fact that these physical properties were processed slower by the visual system. Similar findings regarding the processing time were reported by (Fogarty & Stern, 1989). While these studies already indicated a role of blinks in sensory processing, our study clearly shows that the modulation is based on the top down (voluntarily or involuntarily) assigned relevance of sensory input. Accordingly, not any sensory input, but task relevant stimuli introduce a suppression in blinking. If the stimulus is predictable in its temporal appearance, the pre-stimulus reduction in blinking might be a preparatory response for processing the incoming input, weighted by the probability of stimulus appearance. If the complexity of a stimulus requires more processing time, the suppression is longer**.**

Importantly, I would like to propose here that the driving factor for blink suppression is not sensory processing itself, but rather externally directed attention. The prediction that follows is that blinking does not show a general correlation with attention, but is specific to externally directed attention. Accordingly, blinking should only be suppressed during externally directed attention such as found during active engagement in stimulus processing.

It would further predict, that attention to internal processes do not lead to a decrease in blinking. Indeed, as I will discuss in more detail further below, tasks that require internally directed attention such as memory retrieval, daydreaming or creativity have not been associated with decreased blinking but rather with an increased blink rate (Salvi et al., 2015; Smilek et al., 2010; Ueda et al., 2016). The focus away from actual processing towards an attention based effect further fits well with the domain generality of the blink modulation. Importantly, the underlying cause for a specific attentional allocation should be irrelevant. As explained for study 1, if the relevance of the stimulus is modulated by sensory input, external attention is modulated alongside. However, the attentional focus can also be modulated via non-sensory driven internal processes. One example is the rhythmic change in spatial attention as observed by (Landau & Fries, 2012) during the detection of bilaterally presented simultaneously stimuli . Such a change in attention might also be at the basis of the perceptual switch experienced during perceptual bistability. In these cases, the internal interpretation of the sensory input alters between two (or more) different possibilities but is not based on changes of the stimulus itself. Previous findings have indicated that attentional focus on the stimulus might be an important prerequisite for the perceptual switches (Alais et al., 2010; Brascamp & Blake, 2012; Dieter et al., 2016; Hol et al., 2003; Kohler et al., 2008; Paffen & Alais, 2011; Paffen & Van der Stigchel, 2010; Schölvinck & Rees, 2009; Stonkute et al., 2012). For instance, it has been reported that diverting attention away from a bistable stimulus can reduce perceptual switching. For instance, Alais et al. (2010) proved that an additional auditory task reduces perceptual switching of a Necker cube and also during house/face binocular rivalry. In another experiment Schölvinck and Rees (2009) tested the influence of attention on motion induced blindness (MIB), which is a bistable stimulus consisting of a stationary visual target that alternatively disappears and reappears when superimposed over

moving distractors. The authors observed that when attention is directed towards the target, it increased the probability of its disappearance. But more importantly, directing attention away from the stimulus itself, decreased the number of switches between target appearance and disappearance. Similar findings have also been obtained for the motion quartet (Kohler et al., 2008). According to these authors, when participants were asked to do an additional detection task, durations of a specific percept were prolonged, or in other words, switching was reduced. These findings reveal that an active processing and engagement with the ambiguous stimulus is essential for the perceptual re-interpretation. Therefore, blink reduction occurs during this active re-interpretation of the stimulus, since one needs to avoid disengagement.

According to my hypothesis, the increase in external attention, which lead to increased sensory processing and in turn to the possibility of a perceptual reinterpretation, should be accompanied by a decrease in blink rate. Interestingly, a few studies have described a modulation of blinking around perceptual switches of bistable stimuli (Junji Ito et al., 2003; L. C. van Dam & R. van Ee, 2005). Since the timing of the actual internal switch is not easily known, these studies analysed blinking with respect to the report of the switch. They found the same ocular inhibitory pattern described by Bonneh et al. (2016), namely that there was a decrease in blinks before the switch report and an increase afterwards. Junji Ito et al. (2003) suggested that the blink decrease was driven by the reorganization and reinterpretation of the stimulus and the cognitive effort in order to report the switch. Nakatani and Van Leeuwen (2005) revealed that people who exhibited frequent switching between percepts of a Necker cube tended to have lower blink rates. They postulate that lower blink rates might be associated with a higher concentration during the task. A similar interpretation has been given by L. C. van Dam and R. van Ee (2005), according to whom, any relevant event during a task,

be it a perceptual switch or motor response might mediate blinking. While these studies all associated the blink modulation to the effort introduced by the task of reporting an event, Study 2 and 3 of this thesis clarified the relationship between blink modulation during bistable perceptual changes. First, I could exclude a motor based influence as there was no modulation of blinking around random key presses. Second, visual as well as auditory bistable perceptual changes are associated with a blink rate modulation. Third, in study 2 and 3 could I was able to decode if the decrease in blinking occurred during the internal re-interpretation of the stimulus or was caused by the perceptual (task relevant) event. I have argued for this in the discussion of study 2 and 3 through the timing of blank induced modulations in blinks and switches. For instance, in study 2, one can see that that blank increased 0.5s before the switch, i.e. that a blank increased the probability of a perceptual switch about half a second later (Figure 14). Since the internal switch was caused by the blank, we can conclude the timing of this event (i.e. the internal switch) as being below 0.5s (with reference to the switch report). However, the blink decrease begins much earlier than 0.5s (Figure 13), indicating that it occurred before or during the internal switch but not as a result of it. Similar results were observed in study 3 (please see Discussion section 4.5.1). It is important to stress that while the same blink decrease was found in the auditory domain (Figure 19), due to the absence of blanks in this experiment I could not decipher if the decrease occurred during the internal re-processing. Nevertheless, a reduction during the reinterpretation, which likely occurs along with an increase in externally focussed attention is in line with the hypothesis that blinking is suppressed when engaging with a stimulus. Importantly, attention on the external input is internally generated and not necessarily voluntarily driven. But I would like to put forth here that even though attention may not be necessarily voluntary driven, the reduction could still be mediated via a top-down suppression just like in the processing of relevant information

during temporal judgements, since, as I had mentioned earlier, the study by (Landau & Fries, 2012) revealed that attention could be modulated via non-sensory driven internal processes. The reason for the top-down driven blink suppression could be due to the fact that blinking would possibly foster a disengagement from the external input. Thereby, there could be a shift towards attention that is internally directed.

Although such a disengagement and shift to internally directed attention has not been put forth before, some authors have loosely suggested that blinking might be associated with an attentional disengagement from visual stimulus (Ang & Maus, 2020; Nakano et al., 2013; Smilek et al., 2010). Smilek et al. (2010) postulated that blinking is a shift away from the external stimulus to internal daydreaming. However, their paper specifically discusses a shift away from a visual stimulus to mind wandering and not a modality-independent disengagement from externally focussed attention to internally focused attention.

7.3 Blinks denote the end of external engagement and a possible shift towards internal consolidation

Blinks are not merely suppressed during stimulus processing, but also increase above baseline level at a certain time after stimulus onset. Previous studies have reported an active increase in blinking above baseline after the stimulus onset (Baumstimler & Parrot, 1971; Y. S. Bonneh et al., 2015; Bonneh et al., 2016; Oh, Jeong, et al., 2012; Poulton & Gregory, 1952; Siegle et al., 2008; Edmund Wascher et al., 2015). Blink rate modulation in the temporal judgment task (study 1) showed that the first blink after stimulus onset always occurs at the end of the relevant information independent if other sensory input is still ongoing. This suggests that a blink can mark the time point when one can disengage from the sensory task. Edmund Wascher et al. (2015) already had put forth that people tend to blink at the end of information processing. However, I would like to argue here that the occurrence of the blink

might have an active role in the process, and it might be that they represents the internal consolidation of the information presented. For instance, in study 1, in the figure showing the temporal modulation of blinks (figure 4), one can see that blinking increases a certain point after the trial onset. In a previous study, Ang and Maus (2020) also put forth a similar idea, stating *„Blinks may reflect transitions in cognition, during which previously attended visual information is consolidated…*". Notably, in the study by Brych and Händel (2020), it was shown that the increase in blink probability was higher for a target as opposed to a distractor in an oddball task. Interestingly, in oddball tasks, EEG studies have revealed that a P300-like amplitude occurs only after targets and not after distractors (Duncan-Johnson & Donchin, 1977; Jang et al., 2011). Such a P300 also reflects information consolidation (Alday & Kretzschmar, 2019; Batterink et al., 2012) and has also been associated with blinks (Bonfiglio et al., 2013; Bonfiglio et al., 2014; Liu et al., 2017). Since consolidation is an internal process following sensory processing, this fits with the idea that a blink is involved in the switch away from external attentional focus.

Findings from the bistable stimulus experiments indeed indicate that blinks mark the end of external attentional engagement and a possible shift towards internal processes. In study 3, I found that blinks are followed by periods of stable percept. Specifically, in both the motion quartet and auditory streaming stimulus, the duration between a blink to a switch was longer than the inter-blink interval (Figure 21). Because a blink is followed by a long duration of a specific percept (Blink to switch is longer, as mentioned), it is possible that a blink likely occurs when no further reprocessing of the stimulus needs to take place. This might also explain the increased blink probability (although not significant in all cases) during the switch report (Figures 13 & 19). As a perceptual switch likely involves attentional engagement with the bistable stimulus, the stable percept after the blink indicates a

disengagement from the sensory input. Accordingly, a blink could mark the shift away from the external stimulus and towards internal processes.

If a blink marks a shift towards internal focus, it is possible that they also facilitate these processes. I had specifically analysed the relationship between blinks and divergent thinking to test this. A link between blinking and divergent thinking has been observed as between-subject effect by earlier studies (Chermahini & Hommel, 2010; Ueda et al., 2016). In study 4, I found that blinking is associated with better performance in divergent thinking, however, only when participants were allowed to move freely. Additionally, this relationship was found only between subjects and not within a subject, i.e. subjects with higher blink rates performed better but within a subject a trial with higher blink rate did not coincide with better performance. It is possible that people who are able to disengage easily, possibly indicated by an overall high blink rate, perform better in divergent thinking tasks, the relationship between blink rate and internal tasks is not clear at this point. Indeed, a more complex measurement of blink behaviour might be necessary to unravel such a relationship.

To summarize, a top-down driven blink suppression takes place when the attentional focus is directed externally, i.e. towards a specific stimulus and its processing. The subsequent blink marks the end of this attentional period and concurrent stimulus processing and represent a the time of the shift from externally to internally directed processes and may even facilitate these processes. Interestingly, both Smilek et al. (2010) and Nakano et al. (2013) mention the default mode network (DMN), but do not explicitly state that this could be a possible mechanism through which blinking might facilitate internally directed processes. It has been put forth that activity in the DMN is suppressed in order to disengage from internally directed processes and in-turn facilitate externally focussed demands (Raichle et al., 2001). Blinking has been associated with increased activation in the DMN (Nakano et al., 2013). More

importantly, the increased activation in the DMN has been associated with better performance in internally directed creativity tasks (Beaty et al., 2014; Kühn et al., 2014). Exploring the relationship of blinking and external vs internal processes with respect to DMN activity could be an important step in future research in order to uncover the role of blinks during internally directed processes such as creativity.

7.4 Blink-related neural activity in the sensory cortex

To further understand the function of blinks, I studied the ongoing neural response in V1 of three rhesus monkeys, around a blink event during sensory processing vs rest. During this experiment, the animal was shown either a movie or a blank screen. The aim was to understand if the neural response differs depending on the attentional state of the animal. Although there was faint light and therefore sensory input even during the blank screen, the movie most likely involved higher attentional engagement and increased processing compared to the blank screen. By analyzing single electrode recordings, I found that multi-unit activity (associated with spiking) around a blink was reduced during the movie, but increased during rest. Additionally, I observed an increase in power during blinks across three different frequency bands, namely theta (4-8Hz), beta (16-30 Hz) and gamma (35-80 Hz) during a blink. The increased power was earlier and stronger during the blank and rather suppressed during the movie.

While it is already puzzling why a motor event such as a blink affects neural activity in early visual cortex, it is even more surprising that this influence is dependent on the state of the monkey and the amount of sensory input. Does this differential effect of blinking mark a single process or two different processes dependent on the situation? As I explained above, blinks might facilitate a disengagement from external attention and therefore need to be suppressed during sensory processing in order to avoid such disengagement. However, not

all spontaneous blinks are under full cognitive control and about 20 to 40% are likely executed for reasons such as moisturizing the cornea. If such a blink occurs during stimulus processing, on-going neural activity might be reduced in order to minimize disengagement. However, when there is no specific stimulus that needs to be processed (for instance, when the animal is shown a blank screen), disengaging does not pose a problem and might even be welcome. The found increase in activity associated with blink during rest might therefore mark such a disengagement process. This of course does not mean that increased activity in V1 would in general represent attentional disengagement. Indeed, just as most researchers prior to me, I have also found an overall higher neural activity during the intense visual input of a movie compared to blank screen. Similarly, the blink-related power increase during a blank might also reflect the possibility to disengage. Other studies have put forth a power increase in the delta range, localized to the precuneus, to be associated with blinking (Bonfiglio et al., 2013; Liu et al., 2017; Liu et al., 2019). As mentioned in the discussion of study 5, the theta power (4-8 Hz) in my study overlapped with the delta band in the Bonfiglio's studies (0-4 Hz). Note that the precuneus is an important structure in the default mode network DMN (Fransson & Marrelec, 2008) and blinking, as I had pointed out, has been found to be associated with increased activation in the DMN. Liu et al. (2017) indeed mention that the DMN is active during internally directed states. However, the studies on increased power in the delta range localized to the precuneus used passive sitting or fixation paradigms. However, one study compared passive fixation and stimulus processing and found a reduction in the delta blink-related oscillation in the precuneus during the latter (Liu et al., 2019). This goes in line with the findings of study 5, namely that there is a suppression of the blink related power increase when there is a stimulus to be attended. But do note that the focus of study 5 was on V1 and not the precuneus or DMN. Nevertheless, the observed delay and suppression of the blink

induced power increase while the monkeys watched the movie might be indicative of the fact that the effect of blinks is reduced when in a state of active external processing. Hence, while the qualitatively different MUAe possibly suggests two different processes, the reduction and delay of the power modulation rather suggests one process that is either fully executed (blank) or suppressed (movie).

To summarize, I found that in the early visual cortex, blinking induces a modulation of multi-unit activity and oscillatory activity which depends in its type on whether the blink is executed during processing of an external stimulus or during reduced sensory input in rest.

7.5 Why do humans blink so much?

If disengagement is a consequence of blinks, does this fit with the observation that humans blink on average as much as 15 times a minute? A possible answer to this question that I would like to put forth is that attentional disengagement is indeed very important in our everyday lives. Because humans are inundated with an extreme amount stimuli on a daily basis, blinks might be one way to avoid that attention is stalled and irrelevant sensory input is processed. This might also explain why blink rates are generally higher during walking (Cao et al., 2020b), since we encounter more stimuli and also more changes in sensory input while walking and might need to disengage more often. Importantly, while blinking might be one way to keep prolonged attention to the external world in check, the studies have also clearly shown that by controlling the timing of a single blink event, a prolonged undisturbed processing of stimuli is also possible when necessary.

7.6 General conclusion

Overall, the findings of this project have put forward considerable evidence that blinks serve an important function during cognitive and perceptual processes. Importantly, it seems

that blinks facilitate a disengagement from the external environment. Therefore, they are suppressed when one needs to avoid such a disengagement; for example, while processing relevant external information. This is true for the visual and the auditory domain. Some evidence further associates increased blinking with better performance in tasks that involve an internal attentional state. However, further research is needed to understand this relationship and establish if it is based on a blink induced facilitation of internal processes. Finally and importantly, the on-going neural activity in the primary visual cortex differs possibly depends on the attention state of the individual.

References

Akbari Chermahini, S., & Hommel, B. (2010). The (b) link between creativity and dopamine: spontaneous eye blink rates predict and dissociate divergent and convergent thinking. *Cognition*, *115*(3), 458-465.

Al-Yahya, E., Dawes, H., Smith, L., Dennis, A., Howells, K., & Cockburn, J. (2011). Cognitive motor interference while walking: a systematic review and meta-analysis. *Neuroscience & Biobehavioral Reviews*, *35*(3), 715-728.

Alais, D., van Boxtel, J. J., Parker, A., & van Ee, R. (2010). Attending to auditory signals slows visual alternations in binocular rivalry. *Vision research*, *50*(10), 929-935.

Alday, P. M., & Kretzschmar, F. (2019). Speed-accuracy tradeoffs in brain and behavior: testing the independence of P300 and N400 related processes in behavioral responses to sentence categorization. *Frontiers in Human Neuroscience*, *13*, 285.

Alexander, G. E., DeLong, M. R., & Strick, P. L. (1986). Parallel organization of functionally segregated circuits linking basal ganglia and cortex. *Annual review of neuroscience*, *9*(1), 357-381.

Almonte, F., Jirsa, V. K., Large, E. W., & Tuller, B. (2005). Integration and segregation in auditory streaming. *Physica D: Nonlinear Phenomena*, *212*(1-2), 137-159.

Ang, J. W. A., & Maus, G. W. (2020). Boosted visual performance after eye blinks. *Journal of Vision*, *20*(10), 2-2.

Attneave, F. (1968). Triangles as ambiguous figures. *The American journal of psychology*, *81*(3), 447-453.

Baker, D. H., & Graf, E. W. G. W. (2010). Extrinsic factors in the perception of bistable motion stimuli. *Vision Research*, 1257–1265.

Baker, R., Andersen, A., Morecraft, R., Smith, C., & Webb, R. (2001). Functional MRI in benign essential blepharospasm: Mapping of cortical and subcortical areas involved in spontaneous and voluntary blinking. Investigative ophthalmology & visual science,

Balaban, M. T., & Taussig, H. N. (1994). Salience of fear/threat in the affective modulation of the human startle blink. *Biological Psychology*, *38*(2-3), 117-131.

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.

Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J. R., De Weerd, P., Kennedy, H., & Fries, P. (2015). Visual areas exert feedforward and feedback influences through distinct frequency channels. *Neuron*, *85*(2), 390-401.

Batterink, L., Karns, C. M., & Neville, H. (2012). Dissociable mechanisms supporting awareness: the P300 and gamma in a linguistic attentional blink task. *Cerebral Cortex*, *22*(12), 2733-2744.

Bauer, L. O., Goldstein, R., & Stern, J. A. (1987). Effects of information-processing demands on physiological response patterns. *Human factors*, *29*(2), 213-234.

Bauer, L. O., Strock, B. D., Goldstein, R., Stern, J. A., & Walrath, L. C. (1985). Auditory Discrimination and the Eye Blink. *Psychophysiology*, 636-641.

Bauer, L. O., Strock, B. D., Goldstein, R., Stern, J. A., & Walrath, L. C. (1985). Auditory discrimination and the eyeblink. *Psychophysiology*, *22*(6), 636-641.

Baumstimler, Y., & Parrot, J. (1971). Stimulus generalization and spontaneous blinking in man involved in a voluntary activity. *Journal of Experimental Psychology*, *88*(1), 95.

Beaty, R. E., Benedek, M., Wilkins, R. W., Jauk, E., Fink, A., Silvia, P. J., Hodges, D. A., Koschutnig, K., & Neubauer, A. C. (2014). Creativity and the default network: A functional connectivity analysis of the creative brain at rest. *Neuropsychologia*, *64*, 92-98.

Bell, C., & Davy, H. (1823). XV. On the motions of the eye, in illustration of the uses of the muscles and nerves of the orbit. *Philosophical Transactions of the Royal Society of London*, *113*, 166-186. https://doi.org/doi:10.1098/rstl.1823.0017

Berardelli, A., Rothwell, J., Day, B., & Marsden, C. (1985). Pathophysiology of blepharospasm and oromandibular dystonia. *Brain*, *108*(3), 593-608.

Betta, E., & Turatto, M. (2006). Are you ready? I can tell by looking at your microsaccades. *Neuroreport*, 1001-1004.

Bhatia, K. P., & Marsden, C. D. (1994). The behavioural and motor consequences of focal lesions of the basal ganglia in man. *Brain*, *117*(4), 859-876.

Binder , M. D., Hirokawa, N., & Windhorst , U. (2008). Aperture Problem. In *Encyclopedia of Neuroscience*. Springer.

Blauert, J. (1938). Psychoacoustic binaural phenomena. In *HEARING—Physiological Bases and Psychophysics* (pp. 182-189). Springer.

Blin, O., Masson, G., Azulay, J., Fondarai, J., & Serratrice, G. (1990). Apomorphine-induced blinking and yawning in healthy volunteers. *British journal of clinical pharmacology*, *30*(5), 769-773.

Boeykens, C., Wagemans, J., & Moors, P. (2019). Biases in the perception of the ambiguous motion quartet across spatial scale. *Journal of Vision*, *19*(10), 152a-152a.

Bologna, M., Fasano, A., Modugno, N., Fabbrini, G., & Berardelli, A. (2012). Effects of subthalamic nucleus deep brain stimulation and L-DOPA on blinking in Parkinson's disease. *Experimental neurology*, *235*(1), 265-272.

Bonfiglio, L., Olcese, U., Rossi, B., Frisoli, A., Arrighi, P., Greco, G., Carozzo, S., Andre, P., Bergamasco, M., & Carboncini, M. C. (2013). Cortical source of blink-related delta oscillations and their correlation with levels of consciousness. *Human brain mapping*, *34*(9), 2178-2189.

Bonfiglio, L., Piarulli, A., Olcese, U., Andre, P., Arrighi, P., Frisoli, A., Rossi, B., Bergamasco, M., & Carboncini, M. C. (2014). Spectral parameters modulation and source localization of blink-related alpha and low-beta oscillations differentiate minimally conscious state from vegetative state/unresponsive wakefulness syndrome. *PloS one*, *9*(3), e93252.

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.

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.

Bonneh, Y., Fried, M., & Adini, Y. (2015). Blinking by Surprise: Eye-Blink Rate and Latency Uncover Stimulus Predictability. *Journal of Vision*, *15*(12), 779-779.

Bonneh, Y. S., Adini, Y., & Polat, U. (2015). Contrast sensitivity revealed by microsaccades. *Journal of Vision*, *15*(9), 11-11.

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), 1-1.

Bosman, C. A., Schoffelen, J.-M., Brunet, N., Oostenveld, R., Bastos, A. M., Womelsdorf, T., Rubehn, B., Stieglitz, T., De Weerd, P., & Fries, P. (2012). Attentional stimulus selection through selective synchronization between monkey visual areas. *Neuron*, *75*(5), 875-888.

Brainard, D. H. (1997). The psychophysics toolbox. *Spatial vision*, *10*(4), 433-436.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 433-436.

Brandt, S. A., & Stark, L. W. (1997). Spontaneous eye movements during visual imagery reflect the content of the visual scene. *Journal of cognitive neuroscience*, *9*(1), 27-38.

Brascamp, J. W., & Blake, R. (2012). Inattention abolishes binocular rivalry: Perceptual evidence. *Psychological science*, *23*(10), 1159-1167.

Bristow, D., Frith, C., & Rees, G. (2005). Two distinct neural effects of blinking on human visual processing. *NeuroImage*, *27*(1), 136-145.

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.

Broadbent, D. (1955). A note on binaural fusion. *Quarterly Journal of Experimental Psychology*, *7*(1), 46-47.

Broadbent, D. (1958). Perception and communication.

Brych, M., & Händel, B. (2020). Disentangling top-down and bottom-up influences on blinks in the visual and auditory domain. *International Journal of Psychophysiology*.

Brych, M., Murali, S., & Händel, B. (2020). How the Motor Aspect of Speaking Influences the Blink Rate. *bioRxiv*.

Brych, M., Murali, S., & Händel, B. (2021). The Role of Blinks, Microsaccades and their Retinal Consequences in Bistable Motion Perception [Original Research]. *Frontiers in psychology*, *12*(947). https://doi.org/10.3389/fpsyg.2021.647256

Buffalo, E. A., Fries, P., Landman, R., Buschman, T. J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. *Proceedings of the National Academy of Sciences*, *108*(27), 11262-11267.

Buisseret, P., & Maffei, L. (1983). Suppression of visual cortical activity following tactile periorbital stimulation; its role during eye blinks. *Experimental brain research*, *51*(3), 463-466.

Burr, D. (2005). Vision: in the blink of an eye. *Current Biology*, *15*(14), R554-R556.

Cao, L., Chen, X., & Haendel, B. F. (2020a). Overground walking decreases alpha activity and entrains eye movements in humans. *Frontiers in human neuroscience*, *14*.

Cao, L., Chen, X., & Haendel, B. F. (2020b). Overground walking decreases alpha activity and entrains eye movements in humans. *Frontiers in Human Neuroscience*.

Cao, L., & Händel, B. (2019). Walking enhances peripheral visual processing in humans. *PLoS biology*, *17*(10), e3000511.

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: a review of its functional anatomy and behavioural correlates. *Brain*, *129*(3), 564-583.

Chermahini, S. A., & Hommel, B. (2010). The (b) link between creativity and dopamine: spontaneous eye blink rates predict and dissociate divergent and convergent thinking. *Cognition*, *115*(3), 458-465.

Collewijn, H., Van Der Steen, J., & Steinman, R. (1985a). Human eye movements associated with blinks and prolonged eyelid closure. *Journal of neurophysiology*, *54*(1), 11-27.

Collewijn, H., van der Steen, J., & Steinman, R. M. (1985b). Human eye movements associated with blinks and prolonged eyelid closure. *Journal of neurophysiology* 11-27.

Colombo, A., De Renzi, E., & Gibertoni, M. (1982). Eyelid movement disorders following unilateral hemispheric stroke. *The Italian Journal of Neurological Sciences*, *3*(1), 25-30.

Colzato, L. S., van Wouwe, N. C., & Hommel, B. (2007). Spontaneous eyeblink rate predicts the strength of visuomotor binding. *Neuropsychologia*, *45*(10), 2387-2392.

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.

Cong, D. K., Sharikadze , M., Staude , G., Deubel , H., & Wolf, W. (2010). Spontaneous eye blinks are entrained by finger tapping. *Hum Movem Sci*, 1–18.

Cox, M. A., Dougherty, K., Adams, G. K., Reavis, E. A., Westerberg, J. A., Moore, B. S., Leopold, D. A., & Maier, A. (2019). Spiking suppression precedes cued attentional enhancement of neural responses in primary visual cortex. *Cerebral Cortex*, *29*(1), 77-90.

Craig, J. (2002). Structure and function of the preocular tear film. *The Tear Film: structure, function and clinical examination*, *1*, 18-50.

Damiano, C., & Walther, D. B. (2019). Distinct roles of eye movements during memory encoding and retrieval. *Cognition*, *184*, 119-129.

Dang, L. C., Donde, A., Madison, C., O'Neil, J. P., & Jagust, W. J. (2012). Striatal dopamine influences the default mode network to affect shifting between object features. *Journal of cognitive neuroscience*, *24*(9), 1960-1970.

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).

Davis, M. (1984). The mammalian startle response. In *Neural mechanisms of startle behavior* (pp. 287-351). Springer.

De Jong, P. J., & Merckelbach, H. (1990). Eyeblink frequency, rehearsal activity, and sympathetic arousal. *International Journal of Neuroscience*, *51*(1-2), 89-94.

Deubel, H., Bridgeman, B., & Schneider, W. X. (2004). Different effects of eyelid blinks and target blanking on saccadic suppression of displacement. *Perception & Psychophysics*, 772–778.

Deuschl, G., & Goddemeier, C. (1998). Spontaneous and reflex activity of facial muscles in dystonia, Parkinson's disease, and in normal subjects. *Journal of Neurology, Neurosurgery & Psychiatry*, *64*(3), 320-324.

Dieter, K. C., Brascamp, J., Tadin, D., & Blake, R. (2016). Does visual attention drive the dynamics of bistable perception? *Attention, Perception, & Psychophysics*, *78*(7), 1861-1873.

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.

Drew, G. C. (1951). Variations in reflex blink-rate during visual-motor tasks. *Quarterly Journal of Experimental Psychology*, *3*(2), 73-88.

Duncan-Johnson, C. C., & Donchin, E. (1977). On quantifying surprise: The variation of event-related potentials with subjective probability. *Psychophysiology*, *14*(5), 456-467.

Dykes, M., & McGhie, A. (1976). A comparative study of attentional strategies of schizophrenic and highly creative normal subjects. *The British Journal of Psychiatry*, *128*(1), 50-56.

Einhauser, W., Stout, J., Koch, C., & Carter, O. (2008). Pupil dilation reflects perceptual selection and predicts subsequent stability in perceptual rivalry. *PNAS*, 1704–1709.

Ellis, S. R., & Stark, L. (1978). Eye movements during the viewing of Necker cubes. *Perception*, 575–581.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research* 1035–1045.

Evinger, C., & Manning, K. A. (1993). Pattern of extraocular muscle activation during reflex blinking. *Experimental brain research*, *92*(3), 502-506.

Fogarty, C., & Stern, J. A. (1989). Eye movements and blinks: their relationship to higher cognitive processes. *International Journal of Psychophysiology*, *8*(1), 35-42.

Fournier, J., Saleem, A. B., Diamanti, E. M., Wells, M. J., Harris, K. D., & Carandini, M. (2020). Mouse visual cortex is modulated by distance traveled and by theta oscillations. *Current Biology*, *30*(19), 3811-3817. e3816.

Fransson, P., & Marrelec, G. (2008). The precuneus/posterior cingulate cortex plays a pivotal role in the default mode network: Evidence from a partial correlation network analysis. *NeuroImage*, *42*(3), 1178-1184.

Freed, W., Kleinman, J. E., Karson, C. N., Potkin, S., Murphy, D., & Wyatt, R. (1980). Eye-blink rates and platelet monoamine oxidase activity in chronic schizophrenic patients. *Biological psychiatry*, *15*(2), 329-332.

Friedman, R. S., Fishbach, A., Förster, J., & Werth, L. (2003). Attentional priming effects on creativity. *Creativity research journal*, *15*(2-3), 277-286.

Fries, P. (2015). Rhythms for cognition: communication through coherence. *Neuron*, *88*(1), 220-235.

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.

Gao , X., Yan, H., & Sun, H.-j. (2015). Modulation of microsaccade rate by task difficulty revealed through between- and within-trial comparisons. *Journal of Vision*, 1–15.

Gawne, T. J., & Martin, J. M. (2000). Activity of primate V1 cortical neurons during blinks. *Journal of neurophysiology*, *84*(5), 2691-2694.

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.

Gelman, A., & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. Cambridge university press.

Genç, E., Bergmann, J., Singer, W., & Kohler, A. (2011). Interhemispheric connections shape subjective experience of bistable motion. *Current Biology*, *21*(17), 1494-1499.

Gengerelli, J. (1948). Apparent movement in relation to homonymous and heteronymous stimulation of the cerebral hemispheres. *Journal of Experimental Psychology*, *38*(5), 592.

Gerfen, C. R., & Bolam, J. P. (2010). The neuroanatomical organization of the basal ganglia. In *Handbook of behavioral neuroscience* (Vol. 20, pp. 3-28). Elsevier.

Girshick, A. R., Landy, M. S., & Simoncelli, E. P. (2011). Cardinal rules: visual orientation perception reflects knowledge of environmental statistics. *Nature Neuroscience* 926–932.

Golan, T., Davidesco, I., Meshulam, M., Groppe, D. M., Mégevand, P., Yeagle, E. M., Goldfinger, M. S., Harel, M., Melloni, L., & Schroeder, C. E. (2016). Human intracranial recordings link suppressed transients rather than'filling-in'to perceptual continuity across blinks. *Elife*, *5*, e17243.

Golan, T., Grossman, S., Deouell, L., & Malach, R. (2018a). Widespread Suppression of High-Order Visual Cortex During Blinks and External Predictable Visual Interruptions. *bioRxiv*.

Golan, T., Grossman, S., Deouell, L. Y., & Malach, R. (2018b). Widespread suppression of high-order visual cortex during blinks and external predictable visual interruptions. *bioRxiv*

Goldman-Rakic, P. S. (1988). Topography of cognition: parallel distributed networks in primate association cortex. *Annual review of neuroscience*, *11*(1), 137-156.

Goldstein, R., Bauer, L. O., & Stern, J. A. (1992). Effect of task difficulty and interstimulus interval on blink parameters. *International Journal of Psychophysiology*, *13*(2), 111-117.

Goldstein, R., Walrath, L. C., Stern, J. A., & Strock, B. D. (1985). Blink activity in a discrimination task as a function of stimulus modality and schedule of presentation. *Psychophysiology*, *22*(6), 629-635.

Gregory, R. (1952). Variations in blink rate during non-visual tasks. *Quarterly Journal of Experimental Psychology*, *4*(4), 165-169.

Grothe, I., Neitzel, S. D., Mandon, S., & Kreiter, A. K. (2012). Switching neuronal inputs by differential modulations of gamma-band phase-coherence. *Journal of Neuroscience*, *32*(46), 16172-16180.

Guilford, J. P. (1967). The nature of human intelligence.

Halsband, U., Ito, N., Tanji, J., & Freund, H.-J. (1993). The role of premotor cortex and the supplementary motor area in the temporal control of movement in man. *Brain*, *116*(1), 243-266.

Hamm, A. O., Cuthbert, B. N., Globisch, J., & Vaitl, D. (1997). Fear and the startle reflex: Blink modulation and autonomic response patterns in animal and mutilation fearful subjects. *Psychophysiology*, *34*(1), 97-107.

Hanakawa, T., Dimyan, M. A., & Hallett, M. (2008). The representation of blinking movement in cingulate motor areas: a functional magnetic resonance imaging study. *Cerebral Cortex*, *18*(4), 930-937.

Hebb, D. O. (1968). Concerning imagery. *Psychological review*, *75*(6), 466.

Higgins, S. J., Irwin, D. E., Wang, R. F., & Thomas, L. E. (2009). Visual direction constancy across eyeblinks. *Attention, Perception, & Psychophysics*, 1607-1617.

Himebaugh, N. L., Begley, C. G., Bradley, A., & Wilkinson, J. A. (2009). Blinking and tear break-up during four visual tasks. *Optometry and Vision Science*, *86*(2), E106-E114.

Hol, K., Koene, A., & van Ee, R. (2003). Attention-biased multi-stable surface perception in three-dimensional structure-from-motion. *Journal of Vision*, *3*(7), 3-3.

Hommel, B. (2015). Between persistence and flexibility: The Yin and Yang of action control. In *Advances in motivation science* (Vol. 2, pp. 33-67). Elsevier.

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.

Hupé, J M, & Rubin, N. (2004). The oblique plaid effect. *Vision Research*, 489:500.

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*, 681-698.

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.

Jang, Y.-S., Ryu, S.-A., & Park, K.-C. (2011). Analysis of P300 Related Target Choice in Oddball Paradigm. *Journal of information and communication convergence engineering*, *9*(2), 125-128.

Jenkins, I. H., Jahanshahi, M., Jueptner, M., Passingham, R. E., & Brooks, D. J. (2000). Self-initiated versus externally triggered movements: II. The effect of movement predictability on regional cerebral blood flow. *Brain*, *123*(6), 1216-1228.

Johansson, R., Holsanova, J., Dewhurst, R., & Holmqvist, K. (2012). Eye movements during scene recollection have a functional role, but they are not reinstatements of those produced

during encoding. *Journal of Experimental Psychology: Human perception and performance*, *38*(5), 1289.

Johansson, R., & Johansson, M. (2014). Look here, eye movements play a functional role in memory retrieval. *Psychological science*, *25*(1), 236-242.

Kal, E., Van Der Kamp, J., Houdijk, H., Groet, E., Van Bennekom, C., & Scherder, E. (2015). Stay focused! The effects of internal and external focus of attention on movement automaticity in patients with stroke. *PloS one*, *10*(8), e0136917.

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.

Kanabus, M., Szelag, E., Rojek, E., & Poppel, E. (2002). Temporal order judgement for auditory and visual stimuli. *Acta neurobiologiae experimentalis*, *62*(4), 263-270.

Karson, C. N. (1983). Spontaneous eye-blink rates and dopaminergic systems. *Brain*, *106*(3), 643-653.

Karson, C. N. (1988). Physiology of normal and abnormal blinking. *Advances in neurology*, *49*, 25-37.

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.

Karson, C. N., Burns, R. S., LeWitt, P. A., Foster, N. L., & Newman, R. P. (1984). Blink rates and disorders of movement. *Neurology*, *34*(5), 677-677.

Kassner, M., Patera, W., & Bulling, A. (2014). Pupil: an open source platform for pervasive eye tracking and mobile gaze-based interaction. Proceedings of the 2014 ACM international joint conference on pervasive and ubiquitous computing: Adjunct publication,

Kawashima, R., Roland, P. E., & O'sullivan, B. T. (1995). Functional anatomy of reaching and visuomotor learning: a positron emission tomography study. *Cerebral Cortex*, *5*(2), 111-122.

Kern, M., Schulze-Bonhage, A., & Ball, T. (2021). Blink-and saccade-related suppression effects in early visual areas of the human brain: Intracranial EEG investigations during natural viewing conditions. *NeuroImage*, *230*, 117788.

Kienitz, R., Cox, M. A., Dougherty, K., Saunders, R. C., Schmiedt, J. T., Leopold, D. A., Maier, A., & Schmid, M. C. (2021). Theta, but not gamma oscillations in area V4 depend on input from primary visual cortex. *Current Biology*, *31*(3), 635-642. e633.

Kim, J. J., & Thompson, R. E. (1997). Cerebellar circuits and synaptic mechanisms involved in classical eyeblink conditioning. *Trends in neurosciences*, *20*(4), 177-181.

Kleiner, M., Brainard, D., & Pelli, D. (2007a). "What's new in Psychtoolbox-3". *Perception*, 1-16.

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

Kleiner, M., Brainard, D., & Pelli, D. (2007b). What’s new in Psychtoolbox-3? Perception 36 ECVP Abstract Supplement. *PloS one*.

Kleiner , M., Brainard , D., & Pelli , D. (2007). “What’s new in Psychtoolbox-3?”. *Perception 36 ECVP Abstract Supplement*.

Kobald, O. S., Wascher, E., Heppner, H., & Getzmann, S. (2019). Eye blinks are related to auditory information processing: evidence from a complex speech perception task. *Psychological Research*, 1281-1291.

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.

Kohler, A., Haddad, L., Singer, W., & Muckli, L. (2008). Deciding what to see: The role of intention and attention in the perception of apparent motion. *Vision research*, *48*(8), 1096-1106.

Kondo, H. M., Kitagawa, N., Kitamura, M. S., Koizumi, A., Nomura, M., & Kashino, M. (2012). Separability and commonality of auditory and visual bistable perception. *Cerebral Cortex*, *22*(8), 1915-1922.

Kugelberg, E. (1952). [Facial reflexes]. *Brain*, *75*(3), 385-396. https://doi.org/10.1093/brain/75.3.385

Kühn, S., Ritter, S. M., Müller, B. C., Van Baaren, R. B., Brass, M., & Dijksterhuis, A. (2014). The importance of the default mode network in creativity—a structural MRI study. *The Journal of Creative Behavior*, *48*(2), 152-163.

Kulisevsky, J., Pagonabarraga, J., & Martinez-Corral, M. (2009). Changes in artistic style and behaviour in Parkinson's disease: dopamine and creativity. *Journal of neurology*, *256*(5), 816-819.

Kuo, C.-Y., & Yeh, Y.-Y. (2016). Sensorimotor-conceptual integration in free walking enhances divergent thinking for young and older adults. *Frontiers in psychology*, *7*, 1580.

Ladd, C. O., Plotsky, P. M., & Davis, M. (2000). Startle response. *George Fink. Encyclopedia of Stress.(ed)*, *3*.

Lakoff, G., & Johnson, M. (1980). Metaphor we live by. *Chicago/London*.

Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Current Biology*, *22*(11), 1000-1004.

Laubrock, J., Engbert, R., & Kliegl, R. (2008). Fixational eye movements predict the perceived direction of ambiguous apparent motion. *Journal of Vision* 1–17.

Lawrence, G. P., Gottwald, V. M., Hardy, J., & Khan, M. A. (2011). Internal and external focus of attention in a novice form sport. *Research quarterly for exercise and sport*, *82*(3), 431-441.

Lawrence, M. S., & Redmond Jr, D. E. (1991). MPTP lesions and dopaminergic drugs alter eye blink rate in African green monkeys. *Pharmacology Biochemistry and Behavior*, *38*(4), 869-874.

Leakey, D., Sayers, B. M., & Cherry, C. (1958). Binaural Fusion of Low-and High-Frequency Sounds. *The Journal of the Acoustical Society of America*, *30*(3), 222-222.

Lenoble, Q., Janssen, S. M., & El Haj, M. (2019). Don't stare, unless you don't want to remember: Maintaining fixation compromises autobiographical memory retrieval. *Memory*, *27*(2), 231-238.

Leopold, D. A., & Logothetis, N. K. (1999). Multistable phenomena: changing views in perception. *Trends in cognitive sciences*, *3*(7), 254-264.

Leopold, D. A., Wilke, M., Maier, A., & Logothetis, N. K. (2002). Stable perception of visually ambiguous patterns. *Nature neuroscience*, *5*(6), 605-609.

Leung, A. K.-y., Kim, S., Polman, E., Ong, L. S., Qiu, L., Goncalo, J. A., & Sanchez-Burks, J. (2012). Embodied metaphors and creative "acts". *Psychological science*, *23*(5), 502-509.

Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013a). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, 764-766.

Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013b). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of experimental social psychology*, *49*(4), 764-766.

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.

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.

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.

Long, G. M., & Toppino, T. C. (2004). Enduring interest in perceptual ambiguity: alternating views of reversible figures. *Psychological bulletin*, *130*(5), 748.

Lundstrom, B. N., Petersson, K. M., Andersson, J., Johansson, M., Fransson, P., & Ingvar, M. (2003). Isolating the retrieval of imagined pictures during episodic memory: activation of the left precuneus and left prefrontal cortex. *NeuroImage*, *20*(4), 1934-1943.

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG-and MEG-data. *Journal of neuroscience methods*, *164*(1), 177-190.

Martindale, C. (1999). Biological bases of creativity.

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.

Mednick, S. (1962). The associative basis of the creative process. *Psychological review*, *69*(3), 220.

Memmert, D. (2007). Can creativity be improved by an attention-broadening training program? An exploratory study focusing on team sports. *Creativity research journal*, *19*(2-3), 281-291.

Mendelsohn, G. A., & Griswold, B. B. (1964). Differential use of incidental stimuli in problem solving as a function of creativity. *The Journal of Abnormal and Social Psychology*, *68*(4), 431.

Mendelsohn, G. A., & Griswold, B. B. (1966). Assessed creative potential, vocabulary level, and sex as predictors of the use of incidental cues in verbal problem solving. *Journal of Personality and Social Psychology*, *4*(4), 423.

Michalareas, G., Vezoli, J., Van Pelt, S., Schoffelen, J.-M., Kennedy, H., & Fries, P. (2016). Alpha-beta and gamma rhythms subserve feedback and feedforward influences among human visual cortical areas. *Neuron*, *89*(2), 384-397.

Miwa, H., Kagohashi, M., Noda, K., Miyashita, N., Tanaka, S., & Mizuno, Y. (2001). Eyelid motor extinction. *Journal of neurology*, *248*(4), 343.

Miwa, H., Nohara, C., Hotta, M., Shimo, Y., & Amemiya, K. (1998). Somatosensory-evoked blink response: investigation of the physiological mechanisms. *Brain: a journal of neurology*, *121*(2), 281-291.

Moraru, A., Memmert, D., & van der Kamp, J. (2016). Motor creativity: the roles of attention breadth and working memory in a divergent doing task. *Journal of Cognitive Psychology*, *28*(7), 856-867.

Murali, S., & Händel, B. (2021). The latency of spontaneous eye blinks marks relevant visual and auditory information processing. *Journal of Vision*, *21*(6), 7-7. https://doi.org/10.1167/jov.21.6.7

Murali, S., & Händel, B. (2022). Motor restrictions impair divergent thinking during walking and during sitting. *Psychological research*, 1-14.

Murphy, B. J., Kowler, E., & Steinman, R. M. (1975). Slow oculomotor control in the presence of moving backgrounds. *Vision Research*, *15*(11), 1263-1268.

Nagano-Saito, A., Liu, J., Doyon, J., & Dagher, A. (2009). Dopamine modulates default mode network deactivation in elderly individuals during the Tower of London task. *Neuroscience letters*, *458*(1), 1-5.

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.

Nakatani, H., Orlandi, N., & van Leeuwen, C. (2011). Precisely timed oculomotor and parietal EEG activity in perceptual switching. *Cogn Neurodyn*, 399–409.

Nakatani, H., & Van Leeuwen, C. (2005). Individual differences in perceptual switching rates; the role of occipital alpha and frontal theta band activity. *Biological Cybernetics*, *93*(5), 343-354.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive psychology*, *9*(3), 353-383.

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.

Nijstad, B., De Dreu, C., Rietzschel, E., & Baas, M. (2010). The Dual Pathway to Creativity Model: Creative Ideation as a Function of Flexibility and Persistence. *European Review of Social Psychology*, *21*, 34-77. https://doi.org/10.1080/10463281003765323

Noest, A., Van Ee, R., Nijs, M., & Van Wezel, R. (2007). Percept-choice sequences driven by interrupted ambiguous stimuli: a low-level neural model. *Journal of Vision*, *7*(8), 10-10.

Norn, M. (1969). Desiccation of the precorneal film: I. Corneal wetting-time. *Acta ophthalmologica*, *47*(4), 865-880.

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.

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.

Ohdra, H. (1995). Analysis of eyeblink activity during self-referent information processing in mild depression. *Perceptual and motor skills*, *81*(3_suppl), 1219-1229.

Ohdra, H. (1995). Analysis of eyeblink activity during self-referent information processing in mild depression. *Perceptual and Motor Skills*.

Ohira, H. (1996). Eyeblink activity in a word-naming task as a function of semantic priming and cognitive load. *Perceptual and motor skills*, *82*(3), 835-842.

Oppezzo, M., & Schwartz, D. L. (2014). Give your ideas some legs: The positive effect of walking on creative thinking. *Journal of experimental psychology: learning, memory, and cognition*, *40*(4), 1142.

Otero-Millan, J., Macknik, S. L., & Martinez-Conde, S. (2012). Microsaccades and Blinks Trigger Illusory Rotation in the "Rotating Snakes" Illusion. *The Journal of Neuroscience,*, 6043– 6051.

Ottemiller, D. D., Elliott, C. S., & Giovannetti, T. (2014). Creativity, overinclusion, and everyday tasks. *Creativity research journal*, *26*(3), 289-296.

Overend, W. (1896). Preliminary note on a new cranial reflex. *The Lancet*, *147*(3784), 619.

Paffen, C., & Alais, D. (2011). Attentional modulation of binocular rivalry. *Frontiers in Human Neuroscience*, *5*, 105.

Paffen, C. L., & Van der Stigchel, S. (2010). Shifting spatial attention makes you flip: Exogenous visual attention triggers perceptual alternations during binocular rivalry. *Attention, Perception, & Psychophysics*, *72*(5), 1237-1243.

Pastukhov, A., Vonau, V., Stonkute, S., & Braun, J. (2013). Spatial and temporal attention revealed by microsaccades. *Vision Research* 45–57.

Patel, P., Lamar, M., & Bhatt, T. (2014). Effect of type of cognitive task and walking speed on cognitive-motor interference during dual-task walking. *Neuroscience*, *260*, 140-148.

Pearce, J. (2008). Observations on the blink reflex. *European neurology*, *59*(3-4), 221-223.

Pelli, D. D. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 437-442.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision* 437-442.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial vision*, *10*(4), 437-442.

Peterson, D. A., & Sejnowski, T. J. (2017). A dynamic circuit hypothesis for the pathogenesis of blepharospasm. *Frontiers in computational neuroscience*, *11*, 11.

Pola, J., Wyatt, H. J., & Lustgarten, M. (1995). Visual fixation of a target and suppression of optokinetic nystagmus: effects of varying target feedback. *Vision Research*, 1079-1087.

Polskaia, N., Richer, N., Dionne, E., & Lajoie, Y. (2015). Continuous cognitive task promotes greater postural stability than an internal or external focus of attention. *Gait & posture*, *41*(2), 454-458.

Ponder, E., & Kennedy, W. (1927). On the act of blinking. *Quarterly journal of experimental physiology: Translation and integration*, *18*(2), 89-110.

Poulton, E. C., & Gregory, R. L. (1952). Blinking during visual tracking. *Quarterly Journal of Experimental Psychology*, *4*(2), 57-65.

Pressnitzer, D., & Hupé, J.-M. (2005). Is auditory streaming a bistable percept. Forum Acusticum, Budapest,

Pullman, S., Watts, R., Juncos, J., Chase, T., & Sanes, J. (1988). Dopaminergic effects on simple and choice reaction time performance in Parkinson's disease. *Neurology*, *38*(2), 249-249.

Radel, R., Davranche, K., Fournier, M., & Dietrich, A. (2015). The role of (dis) inhibition in creativity: Decreased inhibition improves idea generation. *Cognition*, *134*, 110-120.

Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences*, *98*(2), 676-682.

Ranti, C., Jones, W., Klin, A., & Shultz, S. (2020). Blink rate patterns provide a reliable measure of individual engagement with scene content. *Scientific reports*, *10*(1), 1-10.

Re, D., Inbar, M., Richter, C. G., & Landau, A. N. (2019). Feature-Based Attention Samples Stimuli Rhythmically. *Current Biology* 693-699.

Rihet, P., Possamaï, C.-A., Micallef-Roll, J., Blin, O., & Hasbroucq, T. (2002). Dopamine and human information processing: a reaction-time analysis of the effect of levodopa in healthy subjects. *Psychopharmacology*, *163*(1), 62-67.

Runco, M. A., & Acar, S. (2012). Divergent thinking as an indicator of creative potential. *Creativity research journal*, *24*(1), 66-75.

Salvi, C., & Bowden, E. M. (2016). Looking for creativity: Where do we look when we look for new ideas? *Frontiers in psychology*, *7*, 161.

Salvi, C., Bricolo, E., Franconeri, S. L., Kounios, J., & Beeman, M. (2015). Sudden insight is associated with shutting out visual inputs. *Psychonomic bulletin & review*, *22*(6), 1814-1819.

Sax, K. W., & Strakowski, S. M. (1998). Enhanced behavioral response to repeated d-amphetamine and personality traits in humans. *Biological psychiatry*, *44*(11), 1192-1195.

Schiller, P. (1933). Stoboskopische Alternativbewegungen [Stroboscopic alternative motion]. *Psychologische Forschung*, *17*, 179-214.

Schluppeck, D., & Engel, S. A. (2010). Oblique effect in human MT+ follows pattern rather than component motion. *Journal of Vision*, 282-282.

Schölvinck, M. L., & Rees, G. (2009). Attentional influences on the dynamics of motion-induced blindness. *Journal of Vision*, *9*(1), 38-38.

Sescousse, G., Ligneul, R., van Holst, R. J., Janssen, L. K., de Boer, F., Janssen, M., Berry, A. S., Jagust, W. J., & Cools, R. (2018). Spontaneous eye blink rate and dopamine synthesis capacity: preliminary evidence for an absence of positive correlation. *European Journal of Neuroscience*, *47*(9), 1081-1086.

Shin, Y. S., Chang, W.-d., Park, J., Im, C.-H., Lee, S. I., Kim, I. Y., & Jang, D. P. (2015). Correlation between inter-blink interval and episodic encoding during movie watching. *PloS one*, *10*(11), e0141242.

Shultz, S., Klin, A., & Jones, W. (2011). Inhibition of eye blinking reveals subjective perceptions of stimulus salience. *Proceedings of the National Academy of Sciences*, *108*(52), 21270-21275.

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.

Slepian, M. L., & Ambady, N. (2012). Fluid movement and creativity. *Journal of Experimental Psychology: General*, *141*(4), 625.

Slepian, M. L., & Ambady, N. (2014). Simulating sensorimotor metaphors: Novel metaphors influence sensory judgments. *Cognition*, *130*(3), 309-314.

Smilek, D., Carriere, J. S., & Cheyne, J. A. (2010). Out of mind, out of sight: eye blinking as indicator and embodiment of mind wandering. *Psychological science*, *21*(6), 786-789.

Spyropoulos, G., Bosman, C. A., & Fries, P. (2018). A theta rhythm in macaque visual cortex and its attentional modulation. *Proceedings of the National Academy of Sciences*, *115*(24), E5614-E5623.

Sterling, L. (2013). Eyeblink Reflexes. In F. R. Volkmar (Ed.), *Encyclopedia of Autism Spectrum Disorders* (pp. 1207-1207). Springer New York. https://doi.org/10.1007/978-1-4419-1698-3_639

Stonkute, S., Braun, J., & Pastukhov, A. (2012). The role of attention in ambiguous reversals of structure-from-motion. *PloS one*, *7*(5), e37734.

Strakowski, S. M., & Sax, K. W. (1998). Progressive behavioral response to repeated d-amphetamine challenge: further evidence for sensitization in humans. *Biological psychiatry*, *44*(11), 1171-1177.

Strakowski, S. M., Sax, K. W., Setters, M. J., & Keck Jr, P. E. (1996). Enhanced response to repeated d-amphetamine challenge: evidence for behavioral sensitization in humans. *Biological psychiatry*, *40*(9), 872-880.

Sweeney, D. F., Millar, T. J., & Raju, S. R. (2013). Tear film stability: a review. *Experimental eye research*, *117*, 28-38.

Taylor, J., Elsworth, J., Lawrence, M., Sladek Jr, J., Roth, R., & Redmond Jr, D. (1999). Spontaneous blink rates correlate with dopamine levels in the caudate nucleus of MPTP-treated monkeys. *Experimental neurology*, *158*(1), 214-220.

Troncoso, X. G., Macknik, S. L., Otero-Millan, J., & Martinez-Conde, S. (2008). Microsaccades drive illusory motion in the Microsaccades drive illusory motion in the. *PNAS*, 16033–16038.

Ueda, Y., Tominaga, A., Kajimura, S., & Nomura, M. (2016). Spontaneous eye blinks during creative task correlate with divergent processing. *Psychological research*, *80*(4), 652-659.

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.

van Dam, L. C., & van Ee, R. (2006). The role of saccades in exerting voluntary control in perceptual and binocular rivalry. *Vision research*, *46*(6-7), 787-799.

van Dam, L. C. J., & van Ee, R. (2005). The role of (micro)saccades and blinks in perceptual bi-stability from slant rivalry. *Vision Research*, 2417–2435.

van Dam, L. C. J., & van Ee, R. (2006). The role of saccades in exerting voluntary control in perceptual and binocular rivalry. *Vision Research*, 787–799.

Van Kerkoerle, T., Self, M. W., Dagnino, B., Gariel-Mathis, M.-A., Poort, J., Van Der Togt, C., & Roelfsema, P. R. (2014). Alpha and gamma oscillations characterize feedback and feedforward processing in monkey visual cortex. *Proceedings of the National Academy of Sciences*, *111*(40), 14332-14341.

van Koningsbruggen, M. G., Peelen, M. V., Davies, E., & Rafal, R. D. (2012). Neural control of voluntary eye closure: a case study and an fMRI investigation of blinking and winking. *Behavioural neurology*, *25*(2), 103-109.

Van Noorden, L. S. (1975). Temporal coherence in the perception of tone sequences. *PhD thesis, Eindhoven University of Technology*.

Veltman, J., & Gaillard, A. (1998). Physiological workload reactions to increasing levels of task difficulty. *Ergonomics*, *41*(5), 656-669.

Veltman, J. A., & Gaillard, A. W. K. (1998). Physiological workload reactions to increasing levels of task. *Ergonomics* 656 - 669.

Volkmann, F. C. (1986). Human visual suppression. *Vision research*, *26*(9), 1401-1416.

Volkmann, F. C., Riggs, L. A., & Moore, R. K. (1980). Eyeblinks and visual suppression. *Science*, *207*(4433), 900-902.

von Cramon, D., & Schuri, U. (1980). Blink frequency and speech motor activity. *Neuropsychologia*, *18*(4-5), 603-606.

von Schiller, P. (1933). Stoboskopische Alternativbewegungen. *Psychologische Forschung 17:179–214*, 179–214.

Wallach, H. (1935). Über visuell wahrgenommene Bewegungsrichtung. *Psychologische Forschung*, *20*(1), 325-380.

Wallach, H. (1935). Über visuell wahrgenommene Bewegungsrichtung. *Psychologische Forschung*, 325–380.

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.

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*, 1207-1218.

Wuerger, S., Shapley, R., & Rubin, N. (1996). "On the visually perceived direction of motion" by Hans Wallach: 60 years later. *Perception*, *25*(11), 1317-1367.

Wulf, G., Dufek, J. S., Lozano, L., & Pettigrew, C. (2010). Increased jump height and reduced EMG activity with an external focus. *Human movement science*, *29*(3), 440-448.

Wulf, G., Höß, M., & Prinz, W. (1998). Instructions for Motor Learning: Differential Effects of Internal Versus External Focus of Attention. *Journal of Motor Behavior*, *30*(2), 169-179. https://doi.org/10.1080/00222899809601334

Wulf, G., Lauterbach, B., & Toole, T. (1999). The learning advantages of an external focus of attention in golf. *Research quarterly for exercise and sport*, *70*(2), 120-126.

Xing, D., Shen, Y., Burns, S., Yeh, C.-I., Shapley, R., & Li, W. (2012). Stochastic generation of gamma-band activity in primary visual cortex of awake and anesthetized monkeys. *Journal of Neuroscience*, *32*(40), 13873-13880a.

Yoon, H. W., Chung, J.-Y., Song, M.-S., & Park, H. (2005). Neural correlates of eye blinking; improved by simultaneous fMRI and EOG measurement. *Neuroscience letters*, *381*(1-2), 26-30.

Zabelina, D. L., Colzato, L., Beeman, M., & Hommel, B. (2016). Dopamine and the creative mind: Individual differences in creativity are predicted by interactions between dopamine genes DAT and COMT. *PloS one*, *11*(1), e0146768.

Zametkin, A. J., Stevens, J. R., & Pittman, R. (1979). Ontogeny of spontaneous blinking and of habituation of the blink reflex. *Annals of Neurology: Official Journal of the American Neurological Association and the Child Neurology Society*, *5*(5), 453-457.

Zhang, W., Sjoerds, Z., & Hommel, B. (2020). Metacontrol of human creativity: The neurocognitive mechanisms of convergent and divergent thinking. *NeuroImage*, *210*, 116572.

Zhou, Y., Zhang, Y., Hommel, B., & Zhang, H. (2017). The Impact of Bodily States on Divergent Thinking: Evidence for a Control-Depletion Account [Original Research]. *Frontiers in psychology*, *8*(1546). https://doi.org/10.3389/fpsyg.2017.01546

Zold, C. L., & Shuler, M. G. H. (2015). Theta oscillations in visual cortex emerge with experience to convey expected reward time and experienced reward rate. *Journal of Neuroscience*, *35*(26), 9603-9614.

Zuber, B. L., Stark, L., & Cook, G. (1965). Microsaccades and the velocity–amplitude relationship for saccadic eye movements. *Science*, 1459-1460.

Appendix

A. Curriculum vitae

B. Acknowledgements

I would first like to thank my primary supervisor, Dr. Barbara Händel for giving me the opportunity to work on this project and for her support and encouragement throughout my PhD. Thank you especially for all the fruitful discussions, suggestions and the open and transparent space to explore my own scientific ideas. And of course, thank you for the much needed support and motivation during the pandemic.

I would also like to thank my second supervisor Prof. Dr. Wilfried Kunde, for his guidance and advice during the course of my PhD. Thank you for all the great input that you have provided during our meetings and seminars. Thank you also to Prof. Dr. Charlotte Förster for agreeing to be my third supervisor. I am very grateful for the expertise, great discussions and useful input that I have received from you during our thesis advisory meetings.

Of course, a big thank you also goes out to my research group and colleagues, Mareike Brych, Liyu Cao and Xinyu Chen for the wonderful working atmosphere and for the useful discussions, input and help that you have provided me over the years. I would also like to express my gratitude towards my colleagues at the Institute of Psychology III for their help and scientific input during the course of my PhD and especially during the seminars.

Finally I would like to thank my family; my parents, N. Murali and Vasanthi Murali, my sister, Ranjani and my husband, Balaji, for their unconditional love, support and encouragement. Thank you for always being there for me, believing in me and encouraging me to fulfill all my goals.

C. Statement of individual author contributions

Publication (complete reference): Murali, S., & Händel, B. (2021). The latency of spontaneous eye blinks marks relevant visual and auditory information processing. Journal of Vision, 21(6), 7-7.					
Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	SM, BH				
Data Collection	SM	BH			
Data Analysis and Interpretation	SM	BH			
Manuscript Writing Writing of Introduction Writing of Materials & Methods Writing of Discussion Writing of First Draft	 SM SM SM SM	 BH BH BH BH			

Explanations (if applicable):

Publication (complete reference): Brych, M., Murali, S., & Händel, B. (2021). The role of blinks, microsaccades and their retinal consequences in bistable motion perception. Frontiers in psychology, 12.					
Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	MB,SM BH				
Data Collection	MB, SM	BH			
Data Analysis and Interpretation	MB, SM	BH			

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

Explanations (if applicable): I, Supriya Murali and Mareike Brych are shared first authors

Publication (complete reference): Murali, S., & Händel, B. (2022). Motor restrictions impair divergent thinking during walking and during sitting. Psychological research, 1-14					
Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	SM	BH			
Data Collection	SM	BH			
Data Analysis and Interpretation	SM	BH			
Manuscript Writing					
Writing of Introduction	SM	BH			
Writing of Materials & Methods	SM	BH			
Writing of Discussion	SM	BH			
Writing of First Draft	SM	BH			

Explanations (if applicable):

Publication (complete reference): Murali, S., & Händel, B. (2021) Spontaneous eye blinks modulate the probability of a perceptual reinterpretation during visual and auditory ambiguity					
Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design	SM	BH			

Methods Development					
Data Collection	SM	BH			
Data Analysis and Interpretation	SM	BH			
Manuscript Writing					
Writing of Introduction	SM	BH			
Writing of Materials & Methods	SM	BH			
Writing of Discussion	SM	BH			
Writing of First Draft	SM	BH			

Explanations (if applicable): This is an unpublished manuscript

Publication (complete reference): Murali, S., Agayby B., Schmid, M., & Händel, B. (2021). Qualitative difference in blink related modulation of V1 activity for different attentive and stimulation states.					
Participated in	**Author Initials,** Responsibility decreasing from left to right				
Study Design Methods Development	BA MS BH SM				
Data Collection	BA	MS			
Data Analysis and Interpretation	SM	BH	BA MS		
Manuscript Writing					
Writing of Introduction	SM	BH	BA MS		
Writing of Materials & Methods	SM	BH	BA	MS	
Writing of Discussion	SM, BH	BA, MS			
Writing of First Draft	SM	BH			

Explanations (if applicable): This is an unpublished manuscript. The title of this manuscript has been altered slightly in the thesis.

The doctoral researcher confirms that she/he 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.

Supriya Murali	18.01.2022	Nürnberg	
Doctoral Researcher's Name	Date	Place	Signature
Dr. Barbara Händel	18.01.2022	Buchen	
Primary Supervisor's Name	Date	Place	Signature

Statement of individual author contributions (Figures)

Publication (complete reference): Murali, S., & Händel, B. (2021). The latency of spontaneous eye blinks marks relevant visual and auditory information processing. Journal of Vision, 21(6), 7-7.					
Figure	**Author Initials,** Responsibility decreasing from left to right				
1	SM	BH			
2	SM	BH			
3	SM	BH			
4	SM	BH			
5	SM	BH			
6	SM	BH			
7	SM	BH			
8	SM	BH			
9	SM	BH			
10	SM	BH			
11	SM	BH			

Explanations (if applicable):

Publication (complete reference):): Brych, M., Murali, S., & Händel, B. (2021). The role of blinks, microsaccades and their retinal consequences in bistable motion perception. Frontiers in psychology, 12.					
Figure	**Author Initials,** Responsibility decreasing from left to right				
1	MB	SM	BH		
2	MB	SM	BH		
3	MB	SM	BH		
4	MB	SM	BH		
5	MB	SM	BH		
6	MB	SM	BH		

Explanations (if applicable): *This is a shared first author publication

Publication (complete reference): Murali, S., & Händel, B. (2022). Motor restrictions impair divergent thinking during walking and during sitting. Psychological research, 1-14.					
Figure	**Author Initials,** Responsibility decreasing from left to right				
1	SM	BH			
2	SM	BH			
3	SM	BH			
4	SM	BH			
5	SM	BH			
6	SM	BH			

Explanations (if applicable):

Publication (complete reference): Murali, S., & Händel, B. (in preparation) Spontaneous eye blinks modulate the probability of a perceptual reinterpretation during visual and auditory ambiguity					
Figure	**Author Initials,** Responsibility decreasing from left to right				
1	SM	BH			
2	SM	BH			
3	SM	BH			
4	SM	BH			
5	SM	BH			
6	SM	BH			
7	SM	BH			
8	SM	BH			
9	SM	BH			

Explanations (if applicable): This is an unpublished manuscript

Publication (complete reference): Murali, S., Agayby B., Schmid, M., & Händel, B. (in preparation). Qualitative difference in blink related modulation of V1 activity for different attentive and stimulation states.					
Figure	**Author Initials,** Responsibility decreasing from left to right				
1	SM	BH	BA	MS	
2	SM	BH	BA	MS	
3	SM	BH	BA	MS	
4	SM	BH	BA	MS	
5	SM	BH	BA	MS	
6	SM	BH	BA	MS	
7	SM	BH	BA	MS	
8	SM	BH	BA	MS	

Explanations (if applicable): This is an unpublished manuscript. The title of this manuscript has been slightly altered in the thesis.

I also confirm my primary supervisor's acceptance.

Supriya Murali

_____

Doctoral Researcher's Name Date Place Signature

D. Affidavit (Eidesstattliche Erklärung)

I hereby confirm that my thesis entitled „Understanding the function of spontaneous blinks by investigating internally and externally directed processes“ 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 „Eine Untersuchung zur Funktion spontaner Lidschläge durch die Differenzierung von extern und intern gerichteten Prozessen“ eigenständig, d.h. insbesondere selbständig 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