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DISSERTATION

The modulation of unconscious visual processing under interocular suppression by spatial attention

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2 AFC	two-alternative forced choice
ACC	anterior cingulate cortex
BCAN	Berlin Center for Advanced Neuroimaging
bCFS	breaking continuous flash suppression
BF	Bayes Factor
BOLD	blood oxygenation level-dependent
CFS	continuous flash suppression
CoA	cost of awareness
EEG	electroencephalography
EKP	ereigniskorrelierte Potentiale
ERP	event-related potential
FFA	fusiform face area
fMRI	functional magnetic resonance imaging
FOV	field of view
FWHM	full width at half maximum
GLM	general linear model
HRF	hemodynamic response function
Hz	Hertz
LOC	lateral occipital complex
MEG	magnetoencephalography
MNI	Montreal Neurological Institute
MPRAGE	magnetization-prepared rapid gradient-echo
min	minute

mm	millimeter
ms	millisecond
MVPA	multi-voxel pattern analysis
PAS	Perceptual Awareness Scale
PPA	parahippocampal place area
rm-ANOVA	repeated measures analysis of variance
ROI	region of interest
RT	reaction time
s	second
SEM	standard error of the mean
SPM	statistical parametric mapping
T	Tesla
TE	echo time
TI	inversion time
TR	repetition time

Abstract

1.1 Abstract (English)

Exploring the scope and limits of unconscious visual processing remains an intriguing but also an elusive challenge to this day. Numerous techniques have been introduced to investigate visual processing outside of awareness. Recently, a new interocular suppression method called Continuous Flash Suppression (CFS) has gained increasing interest in experimental psychology and cognitive neuroscience. Its potential to suppress stimuli from reaching awareness for an extended period of time makes it a powerful tool to explore visual perception under the limen of consciousness. Yet there are divergent, even conflicting reports regarding the extent of unconscious processing under CFS. To reconcile these findings, attention has been introduced as an explanatory factor that modulates the processing of a stimulus when it is suppressed by CFS. According to a previous study by Eo et al. (2016), the semantic information of words is boosted when attention is diverted away from the suppressed stimulus. Based on event-related potential (ERP) responses, they proposed that inattention attenuates interocular suppression and enables unconscious semantic processing, possibly reconciling conflicting evidence in the literature. The two studies presented within this dissertation aimed to further investigate the influence of attention on CFS and whether inattention facilitated unconscious higher-level processing in a neuroimaging and in a behavioural experiment.

The first study explored unconscious object categorization under CFS using functional magnetic resonance imaging (fMRI) and multi-voxel pattern analysis (MVPA). In a spatial cueing task, we tested whether the decodability of an object category increases when attention is diverted away from a suppressed stimulus. Our results provide no evidence for a significant modulation of CFS by attention. Additionally, we presented fully visible stimuli and observed that attention towards an object increased its decodability in higher visual areas.

The second study tested whether unconscious numerical processing occurs under inattention and CFS. In this behavioural priming experiment, we probed whether unattended number primes under CFS facilitated responses to a subsequent visible target number. We found no evidence for unconscious number priming and no modulation of CFS by attention. When we presented visible prime stimuli, we observed an inverse priming effect.

Our results indicate that there is no significant modulation of CFS by attention. This is in line with the increasing notion that high-level processing under CFS is strongly limited.

1.2 Abstract (Deutsch)

Das Erforschen der Möglichkeiten und Grenzen unbewusster visueller Verarbeitung ist bis heute eine faszinierende, aber auch schwer fassbare Herausforderung. Zahlreiche Techniken wurden eingeführt, um die visuelle Wahrnehmung außerhalb des Bewusstseins zu untersuchen. Erst kürzlich hat eine neue interokulare Suppressionsmethode, genannt Continuous Flash Suppression (CFS), zunehmendes Interesse in der experimentellen Psychologie und den kognitiven Neurowissenschaften gewonnen. Das Potential, visuelle Reize über einen längeren Zeitraum zu supprimieren, bevor sie das Bewusstsein erreichen, macht diese Methode zu einem vielversprechenden Werkzeug, um die visuelle Wahrnehmung unterhalb der Schwelle des Bewusstseins zu erforschen. Jedoch gibt es unterschiedliche, sogar widersprüchliche Berichte über das Ausmaß der unbewussten Verarbeitung unter CFS. Um diese Ergebnisse in Einklang zu bringen, wurde Aufmerksamkeit als erklärender Faktor angeführt, der die Verarbeitung eines Reizes moduliert, wenn dieser durch CFS unterdrückt wird. Laut einer früheren Studie von Eo et al. (2016) wird die semantische Information eines Reizes verstärkt, indem die Aufmerksamkeit vom unterdrückten Reiz abgelenkt wird. Basierend auf Messungen ereigniskorrelierter Potentiale (EKP) wurde vorgeschlagen, dass Unaufmerksamkeit die interokulare Suppression abschwächt und eine tiefere unbewusste semantische Verarbeitung ermöglicht. Dies könnte bisherige widersprüchliche Ergebnisse in der Literatur in Einklang bringen. Die beiden vorliegenden Studien dieser Arbeit zielten darauf ab, den Einfluss der Aufmerksamkeit auf CFS weiter zu erforschen und zu explorieren, ob Prozesse auf höherer Ebene unbewusst ablaufen können.

Die erste Studie untersuchte die unbewusste Kategorisierung von Objekten unter CFS mittels funktioneller Magnetresonanztomographie (fMRI) und Multi-voxel Pattern Analysis (MVPA). In einem Spatial-Cueing-Paradigma testeten wir, ob die Dekodierbarkeit der Objektkategorie aus neuronalen Aktivitätsmustern zunimmt, wenn die Aufmerksamkeit von einem unterdrückten Reiz abgelenkt wird. Unsere Ergebnisse liefern keine Hinweise auf eine signifikante Modulation von CFS durch Aufmerksamkeit. Darüber hinaus präsentierten wir vollständig sichtbare Reize und beobachteten, dass die Aufmerksamkeit auf ein Objekt seine Entschlüsselbarkeit in höheren visuellen Bereichen steigerte.

Die zweite Studie überprüfte, ob unbewusste numerische Verarbeitung unter Unaufmerksamkeit und CFS auftritt. In diesem behavioralen Priming-Experiment wurde untersucht, ob nicht attendierte Prime-Zahlen unter CFS Reaktionen auf eine nachfolgende Zielzahl erleichterten. Wir fanden keine Hinweise auf unbewusstes numerisches Priming und keine Modulation von CFS

durch Aufmerksamkeit. Wenn sichtbare Prime-Stimuli präsentiert wurden, beobachteten wir einen inversen Priming-Effekt.

Unsere Ergebnisse deuten darauf hin, dass es keine signifikante Modulation von CFS durch Aufmerksamkeit gibt und stimmen mit der zunehmenden Annahme überein, dass die Verarbeitung auf höherer Ebene unter CFS stark eingeschränkt ist.

2 Introduction

What is the extent of our unconscious minds and how do unconscious processes influence our behaviour? To date, these questions remain a hotly debated issue in the literature. A common example of how unconscious processes are claimed to navigate our decisions is the allegation made by James Vicary in the 1950s. He asserted that by displaying imperative sentences ("Drink Coca Cola" or "Eat popcorn") to the audience, sales of the advertised products would increase noticeably. The fascinating aspect about his postulation was the fact that these phrases were to be presented for a few milliseconds only – too briefly to be perceived consciously (Karremans et al., 2006). Since then, several studies about the scope and limits of unconscious visual processing as well as its investigation have been discussed in cognitive neuroscience and experimental psychology (Eriksen, 1960; Dixon, 1971; Holender, 1986; Sterzer et al., 2014; Dubois and Faivre, 2014; Breitmeyer, 2015; Hesselmann and Moors, 2015). The implemented methods that aim to study visual processing outside of awareness are as heterogeneous as their findings. Just recently, a technique called Continuous Flash Suppression (CFS) was introduced, which suppresses stimuli from reaching awareness by displaying high-contrast flashing masks to one eye and presenting a low-contrast image to the other eye. This method has led to divergent conclusions regarding the extent to which unconscious visual processing can occur. To reconcile these findings, attention may act as an explanatory factor, since a previous study indicated that attention plays a significant role in rendering visual stimuli invisible (Zhang et al., 2011; Brascamp and Blake, 2012; Ling and Blake, 2012; Eo et al., 2016). However, the evidence for this hypothesis is rather sparse. The following studies aimed to further explore how spatial attention modulates CFS by using behavioural and functional magnetic resonance imaging (fMRI) measurements.

2.1 Unconscious visual processing

Various models on how conscious perception differs from unconscious processes have been presumed to this day. It has been suggested that unconscious processes are not any different from conscious operations and that the cognitive executions of a conscious mind can also be conducted unconsciously (Chalmers, 1996). In contrast, some authors proposed that the mind cannot interpret visual information in a meaningful way when conscious access is lacking, limiting unconscious visual perception to the lowest perceptual levels (Perruchet and Vinter, 2002; Holender and Duscherer, 2004). In addition to these extreme positions, we can find a rather graded understanding of unconscious processing. According to previous studies, the processing of low-level features can occur under the limen of consciousness (Kanai et al., 2006; Lin and He, 2009; Shin et al., 2009;

Kaunitz et al., 2011). Furthermore, it has been suggested that high-level processes can be performed without awareness, e.g., the perception of faces (Sterzer et al., 2009) and tools (Fang and He, 2005; Almeida et al., 2008). One theory, the global workspace model by Dehaene et al. (2006), explains performances on a high cognitive level by distributed information units that can work independently. As specified by the model, consciousness acts as a mediator that links unitary, widespread presentations and generates a percept that we become aware of.

To explore unconscious visual processing in a typical psychophysical experiment, awareness of a stimulus, which is meant to be kept from reaching conscious access, is assessed by subjective and objective reports of the participant. Subjective visibility ratings attempt to capture visual awareness, e.g. in shape of rating scales as introduced by Sergent and Dehaene (2004) or Ramsøy and Overgaard (2004). Objective reports often include two-alternative forced choice (2 AFC) tasks that prompt the participant to decide between one answer or the other. Performances above a chance level of 50% serve as an indicator for, at least partially, conscious perception. In many cases, subjective and objective reports are both employed within one experiment, due to a phenomenon called “blindsight”, which describes a perceptual state where subjective and objective reports dissociate (Meeres and Graves, 1990; Lau and Passingham, 2006; Schwiedrzik et al., 2011). Nevertheless, measuring unconscious perception remains a complex issue, as subjective reports are prone to bias and therefore hard to control for (Malach, 2007; Seth et al., 2008; for a review see Sterzer et al., 2014). Moreover, Stein et al. (2021) recently demonstrated that claims on the extent of unconscious neuronal processing may differ with the applied measurement, i.e., subjective or objective awareness measures.

2.1.1 Subliminal, subconscious, conscious

The taxonomy to describe distinct states of visual perception needs to be considered carefully when talking about different stages of processing. Studies often discriminate between a subliminal and supraliminal state, which should rather be understood as two limiting points on a continuum than a binary classification. The subliminal state comprises all processes that occur under the limen of consciousness, ranging from low-level executions such as orientation or colour perception, to high-level functions, such as face perception. Supraliminal percepts exceed the threshold of reaching awareness, without necessarily describing where the limen is located (see Figure 1). The defining differentiation to subliminal states refers to what is perceived by an individual and is dependent on the implemented awareness measure. The global workspace model extended this taxonomy and introduced a distinction into subliminal, subconscious, and conscious states. According to Dehaene et al. (2006), the subliminal state describes mental processes that occur at the early stage of visual perception. Neural processing in the primary visual cortex is limited to low-level features like shape, orientation, or colour. Further up the visual pathway, we encounter more complex structures that enable us, for example, to assign a percept to a certain category, such as faces or scenes. If incoming information exceeds the early visual cortex, mental representations can be developed and distributed over the entire cortex. What isolates consciousness is the absence of attention that promotes these representations to a coherent percept in the neuronal network.

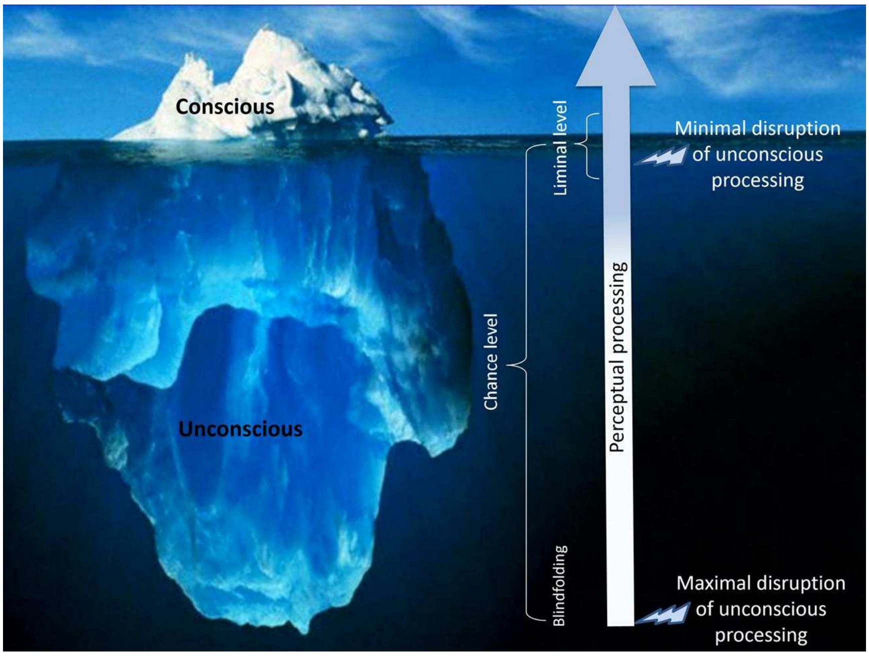

Figure 1. Illustration of awareness assessment under the limen of consciousness
Performance at chance level in objective awareness measures does not directly indicate whether unconscious processing of a suppressed stimulus occurs just under the limen of consciousness or whether the stimulus is completely disrupted from visual processing. If unconscious processes can be observed using one method but not when using another, it may simply be that the selected stimulus parameters pushed visual perception of the stimulus further away from the limen relative to the other (Peremen and Lamy, 2014).

2.1.2 The global workspace theory

The global workspace theory was first introduced by Dehaene et al. in 2006 and distinguishes three mental states of visual processing, namely the subliminal, the preconscious and the conscious state (Figure 2). It presumes that high-level mental operations are not restricted to a conscious mind per se, but rather implements the idea of disparate units that can operate independently and, importantly, unconsciously.

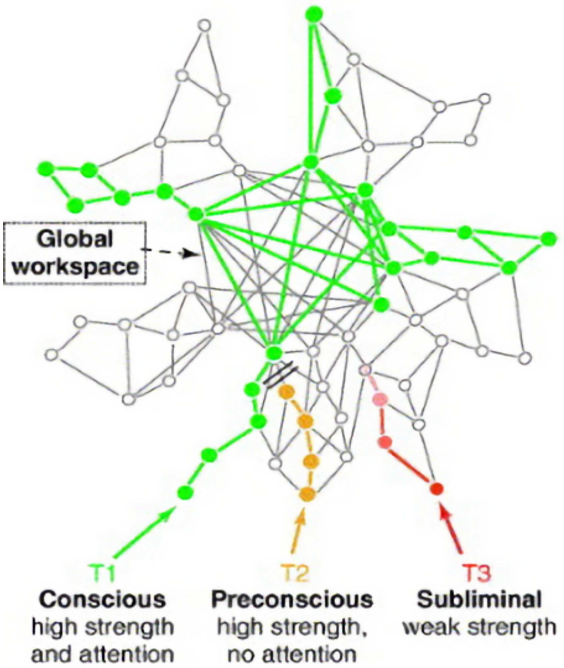

Figure 2. The global workspace model
Three distinct perceptual states as proposed by the global neuronal workspace model (Dehaene et al., 2006). Mental states are distinguished into a conscious state with access to conscious report, a preconscious state with no access to conscious report due to inattention, and an unconscious subliminal state in which activation remains weak and vanishes rapidly.

According to the model, conscious perception, what is referred to as "access to conscious report", depends on three distinct phenomena: vigilance, bottom-up processes and long-distance connections that connect perceptual units with high-level association cortices, including the prefrontal, parietal, and anterior cingulate cortex. Bottom-up information comprises the characteristics of a stimulus itself. For instance, sharp onsets or strong emotional content can alter signal intensity and lower the threshold to conscious perception of a stimulus. Once the signal strength meets a certain threshold, it can be amplified and integrated in a global neuronal network. If insufficient, the responses will diminish rapidly without entering large-scale networks of long-range axons. Weak activation and non-transition of stimulus information are the defining characteristics of the subliminal state. Preconscious percepts contain sufficient information to potentially promote a conscious percept. They are temporarily stored for a few hundred milliseconds, possibly within medium range connections, and upheld by resonant loops. Information in a preconscious state is accessible, but not yet reportable. Attention is the key factor that assembles distant presentations, and sparks intense activation as well as global synchrony. Entering this state enables us to perform intentional actions and allows information to be reported. The global workspace theory can successfully be applied to several phenomena in visual perception and allows a clear distinction between the influence of exogeneous and endogenous factors, i.e., characteristics of a stimulus and attentional amplification, respectively.

2.1.3 Suppression techniques

To study visual perception outside of awareness, several methods have been implemented to render stimuli invisible. As stated by Breitmeyer (2015), at least 24 "blinding" methods have been described in the literature. These include, among others, binocular rivalry (Blake and Logothetis, 2002; Tong et al., 2006; Lin and He, 2009), continuous flash suppression (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006), metacontrast suppression (Breitmeyer and Öğmen, 2006), attentional blink (Raymond et al., 1992), backward pattern masking (Breitmeyer and Öğmen, 2006; Almeida et al., 2013) and inattentional blindness (Mack and Rock, 1998). Each method involves specific characteristics regarding its effectiveness and duration to successfully keep stimuli from reaching awareness (see Figure 3).

Apart from the blinding method itself, one needs to consider the distinct features of a visual stimulus when drawing conclusions on the nature and mechanisms of unconscious perception (Breitmeyer, 2015). For instance, the orientation or size of a stimulus might survive interocular suppression (Blake and Fox, 1974), whereas the lexical or sematic features of words may not (Blake, 1988; Cave et al., 1998). In contrast, the semantic priming of words may still be present when other blinding methods such as sandwich masking or metacontrast masking are applied (Wernicke and Mattler, 2019).

It is crucial to keep in mind that suppression techniques enable us to explore informational content of unconscious processes and do not, importantly, reveal the underlying anatomical substrate per se. As the global workspace model implies, mental representations are not necessarily restricted to anatomical regions, since they are highly dependent on interconnections. Additionally, null findings, i.e., the absence of evidence for unconscious processing, do not automatically indicate that the examined mechanism cannot exist unconsciously. False-negative results can be a consequence of the suppression technique itself, for example when the suppression was too deep to allow further processing of the stimulus (Sterzer et al., 2014). Moreover, although present, one might exclude a significant effect due to weak neuronal signals that did not exceed the necessary threshold to be detected by the applied measurement (Sterzer et al., 2014).

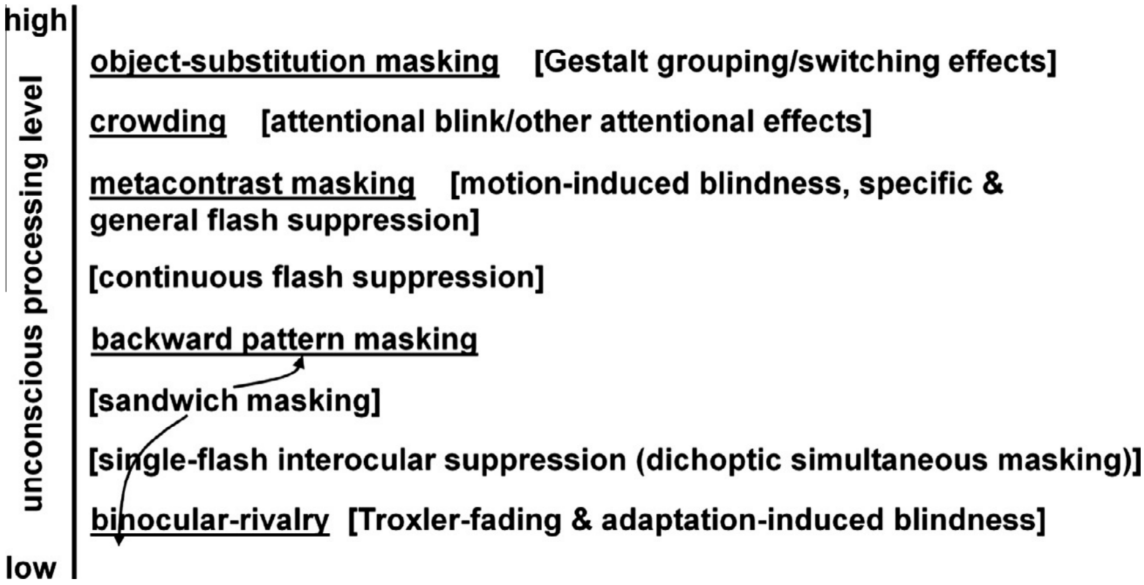

Figure 3. The functional hierarchy of psychophysical blinding methods
Psychophysical blinding methods and the related levels of unconscious stimulus processing as introduced by Breitmeyer (2015). Underlined methods are ranked by empirical findings. Rankings of methods in brackets are based on empirical and theoretical grounds but are rather speculative. Arrows emanating from "[sandwich masking]" indicate an intermediate ranking relative to higher and lower functional levels.

2.1.4 Interocular suppression

To render stimuli invisible, interocular suppression is induced by presenting dissimilar input to the two eyes – known as dichoptic stimulation. The umbrella term "Interocular Suppression" comprises the following methods: binocular rivalry (Wheatstone, 1838; Breese, 1909), flicker & switch rivalry (Logothetis et al., 1996), flash suppression (Wolfe, 1984), generalized flash suppression (Wilke et al., 2003), CFS (Tsuchiya and Koch, 2005), and breaking CFS (bCFS; Jiang et al., 2007; Stein et al., 2011).

Binocular rivalry occurs when each monocularly presented image is equally potent to compete for dominance, allowing perception to alternate between the two stimuli. One stimulus reaches awareness, whereas the other image remains unconscious. In comparison to many other blinding methods (see Breitmeyer, 2015), a substantial advantage of binocular rivalry is its potential to suppress images for several seconds and to explore unconscious processing under various viewing conditions (Kim and Blake, 2005; Baker, 2010). However, the dynamics of binocular rivalry are complex (Fox and Herrmann, 1967; Levelt, 1965; Blake and Logothetis, 2002; Paris et al., 2017; Skerswetat et al., 2018) and awareness of a stimulus can solely be assessed by subjective reports. In flash suppression paradigms (Wolfe, 1984), one of two competing stimuli is presented monocularly first, before suddenly becoming suppressed by displaying both rivalry stimuli to the two eyes. CFS, put simply, can be understood as an extended version of flash suppression. While a low-contrast target stimulus is displayed to one eye, high-contrast dynamic masks are flashed to the other eye, suppressing the low contrast stimulus for up to several minutes (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006). CFS has gained increasing interest in the study of unconscious visual processing, as its ability to keep images from reaching awareness for an extended period of time makes it a powerful tool to explore unconscious visual processes, not only by observing behaviour but also by means of brain imaging methods with poorer time resolution, like fMRI. In the bCFS paradigm, the measured time that a stimulus needs to overcome suppression by the CFS masks serves as an indicator for unconscious processing of the stimulus (Jiang et al., 2007; Stein et al., 2011; Stein and Sterzer, 2014; Gayet et al., 2014). The profound suppression of CFS can be achieved by highly dominant, dynamic patterns. These so-called Mondrian masks, which typically consist of circles and squares of different sizes and colours (originally inspired by the Dutch painter Piet Mondrian), are usually flashed to one eye at a frequency of 10 Hz and achieve a reliable suppression of stimuli for up to several seconds and even minutes (Tsuchiya and Koch, 2005; Tsuchiya et al., 2006). Numerous studies have investigated unconscious processing under CFS (Jiang et al., 2007; Yang et al., 2007; Mudrik et al., 2011; Stein et al., 2012; Gray et al., 2013; Moors et al., 2016; Hung et al., 2017; Rabagliati et al., 2018; Abir et al., 2018), aiming to explore various study fields like awareness (Yang et al., 2014; Lunghi et al., 2017), semantic priming (Zabelina et al., 2013; Peel et al., 2019), and object categorization (Fang and He, 2005; Sterzer et al., 2008; Almeida et al., 2008; Sakuraba et al., 2012).

2.1.5 Unconscious processing under interocular suppression

Behavioural studies have indicated that under CFS low-level features seem to be processed in the absence of awareness, e.g., contrast (Shin et al., 2009), motion (Kaunitz et al., 2011), or stimulus orientation (Kanai et al., 2006). On a more complex level, semantic word priming and numerical priming were observed by Sklar et al. (2012) when stimuli were rendered invisible by CFS. Kang et al. (2011) challenged this finding by showing that semantic information of lexical units could not be processed unconsciously. Yet, unconscious processing of eye gaze has been found under CFS (Chen and Yeh, 2012; Xu et al., 2018) as well as categorical information of tools (Almeida et al., 2008). However, the latter has been questioned by Hesselmann et al. (2016), who showed that the reported priming effects were more likely due to shape than to category. Examining binocular rivalry, Costello et al. (2009) reported unconscious semantic priming of words, which is in contrast to earlier work that did not find semantic priming effects (Zimba and Blake, 1983; Cave et al., 1998). Some authors have claimed that perceptual grouping is present under binocular rivalry (Kovács et al., 1996) and that rivalry depth increases along the two visual pathways (Nguyen et al., 2003).

Previous studies on neural processes of visual perception under interocular suppression have led to divergent findings regarding unconscious low-level and high-level processing (for reviews, see Tong et al. [2006] and Sterzer et al. [2014]). fMRI studies revealed that stimulus awareness is directly linked to activity patterns in the early visual cortex during binocular rivalry (Polonsky et al., 2000; Tong and Engel, 2001; Lee et al., 2007). Similarly, Yuval-Greenberg and Heeger (2013) found a significant modulation of neural activity in V1 by CFS, although it has been questioned whether visual awareness or attention drive this effect (Watanabe et al., 2011). Further studies found that visual information was present even in higher-visual cortices when stimuli were suppressed by CFS (Fang and He, 2005; Sterzer et al., 2008). In addition, emotional information seems to be processed under binocular rivalry, as indicated by the study of Williams et al. (2004), who reported a significant increase of neural activity in the amygdala when contrasting fearful versus neutral faces, which is in line with previous results of Pasley et al. (2004). Troiani et al. (2014) extended these findings by showing that emotional stimuli under binocular rivalry increased activity not only in the amygdala, but also in higher visual areas. However, these results failed to be replicated by Troiani and Schultz (2013), wherein stimuli were suppressed by CFS. This is consistent with previous work of Jiang and He (2006), which did not find emotional information of face stimuli in high-visual areas, even though categorical information was processed when fMRI (Jiang and He, 2006) and Electroencephalography (EEG) measurements (Jiang et al., 2009) were applied. Yet, additional evidence for the categorical processing of objects in the ventral visual cortex is missing (Pasley et al., 2004; Williams et al., 2004). Interestingly, an fMRI study by Fang and He (2005) suggested that object processing might occur in a so-called vision-for-action stream or vision-for-perception stream, as responses to suppressed tools only occurred in the dorsal stream. However, these findings could not be replicated by Hesselmann and Malach (2011).

2.1.6 Modulation of interocular suppression by attention

In essence, visual attention can be divided into voluntary and involuntary attention, also known as endogenous and exogenous attention, respectively. Voluntary attention is a conscious allocation of attention by a so-called top-down process, whereas involuntary attention is caught by a salient stimulus, which is described as bottom-up process. Moreover, we can differentiate other forms of attention, e.g., spatial attention and feature-based attention (Li et al., 2015).

When dissimilar competing images are presented to the two eyes, attention may act as a modulator that interferes with the dynamics of rivalry, changing the rate of alternations between the images (Paffen et al., 2006; Kohler et al., 2008; Kornmeier et al., 2009; Alais et al., 2010) or influencing visual perception by an attended perspective (Chong et al., 2005; Dieter et al., 2015; for a review, see Dieter and Tadin, 2011). Under interocular suppression, it has been suggested that attention leads to an information boost of low-level features at spatially attended locations (Shin et al., 2009), enhances adaption after-effects (Yang et al., 2010), and influences sensitivity to features like colour or orientation (Kanai et al., 2006; Bahrami et al., 2007). Interestingly, Kanai et al. (2006) reported that feature-based attention facilitated stimulus processing when suppressed by continuous flash suppression, but did not find significant effects for spatial attention. Similarly, previous work has indicated that feature-based cues modulate the dynamics of rivalry (van Ee et al., 2009; Dieter et al., 2015) and that spatial attention influences binocular rivalry only minimally (van Ee et al., 2009). Object-based attention under binocular rivalry also altered perceptual dominance in a study of Mitchell et al. (2004), possibly by unconscious selection mechanisms (Lin and He, 2009).

A question that remains debated is whether interocular suppression and attention are directly cross-linked or whether interocular suppression can persist under inattention. It has been argued that attention influences response-gain under interocular suppression and that competition under interocular suppression is highly dependent on attention (Ling and Blake, 2012). Additionally, evidence is lacking for information being processed in the early visual cortex under interocular suppression when attention is withdrawn (Watanabe et al., 2011). However, two studies reported that interocular suppression continued even when attention was diverted away from the stimuli (Moradi and Heeger, 2009; Yuval-Greenberg and Heeger, 2013).

Interestingly, a previous fMRI study by Lee et al. (2007) observed cortical activity during binocular rivalry when stimuli were unattended. In their study, a low-contrast image was presented to one eye, while the other eye viewed a high-contrast stimulus. Once the high-contrast image became dominant, the contrast of the low-contrast image was increased to induce a perceptual shift of the consciously perceived stimulus. These dynamics could be visualized in the early visual cortex and, astonishingly, persisted when attention was diverted, albeit restricted to V1. Similar results were found in a study by Roeber et al. (2011), who found event-related potentials (ERP), i.e., electric neural responses to a presented stimulus, as measured by scalp electrodes (Luck, 2005), under binocular rivalry in the absence of attention. However, no such effect could be found in subsequent fMRI studies when stimuli were rendered invisible by flash suppression (Moradi and Heeger, 2009) and CFS (Watanabe et al., 2011).

Shortly after, Brascamp and Blake (2012) published a behavioural study on rivalry dynamics, in which the rivalry of two images was manipulated using flash suppression. Participants attended the two stimuli and perceptual alternations were induced by the flash. However, once participants shifted their attention to an occupying task and returned to the rivalry stimuli, each of the two stimuli possessed the same likelihood to become dominant first. This led to the conclusion that binocular rivalry is abolished when unattended (Brascamp and Blake, 2012). Similar results were found by Ling and Blake (2012), who demonstrated that negative afterimages became negligible under inattention.

Interestingly, Eo and colleagues (2016) introduced another model in which interocular suppression is affected by attention, albeit counterintuitively. In an ERP study, they presented words under CFS at a spatially attended and unattended location. They found that an N400 effect, which is an established marker of semantic processing, was only present when attention was diverted away from the stimulus. Hence, they concluded that inattention attenuates the depth of interocular suppression, akin to previous findings (Brascamp and Blake, 2012). In the following, this theory will be referred to as the "CFS-attenuation-by-inattention" model.

2.1.7 The "CFS-attenuation-by-inattention" model

The "CFS-attenuation-by-inattention" model refers to previous findings of Eo and colleagues (2016), who investigated the semantic relatedness of words in an EEG and a behavioural experiment. In their study, they presented visible prime words at a central location before participants allocated their covert attention as indicated by a central arrow. Subsequently, a target word, which was suppressed by CFS, appeared at either the attended or unattended location. Participants had to judge whether the prime and target were semantically related. In a separate experiment, awareness of the target stimuli was assessed by a location judgement and word recognition task.

The most interesting finding in their study was the observation that an N400 signal was present, but only when the suppressed target stimuli were unattended, while this effect was absent in the invisible attended condition. Moreover, semantic judgement was at chance level for invisible unattended targets, whereas it was above chance for attended targets. Crucially, they found that location judgement was negatively correlated with the presence of the N400 effect. Hence, they reasoned that semantic analysis of words was processed under inattention and CFS. The authors suggested that spatial attention counterintuitively modulates interocular suppression, and more specifically that inattention attenuates interocular suppression and makes semantic information available outside of awareness. This might indicate that in previous studies, which did not evidence higher-level processing under CFS, semantic processing was indeed present, but activity did not have the strength to influence behavioural responses. Furthermore, the authors suggested that spatial inattention may explain previous results that reported high-level processing under CFS. However, Heyman and Moors (2014) and Moors et al. (2016) found no higher-level processing in a bCFS paradigm, although spatial ambiguity was employed in their study designs. Furthermore, Alsius and Munhall (2013), Gobbini et al., (2013) and Lupyan and Ward (2013) presented stimuli at a central location and reported higher-level effects as indicated by the speed of stimulus detection. This might imply that the "CFS-suppression-by-attention" model will need to be extended.

Nevertheless, the findings of Eo et al. (2016) suggest that attention significantly modulates the depth of CFS and that unconscious higher-level processes may occur under inattention. This questions the ranking of CFS in the functional hierarchy of psychophysical blinding methods and may implicate its reallocation. Furthermore, if higher-level processes can indeed be executed under CFS and inattention, the extent of unconscious processing under CFS should rather be assigned to a preconscious state than to a subliminal state of the global neuronal workspace model.

2.2 Functional magnetic resonance imaging

First introduced in the early 1990s, fMRI has become a powerful method to investigate human brain activity and function (Gore, 2003; Amaro and Barker, 2006; Le Bihan, 2012; Uğurbil and Ogawa, 2015). As a non-invasive method, it has been used to study heterogenous fields such as language (Woermann et al., 2003; Centeno et al., 2014), memory (Machulda et al., 2003; Sidhu et al., 2015), attention (Vuilleumier et al., 2001; Markett et al., 2014), unconscious visual perception (Sterzer et al., 2008) and, astonishingly, even politics (Knutson et al., 2006). In essence, fMRI uses magnetic characteristics of oxygenated and deoxygenated haemoglobin, and provides a so-called blood oxygenation level-dependent (BOLD) signal. This response serves as an indicator of neuronal activity, and reflects oxygenation, cerebral blood flow and volume (Soares et al., 2016). Perhaps the greatest potential of fMRI is its high spatial resolution that allows the distinguishing of functional brain areas more precisely than other methods like EEG or Magnetoencephalography (MEG), albeit with reduced time resolution (Soares et al., 2016). The impaired resolution of time is due to the dynamics of the hemodynamic response. When neural activity rises, the hemodynamic response, i.e., the increase of regional vasodilatation and blood flow, peaks with a delay of ~ 4-6 s, before returning to the baseline ~ 12 s after stimulus presentation (Handwerker et al., 2012; Miezin et al., 2000). To address this issue, the BOLD signal can be characterized by a so-called hemodynamic response function (HRF) for further analysis (Buxton et al., 2004).

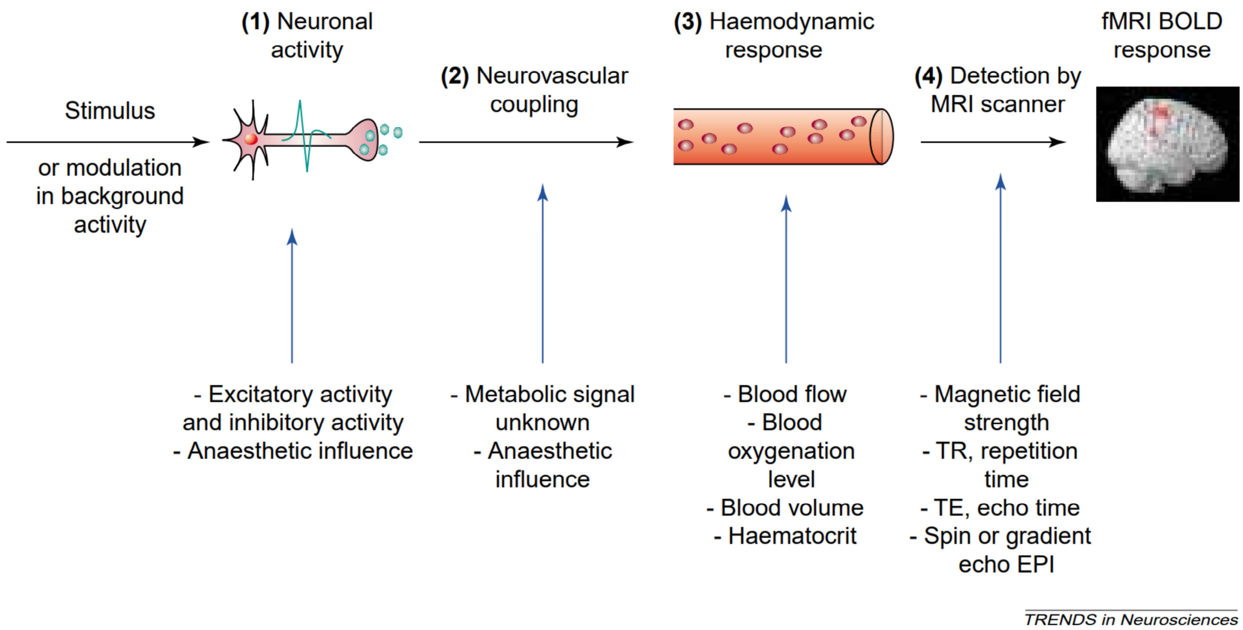

Figure 4. The pathway from stimulus presentation to the final fMRI response map
The BOLD signal is characterized by (1) neuronal responses to a stimulus or background modulation, (2) neurovascular coupling (interaction between neuronal activity and a haemodynamic response), (3) the haemodynamic response, and (4) response detection by an MRI scanner. Illustration by Arthurs and Boniface (2002).

2.2.1 Multi-voxel pattern analysis

When analysing fMRI data, assumptions need to be made on how information is distributed in the brain. Mass univariate analysis has been a popular approach for decades and focuses on analysing each voxel of a functional image separately. Since mental representations are increasingly understood as distributed neuronal patterns (Kahnt et al., 2014), a new method called Multi-voxel pattern analysis (MVPA) has gained interest as a means for disentangling cortical responses (Kamitani and Tong, 2005; Haynes and Rees 2005). It presumes that stimulus information is represented at a sub-voxel scale (Kamitani and Tong, 2005), which potentially increases sensitivity to detect mental representations in comparison to single-voxel-based analyses (Norman et al., 2006). Moreover, it is a powerful tool for exploring how information is represented in the brain

(Norman et al., 2006). A previous study by Haxby et al. (2001), for example, demonstrated that numerous categories of objects were associated with distinct representational activity patterns in the ventral temporal cortex. To detect specific neuronal activity patterns, classifiers (Pereira et al., 2009) are trained to distinguish between two classes in a data set. This decoding procedure is often performed by means of machine-learning techniques such as Support Vector Machine (Cortes and Vapnik, 1995). For cross-validation of decoding results, fMRI studies typically use a leave-one-run-out iteration scheme. This means that one part of the data serves to train the classifier to distinguish between two classes, while the remaining data are used as a test set to probe the classifier's performance, until every fraction of the data has functioned as a test set once. The performance of a classifier is then reflected by the average decoding accuracy across iterations, which is typically expressed as the percentage of correct classifications and serves as indicator for informational content.

2.2.2 Modulation of activity patterns by attention

Previous findings of fMRI studies, which applied univariate analyses, have demonstrated that spatial attention significantly enhances the amplitudes of BOLD signals and that neural responses become suppressed due to inattention (Brefczynski and DeYoe, 1999; Gandhi et al., 1999; Somers et al., 1999). This influence of attention was detected not only in the early visual cortex (Brefczynski and DeYoe, 1999; Gandhi et al., 1999; Martínez et al., 1999), but also in higher level areas, i.e., the ventral and dorsal visual stream (Wojciulik et al., 1998; Dugué et al., 2020).

Analyses of multi-voxel patterns revealed that spatial attention seems to amplify neural responses to task-relevant features in the early visual cortex (Jehee et al., 2011). Moreover, attention increases object representation in the lateral occipital complex (LOC), as previously demonstrated in a study by Guggenmos et al. (2015). In addition, Goddard and Mullen (2021) showed that spatial attention enhances informational content around the central stimulus area and its surroundings in high-level visual areas, whereas V1, V2, V3, and hV4 displayed asymmetric responses to attention. Importantly, care must be taken when interpreting such findings, as previous results were challenged by Cohen and Tong (2015), who argued that brain responses do not necessarily reflect informational gain by attention.

2.2.3 Fusiform face area and parahippocampal place area

The fusiform face area (FFA) has been shown to play a significant role in face perception and is located in the fusiform gyrus. It responds to a wide range of face stimuli when explored by fMRI

(Kanwisher et al., 1997; Grill-Spector, 2003). The parahippocampal place area (PPA) has been detected in the parahippocampal gyrus and primarily processes scene and house stimuli (Epstein and Kanwisher, 1998; Epstein et al., 1999). Studies on unconscious visual perception revealed that responses to face and house stimuli can still be found in the corresponding regions when stimuli are rendered invisible by interocular suppression (Sterzer et al., 2008; Haynes and Rees, 2006). Norman et al. (2006) successfully decoded stimulus information from neuronal activity patterns, although images remained invisible to the participants. Using a binocular rivalry paradigm, Williams et al. (2004) presented images of happy, neutral or fearful faces to one eye and house images to the other eye. Interestingly, the dominance of a perceived object was also reflected in greater activation in the FFA and PPA, respectively.

2.3 Research question and hypotheses

The aim of this dissertation was to further explore the mechanisms underlying unconscious visual processing by testing the "CFS-attenuation-by-inattention" model, as previously introduced by Eo et al. (2016). In their study, unconscious semantic processing of words was intact when stimuli were displayed at a spatially unattended location and suppressed by CFS. By probing the "CFS-attenuation-by-inattention" model, the two present studies aimed to further investigate unconscious high-level functioning in a neuroimaging and in a behavioral experiment. To probe categorical processing of invisible stimuli, we used fMRI and MVPA to measure neural responses to face and house stimuli in the FFA and PPA, respectively. In a spatial cueing paradigm, we tested whether spatial attention had a significant effect on object processing when stimuli were either invisible, due to the CFS masks, or fully visible. We hypothesized that the decodability of face and house stimuli increases when stimuli are unattended and suppressed by CFS. Furthermore, we explored unconscious numerical processing by incorporating the "CFS-attenuation-by-inattention" model in a number priming experiment, which probed whether unattended numbers under CFS facilitate responses to a related target number. The present studies aimed to evaluate whether the extent of unconscious visual processing under CFS and inattention can be related to a subliminal or preconscious state of the global workspace model (Dehaene et al., 2006), and whether the "CFS-attenuation-by-inattention" model might require a reallocation of CFS within the functional hierarchy of psychophysical blinding methods (Breitmeyer, 2015). The specific hypotheses for our studies were as follows:

Hypothesis 1a: Unattended stimuli of faces have significantly better decodability in the FFA than attended face stimuli when images are rendered invisible by CFS. (Study 1)

Hypothesis 1b: Unattended stimuli of houses have significantly better decodability in the PPA than attended house stimuli when images are rendered invisible by CFS. (Study 1)

Hypothesis 2: Unattended stimuli of numbers induce significantly larger priming effects than attended number stimuli when prime images are rendered invisible by CFS. (Study 2)

3 Study 1. Attentional modulation of the perception of object category under CFS: an fMRI study

3.1 Introduction

This study aimed to investigate the “CFS-attenuation-by-inattention” model by probing categorical processing of face and house stimuli using fMRI and MVPA. In a spatial cueing paradigm, we tested whether attention had a significant effect on object related representational activity patterns of stimuli that were either visible or rendered invisible by CFS. According to the “CFS-attenuation-by-inattention” model (Eo et al., 2016), we predicted that decoding accuracies of unattended stimuli would be significantly higher than decoding accuracies of attended stimuli when images were suppressed by CFS. Inversely, we presumed that attention towards visible stimuli would enhance object decodability in high-level visual areas, as previous findings have indicated (Guggenmos et al., 2015). By means of fMRI measurements, we expected to find responses to face and house stimuli in the corresponding cortical regions, namely the FFA and PPA, respectively.

3.2 Methods

3.2.1 Participants

Twenty-five volunteers were recruited for this study (age range: 20 – 35 years, mean age: 25 years, 16 female, 17 right-handed). This sample size was estimated by a power analysis based on previous work by Guggenmoos et al. (2015). In their study, spatial attention significantly enhanced the decodability of objects in the LOC (Cohen’s d = 1.12). We figured that for an effect of half the size and a power of 0.85, a total number of 25 subjects would be mandatory (one-tailed paired t-test, alpha = 0.05), as indicated by G*Power 3 (Faul et al., 2007). One participant had to be excluded due to a coding error in the localizer script. Participants had normal vision or corrected-to-normal vision by contact lenses and no history of psychiatric or neurological disorders. The hole-in-the-card test (Miles, 1930) was used to determine the dominant eye of each participant (dominant right eye: 17). Volunteers were naïve to the experiment, were paid €8/hour for participation, and gave written informed consent. The study was conducted at the Department of Psychiatry and Neurosciences, Charité - Universitätsmedizin Berlin, Germany, and approved by the Ethical Committee of the German Association of Psychology (Deutsche Gesellschaft für Psychologie, DGPs).

3.2.2 Stimuli

The stimulus set consisted of five faces and five houses, as shown in Figure 5. We used greyscale images that resembled each other in shape and structure (e.g., eyes and windows), and matched luminance histograms as well as the rotational average of the Fourier spectra via the SHINE toolbox (Willenbockel et al., 2010). All stimuli were low-pass filtered using a 2D-Gaussian filter with a standard deviation of 30 cycles/image in the frequency domain. Additionally, we created five vertical Gabor patches with a randomly generated phase (1.65 cycles per degree, 3 cycles per 100 pixels, sigma = 30, mean = 0.79, amplitude = 0.95) using Yuki Kamitani's image tools (https://bicr.atr.jp/~kmtn/imageMatlab/index.html), one of which was randomly selected for each trial. Furthermore, 25 CFS masks were created with random, greyscale squares and circles that covered 4% to 18% of the size of a mask. To enable conscious perception of the stimuli in the visible condition, we used CFS masks with superimposed images. All images measured 3.33° x 3.33° of visual angle. They were generated by Matlab 7.9.0 (MathWorks, Natick, MA) and the Psychophysics toolbox 3.0.12 (Brainard, 1997).

Figure 5. Stimulus set (fMRI study)
Sample of stimuli, as used in the main and localizer experiment. There were two categories, faces and houses, and each contained a set of five images.

3.2.3 Experimental design

3.2.3.1 Setup

Participants viewed the presentation through a mirror system, which was fixed to the head coil, on a ground-glass screen placed at the head of the scanner. All images were projected on the screen with a spatial resolution of 1024 x 768 pixels by a Sanyo LCD at 60 Hz. As the total viewing distance was 72 cm, each pixel resulted in approximately 0.02° of visual angle. Participants wore prism glasses without vision correction to obtain dichoptic stimulation and binocular fusion. A cardboard divider between head coil and screen was installed to prevent crosstalk between the eyes (Schurger, 2009). Due to configurational restrictions in implementing binocular fusion, the presentation was shifted towards the upper left side of the screen.

3.2.3.2 Procedure

To get acquainted with the task first, participants performed a training session outside the fMRI scanner. In the scanner, contrasts of the stimuli were adjusted for each participant individually. To determine the highest stimulus contrast at which images of faces and houses could not be seen anymore due to suppression by CFS, we adjusted the contrasts of the stimuli using a logarithmic function in a 1-up-1-down staircase procedure. The 4-point Perceptual Awareness Scale (PAS, Ramsøy and Overgaard, 2004) was used to measure awareness of the stimuli by reporting "no experience" (PAS = 1), "weak experience" (PAS = 2), "almost clear experience" (PAS = 3) or "clear experience" (PAS = 4). Starting with a medium contrasted image, contrast increased if participants reported "no experience" (PAS = 1) of the stimulus, while otherwise it decreased. The staircase procedure consisted of 20 trials. When the contrast curve was not plausible (i.e., bumpy), we repeated this sequence, as some participants needed additional time to adapt to the speed of the task. The highest contrast at which participants reported no experience of the stimulus was selected for the main experiment. Subsequently, the main experiment was conducted followed by a localizer experiment (see methods section "Localizer experiment").

3.2.3.3 Main experiment

A grey rectangle with a central fixation cross within a black framed diamond was presented to each eye of the participant. Black and white striped frames facilitated binocular fusion of the two images, resulting in outer dimensions of 413 x 189 pixels (7.53° x 3.45° of visual angle) and inner dimensions of 409 x 185 pixels (7.46° x 3.38° of visual angle).

First, participants viewed a blank fixation screen for 2000 – 4000 ms. They were instructed to maintain fixation during each trial. Subsequently, a red arrow appeared on the left or right side of the diamond for 450 ms, which indicated the direction of attentional allocation. After another blank screen for 250 ms, a face or a house stimulus emerged on the left or right side of the rectangle, while a Gabor patch appeared on the opposite side (0.34° of visual angle offset from the fixation cross). All stimuli, including the Gabor patch, were presented upright or tilted 10° clockwise to the non-dominant eye only. These spatial rotations were independently randomized for each stimulus. In the invisible condition, CFS masks were flashed to the dominant eye on either side of the second box (0.34° of visual angle offset from fixation cross) with a frequency of 10 Hz. In contrast, CFS masks with superimposed stimuli appeared in the visible condition. The total duration of stimulus presentation equaled 600 ms, and included six frames. Afterwards, participants were instructed to report the orientation of the attended stimulus by button press and to guess the answer when the stimulus was invisible. The central fixation cross would turn blue if their response was registered in time. Subsequently, participants were asked to indicate the visibility of the face or house image, whether attended or not, using the 4-point PAS. Corresponding to the scale points, four vertically arranged crosses were drawn in the center of each rectangle. Once participants had rated the visibility of the stimulus, an "x" replaced the corresponding cross. Each task had to be completed within a maximum period of 1500 ms. Figure 6 illustrates a trial sequence of the experiment.

There were 9-10 experimental runs with 48 trials each, lasting 5 min 30 s per run. The factors visibility (visible, invisible), stimulus category (face, house) and attention (attended, unattended) were counterbalanced. All conditions were presented in random order, including the presentation side and orientation of the stimuli.

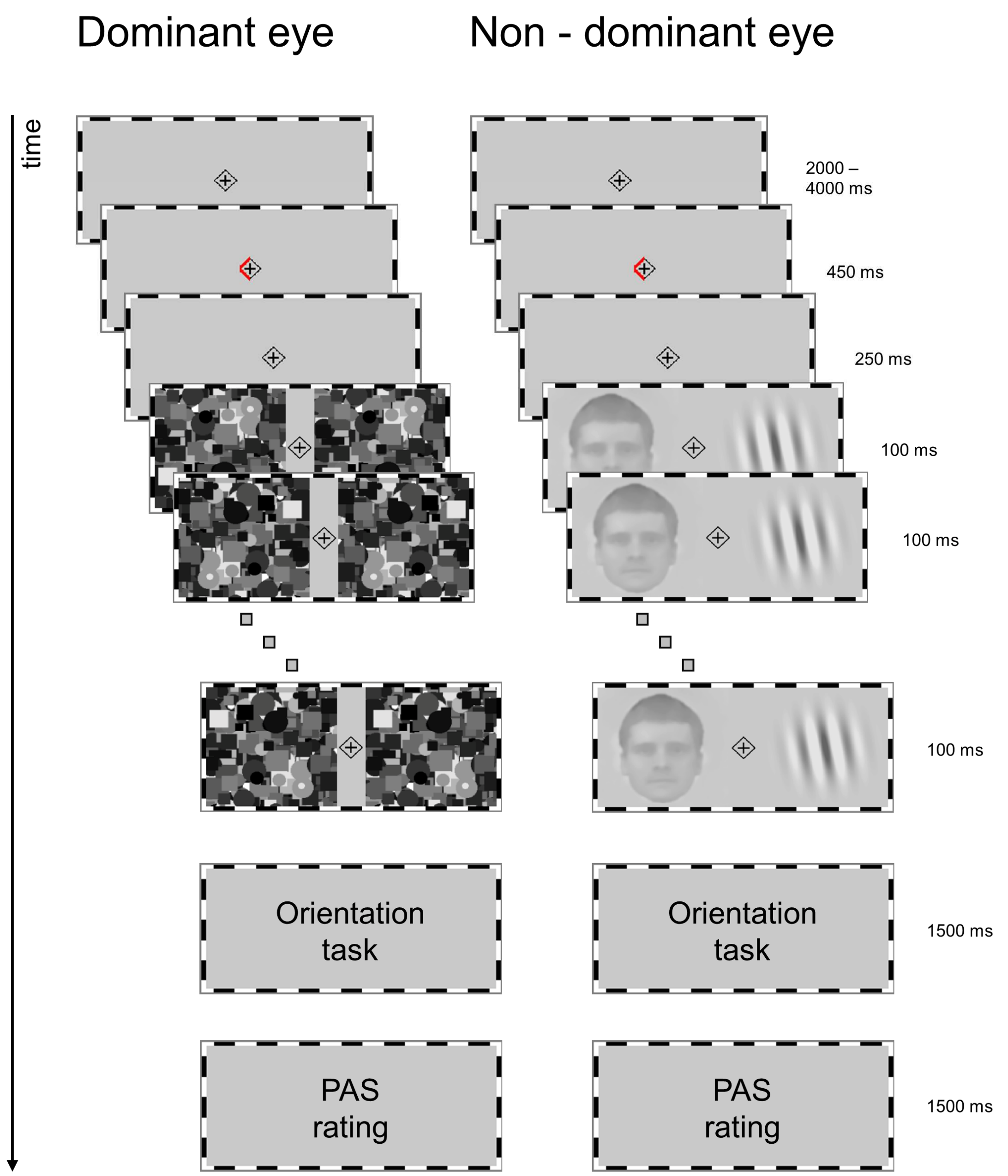

Figure 6. Experimental paradigm (fMRI study)
Participants maintained fixation throughout the experiment and allocated their covert attention towards the left or right side of the fixation cross as denoted by a centrally displayed red arrow cue. A face or house stimulus was presented at either the attended or unattended location, while a Gabor patch appeared on the opposite side. All stimuli, i.e., face/house and Gabor stimuli, obtained an upright or tilted orientation and were shown to the non-dominant eye only. CFS masks were drawn to render stimuli invisible and were presented to the dominant eye. Subsequently, participants had to discriminate the orientation of the attended stimulus and report the visibility of the face or house stimulus. In the visible condition (not shown), face/house and Gabor stimuli were presented to both eyes by superimposing the stimuli on the CFS masks.

3.2.4 Localizer experiment

After the main experiment, participants conducted a short localizer experiment in the scanner. For binocular presentation, the prism glasses were taken off and the divider was removed from the scanner in order to stimulate the central visual field, since response amplitudes seem to decrease with increasing eccentricity (Wu et al., 2013). Each block started with a fixation period (500 ms), which was followed by an intact or scrambled image (500 ms). Subsequently, the fixation cross and images were displayed in turns (500 ms each). One block contained 10 upright images of one category, and participants conducted a one-back task by button press. Thus, attention needed to be maintained throughout the localizer experiment. Intact and scrambled stimuli were displayed separately. Houses, faces and scrambled images were represented by 10 blocks of each category. All blocks were shown in random order and yielded a total duration of 6 min 42 s.

3.2.5 Data acquisition and analysis

3.2.5.1 Behavioural data

Visibility ratings of the four experimental conditions - “visible attended”, “visible unattended”, “invisible attended” and “invisible unattended” - were analyzed separately. Visible trials comprised all trials that included CFS masks with superimposed images. Invisible trials included trials with CFS masks only. For each participant, we computed the relative frequencies of PAS responses. Additionally, the visibility ratings of all subjects were averaged for each condition. To test for significant differences between attended and unattended trials in the visible and invisible condition, we used parametric and non-parametric tests (two-tailed paired-sample t-test and Wilcoxon test, respectively). Orientation discrimination was analyzed for visible attended and invisible attended stimuli. Notably, participants always responded to the attended image, thus there is no response to unattended stimuli.

3.2.5.2 Eye-tracking data

An infrared video eye-tracking system (IVIEW X™ MRI-LR, 50 Hz, SensoMotoric Instruments, Teltow, Germany) tracked the participant’s left eye throughout the experiment. Data were preprocessed by run-wise horizontal and vertical drift correction and a low-pass filter of five data points. Gaze points exceeding the left part of the screen were excluded. Further eye-tracking analysis was applied on participants with > 40% available data during stimulus presentation (600 ms). Individual fixation coordinates were estimated for each participant by the mean value of all gaze points during a blank fixation screen. Successful fixation was specified by gaze data points on the horizontal axis within 0.58° visual angle from the fixation cross during stimulus presentation, which corresponds to the area between fixation cross and inner edges of the largest stimulus.

3.2.5.3 fMRI data

3.2.5.3.1 Data acquisition

fMRI data were collected on a 3T MRI scanner (Tim Trio, Siemens, Erlangen) in the Berlin Center for Advanced Neuroimaging (BCAN), including whole-brain BOLD and anatomical images. Functional images were acquired by T2*-weighted gradient-echo echo-planar imaging (33 slices, repetition time (TR): 2000 ms, echo time (TE): 30 ms, field of view (FOV): 192 mm x 192 mm, flip angle: 78°, interslice gap: 10%, voxel size: 3 x 3 x 3 mm). There were 178 volumes in total for each run of the main experiment and 201 images in the localizer experiment. Anatomical volumes were recorded with a T1-weighted MPRAGE sequence (192 slices, TR: 1900 ms, TE: 2.52 ms, inversion time (TI): 900 ms, FOV: 256 mm x 256 mm, flip angle: 9°, voxel size: 1 x 1 x 1 mm).

3.2.5.3.2 Data preprocessing

All images were preprocessed by means of statistical parametric mapping (SPM12, Wellcome Centre for Human Neuroimaging, United Kingdom; https://www.fil.ion.ucl.ac.uk/spm/software/spm12/). Functional scans of the main experiment were preprocessed in the following steps: realignment to the first scan of a run, slice-timing, coregistration to the anatomical image and spatial smoothing with a 4 mm full width at half maximum (FWHM) Gaussian kernel. Functional volumes of the localizer experiment were realigned to the first image of a run, slice-time corrected, coregistered to structural volumes, spatially smoothed with an 8 mm FWHM Gaussian kernel and normalized into Montreal Neurological Institute (MNI) space using segmentation.

3.2.5.3.3 General linear model

We estimated a general linear model (GLM) for each subject using an event-related design, convolved with a canonical hemodynamic response function (HRF) as implemented in SPM12. In the main experiment, regressors of interest were "visible attended faces", "visible unattended faces", "visible attended houses", "visible unattended houses", "invisible attended faces", "invisible unattended faces", "invisible attended houses" and "invisible unattended houses", defined by stimulus onsets. Furthermore, we modelled the "Task response screen" as an additional regressor of no interest and included six rigid-body realignment parameters with a max. translation of 5.8 mm (mean = 1.5 mm) and a max. rotation of 5.2° (mean = 1.6°). All regressors were designed for each run and each condition. Analysis of the localizer experiment comprised the regressors "intact faces", "intact houses", "scrambled faces", "scrambled houses" and six realignment parameters. We used a boxcar function to model regressors of interest and convolved the function with the canonical HRF. Data were filtered using a high-pass filter with a frequency of 1/128 Hz. For each participant, we estimated statistical parametric maps and generated beta images for each regressor of interest.

3.2.5.3.4 Regions of interest

To explore categorical processing of face and house stimuli, we included the well-established fusiform face area (FFA) and the parahippocampal place area (PPA) as regions of interest (ROI; Kanwisher et al., 1997; Epstein and Kanwisher, 1998; Epstein et al., 1999; Kanwisher, 2001; Grill-Spector, 2003). By means of the Anatomy toolbox (Eickhoff et al., 2005), we extracted the bilateral mid fusiform gyrus for FFA analysis and the parahippocampal gyrus for PPA analysis. As responses to face stimuli have been found most consistently in the middle segment of the fusiform gyrus (Kanwisher et al., 1997; Gauthier et al., 1999; Rossion et al., 2003), we confined the FFA to this section. Next, we created a sphere with a radius of 9 mm around each peak voxel of the whole-brain group localizer contrasts "faces > houses" (FFA) and "houses > faces" (PPA), thresholded at $p < 0.05$, uncorrected. The coordinates of peak voxels were [43 -51 -19] for right FFA, [-42 -51 -22] for left FFA, [22 -39 -10] for right PPA and [-29 -42 -8] for left PPA. After reverse normalization into native space, the individual peak within each transferred mask were used as the center of a 9 mm spherical ROI.

3.2.5.3.5 Multi-voxel pattern analysis

MVPA was performed on beta maps of each participant, using a support vector machine as implemented in The Decoding Toolbox (Hebart et al., 2015). The classifier was trained to distinguish between attended and unattended stimuli for each category (face, house) and visibility condition (visible, invisible), as follows: "visible attended faces" vs. "visible unattended faces", "visible attended houses" vs. "visible unattended houses", "invisible attended faces" vs. "invisible unattended faces" and "invisible attended houses" vs. "invisible unattended houses". In a leave-one-run-out cross-validation procedure, the classifier used each run as a test set once, while the remaining runs served as training sets. There were 9-10 iterations of this procedure, corresponding to the total number of runs of each participant, and prediction accuracies were averaged across all iterations for every subject. Group performances were calculated by the mean decoding accuracies of all subjects. We used two-tailed t-tests to check whether attention had a significant effect on decodability and carried out a two-paired repeated measures analysis of variance (rm-ANOVA) to test for an interaction between the factors visibility (visible vs. invisible) and attention (attended vs. unattended). Bayesian analysis was used to determine the strength of evidence for the hypotheses. The Bayes Factor (BF) is calculated by the ratio of the likelihood of data given an alternative hypothesis and the likelihood of data given a null hypothesis. We report BF_{10}, i.e., the likelihood of our data given the alternative hypothesis over the null hypothesis, and used categorical interpretation as introduced by Harold Jeffereys (1961) as well as Lee and Wagenmakers (2013). It should be noted that our alternative hypothesis differed between the two visibility levels: for invisible stimuli, our alternative hypothesis was that unattended stimuli were significantly better decodable than attended stimuli, whereas for visible stimuli, the alternative hypothesis was that attended stimuli were significantly better decodable than unattended stimuli. Test statistics were computed using JASP 0.14.1.0 (jasp-stats.org) and SPSS 24.0 (IBM).

3.3 Results

3.3.1 Behavioural data

CFS successfully decreased awareness of the stimuli, as indicated by the PAS ratings, from high visibility ratings in the visible condition to low visibility ratings in the invisible condition (Figure 7). Conversely, the effects of spatial attention on reported stimulus awareness were numerically small. Under CFS, the mean PAS rating for attended stimuli was 1.4 ± 0.04 SEM, and 1.3 ± 0.13 SEM for unattended stimuli. Though small, this difference was significant in parametric ($t(23) = 3.0$, $p = 0.006$) and non-parametric tests (Wilcoxon: $p = 0.010$). In visible trials, mean PAS ratings were not significantly different between attended and unattended stimuli (3.8 ± 0.04 and 3.7 ± 0.04, respectively, $t(23) = 1.41$, $p = 0.172$, Wilcoxon: $p = 0.082$).

To assess whether participants allocated their attention as indicated by the red arrow cue, orientation judgement of the attended stimulus was reported independent of visibility. In 90.71% ± 1.40 SEM of the visible trials, orientation discrimination was performed correctly. For suppressed stimuli, performance of orientation discrimination was at chance level (49.94% ± 0.87 SEM), indicating that the orientation of the invisible stimuli could not be discriminated.

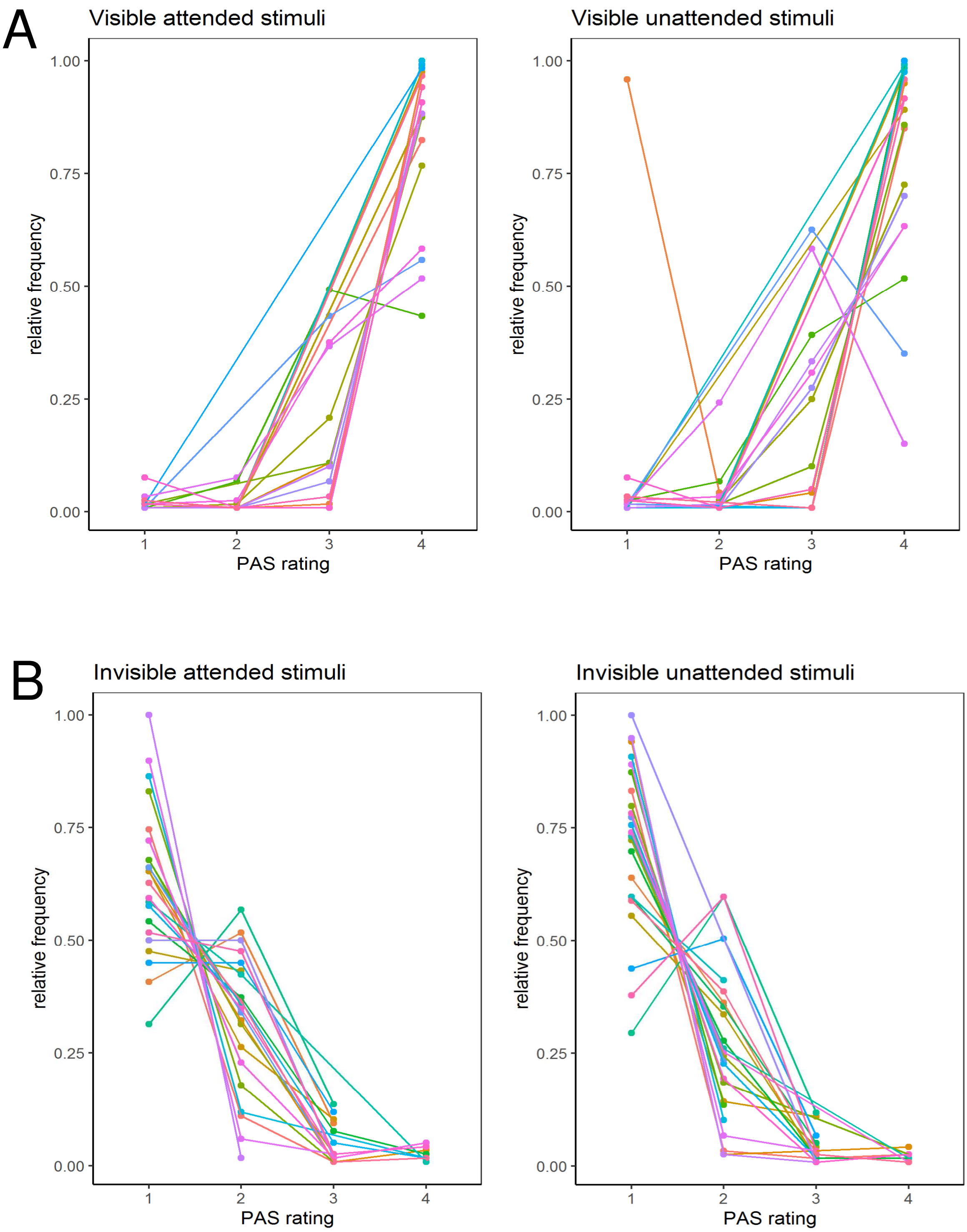

Figure 7. Behavioural results (fMRI study)

A) Relative frequencies of individual PAS ratings in the visible conditions (attended, unattended). B) Relative frequencies of individual PAS ratings in the invisible conditions (attended, unattended). Each colour represents one participant. PAS levels included: "no experience" (PAS = 1), "weak experience" (PAS = 2), "almost clear experience" (PAS = 3) or "clear experience" (PAS = 4). The outlier in the top right panel (orange colour) depicts data from a participant who reported very low PAS ratings in the "visible unattended" condition.

3.3.2 Eye-tracking data

We included 20 participants with > 40% available data during stimulus presentation (600 ms) in all further eye-tracking analyses. 85.6% ± 0.03% (mean ± SEM) of the recorded gaze points were located within the defined fixation area. Participants maintained central fixation in 81.8% ± 0.04 SEM of the trials when stimuli were attended. In trials with unattended stimuli, successful fixation was carried out in 82.77% ± 0.17 SEM of recorded gaze data (see Figure 8 for gaze data distribution). Therefore, the effects of attentional shifts are unlikely to be driven by drifting eye movements throughout the experiment, as fixation was maintained in most of the trials. The amount of available data is shown in Figure 9.

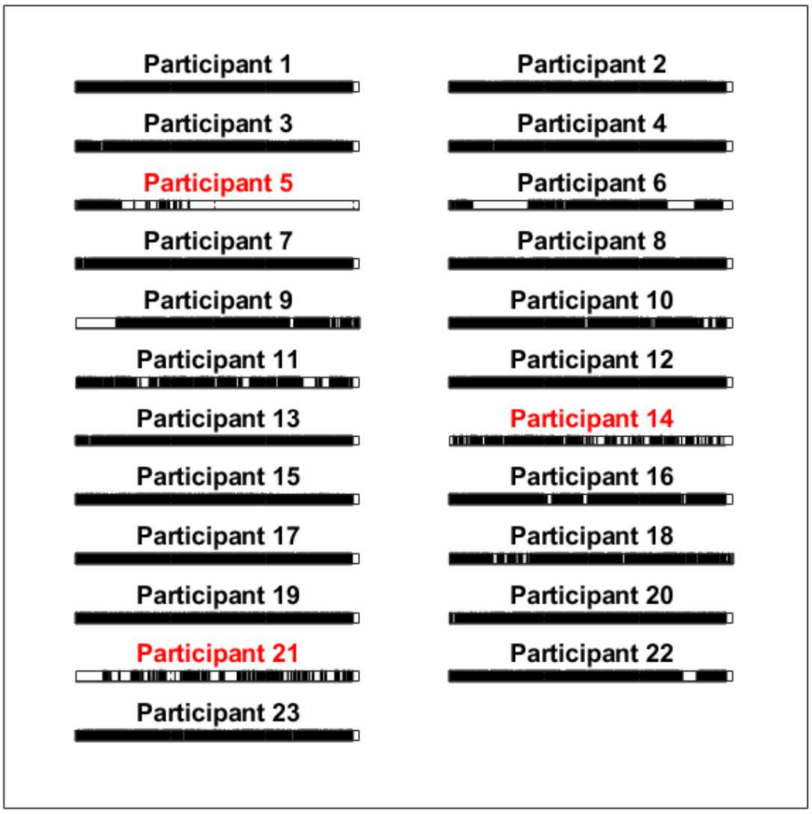

Figure 8. Tracked gaze data (fMRI study)
Percentage of tracked data during stimulus presentation for each participant. Each bar represents a timeline over the main experiment. Black stripes denote recorded data, white areas denote missing data. Three participants, marked in red, had to be excluded due to insufficient data for further analysis.

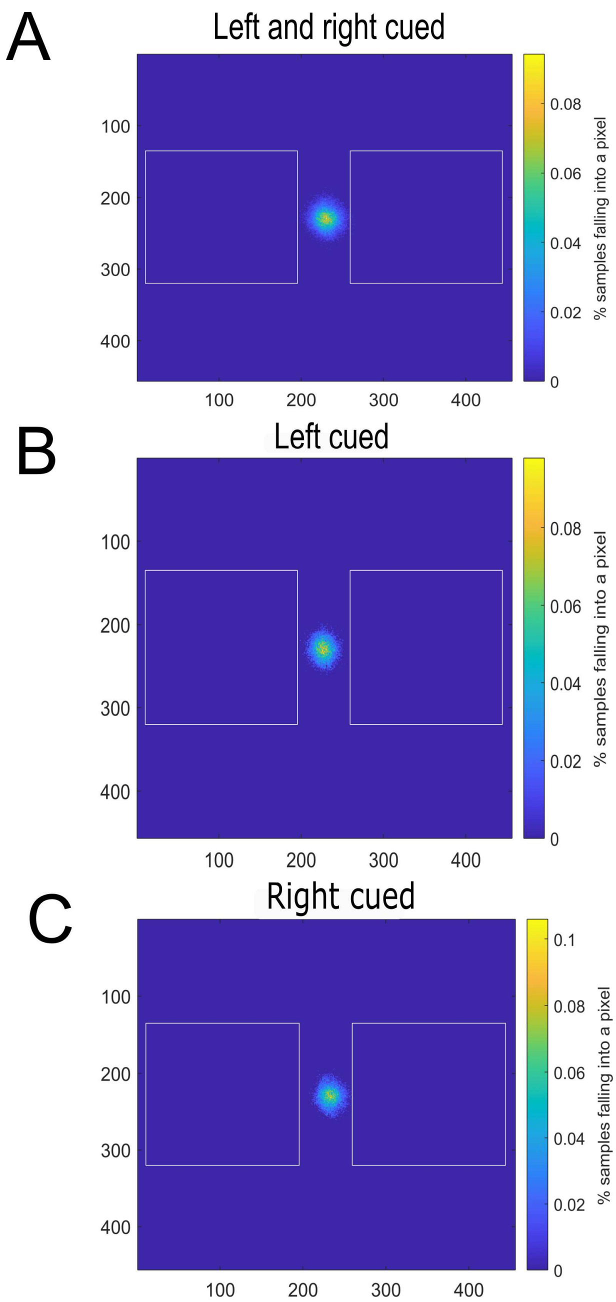

Figure 9. Heatmap of eye-tracking data (fMRI study)
Gaze data of all participants during stimulus presentation. A) Gaze points irrespective of attention allocation. B) Gaze points when the left stimulus was attended. C) Gaze points when the right stimulus was attended. Brighter colours depict a larger amount of gaze data falling into a pixel. The left and right white framed squares represent the two boxes where stimulus and Gabor patch were displayed. Note that the participant's left eye was tracked and that this figure shows the left side of the screen only.

3.3.3 fMRI data

The "CFS-attenuation-by-inattention" model predicts that spatial inattention attenuates suppression of a stimulus when it is rendered invisible by CFS. Hence, inattention facilitates unconscious high-level processing under CFS (Eo et al., 2016). Accordingly, we hypothesized that spatial inattention towards suppressed stimuli of faces and houses should boost their neural representation in the FFA and PPA, respectively (see Figure 10). If unconscious object categorization is enhanced due to informational gain, the decodability of associated activity patterns should increase.

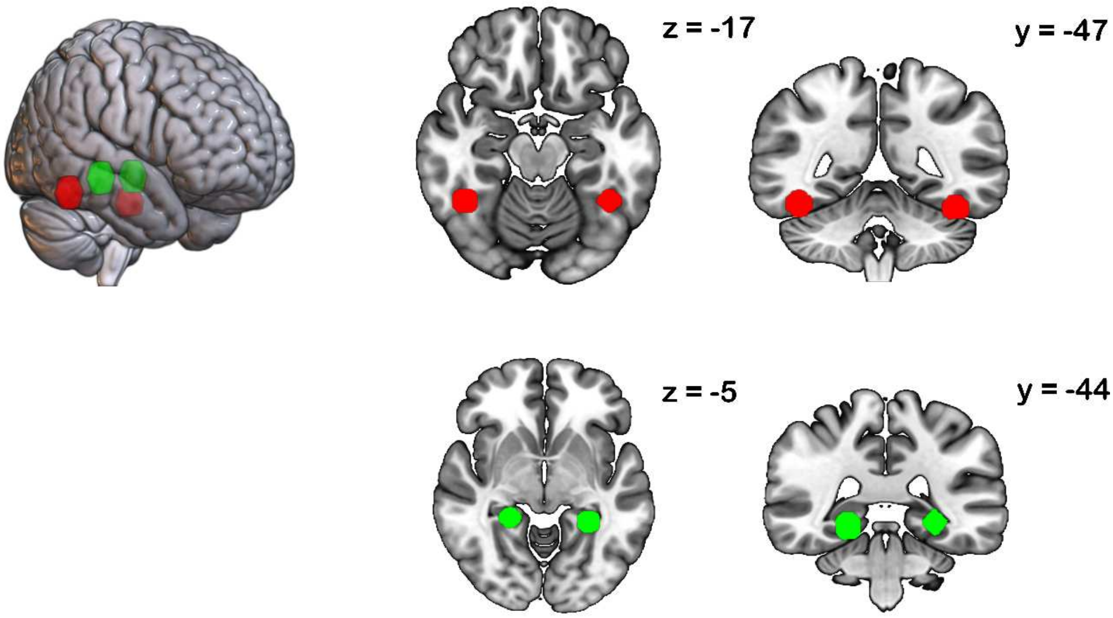

Figure 10. Regions of interest for FFA and PPA
In a first step, a sphere with a 9 mm radius was drawn around the peak voxel of the whole-brain group localizer contrasts "faces > houses" (FFA, red) and "houses > faces" (PPA, green) within the mid fusiform gyrus (FFA) and parahippocampal gyrus (PPA), thresholded at $p < 0.05$, uncorrected. After normalization into native space, the peak voxels within the normalized masks were used to define the center of individual spherical ROIs with a 9 mm radius for each subject.

To test this hypothesis, we performed an rm-ANOVA with the factors visibility (visible, invisible) and attention (attended, unattended). Analysis of FFA data indicated that the main effects of visibility ($F(1,23) = 29.59$, $p < .001$, $\eta p^2 = .56$) and attention ($F(1,23) = 4.73$, $p = .040$, $\eta p^2 = .17$)

reached significance. Moreover, there was a significant interaction between the factors visibility and attention ($F(1,23) = 4.40$, $p = .047$, $\eta p^2 =.16$). Post-hoc t-tests revealed that a significant effect of attention was present in visible trials only, where decoding accuracies resulted in 69.7% ± 2.73 SEM for visible attended stimuli and 61.7% ± 3.2 SEM for visible unattended stimuli ($t(23) = 3.24$, $p = 0.004$, two-tailed paired t-test, $BF_{10} = 11.46$). These findings are in line with previous results which demonstrated that attention induces an information boost in higher visual areas when it is directed towards visible stimuli (Guggenmos et al., 2015). In contrast, we predicted to find an inverse effect of attention in the invisible condition. If inattention attenuates the suppression depth of an invisible stimulus and facilitates unconscious processing, we expected that invisible unattended stimuli would be significantly better decodable than invisible attended stimuli. However, statistical analysis revealed no significant difference between prediction accuracies in the invisible attended and invisible unattended condition, with 50.7% ± 1.85 SEM for attended stimuli versus 50.5% ± 2.22 SEM for unattended stimuli ($t(23) = 0.07$, $p = 0.948$, two-tailed paired t-test, $BF_{10} = 0.22$). In fact, they did not differ from a chance level of 50%, either for invisible attended stimuli ($t(23) = 0.38$, $p = 0.711$, one sample t-test) or for invisible unattended stimuli ($t(23) = 0.23$, $p = 0.821$, one sample t-test). Thus, the interaction between the factors attention and visibility in the rm-ANOVA was solely driven by the difference between attended and unattended visible stimuli, while there was no significant difference between attended and unattended invisible stimuli.

Similarly, we computed an rm-ANOVA on PPA decoding accuracies, in which only the main effect of visibility reached significance ($F(1,23) = 15.26$, $p = .001$, $\eta p^2= .40$). In contrast to the FFA, there was no significant main effect of attention ($F(1,23) = 2.14$, $p = .157$, $\eta p^2 = .09$). The interaction between the factors visibility and attention indicated a slight trend in the rm-ANOVA ($F(1,23) = 3.68$, $p = .067$, $\eta p^2 =.14$), but did not reach significance. Since we had a strong directional hypothesis for the effect of attention on stimulus suppression and processing, we computed additional post-hoc t-tests. However, we found no significant difference between decoding accuracies of invisible attended stimuli with 50.2% ± 2.02 SEM and 51.1% ± 2.40 SEM for invisible unattended stimuli ($t(23) = 0.08$, $p = 0.779$, two-tailed paired t-test, $BF_{10} = 0.22$). Indeed, they were not significantly above a chance level of 50% in the attended ($t(23) = 0.11$, $p = 0.91$, two-tailed paired t-test) and unattended condition ($t(23) = 0.47$, $p = 0.640$, two-tailed paired t-test). The effect of spatial attention on the decoding of visible stimuli was similar for the PPA and FFA, as PPA decoding accuracies in the visible attended condition (63.3% ± 2.63 SEM) were also significantly higher than in the visible unattended condition with 55.2% ± 2.69 SEM (t(23)=2.23, p = 0.035, BF_{10} = 1.71). Thus, there was only anecdotal evidence for the alternative hypothesis. The mean group decoding accuracies are shown in Figure 11.

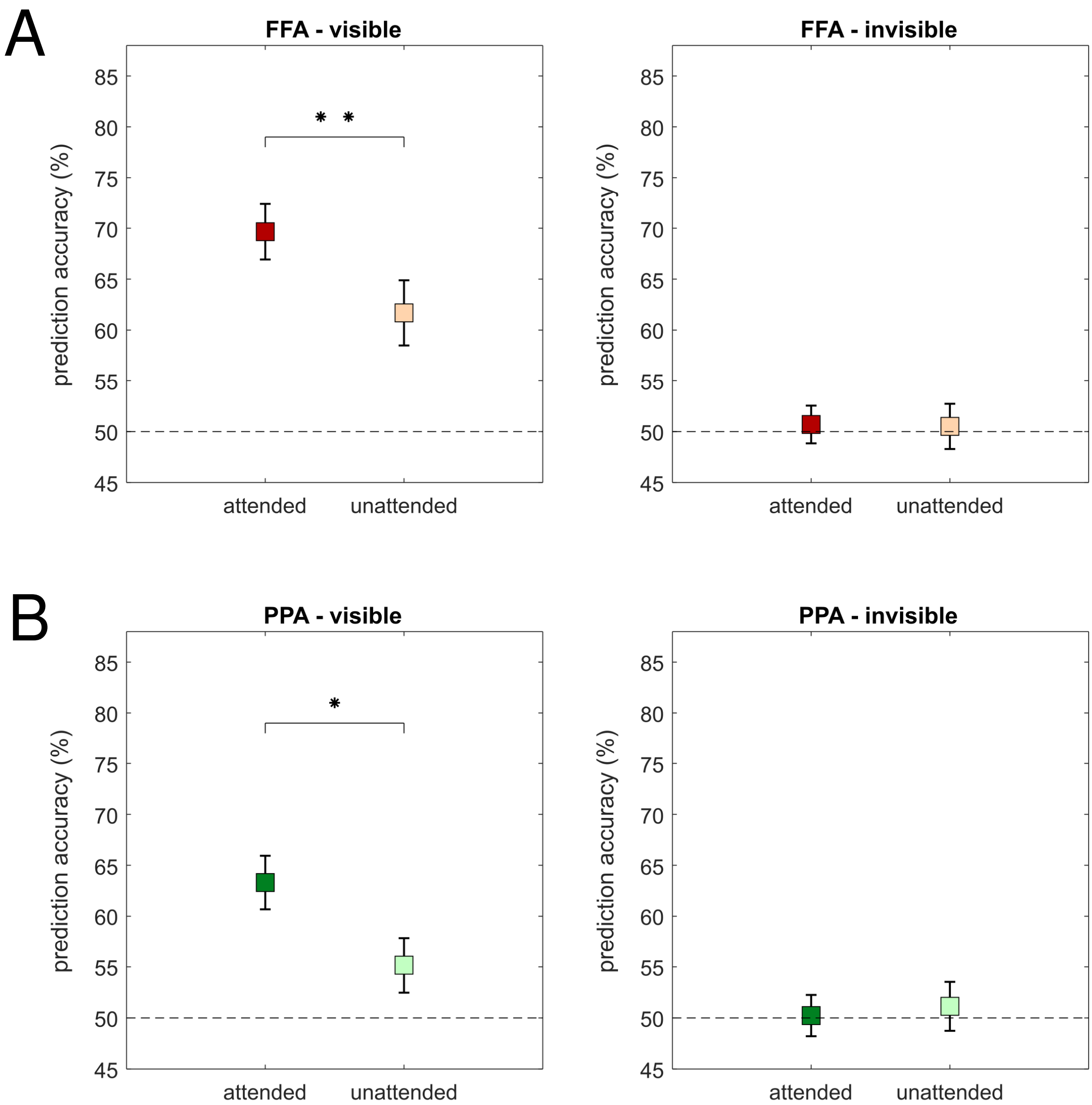

Figure 11. Group mean decoding accuracies in FFA and PPA
FFA (A) and PPA (B) prediction accuracies for attended and unattended stimuli as indicated by brightness level. Left panels show decoding accuracies for visible stimuli, right panels depict decoding accuracies for invisible stimuli. Chance level is marked by the dashed line. Error bars stand for ± 1 SEM. Asterisks: *: $p < 0.05$; **: $p < 0.01$.

3.4 Discussion

This study aimed to explore unconscious visual processing of object category by probing the "CFS-attenuation-by-inattention-model" as introduced by Eo et al. (2016). In their study, they observed unconscious semantic word processing of unattended word stimuli under CFS. Based on the study design by Eo at al. (2016), we incorporated voluntary spatial attention and CFS in our experimental paradigm. We predicted that spatially unattended stimuli of faces and houses would be significantly better decodable than spatially attended stimuli when images were suppressed by CFS. However, there was no evidence of unconscious high-level processing in the form of object categorization in our study. Neither behavioural nor fMRI data indicated a significant response to suppressed stimuli. This might implicate that our experimental design was not suited to testing the model, or that the effect of spatial attention on CFS is very weak.

The absence of evidence was perhaps due to a lack of sensitivity in our study. ERP measurements, as used in the study of Eo et al. (2016), might be better suited to capture stimulus processing under CFS in comparison to fMRI. To address this question, it may be an intriguing approach to test our experimental paradigm while recording ERP responses. Exploration of the N170 effect, an ERP marker that preferentially responds not only to faces but also to house stimuli (Rossion et al., 2000; Itier and Taylor, 2004; Corrigan et al., 2009), could help to further elaborate this hypothesis. Additional support for this approach comes from a study by Corrigan et al. (2009), which has demonstrated that, appealingly, N170 related activity is highly represented in fMRI activity maps.

The absence of a difference between attended and unattended invisible stimuli in our study may also indicate a lack of statistical power, despite our a priori calculation of statistical power being based on the study by Guggenmos et al. (2015), which showed a significant effect of attention on the object decodability of visible stimuli. Overestimation of the effect size possibly led to a sample size that was too small and therefore insufficient.

Another critical difference between our study and the study by Eo et al. (2016) is that we used images of faces and houses that were suppressed from awareness, while Eo et al. (2016) studied words which were rendered invisible by CFS. Thus, it is conceivable that semantic processing of words can occur under CFS, whereas the processing of faces and houses might be largely abolished under CFS. Indeed, it has been observed that the meaning of words can be extracted under interocular suppression. Sklar et al. (2012) as well as Yang and Yeh (2011) investigated semantic word processing in a bCFS paradigm and reported significant but contrary effects, as RTs were either shorter or longer, respectively (also see Jiang et al. [2007] and Costello et al. [2009]). It should be noted, however, that Rabagliati et al. (2018) failed to replicate these findings. Additional evidence of sematic or lexical processing of words under interocular suppression is lacking (Kang et al., 2011). Cheng et al. (2019) incorporated spatial ambiguity in their study design and found that emotional words did not break CFS faster or slower and that word processing was not influenced by word length, agreeing with previous results by Heyman and Moors (2014). Former studies on unconscious visual processing of faces under interocular suppression indicated that facial expression is accessible under interocular suppression (Jiang and He, 2006; Yang et al., 2007; Sterzer et al., 2011; Stein et al., 2013; Yang and Yeh, 2018, but see Schlossmacher et al., 2017), as well as face dominance and untrustworthiness (Stewart et al., 2012; Stein et al., 2018). In addition, upright faces seem to break suppression faster than inverted faces (Yang et al., 2007; Stein et al., 2011) and evoke measurable electromagnetic responses (Sterzer et al., 2009). Unconscious processing of faces also seems to be affected by gender (Wang et al., 2019). Furthermore, evidence for unconscious processing of houses under CFS has been reported by Sterzer et al. (2008), who successfully decoded stimulus related fine-scale activity patterns using fMRI MVPA. Hence, we predicted that our stimuli would be equally suited to being accounted for by the model. Nevertheless, a fallacy needs to be considered, namely to not falsely assume unconscious high-level functioning when actually low-level features drive this effect (Stein and Sterzer, 2012; Stein et al., 2013; Gelbard-Sagiv et al., 2016; Webb and Hibbard, 2020). It might be an intriguing approach for future studies to explore the model with a larger or dissimilar stimulus set.

Taken together, our data do not imply whether the predictions by the "CFS-attenuation-by-inattention" model could be reinforced with different methodological or technical approaches. Although this study provides further evidence that spatial attention enhances the decodability of visible stimuli, it did not reveal an effect of attention on suppressed stimuli under CFS. Our findings seem to be in line with the increasing doubt that higher-level processes can be executed under CFS (Hesselmann and Moors, 2015; Moors et al., 2019).

4 Study 2. Attentional modulation of numerical priming under CFS: a behavioural study

4.1 Introduction

Behavioural priming describes an experimental psychological method that investigates responses to a target stimulus and its neural representation when associated with a so-called prime stimulus. Previous studies have demonstrated that a target-related prime can alter reaction times (RT) to a target (Kouider and Dehaene, 2007; Van den Bussche et al., 2009). This effect can be driven by low-level sensory features like shape (Hesselmann et al., 2016) or high-level qualities like semantics (Van den Bussche et al., 2009). In a typical priming experiment, a briefly presented prime stimulus is followed by a target, the latter usually being associated with a certain task. By responding to the target, e.g., with a speeded decision on a 2 AFC task, RTs can be recorded and are taken as an indicator for mental processes. It has been observed in several studies that congruent (i.e., related) primes fasten responses to a target stimulus, while incongruent prime-target relations lead to slower RTs. These congruency effects not only occur when prime and target stimulus are clearly visible, but have also been observed when stimuli were kept from reaching awareness (for a review, see Kouider and Dehaene, 2007). To this day it remains debated whether number priming can occur under the limen of consciousness. Unconscious number processing has been observed in various experimental settings, such as masking (Dehaene et al., 1998; Naccache and Dehaene, 2001a) and visual crowding (Huckauf et al., 2008), as well as in patients suffering from hemineglect (Sackur et al., 2008). Dehaene et al. (1998) demonstrated that numerical priming in a number comparison task caused measurable activity in ERP responses. Notably, Naccache and Dehaene (2001b) extended these findings by showing that congruency effects were also present when participants had to discriminate whether a target number's value (1, 4, 6, 9) was smaller or larger than five. As predicted, response times in congruent trials, i.e., when targets were primed by a number of the same category (smaller or larger than five), were significantly shorter than in incongruent trials. They corroborated their findings by showing that priming effects evoked responses in fMRI and ERP measurements. In another study by Bahrami et al. (2010), participants performed an arithmetic enumeration task and the authors reported a significant congruency effect. These findings were also in line with previous studies, which indicated that response latencies decrease when decreasing the absolute target–prime distance (Dehaene et al., 1998; Koechlin et al., 1999), potentially due to representational overlap of prime and target (Van Opstal et al., 2008). Furthermore, Sklar et al. (2012) asserted that a significant numerical priming effect was present for subtraction but not for addition equations. This effect seemed to be replicated by Karpinski et al. (2016), albeit to a smaller degree. However, the results of these studies have been critically questioned by several authors (Shanks, 2017; Moors and Hesselmann, 2018).

In this study, we explored whether unconscious number priming can be evidenced when prime stimuli were unattended and suppressed by CFS. According to the "CFS-attenuation-by-inattention" model (Eo et al., 2016), diverted attention should attenuate interocular suppression and facilitate processing of an unattended prime stimulus. Hence, invisible unattended number primes should induce significant congruency effects.

4.2 Methods

4.2.1 Participants

Twenty-nine participants took part in this study (mean age: 24 years, age range: 18-42, 23 female, right handed: 28, dominant right eye: 27), and were recruited via student mailing lists. They had normal or corrected-to-normal vision and no history of neurological or psychiatric disorders. All participants were naïve to the experiment, provided written informed consent and received payment (€8/h) for participation. Eye dominance was determined by the hole-in-the-card test (Miles, 1930). Four participants were excluded from behavioural analysis, due to incomprehensible visibility ratings (n = 1) and inaccurate task execution (n = 3). This study was conducted at the Department of Psychiatry and Neurosciences, Charité - Universitätsmedizin Berlin, Germany, and approved by the Ethical Committee of the German Association of Psychology (Deutsche Gesellschaft für Psychologie, DGPs).

4.2.2 Stimuli

The stimulus set comprised images of four black numbers (1, 3, 5, 7) and five black letters (K, X, T, N, F), as shown in Figure 12. They were presented in an upright orientation or with a rotation angle of 10° degrees clockwise. Additionally, 25 greyscale CFS masks with random circles and masks (covering 4% to 18% of the mask area) were created using Matlab 7.9.0 (MathWorks, Natick, MA) and the Psychophysics toolbox 3.0.12 (Brainard, 1997). These masks were flashed to the dominant eye with a frequency of 10 Hz. To achieve stimulus visibility, stimulus images were superimposed onto the CFS masks. All images of black numbers and black letters on a grey background were cropped and resulted in 6.21° x 6.21° of visual angle, but it should be noted that the edges of numbers and letters did not extend to the borders of the stimulus square (see Figure 13). Accordingly, the CFS masks obtained 6.21° x 6.21° of visual angle.

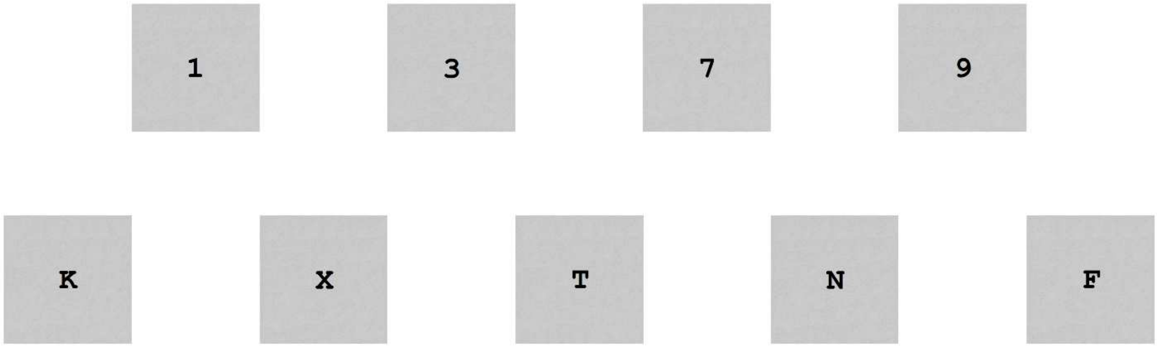

Figure 12. Stimulus set (behavioural study)
Sample of prime stimuli as used in the main and control experiments. The stimulus set consisted of four numbers and five letters. There were two numbers for each category (smaller or larger than five).

4.2.3 Experimental design

4.2.3.1 Setup

Participants performed the experiment in a dark environment and placed their head on a chin rest. For dichoptic presentation, participants viewed the stimuli through a mirror stereoscope. With a total viewing distance of 47 cm, the presentation was displayed on a screen with a resolution of 1280 x 960 pixels. Hence, one pixel resulted in approximately 0.03° of visual angle.

4.2.3.2 Procedure

In a staircase procedure, individual contrasts of the stimuli were set using a logarithmic 1-up-1-down procedure. Participants viewed a grey filled black and white framed rectangle and fixated a central fixation cross within a black rhombus. A red cue appeared on the left or right side of the rhombus and directed to the location (left or right) to which attention had to be allocated. Participants reported whether they had seen the attended stimulus ("seen", "not seen") by button press. Contrast of an image increased if participants had not seen the stimulus or otherwise decreased. Twenty-five trials were performed in the staircase procedure. If necessary, additional trials were conducted as some participants required more time to get used to the task. Afterwards, we selected the highest contrast at which stimuli remained suppressed from reaching awareness.

The main experiment consisted of two blocks with a separate secondary task, comprising a visibility rating and orientation discrimination. One half of the participants performed visibility ratings first, classifying their impression of a stimulus into "no experience" (PAS = 1), "weak experience" (PAS = 2), "almost clear experience" (PAS = 3) or "clear experience" (PAS = 4). The other half of the subject pool was assigned to start with orientation judgements. Task reports were sampled at the end of each trial. To get acquainted with the task, a training session of 32 trials preceded each block. Immediately after the main experiment, we conducted two control experiments. The setup was identical to the main experiment. In a first control experiment, we checked whether awareness of the prime stimuli increased during the experiment, as previous results by Ludwig et al. (2013) indicated that participants learn to better identify a suppressed stimulus over the course of an experiment. The second control experiment tested whether subjects correctly discriminated the prime stimuli when no CFS masks were presented. There were 128 trials for each control experiment.

4.2.3.3 Main experiment

A grey rectangle was presented to each eye of the participant, framed by black and white stripes to stabilize binocular fusion. Their inner dimensions resulted in 15.92° x 6.21° of visual angle, and the outer dimensions were 16.11° x 6.43° of visual angle. In the middle of each rectangle, a black fixation cross was drawn within a black rhombus. Participants were instructed to maintain fixation whenever a fixation cross was displayed. At the beginning of each trial, a blank fixation screen was shown for 500 ms. Next, a red arrow appeared on the left or right side of the rhombus for 450 ms, denoting the direction that covert attention needed to be shifted to. After another blank fixation screen for 250 ms, a prime and a letter stimulus were presented to the non-dominant eye for 200 ms, one of which randomly appeared on the left side of the rectangle, while the other stimulus was shown on the right side. In the invisible condition, two CFS frames were flashed to the dominant eye at 10 Hz. Each frame contained two CFS masks that were located at the corresponding positions on either side of the rectangle. CFS masks with superimposed number or letter stimuli were presented in the visible condition. Stimulus images and CFS masks were presented with an offset of 1.78° of visual angle from the fixation cross. Notably, the stimuli consisted of black numbers and letters on a grey filled square. This reported offset corresponds to the borders of the grey square. Hence, the offset of numbers and letters differed slightly (see Figure 13). Subsequently, a red target number (i.e., 2, 4, 6 or 8) was displayed binocularly at the centre of each eye's screen. Participants had to report whether the number was smaller or larger than five as quickly and accurately as possible, using the left (< 5) or right (> 5) arrow key. There were different secondary tasks in the two blocks. One task required participants to discriminate whether the attended stimulus was tilted or not. Both options ("upright", "tilted") were written above each other, and participants had to manoeuvre a cursor to their preferred answer using arrow keys, confirming their selection by pressing the space bar. One option would always be randomly preselected by the cursor. The remaining block comprised visibility ratings of the attended stimulus, rating subjective awareness by means of the PAS. Once again, options were displayed and selected as described in the orientation discrimination task. Three hundred twenty trials were performed in each block, adding up to 640 trials in total. The duration of the experiment, including staircase, main and control experiments, amounted to 90 min approximately.

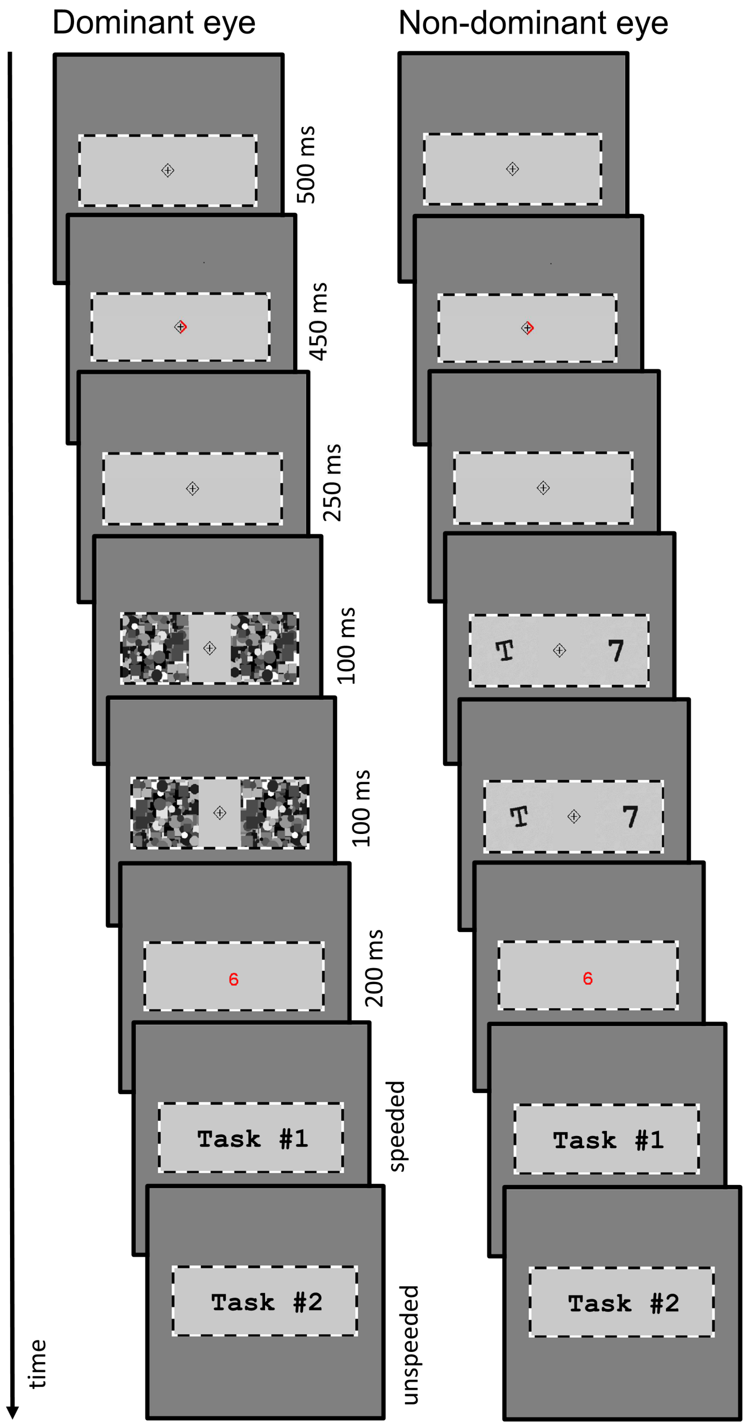

Figure 13. Experimental paradigm (behavioural study)
Participants fixated the central fixation cross and allocated their spatial attention to the left or right side of the black rhombus as indicated by a central red arrow cue. A number prime and a letter stimulus were presented simultaneously, one stimulus at the attended location and the other stimulus at the unattended location. All stimuli obtained either an upright or a tilted orientation. CFS masks were shown to the dominant eye to render stimuli invisible. In the visible condition (not shown), stimuli were superimposed on CFS masks. Subsequently, a central red target number appeared and was to be assigned to one of the two categories (i.e., smaller or larger than five) as accurately and quickly as possible. In one block, the secondary task included an orientation discrimination of the attended prime stimulus. The remaining block contained a visibility rating of the number prime, irrespective of attention.

4.2.3.4 Control experiment 1

As previously shown by Ludwig et al. (2013), perception of suppressed stimuli can improve when performing several trials on the same task. To rule out this scenario, we presented the prime stimuli as in the main experiment. They were either invisible or visible and appeared at an attended or unattended location. In contrast to the main experiment, no targets appeared after prime presentation. Subsequently, participants had to report whether the presented number prime was smaller or larger than five. Additionally, visibility of the attended stimulus was to be rated by the PAS. Responses were registered via button press, akin to the procedure of the main experiment.

4.2.3.5 Control experiment 2

By means of 2 AFC and visibility ratings, the second experiment aimed to ensure that perception of the prime stimuli was precise and correct when no CFS masks were presented. The design was similar to the paradigm of the main experiment, with the exception that only visible primes with no CFS masks were used and no targets were displayed. First, participants had to indicate whether the prime number was smaller or larger than five, independent of spatial attention. Secondly, the visibility of the attended stimulus was registered by the PAS. All feedback was given via button press and unspeeded.

4.2.4 Data acquisition and analysis

4.2.4.1 Behavioural data

4.2.4.1.1 Visibility ratings and orientation discrimination

Subjective awareness of prime stimuli was analyzed based on PAS ratings in each experimental condition. Awareness of a stimulus was categorised into “no experience”, “weak glimpse”, “almost clear” or “fully visible”. Experimental conditions comprised “visible attended”, “visible unattended”, “invisible attended” and “invisible unattended”, according to the presentation of the prime stimulus. To test for significant differences between attentional conditions of each visibility level, we applied two-tailed paired t-tests (parametric) and Wilcoxon tests (non-parametric). Single subject performances were computed as relative frequencies. For group analysis, all visibility ratings were averaged for each condition.

Task performance on orientation discrimination was calculated by the mean percentage of correct responses to visible attended and invisible attended stimuli. We included this task to control for correct and reliable allocation of spatial attention.

4.2.4.1.2 Reaction times

Analysis of the main experiment was only carried out on trials with correct target response. Outliers in RTs were defined by shorter RTs than the first quartile minus 1.5 times the interquartile range, or longer than the third quartile plus 1.5 times the inter-quartile range. Furthermore, we excluded trials with anticipatory RTs (i.e., <100ms) from further analysis (Whelan, 2008). For each condition and each subject, the reaction times of all trials were averaged. To control whether awareness of a prime stimulus modulated target response, we tested for significant difference in response times between visible and invisible trials. Additionally, RTs of incongruent and congruent (prime-target) trials were calculated for each visibility level and attention condition. To test for differences in response priming, RTs of congruent trials were subtracted from RTs of incongruent trials. Two-tailed paired t-tests as well as rm-ANOVA were applied for statistical analysis of conditional group differences.

4.2.4.2 Eye-tracking data

Eye-tracking data were collected with a high-speed video-based eyetracker (Cambridge Research Systems, UK; sampling rate: 100 - 250 Hz; spatial accuracy: 0.05°), using a chin rest to allow a steady view. In a first step, we removed all data points that exceeded the dimensions of the screen. Additionally, motion correction was performed by horizontal and vertical drift correction for each run. For noise reduction, we applied a low-pass filter with a sliding window of five data points. Participants were excluded from further analysis if available gaze data represented less than 40% valid data during prime presentation. Coordinates of the fixation cross were calculated individually for each participant by the mean gaze coordinates during fixation screens only. Successful fixation was defined by detected gaze positions on the horizontal axis within 1.71° of visual angle from the fixation cross, corresponding to the distance of the largest stimulus from fixation cross, while prime stimuli were presented. Within this period, fixation performance was computed by the percentage of successful fixation of the recorded gaze data.

4.3 Results

Four subjects had to be excluded from further analysis of the main experiment and control experiments. One subject was excluded since he reported the correct stimulus orientation in only ~50% of the visible trials and ~60% of the invisible trials. Three additional participants were rejected as they falsely performed the number comparison task on the prime stimulus.

4.3.1 Visibility ratings and orientation discrimination

Figure 14 shows the visibility ratings for each condition. Analysis of perceptual awareness reports yielded a mean PAS rating of 1.73 ± 0.09 SEM for invisible attended stimuli and 1.66 ± 0.08 SEM for invisible unattended stimuli. Although small, this difference reached significance or trend level in parametric ($t(24) = 2.07$, $p = 0.0498$; two-tailed paired t-test) and non-parametric tests (Wilcoxon: $p = 0.071$). For visible stimuli, the mean PAS rating for attended stimuli was 3.82 ± 0.04 SEM and 3.75 ± 0.04 SEM for unattended stimuli. This difference was also minimal, but reached statistical significance ($t(24) = 2.11$, $p = 0.046$, Wilcoxon: $p = 0.0495$). Orientation discrimination was performed correctly in 81.62 % ± 0.02 SEM of visible trials. In contrast, correct orientation was reported in 53.01% ± 0.01 SEM of the trials when stimuli were suppressed by CFS. It should be noted that this result was significantly different from chance ($t(24) = 3.11$, $p = 0.002$; one-tailed t-test).

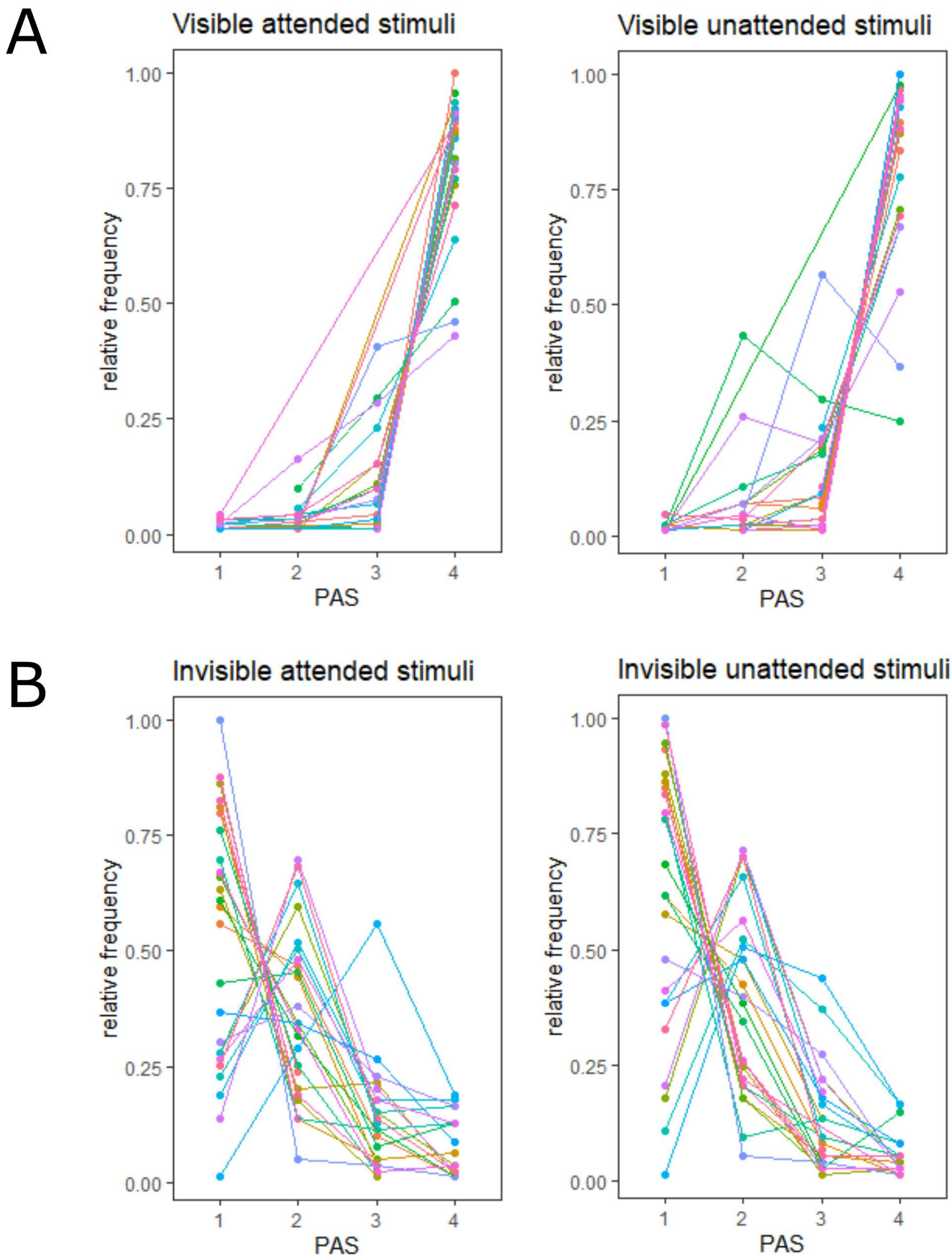

Figure 14. Behavioural results (behavioural study)
A) PAS ratings and relative frequencies in visible trials and invisible trials (B). Each colour represents a participant. Ratings of attended stimuli are shown on the left while the right panels depict responses to unattended stimuli. The difference between visibility ratings of attended and unattended trials was only small in the visible (A) and invisible condition (B).

4.3.2 Main experiment

Only trials with correct responses to target numbers (97.12% ± 0.004 SEM) were included in further analysis. Additionally, we excluded all trials with outliers in RT, which applied to 6.77% of the trials.

4.3.2.1 Priming effects in invisible trials

As positive response priming facilitates responses towards a congruent target, we expected RTs in congruent trials to be faster than in incongruent trials. Following the "CFS-attenuation-by-inattention" model, we predicted that priming effects for unattended prime stimuli would be significantly larger than priming effects for attended stimuli. To address this question, congruency effects were calculated and submitted to statistical analysis for both attentional conditions. Unattended trials revealed no significant difference between congruent (823 ms ± 46 SEM) and incongruent (819 ms ± 46 SEM) prime-target relations ($t(24) = -0.44$, $p = 0.664$; two-tailed paired t-test). There was a slight trend of a congruency effect for invisible attended trials, as mean RTs of congruent and incongruent trials were 822 ms ± 47 SEM and 834 ms ± 48 SEM, respectively ($t(24) = 1.76$, $p = 0.091$; two-tailed paired t-test). Contrary to our prediction, statistical analysis of priming effects between the invisible attended (13 ms ± 7 SEM) and invisible unattended condition (-4 ms ± 9 SEM) failed to reach significance ($t(24) = -1.49$, $p = 0.150$; two-tailed paired t-test). Figure 15 depicts the mean RTs and priming effects of each attentional condition. Additionally, the joint result of RTs of invisible trials (Figure 17), independent from attentional allocation, showed no significant congruency effect (congruent: 822 ms ± 46 SEM, incongruent: 827 ms ± 47 SEM; $t(24) = 0.75$, $p = 0.459$; two-tailed paired t-tests). A two-way rm-ANOVA indicated no main effect of congruency ($F(1,24) = 0.64$, $p = .432$) or attention ($F(1,24) = 0.65$, $p = .150$). Furthermore, there was no significant interaction between the factors attention and congruency ($F(1,24) = 2.21$, $p = .150$).

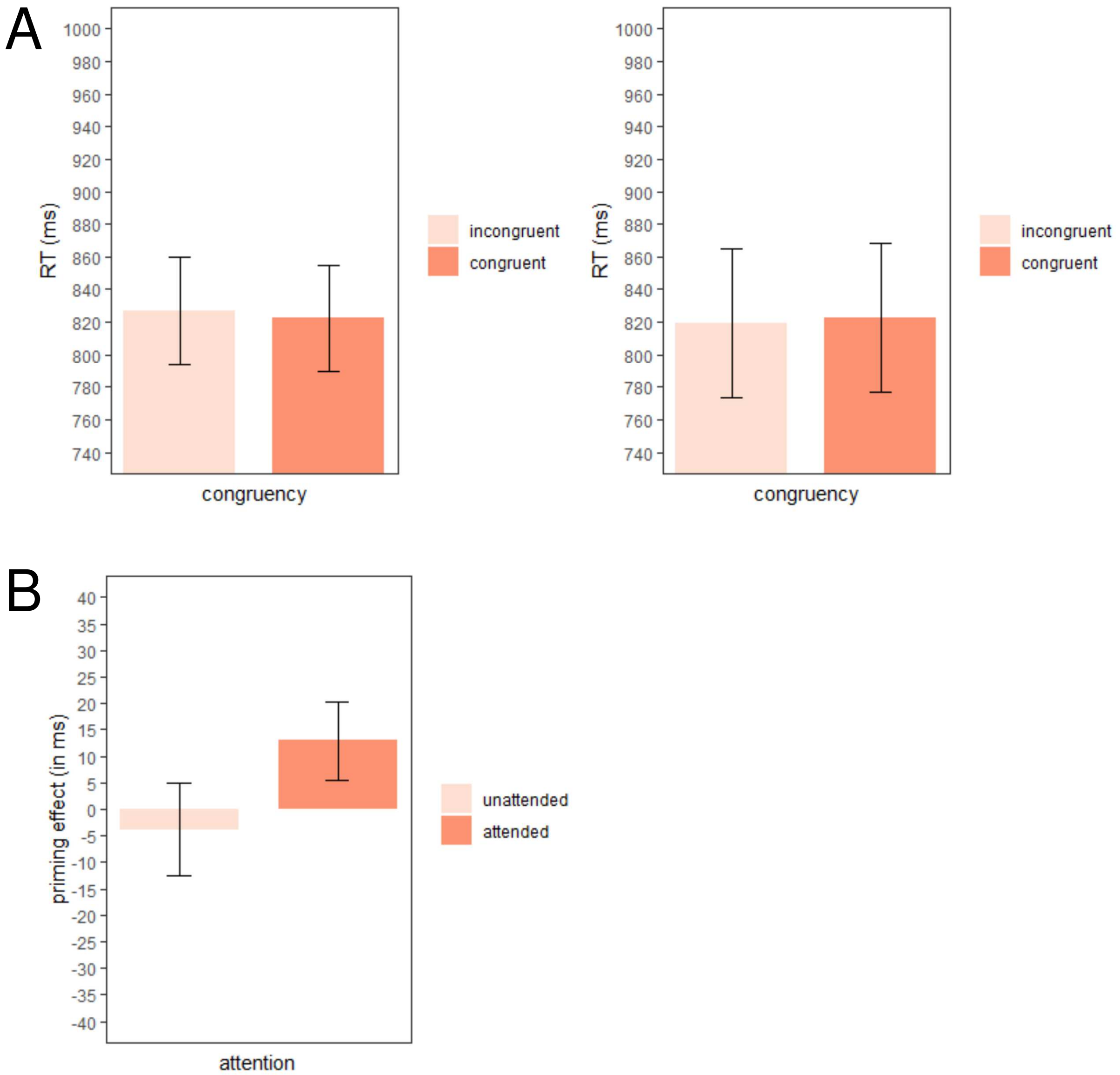

Figure 15. Response times and priming effects in the invisible condition
A) Mean RTs for invisible attended (left) and invisible unattended trials (right). B) Priming effects of trials in the invisible attended and invisible unattended condition. Error bars: ± 1 standard error of the mean.

4.3.2.2 Priming effects in visible trials

In contrast to our prediction that related prime-target relations would facilitate task performance, RTs in trials with superimposed prime images showed a significant inverse priming effect (Figure 16), as the average response times were 880 ms ± 51 SEM for congruent trials and 859 ms ± 46 SEM for incongruent trials ($t(24) = -2.85$, $p = 0.009$; two-tailed paired t-test). When separating the attentional conditions, we found that this effect was present in trials with visible unattended primes only, where response times in the congruent condition resulted in 870 ms ± 47 SEM and 853 ms ± 44 SEM in the incongruent condition ($t(24) = -2.41$, $p = 0.024$). This trend was also found in visible attended primes, as RTs to congruent targets were 890 ms ± 56 SEM and for 866 ms ± 49 SEM for incongruent prime-target relations. However, this result was not significant ($t(24) = -1.891$, $p = 0.071$). Comparing the response priming effects for visible attended primes (-24 ms ± 13 SEM) and unattended primes (-17 ms ± 7 SEM) showed no statistical interference ($t(24) = 0.45$, $p = 0.657$). A two-way rm-ANOVA revealed a significant main effect of congruency ($F(1,24) = 7.87$, $p = .010$), but there was no significant main effect of attention ($F(1,24) = 2.93$, $p = .100$). If inattention attenuates suppression of the prime stimulus and thus facilitates responses to a congruent target, we expected to find a significant interaction of the factors attention and congruency. However, the rm-ANOVA did not indicate that the two factors interacted significantly ($F(1,24) = 0.20$, $p = .657$). Figure 16 shows the average RTs and congruency effects for visible trials.

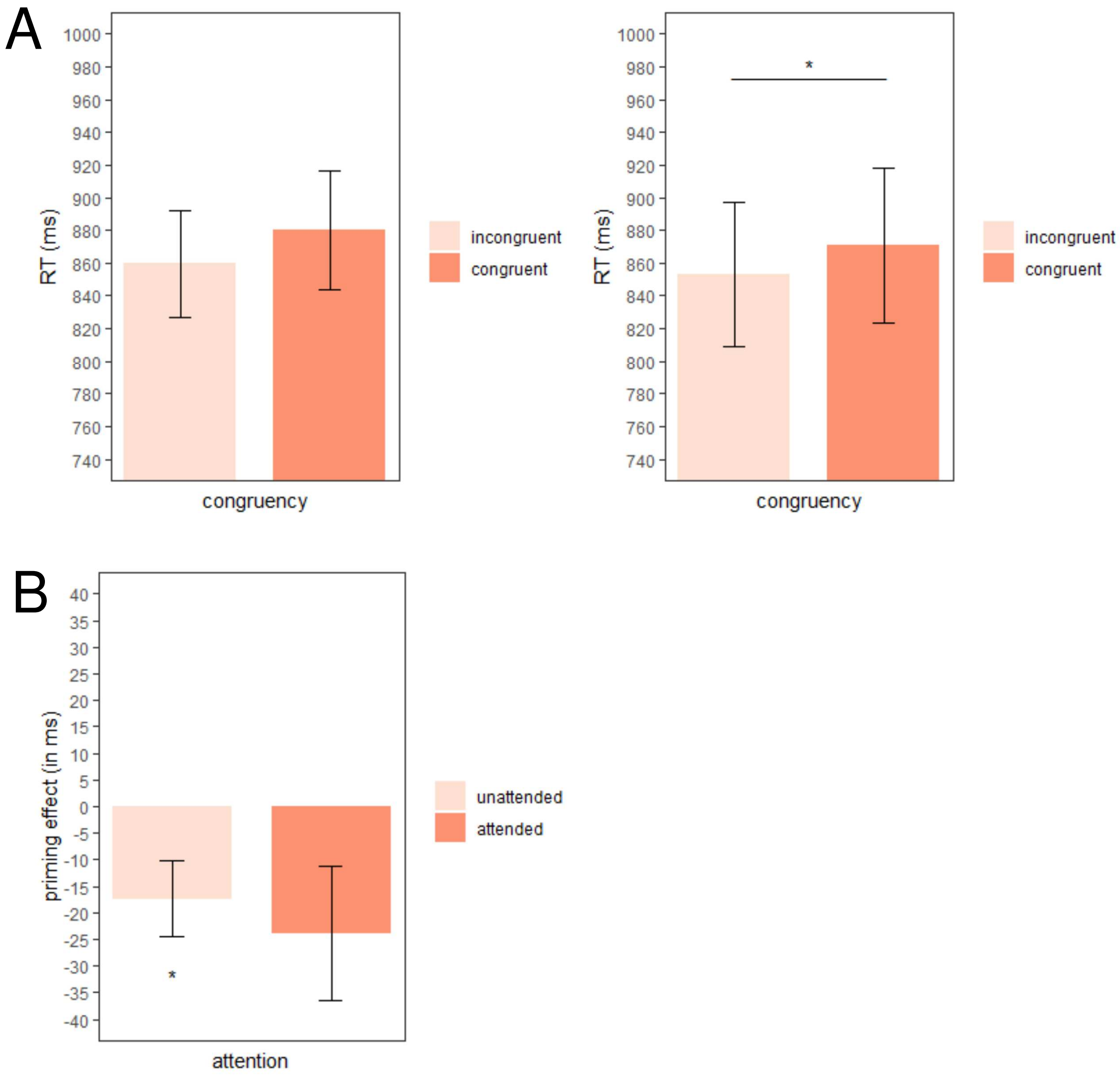

Figure 16. Response times and priming effects in the visible condition
A) Mean RTs for visible attended (left) and visible unattended trials (right). B) Priming effects of trials in the visible attended and visible unattended condition. Error bars depict ± 1 SEM. Asterisks: *: $p < 0.05$.

4.3.2.3 Response times in visible and invisible trials

Previous studies have demonstrated that, in contrast to subliminal primes, response times appear to be slower when presenting supraliminal prime stimuli (Dehaene et al., 2003; Langdon et al., 2013). Dehaene et al. (2003) suggested that the processing of an unmasked prime and a target stimulus requires additional capacities in order to resolve conflicting input, which leads to prolonged response times. Accordingly, we expected RTs in visible primes to be slower than in invisible primes. Indeed, a comparison of mean RTs between visible and invisible trials revealed that RTs in visible trials (870 ms ± 49 SEM) were slower than in invisible trials (824 ms ± 46 SEM). This difference reached significance in a two-tailed paired t-test (t(24) = 2.92, p = 0.007). Figure 17 depicts the mean response times of visible and invisible trials. An rm-ANOVA revealed that of the main factors, only the main effect of visibility reached significance (F(1,24) = 8.45, p = .008). The main effects of attention and congruency did not reach the significance level (attention: F(1,24) = 3.01, p = .096, congruency: F(1,24) = 3.67, p = .067). Moreover, a three-way rm-ANOVA with the factors visibility, attention and congruency revealed no significant interaction (F(1,24) = 1.52, p = .230).

As attention has been shown to boost the representation of object information (Guggenmos et al., 2015), we hypothesized that attention increases the conscious conflict when stimuli are visible and attended. Hence, unattended stimuli that contain less available information, akin to suppressed stimuli, would be associated with an attenuated conflict in stimulus processing. Thus, RTs of unattended trials should be faster. In fact, there was a trend in our data for this hypothesis, as mean RTs of visible attended trials were 878 ms ± 34 SEM and 861 ± 32 SEM for visible unattended primes. However, this trend was not significant (t(24) = 1.70, p = 0.101; two-tailed paired t-test). Similarly, we found no significant difference of invisible attended and invisible unattended stimuli (attended: 878 ms ± 37 SEM, unattended: 862 ms ± 32 SEM; t(24) = 0.801, p = 0.431; two-tailed paired t-test).

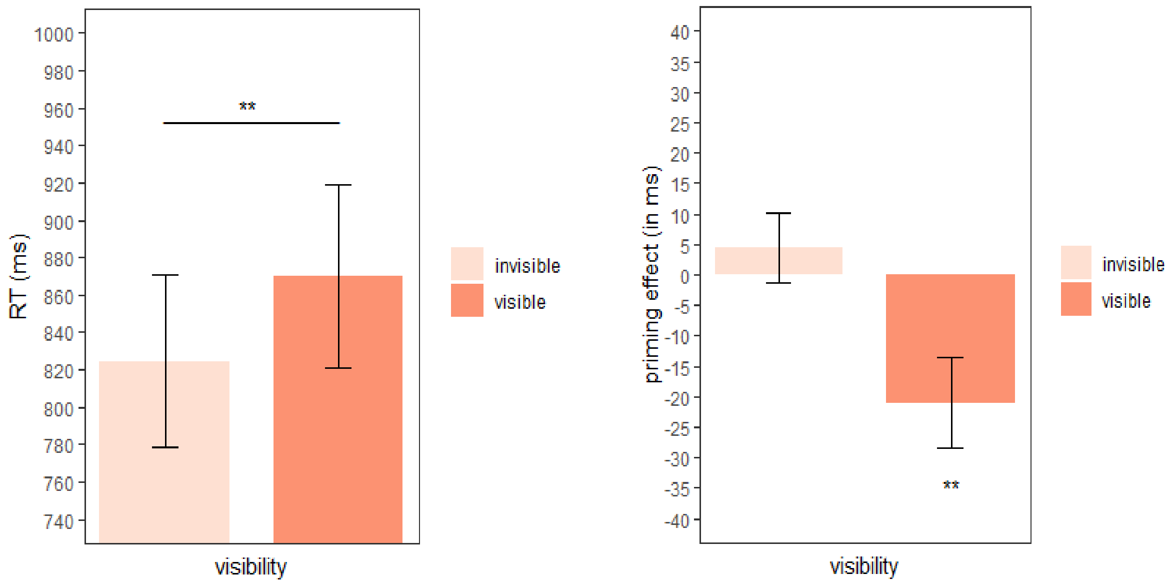

Figure 17. Response times and priming effects in visible and invisible trials
Mean RTs (left) and priming effects (right) include attended and unattended trials in the visible and invisible condition. Error bars depict ± 1 SEM. Asterisks: **: $p < 0.01$.

4.3.3 Control experiment 1

To rule out that participants learned to better perceive the suppressed prime stimuli during the experiment, we analysed the PAS ratings of prime images that were either presented as superimposed images on CFS masks (visible condition) or suppressed by CFS (invisible). The mean PAS rating of suppressed prime stimuli was 1.53 ± 0.08 SEM, indicating that awareness of the prime images did not increase over the course of the experiment. In trials with supraliminal primes, the mean rated visibility yielded 3.86 ± 0.03 SEM. Notably, participants were significantly above chance in discriminating the orientation of the prime stimulus, despite CFS being applied (mean performance of 62.00% ± 0.03 SEM; $t(24) = 4.60$, $p < 0.0001$; one-tailed t-test), which provides further evidence for previous findings by Ludwig et al. (2013). When visible, the orientation discrimination was 95.31% ± 0.02 SEM.

4.3.4 Control experiment 2

In the second control experiment, we tested whether perception of the prime stimuli was correct when they were not suppressed by CFS. The prime stimulus was displayed to each of the two eyes and no CFS masks were presented. Hence, the stimuli should have been perceived consciously. Indeed, the mean PAS rating was 3.80 ± 0.07 SEM. Orientation of the stimuli was correctly discriminated in 96.88% ± 1.40 SEM.

4.3.5 Eye-tracking data

In total, gaze data was successfully recorded in 15 participants. Due to calibration difficulties and technical errors, nine participants were excluded from further analysis. Two additional participants had to be rejected since their recordings did not meet the required percentage of available data (Figure 18). Overall, 98.46% ± 0.52 SEM of analysed gaze points during stimulus presentation confirmed that fixation was successfully performed in the main experiment. This allowed us to rule out that any differences in priming effects were falsely attributed to attention, when in fact eye movements were driving the effect. Group data of eye movements are depicted in Figure 19.

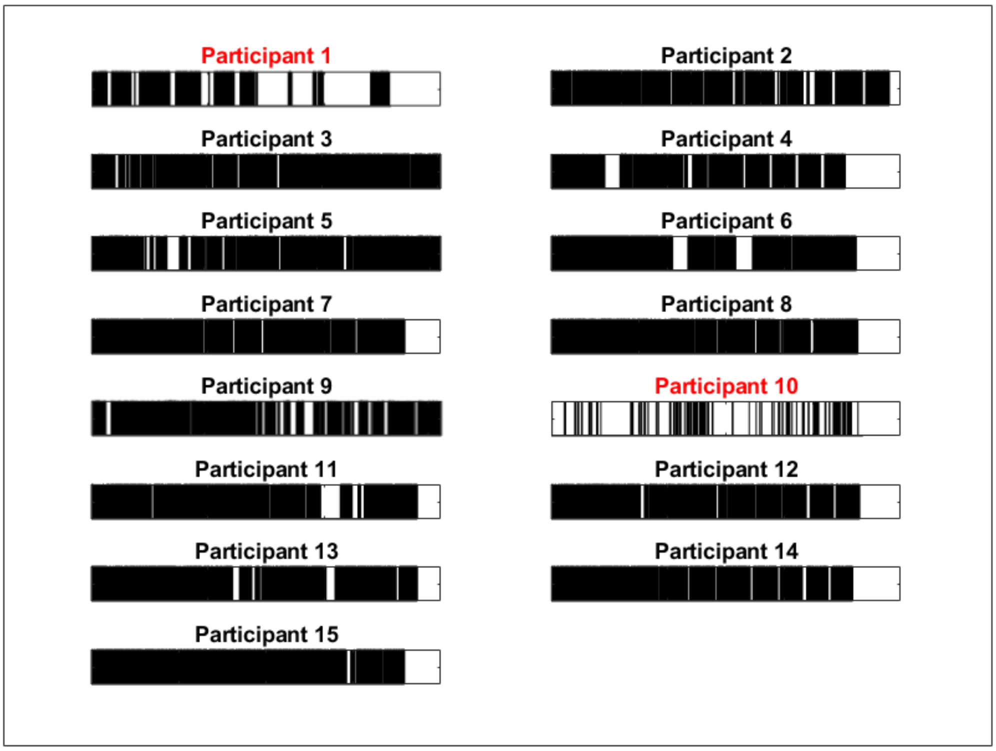

Figure 18. Tracked gaze data (behavioural study)
Each bar illustrates a timeline of the main experiment and shows available data for each participant during stimulus presentation. Black stripes correspond to registered gaze data, white areas represent missing data. Two participants were excluded due to insufficient recorded data (marked in red).

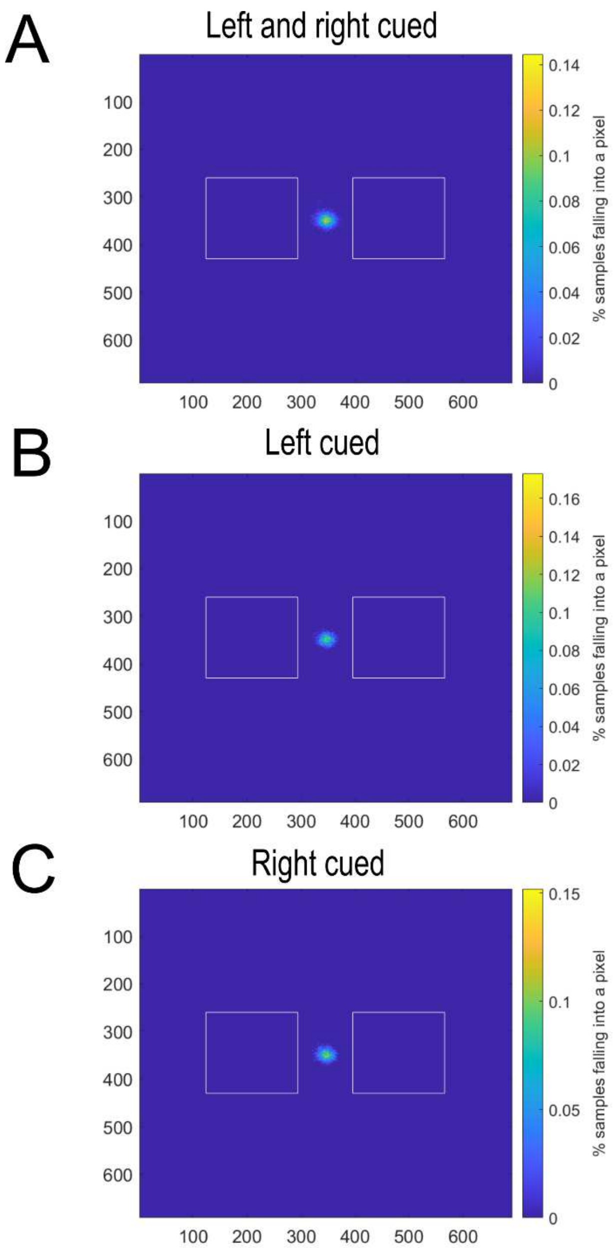

Figure 19. Heatmap of eye-tracking data (behavioural study)
A) Group gaze data irrespective of indicated attention allocation. B) Gaze data of trials with left cued stimuli. C) Gaze data of trials with right cued stimuli. Colour brightness illustrates the quantity of gaze points falling into a pixel. Number and letter stimuli were shown in the left and right squares. This figure displays the left side of the screen, as the participant's left eye was tracked during the experiment.

4.4 Discussion

This study aimed to investigate unconscious numerical priming by probing the "CFS-attenuation-by-inattention" model as introduced by Eo et al. (2016). We predicted to find significant priming effects when number primes were unattended and suppressed by CFS. Akin to a previous study design by Naccache and Dehaene (2001b), participants responded to a centrally displayed target number (2, 4, 6, 9), which was preceded by an attended or unattended number prime (1, 3, 5, 7), and reported whether its value was smaller or larger than five. The prime stimuli were either presented at a spatially attended or unattended location. Following the "CFS-attenuation-by-inattention" model, we hypothesized that number prime effects of unattended numbers would be significantly larger than prime effects of attended numbers.

We found no evidence for unconscious number priming under CFS and inattention. In fact, congruency effects were absent in invisible trials, irrespective of attention. This might indicate that the duration of prime presentation might have been too short to allow subliminal processing of number stimuli. However, this seems to be contrary to previous results by Barbot and Kouider (2012), who demonstrated that, in particular, primes with short durations (60 ms) were more potent for inducing significant priming effects than long prime durations (1000 ms).

Moreover, the task of repetitive attention allocation was highly demanding in our study. Participants reported that they found it difficult to maintain attention and the required speed, suggesting that motivation and performance might have decreased over the course of the experiment. Though the participants continued to respond correctly to the target in more than 90% of the trials, the average response times are noticeably long. Hence, sensitivity in detecting congruency effects might have been significantly impaired and led to false negative results.

Nevertheless, our results may provide further evidence that unconscious number priming does not occur under CFS. This is in line with previous findings which questioned the existence of unconscious numerical priming (Hesselmann et al., 2015). Furthermore, it remains a hotly debated question whether previous findings of unconscious number processing were due to a true effect or are, in fact, false positive results. Several authors have critically examined previous work and showed that, when considering the data analysis carefully, they did not find evidence for unconscious number processing (Moors and Hesselmann, 2018; Moors et al., 2019; Zerweck et al., 2021).

Surprisingly, our study revealed an inverse priming effect when participants were aware of the prime stimulus, as the average RTs of incongruent trials were significantly shorter than the mean RTs of congruent trials. Huber et al. (2002) introduced the "responding optimally with unknown sources of evidence" (ROUSE) model, which aims to explain RT latencies of congruent prime-target relations when stimuli are fully visible. In short, it predicts that features of a prime, mask and target stimulus produce an information source confusion, which needs to be resolved for a target response. Source confusion triggers an estimation of the likelihood - or to what extent – that the induced activity belongs to the prime or the target. Subsequently, prime associated features might be detracted from the processing of the target, misleadingly, if the prime and target stimuli share the same feature (Boy and Sumner, 2010). An overestimation of the prime's feature related activity can deteriorate task responses to the target by deducting relevant information from target processing. In our study, information discounting may have occurred due to congruent stimulus features of number stimuli. Similarly, Mattler (2006) has argued that inverse priming effects are induced by an interaction between features of the prime and target stimulus. Previous results have indicated that negative priming effects can occur when prime and target stimuli share perceptual similarities and that latencies in RTs are possibly due to stimulus interactions at perceptual levels of processing. Moreover, a study by Eimer et al. (2002) revealed that inverse priming effects were absent when the displayed prime and target were dissimilar. Hence, the stimuli used in our experiment may have shared several similarities that led to prolonged task responses.

Additionally, we observed that RTs in visible trials were significantly slower compared to invisible trials. Dehaene et al. (2003) explored this effect by presenting masked and unmasked primes to patients suffering from schizophrenia and healthy subjects. They argued that latencies in trials with unmasked (i.e., visible) primes were due to the control of conscious conflict. As indicated by fMRI measurements, visible primes and targets induced a strong activation of the anterior cingulate cortex (ACC). Dehaene et al. (2003) reasoned that the ACC plays a central role in conflict resolution, underlining previous findings (Carter et al., 2000; MacDonald et al., 2000; Botvinick et al., 2001). However, the prolonged RTs in our visible prime condition may also be explained by the so-called information theory. This model was introduced by Fan (2014) and states that conscious conflict might trigger executive control of attention, aiming to resolve the conflict and prioritize the processing of a target. There is no direct implication in our study as to which model may provide the best fit to the observed data, but it might indicate that attention plays a significant role in resolving conscious conflict.

In addition, performance costs might also be caused by a so-called cost of awareness (CoA). Ophir et al. (2020) defined the cost of awareness based on an observed phenomenon in attentional blink paradigms, namely that an impaired identification of a target occurs when a previously displayed stimulus is perceived consciously (Broadbent and Broadbent, 1987; Raymond et al., 1992). Target responses are most impaired when the target appears around 200-300 ms after the previously perceived stimulus, before returning to baseline approximately 600 ms afterwards (Chun & Potter, 1995). Appealingly, Ophir et al. (2020) incorporated spatial attention in an attentional blink paradigm and presented visible and invisible cues that preceded a target letter. In their study, they found that target responses were only impaired in trials with visible cues. When the cue was suppressed by CFS, this effect was absent. Based on this finding, they defined the CoA as an impaired task performance on trials with visible cues relative to trials with invisible cues. Moreover, the cost of awareness peaks at around 200-300 ms after cue onset and was larger when cue and target appeared at different locations. This might indicate that visible primes in our study led to an impaired target identification due to the CoA, especially since prime and target appeared at different locations. Therefore, participants may have acquired more time to identify and respond to the target.

5 General discussion

The study of unconscious visual processing has created a diverse spectrum of psychophysical blinding methods that are yet to be fathomed. CFS, an interocular suppression method, has become an intriguing and widely-used technique to explore visual perception outside of awareness and has led to diverging, even contradictory conclusions. To reconcile these findings, spatial attention has been suggested as a possible explanatory key factor. As demonstrated in a previous study (Eo et al., 2016), the withdrawal of spatial attention from a suppressed stimulus attenuated CFS and facilitated unconscious semantic processing of words. The aim of this dissertation was to elucidate the role of attention in high-level visual processing under CFS. By integrating supraliminal stimulation in the experimental paradigms, additional conclusions on response modulation due to spatial attention could be drawn. The first study on object categorization in the FFA and PPA did not reveal significant differences in representational activity patterns between unattended and attended stimuli under CFS. In fact, no signs of unconscious processing on a high visual level could be found independent of attention. However, a significant information gain in neuronal response patterns was present when stimuli were attended and consciously perceived. The second study found no significant effect of spatial attention on numerical response priming when prime stimuli were suppressed by CFS. Irrespective of attention, invisible number primes did not trigger significant congruency effects. Visible primes led to longer RTs and provoked an inverse priming effect. In the following discussion, the findings and limitations of these studies will be discussed in detail and an outline for future studies will be presented.

5.1 Missing evidence of Continuous Flash Suppression modulation by spatial attention

The present studies could not find further evidence for unconscious high-level processing when stimuli were unattended and rendered invisible by CFS. Neither behavioural data nor fMRI analysis suggest that unconscious numerical processing and object categorization can be executed under CFS, contrary to predictions made by using the "CFS-attenuation-by-inattention" model. In fact, responses to stimuli did not differ from chance level in the two studies. To interpret these findings, several considerations need to be taken into account.

5.1.1 The Continuous Flash Suppression method

The lack of evidence across the two studies does not necessarily indicate an absence of unconscious high-level processing per se. Heterogeneous findings might be due to specific techniques when applying CFS. For example, different designs of the CFS mask may lead to incongruent suppressor strength. Shared characteristics of mask and stimulus have been shown to deepen suppression (Hong and Blake, 2009; Zadbood et al., 2011; Yang and Blake, 2012). Ludwig et al. (2016) directly addressed this question and demonstrated that different mask contrasts were associated with distinct parametric detection thresholds, while keeping the visibility level constant. At the same time, they found no difference in category-selective activity in ventral and dorsal areas when CFS mask contrast was manipulated parametrically. Han et al. (2018) extended these findings and showed that by decreasing the difference in temporal frequency between mask and target, the duration of stimulus suppression as well as target contrast threshold increased. We are unable to rule out that the designs of the CFS masks, as used in our experiments, induced a stimulus suppression that was too deep to allow for unconscious processing. Inevitably, false-negative results might have led to wrong conclusions (Sterzer et al., 2014).

Moreover, CFS can uphold suppression for several seconds and even minutes (Shimaoka and Kaneko, 2011), building up over time and reaching its maximum at around 500 ms (Tsuchiya et al., 2006; Yang et al., 2014). A key difference between our experiments and the study design of Eo et al. (2016) is the starting point of stimulus presentation. Whereas stimuli and CFS masks appeared simultaneously in both our studies, Eo and colleagues (2016) abruptly displayed the stimuli 300 ms after the onset of CFS. As previously shown, flashing leads to stronger processing of the emerging stimulus (Moradi and Heeger, 2009), possibly enabling more pronounced neural processing.

Additionally, individual contrasts of the stimuli need to be taken into account. As demonstrated previously (Gray et al., 2013), stimuli under CFS become more salient with high stimulus contrast, and may thus experience enhanced visibility and processing. In this regard, individual contrasts in our studies might have been too low, or, while in the case of Eo et al. (2016), they may have been too high. Finding the right measure here remains a complex issue as it is dependent on awareness reports, which remain subjective and are prone to bias.

5.1.2 Unconscious processing under Continuous Flash Suppression

To date, the hotly debated questions remain as to which level CFS interferes with the processing of a visual stimulus, and to what extent CFS allows for unconscious processing. Previous findings indicated that low-level features can be processed under CFS, such as spatial orientation (Kanai et al., 2006), stimulus contrast (Shin et al., 2009) as well as motion (Kaunitz et al., 2011), and colour (Hong & Blake, 2009). Additionally, Hesselmann et al. (2016) suggested that the shape of an object can still be processed under CFS. Further studies, which investigated higher-level processing under interocular suppression, have created a more heterogeneous landscape of findings. The optimistic view that unconscious processes can basically perform the same functions as conscious processes (Hassin, 2013) becomes tempered by the increasing criticism that previous work might have been precipitous (Hesselmann and Moors, 2015). As former results have failed to be replicated and reprovals of methodological and statistical confounds have been rising, the fascination regarding the extent of unconscious processing under interocular suppression has increasingly been critically scrutinised. For example, Sklar et al. (2012) claimed that numerical processing can be executed unconsciously. However, Moors and Hesselmann (2019) applied 250 analyses to further examine the findings of Sklar et al. (2012) and concluded that there is no evidence for unconscious numerical processing when statistical, methodological and theoretical confounds are considered carefully. Bahrami et al. (2010) reported numerical priming under CFS, but it was argued that the design and analysis of this study may be inconclusive and confounded by target numerosity (Hesselmann and Knops, 2014). More support for the notion that numerical processing is largely abolished under CFS comes from Hesselmann et al. (2015) and Zerweck et al. (2021), who also did not find significant numerical priming effects. The results of our behavioural study are in alignment with studies that reported the absence of unconscious numerical processing when stimuli are suppressed by CFS. Additionally, it was suggested that the meaning of Chinese words can be extracted under interocular suppression (Yang and Yeh, 2011). Cheng et al. (2019) aimed to replicate these findings, but did not find evidence for this hypothesis. Still, previous work claimed that semantic processing of words is intact under interocular suppression (Costello et al., 2009; Sklar et al., 2012; Eo et al., 2016), but it should be noted that this optimism may be premature (Kang et al., 2011; Hesselmann and Knops, 2014). The processing of scene congruency has been observed in the absence of visual awareness (Mudrik et al., 2011) by showing that scenes with incongruent object–background relations escaped suppression faster than scenes with a congruent background. However, Moors et al. (2016) could not replicate this effect when applying Bayesian analysis and investigating possible confounds due to stimulus features. Appealingly, categorical processing of tools under CFS was demonstrated in a study by Almeida et al. (2008), which suggests that dorsal stream processes can survive interocular suppression in contrast to ventral stream processes. This finding was challenged by Hesselmann et al. (2016), who argued that the reported priming effects by Almeida et al. (2008) were more likely due to the low-level processing of shape rather than the high-level processing of category. This confound, namely that observed high-level processes may be driven by differences in low-level features, is a critical aspect in several other studies investigating high-level unconscious processing. For instance, Jiang and He (2006) reported unconscious processing of facial expression and facial identity, whereas other studies revealed that differences in low-level features, such as spatial frequency, might have possibly been falsely attributed to the emotional categories of faces in previous studies (Gray et al., 2013; Hedger et al., 2016; Stein and Sterzer, 2014). Hence, care needs to be taken to not falsely claim high-level processing as being responsible for this effect when it is actually low-level features (Moors, 2019). Therefore, it seems more likely that face processing cannot occur under interocular suppression. Accordingly, more studies have failed to provide evidence for unconscious face processing under CFS (Moradi et al., 2005; Shin et al., 2009; Yang et al., 2010; Stein and Sterzer, 2011). Neuroimaging data indicate that CFS reduces stimulus related activity in the early visual cortex, as reported by Yuval-Greenberg and Heeger (2013). They suggested that CFS reduces the contrast of a target by reducing its gain to neuronal responses. Further studies reported the processing of visual information even in higher-visual cortices when stimuli were suppressed by CFS (Fang and He, 2005; Sterzer et al., 2008). However, the findings of Fang and He (2005), namely that objects were unconsciously processed in the dorsal visual stream, could not be replicated by Hesselmann and Malach (2011). The present fMRI study also seems to be in contrast to the findings of Sterzer et al. (2008), who successfully decoded face and house stimuli in the FFA and PPA, respectively. In both studies, stimuli were suppressed by CFS and MVPA was applied for data analysis. Conversely, Sterzer et al. (2008) used high-resolution functional neuroimaging, indicating that our study may have lacked sensitivity when recording neural responses. Moreover, stimulus sizes were much larger in their study and they presented the stimuli foveally, whereas in our study, images were displayed in the peripheral visual field. Since neural responses decrease with increasing eccentricity and decreasing stimulus size (Wu et al., 2013), signal strength might have been too weak to be detected in our study. As the duration of stimulus presentation (600 ms) was equal in the two studies and the stimulus sets comprised a similar amount of greyscale images per category, i.e., 8 and 5 images per category in the study of Sterzer et al. (2008) and our study, respectively, it is not likely that the cause of the divergent findings can be reduced to the employed stimuli. Of note, two further studies could not find evidence for categorical processing of objects in the ventral visual cortex (Williams et al., 2004; Pasley et al., 2004). However, these studies applied univariate analyses, which was one of the main differences in comparison to the study by Sterzer et al. (2008).

Having outlined these conflicting results, one enters a greater realm of potential interpretations of how these divergent observations in behavioural and neuronal measurements may be reconciled. Importantly, care needs to be taken when comparing such varied study designs and analyses. It is crucial to note that behavioural responses do not necessarily reveal the underpinning neuronal mechanism of a direct response (Breitmeyer, 2015). As the global workspace model suggests, neuronal representations of stimulus information are rather distributed over the entire cortex (Dehaene et al., 2006). Hence, an absence of evidence in recorded neuronal responses should not exclude a behavioural response and vice versa. Referring to the study of Eo et al. (2016), the N400 effect was most pronounced when the location judgement was not performed accurately. The authors reasoned that the stimulus was processed preconsciously but did not have the strength to influence behavioural responses. However, our results indicate that neither behavioural nor neuronal responses were modulated by inattention under CFS. This does not exclude unconscious processing of number stimuli or object category, but it might indicate that the effects of attention are very weak or that the model might need to be extended. There is little evidence for unconscious processing in higher-visual areas under CFS inattention. Interestingly, a study by Stein et al. (2015) found that unattended split objects significantly facilitated RTs towards intact target objects. However, this effect was significantly larger in trials with spatially attended prime objects, which rather contradicts the model proposed by Eo et al. (2016). Furthermore, previous studies indicate that the processing of stimulus information under interocular suppression is especially amplified when attention is directed to that stimulus. For example, in a study by Shin et al. (2009), unconscious processing of low-level features was enhanced by spatial attention directed towards the respective stimulus. Moreover, increased adaption aftereffects were observed when attention was directed to a stimulus under interocular suppression. Previous results by Bahrami et al. (2007) also indicate that spatial attention increases the sensitivity to orientation. Moreover, Kanai et al. (2006) found that feature-based attention facilitated tilt aftereffects when adaptors were rendered invisible by CFS, but did not report significant effects of spatial attention. These findings suggest that the influence of attention seems to be rather multifaceted. Further studies are needed to explore the influence of inattention on CFS and interocular suppression in general. For instance, attention or inattention may facilitate unconscious object categorizations of houses and faces, but this might rather be evidenced with different methodological approaches. For instance, probing the model by investigating the face-specific ERP component N170 might be an intriguing avenue for future research.

5.1.3 Attention and interocular suppression

It is still unclear how attention influences interocular suppression and whether the same mechanism applies to binocular rivalry and CFS. Earlier studies have come to different conclusions on how attention modulates interocular suppression. It remains an open question as to whether extenuated rivalry continues in the absence of attention, or whether it is completely abolished (Cavanagh and Holcombe, 2006; Brascamp and Blake, 2012). As previously demonstrated, binocular rivalry seems to be attenuated under inattention (Lee et al., 2007; Roeber et al., 2011; Zhang et al., 2011). Moreover, Brascamp and Blake (2012) reported that rivalry was completely abolished when attention was diverted away from the competing stimuli. In their study, the dynamics of binocular rivalry diminished once attention was withdrawn, resembling the initial dynamics that can usually be found at the very start of rivalry. Based on this result, Eo and colleagues (2016) suggested that attention also acts as a modulator of CFS, namely that inattention to a stimulus under CFS attenuates the depth of its suppression. Eo et al. (2016) successfully tested this hypothesis and demonstrated that unconscious semantic processing of words occurred when probing the "CFS-attenuation-by-inattention" model. However, the literature indicates that unconscious processing under inattention and interocular suppression is rather limited. For example, Cheng et al. (2019) reported that unattended emotional words did not alter RTs in breaking CFS, and neither did frequent words (Heyman and Moors, 2014) nor scene congruency (Moors et al., 2016). In fact, there is evidence that attention facilitates unconscious processing rather than inattention. Previous studies revealed that processing of a suppressed stimulus under CFS was enhanced when it was attended (Shin et al., 2009; Yang et al., 2010; Zhang et al., 2011; Alais, 2012), which contradicts the model of Eo et al. (2016). It remains debated whether even low-level features can survive interocular suppression when unattended. For instance, unattended stimuli were insufficient to elicit afterimages as reported by Ling and Blake (2012), who employed binocular rivalry and flash suppression in their study. This seems to be in line with previous neural findings, which indicated that the withdrawal of attention declines the BOLD signal in early visual cortex when stimuli are suppressed by CFS (Watanabe et al., 2011), potentially reducing target contrast (Yuval-Greenberg and Heeger, 2013).

Interestingly, another concept suggests an intermediate state, where dissonant input of the two eyes is being fused under binocular rivalry and inattention, as suggested by Zhang et al. (2011). In their study, which incorporated rivalry checkerboards, spatial inattention and EEG measurements, unattended and conflicting dichoptic stimuli elicited large amplitudes at intermodulation frequencies. These frequencies indicated that, by inattention, the two images were fused binocularly. They argued that the signals of the two eyes are combined in the visual cortex, which is difficult to reconcile with the idea that information of each stimulus can be preserved and interpreted further up the visual pathway. Appealingly, a novel explanatory framework could cast light onto this issue, namely patchwork rivalry. Just recently, Qian et al. (2019) argued in favor of a mosaic-like processing of two competing stimuli. For instance, Qian et al. investigated visual aftereffects and found that two conflicting unattended stimuli under binocular rivalry were equally processed, rather than merging both images into one presentation. Hence, they reasoned that attention is more likely to link certain fractions of a stimulus, which was complementary to former studies addressing attention as such (Lin and He, 2009; Moors et al., 2017). Similarly, Moors et al. (2017) and Zadbood et al. (2011) argued that, also under CFS, stimuli are rather fractioned. It is reasonable to question the impact of fractured stimuli, but even so, the concept might clarify why certain features appear to be preserved under interocular suppression and others seem not to, e.g., why letters of a word can be extracted but not their meaning (Kouider and Dupoux, 2004). After all, this conflicts with the results of Eo et al. (2016), who demonstrated that high-level, semantic processing occurred especially when the stimuli could not be located. Importantly, interocular suppression methods exhibit substantial differences and it is crucial to consider their individual features and potentials (Stein and Sterzer, 2014; Breitmeyer, 2015; Dieter et al., 2016) as well as their inter-subject variability (Gayet and Stein, 2017; Blake et al., 2019). If inattention abolishes binocular rivalry, it is still unclear whether the same or comparable mechanism can be held for the model of “CFS-attenuation-by-inattention”.

5.1.4 Assessing visual awareness

Subjective and objective awareness measures are the key elements to determine whether a stimulus, or at least parts of it, may have reached awareness. However, the critical issue remains of how to determine the right measurement when an experimenter wants to rule out whether an observed effect may have been due to visibility (Azzopardi and Evans, 2007; Sterzer et al., 2014). The main dilemma arises from the fact that subjective awareness can only be reported by the participant and is yet unable to be controlled for (Malach, 2007; Seth et al., 2008). Hence, previous findings, which reported unconscious higher-level processing, might have been due to partial visibility of the presented stimulus.

When revisiting the results of the orientation judgements in our behavioural study, we observed that correct task performance was significantly above chance in the first control experiment. Consequently, it cannot be ruled out that stimulus visibility increased over the course of the experiment, even if not directly reflected by the average PAS ratings. Nevertheless, this would rather favour the detection of a congruency effect under CFS, which was missing in our study. The difficulty of awareness checks remains a central issue in studying unconscious processing, but it could be addressed by recording visibility ratings online and strictly isolating trials in which participants reported no experience of the stimulus (Stein and Sterzer, 2011; Stein et al., 2012). Additionally, it has been suggested that trials with indicated partial awareness could be consulted in order to draw comparisons with trials in which the stimuli were fully invisible (Stein and Sterzer, 2011; Stein et al., 2012).

5.2 Limitations

5.2.1 Statistical power and analysis

We cannot rule out that the lack of evidence in the two studies might be due to a lack of statistical power. Although a power analysis was conducted for the fMRI study, our estimates might have been incorrect and led to false negative findings. The power analysis was based on the study by Guggenmos et al. (2005), who showed that attention significantly enhanced object decodability in the lateral occipital complex. When effect sizes are overestimated, the resulting sample sizes are often too small to find an effect, which may apply to our studies. However, underestimating power reduces the chance to prove a true effect (Button et al., 2013), which we took carefully into consideration. Interestingly, Button et al. (2013) demonstrated that the average statistical power of studies in cognitive neuroscience is most likely between ∼8% and ∼31%. Hence, previous studies that reported positive findings might have been biased by low statistical power, reducing the likelihood that a significant result had genuinely reflected a true effect.

5.2.2 Attention allocation

Ensuring that participants correctly allocate their attention over the course of the experiment remains a critical issue. We considered that participants might not allocate their attention as indicated by the central arrow cue, possibly biasing the conclusions that are drawn from each of the two studies. For this reason, we implemented an additional attention control task, in which participants were instructed to report the orientation of an attended stimulus. Although participants showed an overall good performance in providing the correct answer for visible stimuli, we cannot rule out that involuntary attention was, as indicated, caught by the unattended stimulus. Previous studies have evidenced that when images were suppressed by CFS, attention can be drawn to emotional facial expressions (Yang et al., 2011), faces with adverted gaze (Xu et al., 2018) and arousing images (Jiang and He, 2006). Moreover, a study by Rothkirch et al. (2012) indicated that participants fixated a task-relevant stimulus under CFS for a significantly longer duration than a task-irrelevant stimulus. Future studies should establish more sophisticated methods that control the accurate allocation of attention.

5.2.3 Technical limitations

The absence of evidence in our studies may also be due to a lack of sensitivity. ERP measurements, and in particular the N400 component which is related to semantic processing and was the central marker in the study of Eo et al. (2016), might be better suited to observe stimulus processing under CFS in comparison to fMRI measurements. As fMRI is characterized by high spatial resolution and poor time resolution, the stimulus related signal strength in our study was present, but possibly too weak to be recorded. Further exploration of our experimental paradigm by means of ERP measurements might help to reconcile the divergent findings. Ultimately, ultra-fine spatial resolution could offer higher sensitivity and allow for additional information gain (Iranpour et al., 2015). Alternatively, two methods may be combined in order to provide high spatial resolution (like fMRI) and high temporal resolution (e.g., EEG or MEG). For instance, an elegant implementation of EEG and fMRI in one study was demonstrated by Hesselmann et al. (2011).

6 Conclusion and outlook

Trying to reconcile the divergent findings in the study of unconscious visual perception under CFS once more revealed how elusive the investigation of unconscious processing is. The two present studies could not find evidence for unconscious high-level processing, irrespective of attention, and question the general applicability of the “CFS-attenuation-by-inattention” model. Our data support the notions that unconscious processing under CFS is rather limited to the subliminal state as described by the global workspace model, and that CFS ranks at a lower level in the hierarchy of psychophysical blinding methods. The results of the two presented studies seem to be in line with the overall trend in the study of unconscious visual processing, namely reporting that there is little evidence for the presence of high-level processing under CFS, if any at all. The lack of consistent and convergent results seems challenging but could be addressed by minimizing the degrees of freedom that are yet to be defined by the experimenter. Setting additional methodological and technical standards, defining these standards by incorporating data which is already accessible and encouraging open science may be promising opportunities to further disentangle our unconscious minds.

7 References

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8 Eidesstattliche Versicherung

„Ich, Juliane Handschack, versichere an Eides statt durch meine eigenhändige Unterschrift, dass ich die vorgelegte Dissertation mit dem Thema:

„Die Modulation visueller Reize unter interokularer Suppression in Abhängigkeit von räumlicher Aufmerksamkeit“ /
”The modulation of unconscious visual processing under interocular suppression by spatial attention“

selbstständig und ohne nicht offengelegte Hilfe Dritter verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel genutzt habe.
Alle Stellen, die wörtlich oder dem Sinne nach auf Publikationen oder Vorträgen anderer Autoren/innen beruhen, sind als solche in korrekter Zitierung kenntlich gemacht. Die Abschnitte zu Methodik (insbesondere praktische Arbeiten, Laborbestimmungen, statistische Aufarbeitung) und Resultaten (insbesondere Abbildungen, Graphiken und Tabellen) werden von mir verantwortet.

[Für den Fall, dass Sie die Forschung für Ihre Promotion ganz oder teilweise in Gruppenarbeit durchgeführt haben:] Ich versichere ferner, dass ich die in Zusammenarbeit mit anderen Personen generierten Daten, Datenauswertungen und Schlussfolgerungen korrekt gekennzeichnet und meinen eigenen Beitrag sowie die Beiträge anderer Personen korrekt kenntlich gemacht habe (siehe Anteilserklärung). Texte oder Textteile, die gemeinsam mit anderen erstellt oder verwendet wurden, habe ich korrekt kenntlich gemacht.

Meine Anteile an etwaigen Publikationen zu dieser Dissertation entsprechen denen, die in der untenstehenden gemeinsamen Erklärung mit dem/der Erstbetreuer/in, angegeben sind. Für sämtliche im Rahmen der Dissertation entstandenen Publikationen wurden die Richtlinien des ICMJE (International Committee of Medical Journal Editors; www.icmje.og) zur Autorenschaft eingehalten. Ich erkläre ferner, dass ich mich zur Einhaltung der Satzung der Charité – Universitätsmedizin Berlin zur Sicherung Guter Wissenschaftlicher Praxis verpflichte.

Weiterhin versichere ich, dass ich diese Dissertation weder in gleicher noch in ähnlicher Form bereits an einer anderen Fakultät eingereicht habe.

Die Bedeutung dieser eidesstattlichen Versicherung und die strafrechtlichen Folgen einer unwahren eidesstattlichen Versicherung (§§156, 161 des Strafgesetzbuches) sind mir bekannt und bewusst.“

Datum   Unterschrift

9 Lebenslauf

Mein Lebenslauf wird aus datenschutzrechtlichen Gründen in der elektronischen Version meiner Arbeit nicht veröffentlicht.

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