Aus der Neurologischen Klinik der Universität Heidelberg (Geschäftsführender Direktor: Prof. Dr. med. Wolfgang Wick)

Influence of arousal and attention on the perception of auditory near-threshold stimuli

Inauguraldissertation zur Erlangung des Doctor scientiarum humanarum an der Medizinischen Fakultät Heidelberg der Ruprecht-Karls-Universität

vorgelegt von

Laura Doll

aus Mannheim

2023

Dekan: Prof. Dr. med. Dr. h.c. Hans-Georg Kräusslich Doktorvater: Prof. Dr. med. Alexander Gutschalk

Contents

List of Figures V				
Li	List of Tables V			
Ał	obrev	iations		VII
1	Introduction			
	1.1	Conscious Perception		. 1
		1.1.1 Theories of consciousness		. 2
		1.1.2 Neural correlates of consciousness		. 3
	1.2	Attention and related brain networks	••••	. 4
	1.3	Arousal, the Locus Coeruleus and the Pupil	••••	. 6
	1.4	Research question	• • •	. 7
2	Mat	erial and Methods		11
	2.1	Data Acquisition		. 11
		2.1.1 M/EEG	· • • •	. 11
		2.1.2 MRI		. 12
		2.1.3 Pupillometry		. 12
		2.1.4 Behavioral data		. 13
	2.2	Presentation of Stimuli and procedure		. 13
		2.2.1 Experiment 1	• • • •	. 13
		2.2.2 Experiment 2	••••	. 14
		2.2.3 Experiment 2b		. 15
		2.2.4 Experiment 3	• • • •	. 15
	2.3	Participants	• • • •	. 16
	2.4	Data Analysis	· • • •	. 16
		2.4.1 Eye Tracking	· • • •	. 16
		2.4.2 M/EEG	•••	. 18
		2.4.3 tMRI	•••	. 19
	o -	2.4.4 Behavioral data	•••	. 20
	2.5	Modeling of neural activity based on Signal Detection Theory .	• • •	. 22
		2.5.1 Bimodal signal distribution	• • • •	. 23
3	Rest	alts		25
	3.1	Experiment 1: Task-related modulation of auditory perception .	••••	. 25
		3.1.1 Behavioral results	••••	. 25
		3.1.2 M/EEG	••••	. 26
		3.1.3 Pupil dilation response	••••	. 27
		3.1.4 Perception of task-irrelevant NT tones		. 29
		3.1.5 Transition probabilities		. 30
	3.2	Experiment 2: Confidence rating of near-threshold perception .		. 31
		3.2.1 Behavioral results		. 33

		3.2.2	M/EEG	34
		3.2.3	Pupil dilation response	36
		3.2.4	Group comparison: conservative vs. liberal listeners	36
		3.2.5	SDT-Model of neural activity: Unimodal vs. Bimodal	40
	3.3	Experi	ment 2b: Comparing rating scales for near-threshold perception	40
	3.4	Experi	ment 3: Attention networks in auditory perception	41
		3.4.1	Behavioral results	42
		3.4.2	Pupil dilation response	43
		3.4.3	Stimulus-evoked BOLD signal	43
		3.4.4	Pre-stimulus BOLD signal and pupil size	50
		3.4.5	Co-variation of BOLD signal and pupil size	51
4	Disc	ussion		53
	4.1	Attent	ional modulation of brain activity	53
	4.2	Influe	nce of arousal	54
		4.2.1	Pupil dilation and performance	55
		4.2.2	Pupil dilation and brain activity	57
	4.3	Correl	ates of conscious perception	58
		4.3.1	P3b	59
		4.3.2	Existence of a perceptual threshold	60
	4.4	Limita	tions and future directions	63
	4.5	Conclu	usion	64
5	Sum	mary		65
6	Zusa	ammen	fassung	67
Bi	bliog	raphy		69
_	0			
Pe	rsona	al publi	cations	81
Da	inksa	gung		83
Ei	desst	attliche	Erklärung	85

List of Figures

1	Behavioral results of Experiment 1	25
2	dSPM-Maps of evoked activity of Experiment 1	27
3	Evoked potentials of Experiment 1	28
4	Pupil dilation response of Experiment 1	29
5	Comparison of listeners who perceived/missed NT tones	30
6	Transition probabilities	31
7	Behavioral results of Experiment 2	33
8	dSPM-Maps of evoked activity of Experiment 2	35
9	Evoked potentials of Experiment 2	35
10	Pupil dilation response of Experiment 2	37
11	Evoked potentials for conservative and liberal participants	39
12	SDT-based models of neural activity	40
13	Response distributions of audibility and confidence ratings	41
14	Results of the pupil analysis in Experiment 3	42
15	Maps of stimulus-evoked activity of Experiment 3	44
16	ROI analysis of cortical BOLD signal	46
17	Maps of subcortical stimulus-evoked activity	49
18	ROI analysis of subcortical BOLD signal	49
19	FIR-Analysis of pre-stimulus BOLD activity	50
20	Co-variation of BOLD signal and pupil size	51

List of Tables

1	Permutation cluster tests of the M/EEG Experiments	32
2	Permutation cluster tests of the PDR' of Experiment 3	43
3	Statistic results of the cortical ROIs	47
4	Statistic results of the subcortical ROIs	48

Abbreviations

AAN	auditory awareness negativity
AC	auditory cortex
ACC	anterior cingulate cortex
AI	anterior insula
AM	amplitude modulated
aMCC	anterior midcingulate cortex
ANOVA	analysis of variance
BOLD	blood oxygenation level-dependent
CON	cingulo-opercular network
CR	correct rejection
DAN	dorsal attention network
DMN	default mode network
dSPM	dynamic statistical parametric mapping
EEG	electroencephalography
FA	false alarm
FDR	false discovery rate
FEF	frontal eye fields
FIR	finite impulse response
FLAIR	Fluid Attenuation Inversion Recovery
fMRI	functional magnetic resonance imaging
GLM	general linear model
GRAPPA	generalized auto-calibrating partially parallel acquisition
Н	hit
HRF	hemodynamic response function
IC	inferior colliculus
ICA	independent component analysis
iPCS	inferior precentral sulcus
IPS	intraparietal sulcus
LC	locus coeruleus
Μ	miss
MCC	midcingulate cortex
MEG	magnetoencephalography
MGN	medial geniculate nucleus
MNE	minimum norm estimate
MPRAGE	Magnetization Prepared Rapid Gradient Echo

MRI	magnetic resonance imaging
NCC	neural correlates of consciousness
NE	norepinephrine
NT	near-threshold
PAG	periaqueductal gray
PCC	posterior cingulate cortex
PDR	pupil dilation response
pMCC	posterior midcingulate cortex
pSTS	posterior superior temporal sulcus
rmANOVA	repeated-measures analysis of variance
ROI	region of interest
RSC	retrosplenial cortex
SC	superior colliculus
SDT	signal detection theory
SMG	supramarginal gyrus
SNR	signal-to-noise ratio
sPCS	superior precentral sulcus
STG	superior temporal gyrus
STS	superior temporal sulcus
ТЕ	echo time
TI	inversion time
ТРЈ	temporoparietal junction
TR	repetition time
VAN	ventral attention network

Chapter 1

Introduction

In daily life, there are many situations, where we consciously perceive a stimulus one time and miss it another time. Imagine, for example, the sound of a vibrating phone: If you are impatiently waiting for a call, chances are that you hear it immediately. But if you are focused on something else, you might need a couple of seconds to hear the sound and maybe a couple more to figure out, where it is coming from. It could even happen that the caller hangs up before you heard it.

But why does this happen? What determines if we perceive a stimulus or not? In the example described above, the main difference between hearing and missing the phone would be selective attention to the expected stimulus, i.e. the sound of the vibration. Another obvious reason would be a difference in (relative) stimulus strength: In a room full of talking people, it would be harder to hear the phone compared to a quite setting. But even in a laboratory setup, where stimulus strength is carefully controlled and attention is systematically varied by introducing specific tasks, physically identical stimuli can be detected in some trials and missed in others. The reasons for this are manifold and have been part of the quest for the neural correlates of consciousness (NCC). In the following section, the concept of conscious perception is outlined together with the most common theories and candidates for the NCC. Afterwards, the two main influences on conscious perception, arousal and attention, are discussed. Finally, everything is brought together to explain the research questions of this thesis.

1.1 Conscious Perception

Conscious perception and its neural correlates have been a much discussed topic during the last decades. First off, the clinical state of being conscious versus unconscious (due to sleeping, being in a coma, etc.) is not of interest for this thesis. In contrast, the focus will be on the consciousness of perception, where the definition is not straight forward. Back in 1995, Ned Block suggested that there are mainly two different kinds of consciousness: While phenomenal consciousness is about the "experience" and its contents, access consciousness is about the availability of that state to other processes like decision making and responding to the stimulus in an appropriate way (Block, 1995). Despite being controversial, this approach is influential to date. Several alternative ways to distinguish levels of (un-)conscious processing were suggested, like preconscious and subliminal processing (Dehaene et al., 2006; Pitts et al., 2018) or partial awareness (Kouider et al., 2010).

In contrast, the definition of the neural correlates of consciousness as "minimal set of neuronal events that gives rise to a specific aspect of a conscious percept" (Crick and Koch, 2003) is widely accepted. However, finding these correlates is not an easy task, as the problem is multifaceted and experimental evidence is equivocal. Consequently, there are many different theories on this topic. A brief overview of the most important ones will be given in the following paragraphs.

1.1.1 Theories of consciousness

Generally, most theories on the NCC can be categorized according to whether they believe the core region of consciousness in the "front" or "back of the brain" (Crick and Koch, 2003). The "front of the brain" theories assume that a fronto-parietal network is necessary for conscious perception, while the "back of the brain" theories focus on local activity in and around the sensory areas.

One representative of the "front of the brain" fraction is the *higher-order theory* (Lau and Rosenthal, 2011). It postulates that a state is only conscious, if one is aware of being in that state, and that for these higher-order thoughts, the prefrontal cortex is substantial.

Arguably the most popular theory of consciousness is the global neuronal workspace theory (Dehaene et al., 1998). While the concept of a global workspace was already introduced by Baars (1988), the theory was expanded by Stanislas Dehaene and colleagues (Dehaene et al., 1998; Dehaene and Naccache, 2001). It predicts that consciousness will arise only, if local neural activity "ignites" the global workspace, from where the information can be accessed by other brain areas for further processing. The ignition of the workspace also results in an amplification of neural activation in the respective sensory areas (Sergent and Dehaene, 2004b). Based on experimental evidence, they postulate that prefrontal, cingulate and parietal cortices play a major role in the global workspace (Dehaene and Naccache, 2001; Sergent and Dehaene, 2004b). This theory includes an important prediction: Because ignition happens only once a threshold of neural activity is crossed, consciousness coincides with a sudden increase in neural activation, which is evident not only in the global workspace, but also in the later time range of the sensory areas. Consequently, a bifurcation of activity between conscious and unconscious events should be detectable (Sergent and Dehaene, 2004b).

The *recurrent processing theory* (Lamme and Roelfsema, 2000) is a "back of the brain" proponent. The general approach is similar to the global workspace theory: feed-forward activation represents unconscious processing and consciousness arises with the feed-back from higher areas. However, this recurrent activity is more local (i.e. stays in the back of the brain). The authors also note that a widespread recurrent activity, which would be equivalent to ignition of the global workspace, can be the next processing step, but is not essential for consciousness.

A growing number of studies suggest that fronto-parietal activation usually can be traced back to task requirements like attention, a behavioral response, or other post-perceptual processing (Koch et al., 2016; Tsuchiya et al., 2015; Pitts et al., 2018; Rutiku et al., 2015). This would argue in favor of a back-of-the-brain correlate of consciousness, but recent evidence for frontal activation in a no-report-paradigm (Hatamimajoumerd et al., 2022) underlines the importance of future studies with rigorous dissociation of all contributing factors.

Similar to the question of where the neural basis of consciousness is, it is also highly controversial whether consciousness is a continuum with different levels of awareness, or an all-or-nothing phenomenon, where a sensory threshold categorizes sensations as conscious or unconscious.

Signal detection theory (SDT) is one example of a threshold-free framework. The theory was developed in the 1950's in mathematics and engineering (Peterson et al.,

1954; Meter and Middleton, 1954), and later transferred to psychology and psychophysics (Tanner Jr. and Swets, 1954; Green and Swets, 1966). Its fundamental concept is to model detection tasks using two gaussian distributions with different means, one for the noise trials, the other one for signal trials (with noise). The distance between these distributions defines the sensitivity, while the decision criterion marks the signal strength, above or below which the observer will respond "signal present" or "absent", respectively (Stanislaw and Todorov, 1999). Although the criterion resembles a threshold, it is - in contrast to a sensory threshold - adopted arbitrarily by the observer and can be raised or lowered (Egan et al., 1959; Green and Swets, 1966, p. 10).

Other theories work with a similar model as the SDT, but include one or more thresholds (Wixted, 2020; Green and Swets, 1966, p. 126-147). Despite variations in the details, they usually have in common that the information, i.e. signal strength, below the threshold cannot be accessed by the observer, hence the corresponding response will be a guess. False alarms either occur because part of the noise distribution exceeds the threshold, or because of invalid guesses on trials below threshold. Above the threshold, similar to a threshold-free model, responses can be based on the signal strength, which means a rating of perceptions is possible. Because of such common features, finding experimental evidence for or against a sensory threshold is difficult, especially when considering models with multiple thresholds, which might be impossible to distinguish from threshold-free models (Green and Swets, 1966, p. 136). This becomes particularly evident when reviewing existing studies arguing for a gradation of perception (with or without threshold, e.g. Overgaard et al., 2006; Roth-Paysen et al., 2022), for the existence of one threshold, i.e. a dichotomy (Sergent and Dehaene, 2004a; Sergent et al., 2021), or even for something in between (Karabay et al., 2022). Therefore, more work is needed to shed some light on this area, and results should always be interpreted carefully from different angles regarding their support of one hypothesis or another.

1.1.2 Neural correlates of consciousness

During the ongoing quest for the NCC, a substantial amount of experimental evidence has been collected, many NCC candidates have been identified, and many have been discarded. An early discovery was synchronized activity in the gamma range (30-70 Hz) in response to visual stimuli (Gray et al., 1989), leading to the conclusion that gamma synchronization is required for consciousness (Crick and Koch, 1990). However, more recent research showed that this might rather be a correlate of attention than consciousness (Wyart and Tallon-Baudry, 2008), as both factors were not properly dissociated in earlier work (Koch et al., 2016).

The P3b, a late component of event-related potentials that appears approximately after 300 ms and can be measured as a parietal positivity (Sutton et al., 1965), is another candidate with a similar history: It is usually observed after the detection of a target and shows a bifurcation between perceived and unperceived trials predicted by global neuronal workspace theory (Sutton et al., 1965; Sergent et al., 2005; Cul et al., 2007; Dehaene and Naccache, 2001). However, in different experimental settings, it has been shown that clearly perceived but task-irrelevant stimuli do not evoke a P3b (Pitts et al., 2012; Pitts et al., 2014), hence it cannot be a correlate of conscious perception (Koch et al., 2016). Instead, it is often related to the behavioral relevance of a stimulus, attention, decision making, response, and other factors that are intertwined with, but distinct from, consciousness (Squires et al., 1975; Twomey et al., 2015; Kamp and Donchin, 2015; Paul and Sutton, 1972; Rutiku et al., 2015).

One of the currently most probable NCC-candidates is the perceptual awareness negativity (Dembski et al., 2021). Since a negativity is oftentimes also measurable for unperceived trials, the authors suggested that to define the awareness negativity as the difference in activation between perceived and unperceived trials. Activation patterns in line with this suggestion were found in the visual (Sergent et al., 2005; Koivisto and Grassini, 2016; Pitts et al., 2014), auditory (Gutschalk et al., 2008; Eklund and Wiens, 2019; Schlossmacher et al., 2021), and somatosensory modality (Schubert et al., 2006; Auksztulewicz et al., 2012). However, some of these authors interpreted the negativity for unperceived trials as an indication that activation of the respective sensory cortex was not sufficient for conscious perception (Sergent et al., 2005; Schubert et al., 2006). The auditory awareness negativity (AAN) usually peaks between 130 and 230 ms, which overlaps with the N1 time range and suggests a relation of the two components (Dembski et al., 2021). Furthermore, it is likely related to a component that has been described as awareness-related negativity (Gutschalk et al., 2008), and to the attention-related N_d , a wave form described as the difference between attended and unattended stimuli (Hansen and Hillyard, 1980). To date, it has not been conclusively clarified whether all of these components are truly independent or just different variations of the same activation.

1.2 Attention and related brain networks

The correlation between attention and consciousness is so tight that it is oftentimes discussed, whether (and how) the two processes can be disentangled, and there is diverging evidence regarding this question.

Attention has been proposed as the process that controls which information become conscious (Posner, 1994; Branch Coslett, 1997; Cohen et al., 2012). Cohen et al. (2012) further argue that there is evidence for attention without awareness but not vice versa, concluding that attention is necessary but not sufficient for awareness. In response to this, it has been suggested to distinguish the effects of bottom-up and top-down attention on conscious perception, since the latter is probably not necessary for the conscious perception of salient stimuli, while the former cannot be dissociated from consciousness (Tsuchiya et al., 2012). Other approaches distinguish between different types of consciousness and propose that attention is required only for some: In an expansion of Dehaene et al. (2006), Pitts et al. (2018) describe a framework of conscious processing, where the final stages depend on the stimulus strength and the amount of attention. In this framework, attention is required to reach consciousness, but the two different kinds of consciousness (phenomenal and access, as in Block, 1995) could rely on different attentional processes. In contrast, Nani et al. (2019) suggest that phenomenal consciousness is possible without attention. Only afterwards, to provide rich "focal" awareness of certain features, attention would be necessary.

In summary, there seems to be consensus that conscious perception is always coupled to some form of attention, but it might be possible to observe attention without consciousness. The diverging opinions emphasize the importance of carefully interpreting results when it comes to the different types of attention and consciousness involved in the respective experiment. To do so, one would also need to know which activation patterns can be traced back to attention. Therefore, the most important brain networks related to attention are introduced in the following sections. The *default mode network* (*DMN*) consists of regions where activity is decreased during task performance compared with resting state (Shulman et al., 1997). From a variety of results, some core regions of this network established over the years, including posterior cingulate cortex (PCC), medial prefrontal cortex, and inferior parietal cortex (e.g., Shulman et al., 1997; Greicius et al., 2003). Fox et al. (2005) called this network "task-negative" and showed that it is anti-correlated with the "task-positive" network, consisting of regions that are activated during performance of various tasks. These regions include the prefrontal cortex, insula, supplementary motor area, intraparietal sulcus (IPS), and frontal eye fields (FEF), and they partially overlap with the dorsal attention network (see below).

Another network related to the execution of tasks is the cingulo-opercular network (CON) consisting of the anterior cingulate cortex (ACC) and the anterior insula (AI). It was previously called task-set system, since it was reliably and steadily activated during the performance of tasks (Dosenbach et al., 2006). Subsequently, Dosenbach and colleagues distinguished it from a frontoparietal network, with a suggested role of adaptive control during performance, while the CON should be responsible for the stable maintenance of the task-set and was called CON going forward (Dosenbach et al., 2007). Later on, it has been called salience network, because it was activated by salient, behaviorally relevant stimuli (Menon and Uddin, 2010). They suggested that the AI serves as a hub to switch between networks for internal and external oriented attention, and that a transient signal form AI helps disengaging brain regions which are not needed for the current task, while engaging areas for attention and other control processes. This could be in line with other studies that found increased pre-stimulus activity in the CON (here AI, ACC, and thalamus) improves performance (Sadaghiani et al., 2009), even when events are unpredictable (Coste and Kleinschmidt, 2016). They conclude that the CON plays an important role for sustaining attention, which is in agreement with maintaining a stable taskset (Dosenbach et al., 2007). In contrast to the characteristics of the DMN described above, they also found that increased activity in DMN-areas enhances performance. Additionally, activity in the so-called dorsal attention network was detrimental for performance, at least for auditory events (Sadaghiani et al., 2009; Coste and Kleinschmidt, 2016).

This *dorsal attention network* (DAN) has been suggested to be in control of topdown attention, such as the selection of stimuli during task performance (Corbetta and Shulman, 2002). Core regions of the network are the FEF and the IPS. The counter part is the *ventral attention network (VAN)*, which is related to stimulus-driven bottom-up attention, and includes the temporoparietal junction (TPJ), frontal gyrus, frontal operculum, and AI (Corbetta et al., 2008). The VAN is activated by the detection of behaviorally relevant stimuli, in particular when they are salient or unexpected, and was suggested to serve as an alerting system, which redirects attention to this stimuli (Corbetta and Shulman, 2002). While both systems complement each other, they also interact: During focused attention, the VAN is suppressed to improve task performance. But when a potentially relevant stimulus is registered, the VAN is activated and signals the DAN to reorient attention towards the new stimuli (Corbetta et al., 2008). The interaction could occur via the prefrontal gyrus, which correlates with both networks (Fox et al., 2006). Evidence for this process was found when examining how signals between the networks influence performance (Wen et al., 2012): Signals from DAN to VAN enhance performance, consistent with the notion of a VAN suppression to filter out unimportant stimuli. In contrast, signals from VAN to DAN impair performance on the current task, as the attentional set is broken in favor of reorienting. But there is also evidence for an involvement of the TPJ in post-perceptual processing and adjustment of expectations instead of reorienting (Geng and Vossel, 2013).

Additional to or as a part of the networks described above, subcortical brain regions are also crucial for attention. For example, the thalamus, which regulates communication between different cortical areas (Arcaro et al., 2018), is an integral part of the CON (Sadaghiani et al., 2009; Coste and Kleinschmidt, 2016). The pulvinar nucleus of the thalamus is particularly known for its role in visual processing (Bourgeois et al., 2020), including attention (Saalmann and Kastner, 2011). But it has been recently proposed that the pulvinar combines information from different sensory modalities and functions as a regulatory hub for adaptive cognition (Froesel et al., 2021). Evidence for the multisensory integration in the pulvinar was found in non-human primates (Vittek et al., 2022). Another important subcortical hub is the superior colliculus (SC), which is also known to be involved in attention, more specifically spatial attention (Krauzlis et al., 2013). While many other regions could be considered in this list, the last one mentioned here will be the locus coeruleus (LC). The LC is the source for cortical norepinephrine (NE) and regulates the level of arousal, which in turn strongly influences perception and performance (Aston-Jones and Cohen, 2005). Therefore, the next section will be dedicated to arousal, its consequences, and the question of why and how to measure it.

1.3 Arousal, the Locus Coeruleus and the Pupil

Arousal describes a general activation level of the brain, which varies between sleep and fatigue at the lower end of the range, and hypervigilance and distractibility at the upper end (Aston-Jones and Cohen, 2005; Maness et al., 2022). The locus coeruleus (LC) is typically considered as main modulator of arousal level by releasing NE via its widespread projections to virtually all parts of the cortex (Aston-Jones and Cohen, 2005; Jones, 1991). But apart from the LC-NE system, other neurotransmitters like acetylcholine, serotonin, or dopamine originating from various sources (basal forebrain, raphe nuclei, periaqueductal gray) are also known to influence arousal (Scammell et al., 2017; Maness et al., 2022).

Arousal is tightly coupled to perception and task-performance: Both low and high levels of arousal deteriorate performance, while medium levels are optimal for task execution (Aston-Jones and Cohen, 2005; McGinley et al., 2015a; Murphy et al., 2011). In a simple model, the beneficial effect of medium arousal on performance is explained by a suppression of unnecessary stimuli and a simultaneously facilitated processing of relevant stimuli (Berridge and Waterhouse, 2003). Aston-Jones and Cohen (2005) expanded this model by proposing two different firing modes of the LC: In the phasic mode, spontaneous firing rates (i.e. tonic activity) are moderate, while the phasic firing in response to stimuli is high. This corresponds to the optimum level of arousal for task performance, where spontaneous activity to irrelevant stimuli is suppressed to exploit the rewards associated with the task. Hence, this mode is also called "exploitation" mode. In the tonic mode, the baseline activity is elevated and phasic responses are diminished, leading to a decrement in performance. Phasic LC responses to task-irrelevant events are not suppressed anymore, leading to distractibility, or the so-called "exploration" of other options beside the current task (Aston-Jones and Cohen, 2005).

This trade-off between exploitation and exploration strongly resembles the interaction between the DAN and VAN (see section 1.2). Consequently, Corbetta et al. (2008) suggested a link between LC activity and the VAN, especially the TPJ, which is activated by salient events during the exploration mode. This parallel is also found in the suggestions of both the VAN and the LC-NE activities as a signal to interrupt ongoing processes for resetting and adapting to new circumstances (Corbetta et al., 2008; Bouret and Sara, 2005).

While LC activity can be directly measured in animals (McGinley et al., 2015a; McGinley et al., 2015b; Joshi et al., 2016), non-invasive methods are necessary for studies with human subjects. One possibility is the measurement of blood oxygenation level-dependent (BOLD) contrast with functional magnetic resonance imaging (fMRI) to determine LC activity (Murphy et al., 2014). But this method is vulnerable to artifacts and high noise levels, especially without the use of dedicated sequences for LC localization and recording (Turker et al., 2021). Additionally, fMRI is expensive, rather slow and may not be suitable for all tasks. A convenient and widely used alternative is pupillometry, since pupil size covaries with LC activity and can therefore be used as a proxy for arousal (Aston-Jones and Cohen, 2005; McGinley et al., 2015a; Joshi et al., 2016; Murphy et al., 2014). Pupil size shows the same nonlinear relationship with performance as LC-activity (Murphy et al., 2011; McGinley et al., 2015a) and has been used to track the transition between exploitation and exploration mode (Gilzenrat et al., 2010). Furthermore, the frequent co-occurrence of the phasic pupil dilation response (PDR) and the P3 component of the event-related potentials, and the similar modulation of both by target probability, performance and more, resulted in the proposal of a close relationship between the two (Nieuwenhuis et al., 2011; Nieuwenhuis et al., 2005; Murphy et al., 2011). However, there is also evidence for a dissociation of both responses (Kamp and Donchin, 2015).

The physiological basis for the correlation of LC activity and pupil size is not yet entirely understood. Simply put, the pupil size dilates either through an increasing influence of the sympathetic nervous system and a stimulation of the dilator muscle, or a decreasing influence of the parasympathetic nervous system with an inhibition of the Edinger-Westphal nucleus and a relaxation of the sphincter muscle (Nieuwenhuis et al., 2011). The LC innervates the Edinger-Westphal nucleus and likely modulates pupil size via this pathway. But there are also projections from LC to SC, which can also directly and indirectly modulate pupil size along different pathways (Joshi and Gold, 2020; Wang and Munoz, 2015). Furthermore, besides NE, other neurotransmitters like acetylcholine are known to play a role (Reimer et al., 2016; Joshi and Gold, 2020; Maness et al., 2022). Other studies showed widespread cofluctuations of cortical activity and pupil size, but with partly divergent results (Schneider et al., 2016; DiNuzzo et al., 2019; Yellin et al., 2015; Murphy et al., 2014), underlining the necessity for more research to understand arousal with all its cortical, subcortical, and peripheral causes and effects.

1.4 Research question

Experiment 1 of this project was designed to investigate auditory perception with different levels of attention and arousal. A combination of magnetoencephalography (MEG) and electroencephalography (EEG) was used to measure the AAN and the decision related P3b. The pupil size was recorded simultaneously as a proxy for

LC activity and arousal. The latter should influence task-performance in a nonlinear way, with optimal performance at medium levels of arousal. Attention was manipulated by switching the role of target and distractor between two competing stimuli of different saliency across the three runs of the experiment. The attentional modulation of evoked brain activity or pupil dilation was expected to be larger for near-threshold compared to more salient stimuli. For example, the near-threshold stimulus was not expected to be perceived, when the salient stimulus was taskrelevant and participants were not yet informed about the near-threshold one. But based on Pitts et al. (2012), perception of this near-threshold stimulus was expected once they have been task-relevant in a previous run. This should provide the opportunity to classify detected vs. undetected stimuli based on the evoked pupil dilation. A successful classification of non-targets (i.e. trials without a button press) would enable an investigation of perceptual awareness without the confounding factors of decision making and response (Tsuchiya et al., 2015; Frässle et al., 2014). Furthermore, this could also be used to test the hearing of impaired individuals or infants who are unable to indicate perceptions.

Experiment 2 also used pupillometry, MEG, and EEG. It was designed based on the findings of Experiment 1 to investigate the influence of the decision criterion. For this aim, several response options were provided, representing the confidence in tone absence or presence in one trial. This served two important purposes: First, reproducing the findings of the first experiment, and evaluate if the decision criterion has any relevance to them. Second, clarifying whether the confidence is directly related to the evoked responses, and if this is an indication for or against a threshold for conscious perception. If there was no such threshold, the gradation of confidence ratings should result in a gradation of neural responses and stimulus-evoked pupil dilation across both detected and undetected tones. In contrast, if a threshold exists, the responses for undetected tones should not degrade further, regardless of the level of confidence.

Experiment 2b, a previously unplanned psychoacoustic extension of Experiment 2, was added because of a recent study with stimuli similar to those of the present experiments (Sergent et al., 2021). This study provided evidence for a perceptual threshold with the use of an audibility rating scale. To find out, how the use of different ratings scales could influence the results, Experiment 2b used two runs of the same detection task, once with the confidence rating used in Experiment 2, and once with the audibility rating used in the study by Sergent et al.

In Experiment 3, fMRI was used for an examination of attentional network under similar task-related modulations of selective attention as in the first experiment. The measurement was again complemented with pupillometry. As in Experiments 1 and 2, a non-linear influence of arousal, i.e. pre-stimulus pupil size, on the detection of near-threshold stimuli was expected. In a similar manner, pre-stimulus activity in certain brain regions, most notably the CON, should differ between subsequently perceived and unperceived tones (Coste and Kleinschmidt, 2016). It was further expected to find evoked activity in the superior temporal sulcus (STS) for all perceived stimuli, based on previous work from our lab (Wiegand et al., 2018). This area is part of the TPJ, thus it also belongs to the VAN and could be correlated to the pupil size, as suggested by Corbetta et al. (2008). Based on these anticipated connections between 1) pre-stimulus pupil size and CON, and 2) pupil dilation response and VAN, a correlation of BOLD activity and pupil size should reveal if and how these - and potentially other networks - covary with the pupil size.

In summary, the experiments were designed to test how arousal and attention influence conscious perception in general, and the activation of different areas in particular. The recording of the pupil size thereby should serve not only as a measure of arousal, but also as an indication of the involvement of subcortical systems such as the LC and SC in the process of conscious perception.

Chapter 2

Material and Methods

2.1 Data Acquisition

2.1.1 M/EEG

MEG and EEG are used to measure changes in the magnetic and electric fields originating from neuronal activity. The advantage of M/EEG over other imaging methods like fMRI is the direct measurement of neuronal activity and the high temporal resolution in the millisecond range (Sommer, 2011). Under ideal circumstances, spatial resolution can be in the millimeter range, but it strongly depends on the signal-to-noise ratio (SNR), the number of sensors, and the analysis method, and it might rise to few centimeters (Hämäläinen et al., 1993; Cohen et al., 1990; Samuelsson et al., 2021). Combining MEG and EEG measurements improves localization accuracy compared to either method alone (Molins et al., 2008). EEG is particularly useful for sources oriented radially to the scalp, as they do not produce a measurable magnetic field outside the head, so MEG sensors cannot capture their activity (Silva, 2010).

For the present study, MEG was recorded with a 122-channel whole-head system consisting of 61 pairs of planar gradiometers (MEGIN Oy, Helsinki, Finland; Ahonen et al., 1993). EEG was recorded with caps and electrodes by EASYCAP GmbH (Wörthsee, Germany) and two SynAmps amplifiers for up to 32 electrodes each by Compumedics Neuroscan (Abbotsford, Victoria, Australia). In the first experiment, 63 equidistant EEG channels were used, this layout extends below the inion to cover as much of the scalp as possible to improve source localization. Additionally, ECG was recorded and later used to correct cardiac artifacts. For the second experiment, only one of the SynAmps amplifiers was available, therefore the standard 10-20 electrode layout with 32 channels was used. In both experiments, preparation began with fitting the cap and applying an electrode gel to the participant's scalp under each electrode to reduce the resistance to below $3k\Omega$. Afterwards, the MEG coils were fixated on the cap. These coils are used to measure the head position relative to the MEG sensors, which is necessary for the correct localization of signals. The positions of these coils, all electrodes, and additional head shape points were digitized using the Polhemus 3D Space Isotrack2 system (Polhemus, Colchester, Vermont, USA). The coordinate system was defined by the left and right pre-auricular points and nasion. The head position of the participant in the MEG was measured in the beginning of each run. The M/EEG data were recorded with a sampling frequency of 1000 Hz and a low-pass filter of 330 Hz.

2.1.2 MRI

fMRI captures neuronal activity indirectly by measuring the BOLD signal. This signal reflects the oxygen supply of the brain, as the magnetic properties of hemoglobin change when oxygen is bound to the molecule (Ogawa et al., 1990). In brain areas with increased activity, the supply of oxygen increases more than the usage (Fox and Raichle, 1986), which results in an increases of signal strength (Kwong et al., 1992). This indirect relationship between brain activity and signal change results in a temporal offset: The peak in signal strength occurs approximately 5 s after the underlying change in brain activity (Sommer, 2011). Furthermore, scans of the whole brain are usually sampled only every few seconds (repetition time, TR), resulting in very low temporal resolution compared to M/EEG. The spatial resolution can, in contrast, be in the millimeter range or even below. The limits depend on technical aspects like field strength, and on the measurement sequence, which is usually a trade of between spatial and temporal resolution: a larger field-of-view or smaller voxels require a longer TR and vice versa.

The fMRI of Experiment 3 were done with a 3T Siemens Magnetom Prisma (Siemens Medical Systems, Erlangen, Germany), using a 32-channel head coil. A T2*-weighted echo-planar imaging sequence with generalized auto-calibrating partially parallel acquisitions was used (GRAPPA; $64 \times 64 \times 32$ voxels of $3 \times 3 \times 4$ mm³, TE=30 ms, TR=2 s, flip angle 80°), 635 volumes were acquired in each run. There was no pause between the acquisition of two volumes to produce a quasi-continuous noise with as little audible transition as possible.

Apart from the fMRI scans, structural MRIs were necessary for both the M/EEG and the fMRI data analysis to ensure proper source localization (see section 2.4 for more info). The measurements for the first two experiments were done with a 3T Siemens Magnetom Trio. For Experiment 3, the structural scans were done with the Siemens Magnetom Prisma, directly before the functional scans. The structural scans consisted of a T1-weighted MPRAGE sequence (Magnetization Prepared Rapid Gradient Echo, $256 \times 256 \times 192$ voxels of 1 mm^3 , TR=1570 ms, TE= 2.67 ms, TI=900 ms, flip angle 9°) and a T2-weighted FLAIR sequence (Fluid Attenuation Inversion Recovery, $192 \times 256 \times 25$ voxels of $0.9 \times 0.9 \times 5.5 \text{ mm}^3$, TR=8500 ms, TE=135 ms, TI=2400 ms, flip angle 170°).

2.1.3 Pupillometry

Eye tracking was performed with the Eyelink 1000 Plus (SR Research Ltd., Ottawa, Canada). The right eye was tracked with a sampling rate of 1000 Hz and pupil area was recorded along with gaze position. Pupil size is measured in arbitrary units, a conversion to millimeters was not necessary here, since only the relative change in pupil size was of interest.

The eye tracker was positioned in the lower part of the participant's visual field directly below the screen. For the MRI measurements, screen and tracker were outside the bore and a first-surface reflecting mirror was used so that the eye could be tracked and the participant could see the screen. Before each run, pupil detection thresholds were checked and adjusted if necessary. This was followed by a calibration and validation procedure, in which the participants had to fixate circles that appeared at nine locations arranged in a 3x3 grid to cover all parts of the screen. During the measurement, participants were asked to fixate a cross in the center of the screen. This was necessary, because the measurement of pupil size can be distorted if gaze position is no longer centered, i.e. the eye is (partially) recorded from the side.

Participants were told that blinking was allowed, but should be kept at a reasonable low amount and not time-locked to the stimulus, if possible.

All measurements of the first experiment were conducted with the lights in the MEG booth turned off, leaving the screen as the only light source. In the following experiments, lights were turned on because the strong contrast between the bright screen and the dark environment was more fatiguing to the eyes.

2.1.4 Behavioral data

In all four experiments, button presses were collected using fiber optic response devices by Current Designs (Philadelphia, Pennsylvania, USA). During the M/EEG measurements, the signal was transferred to the stimulation channels of the MEG and saved within the M/EEG file. In the psycho-acoustic experiment, the responses were transferred to the stimulation computer and recorded with MATLAB and Psychtoolbox. Finally, in the fMRI experiment, button presses were again transferred to the respective stimulation computer, where they were processed in the Experiment Builder Software provided by the eye tracker manufacturer (SR Research) and saved in the eye tracking result file.

2.2 Presentation of Stimuli and procedure

For the M/EEG experiments and the psychoacoustic experiment, an in-house developed program based on MATLAB (The MathWorks Inc., Natick, Massachusetts) was used to create the stimuli in real-time during the experiment and present them with a sampling rate of 48 kHz. The stimulation was delivered with a programmable attenuator (PA5, Tucker-Davis Technologies (TDT), Alachua, FL, USA), headphone amplifier (HB7, TDT), and ER-3 earphones with custom tubes (Etymotic Research, Elk Grove Village, IL, USA). This was combined with Psychtoolbox (Brainard, 1997) and the Eyelink Developer's Kit (SR Research) to control the eye tracker during the acoustic stimulation.

For the fMRI experiment, stimuli were also created in MATLAB, but saved as audio files. The playback during the experiment was done with the Experiment Builder software, which also controlled the pupil recording. The stimuli were also delivered with the PA5 attenuator and the HB7 headphone amplifier, but combined with MRI compatible earphones (S14 by Sensimetrics, Gloucester, MA, USA).

The only visual elements during the three main experiments were the calibration screens for the eye tracker and a black fixation cross presented on an otherwise gray screen during the whole course of the measurement. These screens were controlled by Psychtoolbox and the Eyelink Developer's Kit during Experiments 1 and 2, and by the Experiment Builder script during Experiment 3.

2.2.1 Experiment 1

The acoustic stimulation in the first experiment consisted of epochs of white noise with a random duration between 3 s and 5 s. There was no pause between the noise epochs and because of the random nature of white noise, transitions between epochs were not audible, creating the impression of continuous noise. At the beginning of each epoch, one of three different stimuli was played:

- A transient amplitude modulation of the noise with a duration of 100 ms, a modulation frequency of 50 Hz, and a modulation depth of usually 25%. The latter was increased to 35% for four participants.
- A pure tone with a frequency of 1000 Hz, a duration of 100 ms including hamming windows of 10 ms at the beginning and the end of the tone, and an SNR close to the 50% detection threshold. The SNR for these near-threshold (NT) tones was usually -21 dB, but increased to -19 dB for one participant.
- A pure tone as described above, but with an SNR of -100 dB, leaving the tone inaudible for the listener. These tones served as catch trials to control the false alarm rate

In each of the three identical runs, 50 amplitude modulated (AM) noise trials, 150 NT tones, and 50 catch trials were presented in a pseudo-random order, i.e. randomized but equal across participants, with a total duration of 17 min for each run. Between the runs, participants stayed seated in the MEG, but could rest as needed. During the first and last run, participants were instructed to indicate the detection of AM noise via a button press with the right hand. In the second run, the task was to detect the NT tones while ignoring the AM noise. Participants were not informed about the presence of the NT tones before the first run. A short example of continuous noise including amplitude modulations was played to familiarize participants with the stimulus before the first run was started. When detection of the AM noise was not reliable in the example set or the first minutes of the actual run, the modulation depth was increased to 35%, before the run was (re-)started. This was the case for four participants.

Before the second run, an adaptive testing procedure based on Lecluyse and Meddis (2009) was conducted to train participants for the detection of the NT tones: Short intervals of white noise were presented with or without a pure tone. After the interval, the participant had to respond, whether a tone was present or not. If a tone was detected successfully, the SNR was decreased for the next interval; if it was missed, the SNR was increased. The test was stopped once the responses switched eleven times between "Yes" and "No", and the 50% detection threshold was estimated as the average SNR across the last seven of those turning points. Apart from the SNR, the tone characteristics were identical to those used in the actual experiment. However, pilot experiments showed that the obtained thresholds' transferability to a longer experimental setting was limited: Subjects with a low threshold value had the tendency for an unusual low hit rate and vice versa. Hence, the SNR was usually set to -21 dB, which proved as a reasonable stable value in the pilot experiments.

After this adaptive test, the second run was started. Performance was monitored and if detection was too low during the first minutes, the run was restarted with an increased SNR. This was the case for one participant, were the final SNR was -19 dB. Before the last run, participants were not informed that NT tones would be present again in the last run. The instruction was only to repeat the task of the first run, i.e. detecting the AM noise. Hence, the main difference between first and last run was the previous experience with the NT stimuli.

2.2.2 Experiment 2

The second stimulation again consisted of white noise epochs containing either nearor subthreshold tones, i.e. target or catch trials. This time, however, the tones appeared between 800 and 1200 ms after the noise onset, and 2s after the tone, the noise stopped. The duration of the following pause was fixed at 1.3s, except for the first participant, where a 1s pause was used. Participants were instructed to report their perception and confidence during this pause. Three buttons were available for each hand: The right hand was used if the participants perceived a tone, and the left hand was used if they did not. On each hand, the index finger button represented high confidence (3) in signal presence or absence, the middle finger button represented medium confidence (2) and the ring finger button represented low confidence (1). These six response options and the presentation of both signal and catch trials resulted in 12 possible outcomes: hit (H), miss (M), false alarm (FA), and correct rejection (CR), each with three different confidence levels.

The stimuli were presented in two runs of 20 min, with 250 NT tones and 50 catch trials each. Participants had the opportunity to rest between the runs if necessary.

2.2.3 Experiment 2b

This psychoacoustic experiment featured the same acoustic stimulation as Experiment 2, but with different rating scales in each of the two runs. During the first run, participants had to rate the audibility on a scale from 0% to 100%. Participants were informed that all tones would be soft, so that they could make use of the whole scale even without salient tones. The scale consisted of one continuous horizontal line and two vertical ticks and the end points, the marker (another vertical line) always appeared at 50%. Participants could move the marker in steps of 2.5% and confirm their final choice via button presses. In the second run, the rating procedure was the same as in Experiment 2 with six different confidence levels ranging from high confidence in the absence of a tone to high confidence in tone presence. In contrast to the previous experiment, the duration of the pause between trials was not fixed in either run, but lasted as long as participants needed to make a response, and the button assignment was shown on the screen for the second run.

Each runs consisted of 240 (210) signal and 40 (35) catch trials for the first (second) half of the participants. The number of trials was reduced after the first half, because the high number of trials combined with a slow response mechanism in the audibility rating resulted in long duration (>40 min) for some participants.

2.2.4 Experiment 3

The auditory stimulation of the fMRI experiment very much resembled that of the first experiment with the previously used NT tones in continuous white noise as main stimuli. In addition to that, the same subthreshold tones (-100dB) were again included as catch trials, and salient AMs tones instead of the AM noise served as distractors. These AM tones had the same frequency (1000 Hz) as the NT tones, but lasted for 200 ms and had an SNR of +22 dB. The modulation frequency was 50 Hz with a modulation depth of 70%. After the structural MRI scan, each participant completed three runs of the same stimulation while functional MRI and pupil size were recorded. The instructions differed for each run: Before the first part, they were not informed about the different stimuli, and the only task was to listen. After this run, subjects were asked whether they had heard the AM tones and were consequently instructed to report their detection by pressing a button with the right hand during the next run. Before the last run, participants were asked whether the had perceived the NT tones. They listened to some short examples containing only the NT tones (with varying SNRs) to get used to the stimulus. Afterwards, they were

instructed to detect the NT tones while ignoring the AM tones, and the final run was started. Performance was observed for the first minutes, and if a subject failed to detect the NT tones, the recording was stopped, further examples were played to them, and the measurement was restarted. In those cases, the SNR was not adjusted to keep the stimuli identical across the three runs.

2.3 Participants

The experiments were part of a study approved by the ethics committee of the Medical Faculty at Heidelberg University (No. S-327/2016), and participants provided written informed consent. All participants were healthy and without any reported hearing impairment.

In the first experiment, 14 participants were recorded and included (6 male, 8 female, 21-32 years of age, mean 25.4) in the analysis. 27 subjects took part in the second experiment, 17 of those were included (9 male, 8 female, 19-35 years of age, mean 24.4), while the rest was excluded because of poor data quality (N=9) or performance (N=1, d'<0, i.e. FA rate was higher than the hit rate). In the psychoacoustic experiment, 10 participants were included (3 male, 7 female 21-30 years of age, mean 26.0), while three were excluded due to small methodological differences in the procedure, which could have biased the results. 30 participants completed the fMRI experiment, but only 20 were included in the final analysis. The remaining 10 were excluded because of their performance (detection rate below 10% in the second/third run, N=1/7, respectively) or artifacts in the data (N=2). Additionally, three of the 20 included subjects had to be excluded from the analysis of PDR, due to their high blink rates, which resulted in no usable epoch for some conditions.

Of all included participants, one took part in Experiments 1 and 2, one in Experiments 2 and 2b, and one in Experiments 2b and 3; all others participated only once.

2.4 Data Analysis

Various software packages were used for data analysis, depending on the type of data or the processing step: Eye tracking data sets were analyzed in MATLAB, M/EEG data sets with MNE-Python (Gramfort et al., 2013), and fMRI data sets with Freesurfer (Fischl, 2012) and MATLAB. The final plots for all types of data were created in MATLAB, while the statistical analysis was done with different programs: MNE-Python was used for permutation cluster tests and repeated-measures analyses of variance (rmANOVAs), MATLAB for t-tests, and SAS (SAS Institute Inc., Cary, NC, USA) for rmANOVAs and contrast analyses. For the ANOVAs, Greenhouser-Geiser correction was applied to correct for sphericity deviations. Furthermore, the BOLD activation maps, the t-tests, and the rmANOVAs of Experiment 3 were corrected for multiple comparisons with a false discovery rate (FDR) correction of α =0.05. More details regarding the statistical tests and corrections can be found in the respective result segments. The different analyses for each data type are explained below.

2.4.1 Eye Tracking

The eye tracking data were imported to MATLAB using the edfmex toolbox provided by SR Research. For the M/EEG experiments, the data files also included the onset times for each stimulus. In the fMRI experiment, only start and end of acoustic stimulation were recorded in the data file, while the timing of the individual stimuli was loaded from a file saved during the creation of the audio file. The following data analysis was done with self-written routines and was mostly identical for the three experiments:

Blinks and otherwise missing data points were identified when the slope exceeded 10/ms in the M/EEG experiments and 5/ms in the fMRI experiment, or when the absolute pupil size dropped below 100. To avoid artifacts around blinks, the data points 100 ms before and after the blinks were also excluded, before all missing samples were reconstructed with a linear interpolation. Afterwards, the data were low-pass filtered with a 4 Hz cut-off. The stimulus onset times were combined with the button presses to define the stimulus type (H, M, FA, CR). Based on this, epochs from 500 ms before to 3000 ms after each events were created from both the PDR and it's first derivative (PDR'). The latter was calculated by taking the difference between two adjacent samples and smoothing across 200 samples (corresponding to a non-casual 5 Hz low-pass filter).

A divisive baseline correction was applied to the PDR epochs, using the mean pupil size during the 200 ms before stimulus onset. In the second experiment, the noise-onset of each epoch caused an increase in pupil size starting before stimulus-onset. This resulted in an offset in PDR' and was removed with a subtractive baseline correction (mathematically corresponding to a linear detrending of the PDR). Epochs with more than 15% (M/EEG) or 30% (fMRI) were excluded, before both the PDR and PDR' were averaged across trials for each condition. This threshold was increased for fMRI, as the pupil recording was less robust due to the more complicated setup, causing a larger amount of missing data points. The data sets were carefully controlled to validate that this change did not have a negative impact on overall data quality. Finally, the results were averaged across participants.

Statistical analysis was conducted on the PDR', as some subtle differences between conditions were more pronounced here, especially in the M/EEG experiments. Additionally, activity in cortical NE neurons has been shown to correlate more with the rapid changes represented in the PDR', while slower changes are more indicative of activity in acetylcholine neurons (Reimer et al., 2016).

A temporal permutation cluster test was used to determine during which time period the PDR' was significantly different from zero (Maris and Oostenveld, 2007), using one-tailed t-tests, a cluster forming threshold of 0.05, and -if possible- 50000 permutations. The number of permutations is limited to $2^N - 1$, with the sample size N corresponding to the number of subjects for the tests conducted here. Therefore, for N<16, the respective maximum value is used instead of 50000. It is additionally noteworthy that for small sample sizes, the number of possible p-values is also lower, hence the possibility of obtaining the same value in different tests increases.

The permutation test was conducted for each condition in the time window from 500 to 1000 ms after stimulus onset in the M/EEG experiments and from 500 to 2000 ms in the fMRI experiment. The time window was extended here, since the pupil dilations lasted longer. Amplitudes of the PDR' were calculated as the mean (M/EEG) or maximum (fMRI) in the corresponding time window. Once again, the analysis was changed for the fMRI experiment because of the longer duration and - more importantly - the obvious latency difference between PDRs evoked by AM and NT tones. T-tests and rmANOVAs were used for comparisons of the amplitudes between conditions.

In the fMRI experiment, the eyetracking data were used for two more analysis: First, the baseline pupil size and the baseline saccade rate were calculated and compared between hit and miss trials. The saccade rate was calculated using a MATLAB

script adapted from Burlingham et al. (2022). Second, the pupil size was used as a regressor, to find areas where the BOLD signal co-variates with pupil size. Details for this analysis can be found in subsection 2.4.3.

2.4.2 M/EEG

The M/EEG data was analyzed using MNE-Python (Gramfort et al., 2013). The three runs of Experiment 1 were analyzed individually, while the two runs of Experiment 2 were combined into one data set. The preprocessing of single subjects data sets included band-pass filtering from 0.05 Hz to 40 Hz, excluding channels without signal or with excessive noise, and artifact correction. The latter was done in two steps: First, signal-space projection (SSP, Uusitalo and Ilmoniemi, 1997) was used on the low frequency (<0.5 Hz) part of the data to find and remove external artifacts, mostly originating from traffic, e.g., street cars. SSP removes noise by projecting the data into a subspace that is orthogonal to the noise signal. For each run/participant (Ex. 1/2), 6 projections were calculated, but only those that visibly reduced the amount of noise were applied, while the rest was discarded. Across all data sets, an average number of 4.4 projections (range 2-6) was used. In a second step, independent component analysis (ICA) was used to decompose the signal into statistically independent components. This method is especially useful to identify and exclude components contaminated with ECG and EOG artifacts. In Experiment 1, the ECG channel was used for an automated search of cardiac artifacts, in Experiment 2, this was done without a reference channel. In both experiments, the electrodes above the eyes were used as reference for EOG artifacts. Visual inspection completed the procedure, and affected components were excluded from the data. The ICA was calculated and applied separately for MEG and EEG.

After artifact correction was completed, rejection thresholds were determined based on the signal variability for both channel types (Jas et al., 2016; Jas et al., 2017) and epochs exceeding one of these thresholds were excluded. Evoked potentials were calculated by averaging across conditions and a linear detrending was applied to the evoked EEG data.

For source analysis, the participant's structural MRI was processed with Freesurfer (Fischl et al., 1999; Dale et al., 1999; Fischl, 2012) to reconstruct the white matter, inner skull, outer skull, and scalp surfaces. Based on the white matter surface, a source space was created with 4098 equally distributed dipoles in each hemisphere (4.9 mm distance between dipoles). The changing conductivities between the different tissue types was modeled using the boundary element method with the triangulated brain, skull and scalp surfaces. For the analysis of MEG data, a model based only on the brain compartment would be sufficient. But for EEG, a three layer model is necessary, with default conductivities of 0.3, 0.006 and 0.3 S/m for the brain, skull, and scalp, respectively. Consequently, this three layer model is used for the present data.

This boundary element model is used to calculate the forward solution, which reports the signal distribution at sensor level for any given dipole of the source space. Further, a noise-covariance matrix is calculated from the pre-stimulus intervals (100 ms before stimulus onset), to estimate the noise in the different channels and weight them accordingly during the calculation of the source estimate. The noise-covariance matrix and the forward model are used to calculate the inverse operator, which can be applied to the evoked data to finally give a source estimate for each condition. The calculation of this source estimate was done both with a minimum norm estimate (MNE) and dynamic statistical parametric mapping (dSPM), which is the

noise-normalized version of MNE (Dale et al., 2000). The dSPM was used for mapping the signal onto the brain, to find the main loci of activation. In the dSPM maps, the medial wall was excluded, as it displays mostly spread from other areas and likely no relevant real activity (Samuelsson et al., 2021).

Wave forms were extracted from the MNE-based source estimate to avoid a bias due to unequal numbers of trials, which is important when comparing the signal strength between conditions. They were extracted from pre-defined regions of interest (ROIs): The Heschl's Gyrus as part of the auditory cortex (AC) and main source of the auditory evoked potentials, including the N1, and an ROI combining the PCC and the retrosplenial cortex (RSC) as potential source of the P3 (Das et al., 2023). To extract a waveform, the time course of signal strength was averaged across all dipoles in the corresponding ROI. The wave forms were finally imported into MATLAB, where they were averaged across hemispheres, after an initial analysis revealed no relevant differences, and an additional 15 Hz low-pass filter was applied before plotting, mainly for aesthetic reasons.

The significance of these waveforms was tested with temporal permutation cluster tests (Maris and Oostenveld, 2007) in the following time windows: 100-400 ms for the AC and 300-800 ms for the PCC/RSC. The permutation test used a cluster forming threshold of 0.05, one-tailed t-tests, and up to 50000 permutations, but refer to subsection 2.4.1 for more details. Amplitudes were calculated as the mean in these time windows, and rmANOVAs were used to compare the amplitudes across conditions.

2.4.3 fMRI

The analysis of the fMRI data sets was done with Freesurfer v6.0 (Fischl, 2012). In the preprocessing, the structural scan was used for coregistration of the volumes, as well as motion and slice timing was corrected. The signal of the cortex was morphed to a surface for each hemisphere, while the subcortical analysis was conducted in the volume. In the surface analysis, the signal was smoothed using a gaussian kernel with a FWHM of 5 mm. The subcortical data sets were not smoothed to avoid further reduction of spatial resolution. For the group average, surface data were transformed to the fsaverage template brain, the volume data was combined in the MNI305 space with 2 mm resolution.

A general linear model (GLM) was fitted to the time course to find which conditions (AM tones, NT tones and detected/missed NT tones) caused changes in BOLD response compared to the catch trials. The canonical hemodynamic response function (HRF), a superposition of two gamma functions (Friston et al., 1998), was used to model the BOLD response in the GLM. Group maps showing the voxels with significant changes were created on the cortical surface and in the subcortical volume. Additionally, the GLM's beta values were extracted from a couple of brain regions to further investigate task modulation and lateralization. To this end, beta values were averaged across all vertices in an ROI, and t-tests as well as rmANOVAs were used for statistical tests.

The cortical ROIs were chosen to cover the main areas of potentially important networks. If possible, predefined labels were used or only small adaptations were made based on previous knowledge. The AC was chosen for the auditory activity; posterior superior temporal sulcus (pSTS) and supramarginal gyrus (SMG) are part of the TPJ), and selected together with the AI and inferior precentral sulcus (iPCS) as representation of the VAN. The DAN is covered by the IPS and the superior precentral sulcus (sPCS), which includes the FEF. The anterior midcingulate cortex (aMCC)

was chosen because of it's importance for attention and as part of the CON (together with the AI), and finally the RSC represents the putative source of the P3b observed in EEG. The ROIs for SMG, iPCS, sPCS, and IPS were taken from the Destrieux Atlas (Destrieux et al., 2010), which is included in freesurfer. The ones for AI, aMCC, RSC, and pSTS were based on this atlas but created manually as a subregion of the original label. The AC-ROI combines two labels of the Heschl's gyrus and the planum temporale, which were used in a previous study (Wiegand et al., 2018).

The subcortical ROIs include the LC, whose activity is correlated to pupil size (Murphy et al., 2014), the SC and pulvinar for their involvement in attention processes, the inferior colliculus (IC) and medial geniculate nucleus (MGN) as part of the auditory pathway, and the PAG to cover large parts of the remaining activity in the midbrain. The ROIs of the PAG, IC, and SC were based on the Paxinos Atlas (Paxinos et al., 2012). For the IC and SC, ROIs from a previous study (Gutschalk and Steinmann, 2014) were recreated as spheres with a radius of 2 mm centered at the following Talairach coordinates: $\pm 5/-35/-7$ (IC) and $\pm 6/-30/-2$ (SC). The PAG has a more complex, none-spherical layout and was therefore drawn manually in the MNI305 space. The ROIs for the thalamic nuclei MGN and pulvinar were created with the thalamus segmentation tool of Freesurfer v7.0 (Iglesias et al., 2018). Finally, the LC ROI was based on Keren et al. (2009). Voxels containing these center coordinates or within their standard distributions were included in the ROI, interpolation of these voxels across slices provided the missing parts.

In a separate analysis, the pupil size was used as regressor for the BOLD analysis. This should reveal regions that co-vary with the pupil size. The preprocessed, i.e. blink corrected pupil size was used for this. A sliding mean, which replaced each time point by the mean of the surrounding 2 s, was applied before downsampling the regressor to 0.5 Hz (TR=2s). Time periods after stimuli (10 s) were excluded from this analysis to avoid contamination with task evoked activity. Since the pupil response is delayed compared to the underlying brain activity, the canonical HRF would not be an appropriate model. Therefore the pupil regressor was not convoluted, but used with different time lags, to calculate an euqivalent of a standard finite impulse response (FIR) analysis. The resulting time course was averaged across the whole brain, after no relevant differences between regions were found, and maps of the brain activity around the positive (0-2 s) and negative (4-8 s) peak were created.

2.4.4 Behavioral data

In the first M/EEG and in the fMRI experiment, "hits" (H) were defined as target stimuli followed by a button press that occured within 1.3s. Responses later than this or after a non-target stimulus were rated as "false alarms" (FA), target or catch trials without a subsequent button press as "miss" (M) or "correct rejection" (CR), respectively. In the second M/EEG experiment and the confidence rating part of the psychoacoustic experiment, target trials followed by any of the "tone present" ratings were rated as hits (H1/2/3 for detected tones with high/medium/low confidence, respectively), the others as misses (M1/2/3). Catch trials followed by a target present/absent rating were rated as false alarms (FA1/2/3) or correct rejections (CR1/-2/3), respectively. Trials with no response were excluded from the analysis, but on average this occurred in only 1.0% of the trials (range 0-4.3%). Reaction times in Experiment 2 were compared using two separate rmANOVA for the factors outcome (4 levels: H, M, FA, CR) and confidence (3 levels: high, medium, low). In the first and last experiment, reaction times were not analyzed, as they are only available for hits and no meaningful comparisons can be made.

Detection and false alarm rates were calculated in all experiments. But note that in Experiment 1 and 3, the false alarm rate defined as the number of false alarms divided by the number of catch trials is somewhat arbitrary: Due to the continuous noise, participants don't have any information about the start or end of a trial, and several false alarms could occur within one trial. In the first experiment, the change of detection rate over time was investigated for NT tones by splitting the trials of the second run in five equal parts and calculating the detection rate in each of these quintiles.

The decision criterion and the sensitivity d' were calculated in the M/EEG experiments based on detection and false alarm rates (Stanislaw and Todorov, 1999). In the second experiment, the median criterion was used to split the participants into two groups. Usually, subjects with a criterion above or below 0 are considered as "conservative" or "liberal", respectively (Stanislaw and Todorov, 1999). Here, all except one subject had a positive criterion, i.e. a bias towards the "signal absent" responses, but for easier reference, the group with criteria below the median will be labeled liberal and the other one conservative.

Detection rate and arousal

To investigate the influence of arousal, measured as the pre-stimulus pupil size, on performance, trials were sorted into quantiles according to their baseline pupil size. Quintiles, i.e. five bins, were used for the M/EEG data sets, but only quartiles in the fMRI experiment. This reduction was necessary because there were fewer trials and otherwise additional participants would have to be excluded due to missing trials in one or more bins. Detection rates in each bin were calculated on a single-subject level before averaging across participants. Contrast analyses were used to test for linear or quadratic effects of pupil bin on detection rate.

Transition probabilities

For both M/EEG experiments, the probability of a particular outcome for the current trial based on the outcome of the previous trial was calculated. This likelihood, subsequently called "transition probability", was calculated for each participant and all possible transitions from event i to j, as the absolute number of the transition $N_{i\rightarrow j}$ divided by the number of all transitions from i $N_{i\rightarrow}$ and the number of all transition to j $N_{\rightarrow j}$ to account for the different prevalence of each event type.

$$P_{i \to j} = \frac{N_{i \to j}}{N_{i \to} \cdot N_{\to j}} \tag{2.1}$$

In both experiments, hits and false alarms were combined as signal present responses ("Yes"), and correct rejections and misses as signal absent responses ("No"). But in the second first and third run of Experiment 1, CR were excluded from the analysis, because (a) they were mostly not perceived and (b) their number was so high (150 NT tones compared to 50 AM noise) that transitions from or to a CR would dominate the whole statistics without being meaningful. In other words, an exemplary sequence of H, CR, and M is counted as transition from H to M, i.e. Yes to No. During the middle run, i.e. the detection of NT tones, it was assumed that most AM noise sequences are also perceived. Therefore they were counted as transition to or from a No response. In the second experiment, all transitions were additionally combined across confidence or across response type, to visualize the individual effects.

Response accuracy

In Experiment 2 the response accuracy was calculated according to Wixted (2020): For each confidence rating i (i=1-3) the accuracy a "Yes" response was calculated as the rate of correct relative to all "Yes" responses (i.e. hit rate HR vs. HR and false alarm rate, FAR). The accuracy for "No" responses was correspondingly calculated with the rates of correct rejections and misses (CRR and MR).

$$A_{Yes_i} = \frac{HR_i}{HR_i + FAR_i} \tag{2.2}$$

$$A_{No_i} = \frac{CRR_i}{CRR_i + MR_i} \tag{2.3}$$

2.5 Modeling of neural activity based on Signal Detection Theory

Experiment 2 raised the question, whether conscious perception is continuous or binary, i.e. whether there is a threshold for neural activity that has to be crossed in order to perceive a stimulus. The decrease in amplitude with confidence suggests a continuum of perception. Signal detection theory (SDT, Green and Swets, 1966) postulates such a continuum, where a decision criterion chosen by the observer determines whether a stimulus is classified as detected.

In order to test whether this assumption models the present data well, the signal and noise distributions and the decision criteria were calculated using the behavioral results. Based on this, the neural activity was predicted and compared to the amplitudes measured in AC, PCC/RSC and the PDR'.

In a first step, the distributions of neural activity for signal and noise trials were defined based on Green and Swets (1966, p. 59). Both are regular gaussian distributions:

$$g(x) = \frac{1}{\sigma \sqrt{2\pi}} \exp^{-\frac{(x-\mu)^2}{2\sigma^2}}$$
(2.4)

The absolute values of the mean μ and the standard deviation σ of one distribution can be chosen freely, since only the relationship between g_{noise} and g_{signal} is important. Hence, the calculations were started with $\mu_{noise} = 0$ and $\sigma_{noise} = 1$. The ratio $\frac{\sigma_{noise}}{\sigma_{signal}}$ was calculated based on the receiver-operating-characteristic curves: Hit and false alarm rates for each criterion were plotted in a double probability plot, where the ratio is then defined as the slope of the linear fit through these points. Afterwards, the only missing parameter for the distributions was μ_{signal} . One approach to find its value is the use of the empirical constant described by Green and Swets (1966, p. 98):

$$\frac{\Delta\mu}{\Delta\sigma} = \frac{\mu_{signal} - \mu_{noise}}{\sigma_{signal} - \sigma_{noise}} = 4$$
(2.5)

An alternative approach is to calculate the criteria for both noise and signal distributions as described below using different values for μ_{signal} . Theoretically, the criteria derived from both distributions should be equal. Consequently, the μ_{signal} with the smallest differences between noise and signal criteria was chosen.

To calculate the five decision criteria for the noise or signal distribution, the behavioral data were used. For each criterion, the number of different ratings were combined and divided by the number of catch or signal trials to give the probability of this rating. For example, $p_{FA,1} = N_{FA1}/N_{catch}$ is the probability of the strictest criterion for the noise, and $p_{H,1} = N_{H1}/N_{signal}$ for the signal trials. For more liberal criteria, the less confident FA and H are included, until the most liberal criterion, where also the low and medium confident CR and M are counted: $p_{FA,5} = (N_{FA1} + N_{FA2} + N_{FA3} + N_{CR3} + N_{CR2})/N_{catch}$ for noise trials, and $p_{H,5} = (N_{H1} + N_{H2} + N_{H3} + N_{M3} + N_{M2})/N_{signal}$ for signal trials, respectively. In the theoretical model, the same probabilities are defined as the area under the curve from the criteria c_i (i=1-5, vertical lines in Figure 12) to infinity. Solving this equation for c_i gives to the desired criteria.

$$p_i = \int_{c_i}^{\infty} g(x) dx \tag{2.6}$$

To find the final μ_{signal} , this calculation was based on the behavioral data averaged across participants and repeated for all μ_{signal} between 0 (μ_{noise}) and 2 ($\mu_{noise} + 2\sigma_{noise}$) in steps of 0.005. Afterwards, the μ_{signal} was chosen, where the difference between c_i derived from the signal and noise distribution was minimal.

With this final μ_{signal} , the criteria were recalculated for each subject base on individual behavioral results. Despite optimizing μ_{signal} , the criteria from signal and noise distribution obviously still differed slightly, but a single set of criteria was necessary for the modeling of neural activity. Hence, each c_i was chosen so that it fulfills Equation 2.5 as well as possible for both distributions. This was achieved by solving the following equation for c_i :

$$\min\left|\int_{c_i}^{\infty} g_{noise}(x) dx - p_{FA,i} + \int_{c_i}^{\infty} g_{signal}(x) dx - p_{H,i}\right|$$
(2.7)

Using these criteria, the average amplitude of neural activity A_i for each rating of the signal trials (i=1-6, from H1 to M1) was calculated.

$$A_{i} = \frac{\int_{c_{i}}^{c_{i-1}} g(\bar{x}) \cdot x \, dx}{\int_{c_{i}}^{c_{i-1}} g(\bar{x}) dx}$$
(2.8)

For the first and last rating, the upper or lower limit of the integrals (c_0 or c_6) are ∞ and $-\infty$, respectively. These amplitudes were averaged across participants. Since A_1 , the average amplitude of M1, was negative, the distributions and consequently all amplitudes were shifted by its absolute value, to move it to 0. Note that this was an arbitrary choice aiming for more meaningful values with only minor influence on the overall results of the model. To compare these predictions with the amplitudes observed in AC, PCC/RSC, and PDR', the four data sets were additionally divided by the mean H1-amplitude across subjects. R^2 , the coefficient of determination, was calculated to indicate how much of the variance in the data could be explained by the model.

2.5.1 Bimodal signal distribution

From advocates of the bimodality of perception, it has been proposed that the neural activity can be modeled by the superposition of two gaussians: One conscious mode with a mean above the perceptual threshold, and one unconscious mode below (Sergent et al., 2021).

$$g_{bi}(x) = \frac{b}{\sigma \sqrt{2\pi}} \exp^{-\frac{(x-\mu_{signal})^2}{2\sigma^2}} + \frac{1-b}{\sigma \sqrt{2\pi}} \exp^{-\frac{(x-\mu_{noise})^2}{2\sigma^2}}$$
(2.9)

The criteria and amplitudes predicted by this bimodal model were calculated using the steps described above, while replacing the unimodal signal distribution g_{signal} with g_{bi} . According to Sergent et al. (2021), the standard deviations of both modes and of the noise distribution are equal. Hence, they were set to 1 here. The detection rate influences *b*, the relative weight of the two modes. It was set to 59% here, which was the average hit rate of the second experiment.

Chapter 3

Results

3.1 Experiment 1: Task-related modulation of auditory perception

The first experiment was a combined measurement of M/EEG and pupillometry, where the presence of two types of stimuli (NT tones and AM noise) allowed the investigation of task-related modulations of the PDR, the P3, and the evoked potentials in the auditory cortex. Recording the pupil size furthermore provided a continuous measure of arousal, which can influence task performance (McGinley et al., 2015a; Murphy et al., 2011). Participants completed three runs with identical stimulation, but alternating task between detection of AM noise and NT tones. They were not informed about the presence of NT tones in the first or last run, when they had to detect the AM noise.

3.1.1 Behavioral results



FIGURE 1: Behavioral results of Experiment 1. (A) Detection and false alarm rates in the three runs. (B) Detection rate in dependence of the pre-stimulus pupil size. Trials are sorted into five equally large bins based on their pupil size and hit rates are calculated for each bin. In both panels, single points represent single subject data, bar heights and error bars mark the average across subjects and the standard error, respectively.

The average detection rate was 74% (40-96%) and 72% (42-96%) for the AM noise in the first and last run, and 35% (range 6-51%) for the NT tones in the second run (Figure 1). False alarm rates were generally low, with averages of 2% (0-8%), 5% (0-11%) and 5% (0-32%) in the first, second and third run, respectively. Together, this results in average decision criteria of 0.8, 1.2 and 0.7 in the three runs. None of the participants reported that they heard NT tones in the first run, but half of them (N=7) reported perception of the NT tones in the last run. This group also had a higher average detection rate during the second run compared to the group who did not perceive any NT tones when not task-relevant (42% vs. 23%, range: 27-49% vs. 6-51%, t-test: t_{12} =2.6 , p=0.025). Overall, the detection rate of the NT tones was lower than the targeted 50%, even though the chosen SNR was in good agreement with the results of the test conducted before the second run. A couple of reasons might contribute to this: First, the testing procedure is much shorter than the actual experiment, hence attention and arousal do not have to be maintained for an extended period of time. This effect of time-ontask was confirmed by a significant decrease in detection rate across time, dominated by a drop in the last fifth of the run (mean rates for the quintiles: 35/39/30/33/21%, rmANOVA: F_{4.52}=4.2, p=0.016). Second, following this line of reasoning, another difference is the decreased number of targets per time compared to the pre-test, which increases the demand on vigilance. Third, the trial-based structure of the test with short periods of noise could increases performance, as the noise onset serves as temporal cue for the tone appearance and might increase arousal. The increased performance in Experiment 2 seems to support this explanation, but this did not hold true after considering the slightly different SNRs (see subsection 3.2.1). Lastly, the presence of the AM noise could have impeded performance. This was not systematically inquired, but one participants spontaneously reported being distracted by it.

The detection of the NT tones was further expected to vary with arousal, measured as the pre-stimulus pupil size (Aston-Jones and Cohen, 2005). While a contrast analysis confirmed a covariation of hit rate and arousal, the relationship was not quadratic ($F_{1,13} = 1.1$, p = 0.32) as shown in a similar experiment in mice (McGinley et al., 2015a), but linear ($F_{1,13} = 12.6$, p = 0.003). A possible explanation for this deviation could be a limited range of arousal during the experiment: Due to the monotonous structure of stimulation, participants might have never experienced high levels of arousal, leaving the second half of the inverted U-shaped curve inaccessible in this experiment. Furthermore, other studies in human also found conflicting results regarding the relationship of arousal and performance, for more details, see subsection 4.2.1

3.1.2 M/EEG

The M/EEG measurement revealed two centers of activation: One in and around the auditory cortex peaking around 180 ms after stimulus onset, the other one in the medial part of the brain, including the PCC and RSC peaking around 500 ms. Consequently, waveforms for further analysis of the activation were extracted from these areas. The exact ROIs are displayed in the top part of Figure 3.

Auditory cortex

The salient AM noise evoked a prominent negativity peaking around 180 ms after stimulus onset in each of the runs. This activity is in line with the fact that participants reported to hear this stimulus in all runs, even when it was not task relevant. The negativity for NT tones is only present in the middle run and extends longer in time. Surprisingly, not only the detected but also the missed NT tones evoked a negative-going AC response. The significance of these findings was tested and confirmed with temporal permutation cluster tests in the time window from 100 to 400 ms; results can be found in Table 1. Additionally, the influence of task on the amplitudes was investigated with one rmANOVA each for the NT tones and the AM noise. In the respective task-relevant runs (1 and 3 for AM noise, 2 for NT tones), the amplitudes of hits and misses were averaged weighted according to the



FIGURE 2: dSPM-Maps of the activity evoked by detected AM noise (combined across run 1 and 3), and detected and undetected NT tones.

hit rate. The results confirmed a task modulation for NT tones, and none for AM noise ($F_{2,26}$ =12.6/0.4, p=0.0004/0.55).

PCC/RSC

The PCC/RSC region is the presumable source of the task and decision related P3b (Das et al., 2023). Hence, a late positive response would be expected for detected targets only. This is indeed the case here, where only detected AM noise in the first and last run and detected NT tones in the middle run evoked prominent positivities. The significance of these components was confirmed with permutation cluster tests between 300 and 800 ms (Table 1).

3.1.3 Pupil dilation response

In response to detected target stimuli, the pupil starts to dilate at approximately 500 ms, peaks for the first time around 1000 ms and again around 1700 ms. After the second peak, the pupil size slowly resumes back towards the pre-stimulus size, which can take longer than 3 s from stimulus onset on. Because of the sluggish nature of the PDR, the statistical analysis is focused on the first derivative (PDR'),



FIGURE 3: Evoked potentials in the auditory cortex (left column) and the PCC/RSC (right column) together with the mean amplitudes in the time windows of interest (gray areas, 100-400 ms for AC, 300-800 ms for PCC/RSC). The significance of each waveform was tested with a permutation cluster test in the respective time window, periods where the activation of one condition significantly differed from zero are marked with a horizontal bar in the respective color. In the amplitude plots, each circle represents one participant, while bar height and error bars mark the mean and standard error of the mean across participants.

were the actual dilation is mostly confined to the time window from 500 to 1000 ms after stimulus onset. This time window was used to test the PDR' for significance, using a temporal permutation cluster test.

As expected, the pupil dilated in response to all detected target stimuli, i.e. the AM noise in the first and last run, and the NT tones in the middle run (Figure 4). The increase amounts to roughly 10%, while being slightly higher for the more salient AM noise compared to the NT tones. Even though participants supposedly perceived the AM noise also in the middle run, the pupil dilates only marginally without reaching significance. This causes a small but equally insignificant peak in the PDR'. In contrast, undetected targets result in a PDR of almost 5% peak amplitude for the AM noise and approximately 2% for the NT tones. In both cases, the PDR' was significant.


FIGURE 4: Pupil dilation response during the Experiment 1. Each row represents one of the three runs from top to bottom. The pupil dilation response relative to baseline is shown in the first column, the first derivative (PDR') in the second column. The significance of the PDR' was tested with a permutation cluster test in the time window of interest (500-1000 ms, gray area), periods where the dilations significantly differed from zero are marked with a horizontal bar in the color of the respective condition. The PDR' amplitudes were measured for each subject as the mean during this time and are plotted in the right column. Each circle represents one participant, while bar height and error bars mark the mean and standard error of the mean across participants.

3.1.4 Perception of task-irrelevant NT tones

While none of the participants noted the NT tones during the first run, half of them reported that they perceived tones in the last run. Therefore the previous analyses of M/EEG waveforms and PDRs were repeated with the two groups of participants, those who perceived the tones (Group 1) and those who did not (Group 2). Consistent with their reports, Group 1 shows visible but small responses to the NT tones in the AC, PDR', and even PCC/RSC (Figure 5), but none of them are significant (Table 1). It should be kept in mind that the informative value of these results is limited by the small sample size in each group (N=7) and the correspondingly few permutations for the cluster test.

Originally, it was planned to classify the NT tones in the last run, mainly based on their pupil dilation response, but potentially including the M/EEG waveforms. The classifier should be trained on the data sets of the second run, were responses provided direct access to whether a tone was detected or not. However, this classification was not successful, and Figure 5 shows why: The average PDR, PDR', and AC activity of NT tones in the last run is not significant and even smaller than that of missed tones in the middle run. Hence, a classifier trained on the trials of run



2, would not be expected to perform well on the last run, as modulation by task is apparently stronger than previously expected.

FIGURE 5: Comparison of the two groups of participants, who perceived (A-D) or missed (E-H) NT tones during the last run. In each panel, responses evoked by NT in the runs 1/2/3 are plotted in red/blue/yellow, respectively, the missed NT during the second run are in bright blue. Evoked responses are from the AC (A/E), PCC/RSC (B/F), PDR (C/G), and PDR' (D/H). Significance was tested by performing a permutation cluster test against zero in the respective time windows (AC: 100-400 ms, PCC/RSC: 300-800ms, PDR': 500-1000 ms).

3.1.5 Transition probabilities

The slow decrease of the PDR after the stimulus together with the confirmed relationship between pre-stimulus pupil size and detection rate raises the question, if the outcome of one trial influences the following one. In other words: If one target was detected and the pupil size is still elevated, does this increase the probability of another detection for the succeeding tone? The transition probabilities in Figure 6A show, that there a no significant differences between the transitions (rmANOVAs for each run with the factor transition, 4 levels: Yes \rightarrow Yes, Yes \rightarrow No, No \rightarrow No, No \rightarrow Yes; F_{3,39}=0.1 /2.3/0.9, p=0.80/0.16/0.37 for run 1/2/3, respectively).

One potentially confounding influence is the presence of distractors: In the first and last run, the number of distractors (NT tones) is much higher than that of the AM noise. On average, there are three epochs with an NT tone and one catch trial in between two AM noise epochs. Therefore, assuming that the vast majority of tones is not perceived and does not evoke a PDR, there is enough time for the pupil size to go back to baseline level, which removes the original reasoning to assume a transition effect. In the second run, this is not so much the case, as there are more tones than AM noise epochs or catch trials, making a transition effect more probable. Nevertheless, about half of the NT tones in the pseudorandomized sequence were not followed by another tone, but by a catch trial or AM noise. Additionally, it can be assumed that the AM noise was perceived most of the time. Even though it did not evoke a significant PDR, this could still influence subsequent detections. But note that the general pattern of transition probabilities in this run did not change when CR of distractors were not included as a No response (data not shown).



FIGURE 6: Transition probabilities of the first (A) and second (B) experiment. Previous trial's outcome (signal absent/present response) are plotted on the y-axis, the current trial's outcome on the x-axis. Note that the values are accounted for the different numbers of occurence for each outcome and therefore not real probabilities, i.e. they do not add up to 1. The colormaps are adjusted for each panel to be centered around the mean across all transition, and with an upper/lower limit of the mean plus/minus three times the standard deviation. A) Three runs of the first experiment (top to bottom). B) All possible transitions of the second experiment (upper), transitions combined across confidence to visualize the effect of response type (lower left), and combined across response type to visualize the effect of confidence (lower right).

3.2 Experiment 2: Confidence rating of near-threshold perception

When assuming a bimodal model of perception, the AC activity and PDR for missed NT tones in the first experiment could be explained by participants classifying perceived tones as unperceived, for example because their confidence in the perception was low. Alternatively, in a threshold free model of perception (like SDT), these evoked components could be explained by a gradual decrease in amplitude, which would correspond to the decreasing strength of perception. In that case, a dicho-tomized analysis would likely contain different levels of perception with different amplitudes, resulting in a measurable evoked potential for missed trials.

The second experiment was designed to examine this possibility: Participants had six different response options depending on their level of confidence in the presence of a stimulus: tone *present* or *absent*, each with high, medium and low confidence (3, 2, and 1, respectively). This procedure allowed the participant to apply different response criteria, which should reduce misclassifications due to low confidence, at least for the most confident signal absent ratings.

TABLE 1: Results of temporal permutation cluster tests of the M/EEG Experiments. Each waveform was tested in a specific time interval around the peaks: 100-400 ms for AC, 300-800 ms for PCC/RSC, and 500-1000 ms for PDR'. One-tailed t-tests were used together with a cluster forming threshold of 0.05. The number of permutations N is limited by the sample size (number of participants) but capped at 50000, and is listed for group of each analyses. When clusters were found, their start and end time, and the corresponding p-value are given. Significant clusters (p<0.05) are marked with an asterisk. If multiple clusters were found for one condition, they are listed in chronological order.

		AC			PCC/RSC			PDR'			
			t [ms]	р		t [ms]	р		t [ms]	р	
Experin	nent 1 (N=16383)			-1			-1			-1	
Run 1	detected AM noise		100-344	0.0064	*	306-774	0.0001	*	500-1000	0.0001	*
			342-368	0.1267							
	missed AM noise		140-146	0.1737		617-666	0.1017		629-977	0.0013	*
	PT		-	-		719-744	0.1782		563-584	0.1477	
									607-619	0.1719	
	Correct rejections		-	-		_	-		-	-	
Run 2	AM noise		100-224	0.0093	*	-	-		577-737	0.0510	
			336-357	0.1733							
			395-400	0.2037							
	detected NT tones		146-400	0.0002	*	386-775	0.0021	*	521-989	0.0001	*
	missed NT tones		157-400	0.0099	*	-	-		625-1000	0.0014	*
	Correct rejections		-	-		_	-		-	-	
Run 3	detected AM noise		116-204	0.0342	*	324-769	0.0001	*	500-995	0.0001	*
	missed AM noise		149-184	0.1112		-	-		577-753	0.0255	*
									883-893	0.1701	
									912-1000	0.0722	
	NT tones		-	-		_	-		647-790	0.0607	
	Correct rejections		-	-		-	-		-	-	
Group	1: NT perceived in Run 3	(N=	=127)								
Run 1	NT tones	(-	-		679-701	0 1875		-	-	
Run 2	detected NT tones		101-400	0.0156		399-700	0.0391	*	537-992	0.0156	*
Ittur 2	undetected NT tones		121-400	0.0156		-	-		633-1000	0.0156	*
Run 3	NT tones		-	-		460-493	0 1641		674-815	0.0859	
ituit o						561-655	0.0547		0,1010	0.0007	
						681-719	0.1563				
Group	2: no NT perceived in Ru	n 3	(N=127)			001712	0.1000				
Run 1	NT tones		-	-		-	-		520-531	0.2266	
									548-594	0.1406	
									613-630	0.1875	
Run 2	detected NT tones		183-400	0.0234		421-718	0.0234	*	512-522	0.2031	
							0.0202		554-918	0.0156	*
	undetected NT tones		-	-		_	-		855-869	0.2031	
Run 3	NT tones		-	-		_	-		-	-	
Experin	nent 2 (N=50000)										
Hit	combined		100-400	0.0003	*	410-764	0.0006	*	500-882	0.0007	*
1110	confidence	3	100-400	0.0001	*	435-737	0.0004	*	500-909	0.0003	*
	connuence	2	110-400	0.0003	*	406-468	0.1214	*	500-874	0.0002	*
		-	110 100	0.0000		486-770	0.0019	*	000071	0.0002	
		1	127-400	0.0014	*	448-468	0 2264		540-790	0.0310	*
		-	12, 100	0.0011		645-677	0.1832		010770	0.0010	
						770-787	0.2387				
Miss	combined		135-400	0.0000	*	789-800	0.2819		-	-	
	confidence	3	220-251	0.1116		-	-		-	-	
		2	174-400	0.0005	*	374-567	0.0120	*	-	-	
		-		5.0000		622-679	0.1177				
						684-710	0.2483				
		1	210-305	0.0233	*	736-753	0.2499		646-775	0.0499	*
Correct	rejections	-	-	-		-	-		-	-	
			1			1			1		



3.2.1 Behavioral results

FIGURE 7: Behavioral results of Experiment 2. Each circle represents the data of one participant, while bar height and error bars mark the mean and standard error of the mean across participants. A) Frequency of each response type with respect the number of signal (N=500) or catch trials (N=100). B) Hit and false alarm rates combined across the three confidence ratings. C) Detection rate in dependence of the pre-stimulus pupil size. Trials were sorted into quintiles according to their baseline pupil size and a detection rate was calculated for each of the five bins. D) Reaction times for each of the response types. Note that not all participants chose all options for catch trials, hence the average is across fewer participants in some conditions: $N_{CR3} = 16$, $N_{FA3} = 5$, and $N_{FA2} = 10$. E) Decision criterion F) Accuracy as a function of confidence. The accuracy of responses was calculated for each confidence rating in both response categories ("Yes" = signal present, i.e. H or FA, "No" = signal absent, i.e. M or CR) as the number of correct responses divided by all responses of this type (see subsection 2.4.4).

The behavioral results of the second experiment are plotted in Figure 7. While the responses for detected tones are almost equally spread across the confidence ratings, there are clear differences for the other outcomes: Misses and correct rejections are less likely for low confidence, while false alarms rarely occur with high confidence. In fact, for the less frequent catch trials not all possible outcomes were present in all subjects: CR 3 were present in 16, FA 2 in ten and the high confidence FA 3 in only five of the 17 data sets. Combined across confidence ratings, the average detection and false alarm rates of 59% and 10% (range 26-87% and 1-34%, respectively) resulted in an average decision criterion of 0.61 (range -0.03 - 1.11). This is lower than in the second run of Experiment 1 (independent-samples t-test, t₂9=3.9, p=0.0005), proving that the different response options indeed allowed participants to be less conservative in their decisions. However, all except one participant still used a positive decision criterion, i.e. were biased towards a No response. The higher detection rate and more liberal criterion compared to Experiment 1 persist, even when all participants with an SNR higher than -21 dB were excluded from the comparison (N=1/5 in Ex. 1/2; average hit rate 32%/55%, t₂₃=-3.2, p=0.004; average criterion 1.14/0.56, $t_{23}=3.6$, p=0.002). However, the sensitivity d' does not change between experiments when only this subset of participants is considered (average d': 1.2/1.4,

 t_{23} =-0.8, p=0.4). Thus, it can be concluded that the trial-based structure of the experiment does not per se increase the detection rate (as suggested in subsection 3.1.1).

The reaction times were measured from noise offset and were shortest for high confidence hits (H3, average 176 ms) and longest for the low confidence correct rejections (CR1, average 479 ms). Since not every subject chose every response option, a combined rmANOVA was not possible. Instead, two separate rmANOVAs with the factor outcome (H/M/FA/CR) or confidence (1/2/3) were calculate on the reaction times averaged across confidence or outcome, respectively. This showed that both factors had an effect on the reaction time ($F_{1,16}$ =12.2/7.6, p=0.0001/0.0039 for outcome/confidence, respectively), with faster responses for higher confidence and for hits compared to misses, FA and CR.

Similar to the first experiment, the influence of pre-stimulus pupil size on the detection rate was analyzed. There was again a significant influence, but this time the effect was quadratic, with a peak performance at medium pupil size (contrast analysis, $F_{1,16} = 15.8/0.4$, p=0.001/0.53 for quadratic and linear effects, respectively). The difference might be caused by an increased range of arousal due to the trial-based structure with noise on- and offsets, compared to the previously used continuous noise. This new finding is in line with previous studies suggesting an "inverted u-shaped" relationship between tonic arousal and performance (Aston-Jones and Cohen, 2005; McGinley et al., 2015a), but see subsection 4.2.1 for more details.

Additionally to the detection rate, the accuracy was calculated for "Yes" and "No" responses (Wixted, 2020). Based on signal detection theory (Green and Swets, 1966), this response accuracy should decrease with confidence: For target-present ratings, decreasing confidence is related to a lower decision criterion, i.e. more false alarms; for target-absent ratings, decreasing confidence means a higher criterion and thus more misses. Both increase the number of mistakes relative to the total amount of the target-present or -absent ratings, which decreases the accuracy. On the other hand, assuming an absolute threshold for perception would imply that differences in signal strength for all trials below the threshold (M and CR) are inaccessible to the observer and thus indistinguishable. Consequently, the response accuracy for No should be invariant across confidence (Wixted, 2020). Here, the average accuracy for a Yes drops from 95% for the high confidence rating to 76% for the lowest rating, while the No accuracy is generally lower but also drops from 70% to 51%. Both effects are significant (*F*_{2,32}=19.2, p<0.0001 for Yes, *F*_{2,32}=5.0, p=0.027 for No). Lastly, transition probabilities were calculated similar to those in Experiment 1. From Figure 6B, it becomes obvious that a highly confident rating, regardless of whether it is Yes or No, is most likely followed by another one of the same kind. Additionally, a high confident "No" is more likely to be followed by a high confident "Yes" than any lower confidence option. A rmANOVA with the factors response transition (4 levels: Yes \rightarrow Yes, Yes \rightarrow No, No \rightarrow No, No \rightarrow Yes) and confidence change (5 levels: -2,-1,0,1,2) confirmed a significant influence of both factors ($F_{12,192}=7.9/7.8$, p=0.003/0.007 for response/confidence), while the interaction was not significant ($F_{12,192}$ =2.3, p=0.075).

3.2.2 M/EEG

The M/EEG maps for detected targets look similar to those of the first experiment, but with a lower amplitude, especially in the later time window (Figure 8). Possible reasons for this might be the trial-based structure, where activity evoked by the noise onset might interfere with the stimulus-evoked activity, as well as the lower



FIGURE 8: dSPM-Maps of activity evoked by detected NT tones combined across the three confidence ratings

density of EEG electrodes used here. The ROI analysis was again confined to AC and PCC/RSC (Figure 9, A and B). Waveforms are always shown once in a dichotomous fashion with hits and misses combined across all confidence ratings, and again for the individual ratings. Correct rejections were only analyzed combined across confidence ratings and false alarms were not analyzed, because their low numbers did not provide a sufficient SNR of the averaged M/EEG data.



FIGURE 9: Evoked potentials of Experiment 2. Waveforms extracted from the auditory cortex (A) and the PCC/RSC (B), are shown together with their mean amplitudes in the time windows of interest (100-400 ms for AC, 300-800 ms for PCC/RSC). Dichotomized curves are shown in the upper row, while all ratings are shown in the lower row. In the amplitude plots, each circle represents single subject data, while bar height and error bars mark the mean and standard error of the mean across participants.

Auditory Cortex

The dichotomized waveforms from the AC reproduce the main findings of the previous experiment: Detected targets evoke a strong negative-going response around 200 ms, missed targets evoke a broad, smaller, but still significant negativity. Results of the permutation cluster test that was used to determine time intervals with significant activity can be found in Table 1. Separating the waveforms into the different ratings shows a decrease in amplitude across conditions. This was confirmed by a rmANOVA with the factor condition (H3-1, M1-3, and Catch; $F_{6.96}$ =4.9, p=0.0095). The negative-going responses for the three hits were significant in the cluster analysis and their amplitudes clearly decreased with confidence. The responses evoked by low and medium confident misses (M1 and M2) were also significant, the one evoked by M3 was not, but these amplitudes did not show considerable differences between the ratings. This might be related to the lower trial count of the M1, which amounts to only about half of the number of M3, leading to a low signal-to-noise ratio for this condition ($N_H = 1601/1393/1683$, $N_M = 769/1035/1496$ combined across subjects for H3/2/1, M1/2/3, respectively; see also Figure 7). Although there is virtually no amplitude difference between the three misses, a rmANOVA confirmed a significant effect of condition (H3-1, M1-3) on the amplitudes (calculated as mean in the time window of interest; $F_{6,96}$ =4.9, p=0.0095), which is obviously dominated by the decrease in the range of detected targets.

PCC/RSC

In the PCC/RSC region, a significant P3b can be observed for the detected tones combined across confidence ratings, as well as for H3, H2, and M2 (Table 1). Lower confidence in signal presence not only caused a decrease in amplitude (rmANOVA with factor condition: H3-1, M1-3, and Catch; $F_{6,96}$ =4.6, p=0.0086), but also seemed to cause an increase in latency. This was most prominent among the hit trials, as confirmed by a significant rmANOVA (factor condition, H1-3; $F_{2,32}$ =8.8, p=0.0014), but the effect was not significant anymore when including the misses (H3-1, M1-3; $F_{5,80}$ =2.4, p=0.077).

3.2.3 Pupil dilation response

In this experiment, the PDR peak around 1000 ms is superimposed by an approximately linear drift, which is present for all trial types: hits, misses and correct rejections (Figure 10). This is caused by the noise-onset about 1s before the tone onset, which itself causes a PDR. To avoid a confounding influence of this on the statistical analysis, an additional baseline correction of the PDR' was performed. After this correction, the dichotomized curves resemble those of Experiment 1. But one difference is remarkable: The second PDR peak, which occured around 1750 ms in the first experiment (1500 ms in the PDR'), is not found this time. This suggests that it might have been caused by the button press, which was delayed in the second experiment. Another possibility is that it is masked by the noise-onset response. In the dichotomized PDR', there are visible peaks for both hits and misses, similar to the previous experiment, but only the one for hits reached significance (Table 1). For the single ratings, the PDR' of H1-3 and M1 are significant, while the M2 and M1 show peaks at approximately the same time, but much lower than the other conditions. The amplitude decrease across conditions was significant (rmANOVA with factor condition: H3-1, M1-3, and Catch; F_{6,96}=5.2, p=0.0036).

3.2.4 Group comparison: conservative vs. liberal listeners

To further evaluate the influence of the criterion on the processing and detection of NT tones, the participants were split into two groups according to their overall



FIGURE 10: Pupil dilation response of Experiment 2. The PDR (A) and it's first derivative PDR' (B) are shown together with the mean amplitudes of PDR' in the time window of interest (500-1000 ms, gray area) for each condition. The dichotomized curves are shown in the upper, individual ratings in the lower row. In the amplitude plots, each circle represents single subject data, while bar height and error bars mark the mean and standard error of the mean across participants.

decision criterion. The main goal was to see, whether the AC activity and PDR for missed NT tones was more pronounced in the conservative group. This should be the case, if a strict criterion, i.e. a misclassification of low confident detections as misses explained this activity.

As Figure 11 shows, amplitudes in the AC are generally smaller in the conservative group and there are differences in the timing of the peak for detected and missed tones: In the conservative group, both have a similar timing and shape, while in the liberal group, the activity evoked by misses is much broader and later. Paired two-sided t-tests confirmed there is a latency difference between hits and misses in the liberal group (t_7 =-5.7, p=0.001) but not in the conservative group (t_8 =2.1, p=0.066). Note that no permutation cluster tests were performed to test the significance of those activations for two reasons: First, it was not the aim of this group comparison. Second, the small group sizes severely limit the number of permutations (to 127 and 255 for liberal and conservative participants, respectively) and therefore the informative value of the results.

To test the main hypothesis, the amplitude ratio of hits and misses were compared. From the grand average waveforms in the AC, the hypothesis seems to be true: The mean amplitude of misses relative to hits is about 68% in the conservative and 33% in the liberal group. However, this is not a consistent effect across participants where the average ratio is 34% (SD 70%) in the conservative, and 55% (SD 57%) in the liberal group. These ratios do not differ significantly between the two groups (two-sided t-test of independent samples: t_{15} =-0.7, p=0.50). In the PDR, the hypothesis was equally refuted (t-test for the M/H ratios across both groups: t_{15} =-1.2, p=0.25). The average ratios of -150% and 82% were dominated by one outlier in the conservative group (median: 35%/82%, SD: 560%/76%, for conservatives/liberals, respectively). This indicates that the evoked activity for undetected tones is likely not caused by

misclassified trials, but can rather be explained by a gradual decrease of amplitudes as postulated by SDT.

Generally, the PDR and PDR' of both groups look similar to the original analysis, although a bit noisier, especially in the liberal group. In this group, the PDR' peaks for M3 and M2 show a higher latency compared to the other conditions. However, post-hoc t-tests comparing M3 and M2 with H1 were not significant (t_7 =-1.5/-1.9, p=0.18/0.09 for H1 vs. M2/M3, respectively).

In the PCC/RSC, the dichotomized analysis resembles that of the whole group, with a significant P3b only for the combined hits. For the single ratings in contrast, the low and medium confident misses also show a P3b in the liberal group. The more striking result the considerable latency difference between the groups: The P3b of the liberal group peaks on average at 432 ms (SD: 154 ms), which is 164 ms earlier than the one of the conservative group (596 ms, SD: 90 ms). This difference is significant, as confirmed by independent two-sided t-tests (t_{15} =2.7, p=0.016).



FIGURE 11: Evoked potentials of the conservative and liberal participants of Experiment 2. Waveforms extracted from the AC (A and D), the PCC/RSC (B and E) and the PDR' (C and F) together with their mean amplitudes in the time windows of interest (100-400 ms for AC, 300-800 ms for PCC/RSC, 500-1000 ms for PDR'). Dichotomized curves are shown in A-C, all confidence ratings are shown in the D-F. In each panel, the data of the conservative/liberal group is shown in the upper/lower row, respectively.

3.2.5 SDT-Model of neural activity: Unimodal vs. Bimodal

The continuous decrease of amplitudes across ratings, expecially in the hit but also partly in the miss range, suggests that the relation between neural activity and perception is continuous. Two different models were used to predict the signal strength based on the behavioral outcome: a unimodal and a bimodal model for testing whether the measured amplitudes are in line with continuous or bifurcated perception. The unimodal model is based on SDT (Green and Swets, 1966), where the probability for a signal strength is described by two separate Gaussian distributions for signal trials and noise trials. In this model, a differentiation between perceived and unperceived trials solely depends on the decision criterion set by the observer: If the signal strengths is higher than this criterion, the trial will be rated as perceived, if the signal strengths falls below the criterion, it will be rated as unperceived. The bimodal model is an extension of this model, where the signal distribution consists of two modes, representing the signal strengths for perceived and unperceived signal trials, as suggested by Sergent et al. (2021).

The results show that both models explain the data well (Figure 12A, AC: $R^2 = 0.84$, 0.83; PCC/RSC: $R^2 = 0.67$, 0.66; PDR': $R^2 = 0.62$, 0.61 for for the uni-/bimodal model, respectively). However, it is also obvious that the two modes of the bimodal signal distribution are only marginally separated, i.e. without an obvious bifurcation. The AC amplitudes are best explained, with the M3 deviating most from the prediction. The drop in P3b and PDR' amplitudes is steeper in the hit range and flattens in the miss range, but overall still well explained by the models.



FIGURE 12: SDT based models of neural activity. A) Noise distribution (grey) and uni-/bimodal signal distributions (red/blue) calculated based on the average behavioral results of Experiment 2. Vertical solid/dashed lines are the five criteria for the uni-/bimodal model, respectively. B) Amplitudes predicted for both models in comparison to the data from AC (grey diamond, dashed), PCC/RSC (grey squares, solid) and PDR' (dark grey triangle, dotted). All data points are averaged across participants, error bars represent the standard error of the mean.

3.3 Experiment 2b: Comparing rating scales for near-threshold perception

In the above mentioned study (Sergent et al., 2021) that postulates bifurcation of neural activity between perceived and unperceived trials, the audibility of stimuli was rated on a continuous scale. For near-threshold stimuli, they observed a clearly bimodal audibility distribution. To examine if the different scales bias the findings

towards evidence for continuous or bifurcated perception, the following psychoacoustic experiment compared the audibility with the confidence rating scale. The results are shown in Figure 13. While the grand average of the audibility rating shows a possible bimodality, with one peak at 0% and a broader one around 60%, this is rarely visible in the single subject data: S1 and S6 show a similar pattern, S9 two peaks towards the ends of the scale. The remaining subjects' distributions are not bimodal. Similar conclusions can be drawn from the confidence rating, where few distributions appear bimodal (S1, S3, S9), but most do not. Consequently, neither of the scales seem to bias towards a specific response or perception dynamic. In the post-experimental interviews, all participants indicated that they preferred the confidence rating scale. The most common reason given was that this scale was easier to use and matched their experience better. Furthermore, participants were asked to estimate at how many different signal-to-noise ratios the tones were presented. The average guess was 6.2 (range 3-12) in the audibility rating and 5.3 (range 1-10) in the confidence rating. So all except one listener, who guessed 1 in the second run, perceived a higher variation in stimuli than presented (which was -21dB for target and -100dB for catch trials).



FIGURE 13: Response distributions of audibility and confidence ratings. Upper left panel shows the grand average distributions of the audibility (upper) and confidence rating (lower); the other panels show single subject data. The probability of a rating for target trials is shown in color, for the catch trials in grey.

3.4 Experiment 3: Attention networks in auditory perception

In this fMRI experiment, the goal was to further investigate the influence of attention on the detection of near- and supra-threshold tones and to find the brain networks involved in this process. Additionally, the correlation between pupil size and these networks was of interest. Potentially relevant networks are the ventral and dorsal attention network (VAN/DAN, Corbetta et al., 2008) and the cingulo opercular network (CON, Coste and Kleinschmidt, 2016). Both tonic and phasic changes in pupil size might be related to the VAN, as suggested by (Corbetta et al., 2008), while the CON network might be correlated with tonic changes in pupil size, as both affect performance (Coste and Kleinschmidt, 2016; Aston-Jones and Cohen, 2005). The stimulation was similar to that of Experiment 1, consisting of continuous white noise with NT tones and supra-threshold AM tones. The AM tones replaced the AM noise as distractor, in an effort to create a more salient stimulus that could be reliably detected even with the additional noise introduced by the MRI scanner. During the three runs, the attention to the NT tones was successively increased from passive listening in the first run, over detection of the AM tones in the second run, to detection of the NT tones in the last run.



FIGURE 14: Results of the pupil analysis in Experiment 3. A) PDR evoked by the different stimuli in the runs 1-3 from left to right, respectively. B) Same as A) but with the first derivative. For statistical analysis, permutation cluster test was performed on the PDR' time courses in the time window from 500 to 2000 ms. Time periods with a significant difference from 0 (p<0.05) are marked with a horizontal bar, results can be found in Table 2. C) Detection rate in dependence of the pre-stimulus pupil size. Trials are sorted into four equally large bins based on their pupil size and detection rates were calculated for each of the five bins. D) Amplitudes of the first derivative calculated as the maximum value in the time window 500-2000 ms. Conditions are sorted by stimulus type (AM tones on white, NT tones on grey background) and run (1-3 from left to right). NT tones in the last run are additionally split into detected and missed trials. In C and D, each circle represents the value of one subject, the bar height indicates the mean across subjects, and the length of the error bars indicates the standard error of the mean.

3.4.1 Behavioral results

During the first run, all but one participant noticed the presence of the salient AM tones, as stated after the run. The hit rate in the second run was 100% for all subjects, with only one participant triggering one false alarm. In the following debriefing, three participants said, they additionally perceived soft tones (i.e. the NT tones). The average detection rate for NT tones in the last run was 60% (range 22-88%) with a false alarm rate of 17% (0-50%). Note, that the false alarm rate was calculated by dividing the number of FA by the number of catch trials and AM tones. But due to the long trial duration (up to 15 s), several FA in one trial are conceivable, so this rate might exaggerate the tendency to respond without having perceived a real stimulus. Similar to the M/EEG experiments, the trials were sorted into quantiles according to arousal, measured as the pre-stimulus pupil size, and the detection rate of NT tones was calculated for each quantile. Because of the lower number of trials compared to the other experiments, only four bins were used. One participant had to be

excluded from this analysis because only two trials with valid pupil data remained (i.e. with less than 30% blinks or otherwise corrupted data). Figure 14A shows that performance again peaked at intermediate levels of arousal, this quadratic effect was significant and no linear effect was found (contrast analysis, quadratic: $F_{1,18} = 9.6$, p = 0.006; linear: $F_{1,18} = 2.1$, p = 0.1696).

3.4.2 Pupil dilation response

Based on the findings of Experiment 1, a PDR was expected for AM tones in the second, and detected and missed NT tones in the third run. Since passively perceived, salient stimuli can elicit a PDR, it was also expected that the AM tones evoke a PDR in the first run. For the third run, two scenarios for the PDR evoked by AM tones were possible: A suppression because attention is directed towards the NT tones (see AM noise in the second run of Ex. 1), or a similar amplitude as in the first run, because the AM tones are much more salient than the AM noise in Experiment 1. In the latter case, it would probably be lower than in the second run, as it was not task-relevant anymore.

Indeed, a significant PDR was observed for AM tones in all runs, and for detected and missed NT tones in the last run (Table 2). The peak amplitudes are plotted in Figure 14C and analyzed with one rmANOVA for each stimulus type (AM/NT tones) with the factor run (1/2/3). This showed a significant task modulation not only for NT tones, but also AM tones, even though they evoked a PDR in all runs ($F_{1,16}$ =27.0/67.8, p=5e-6/5e-8, for AM/NT respectively). The attenuation of the PDR evoked by AM tones in run 3 compared to run 2 was additionally analyzed with post-hoc t-tests. There was no significant difference in peak amplitude for the first derivative, but the PDR was significantly attenuated (t_{16} =1.8/6.5, p=0.09/8e-6, for PDR'/PDR, respectively).

TABLE 2: Results of the permutation cluster tests of the PDR' of Experiment 3. The tests were performed in the time window from 500 to 2000 ms with one-sided t-tests, a cluster forming threshold of 0.05, and 50000 permutations. When clusters were found, their start and end time are given with the corresponding p-value. Significant clusters (p<0.05) are marked with an asterisk. For some conditions, more than one cluster was found. consequently, both are listed in chronological order.

Experii	nent 3	start [ms]	end [ms]	р	
Run 1	AM tones	501	819	0.0008	*
		1191	1486	0.0519	
	NT tones	-	-	-	
	Catch	-	-	-	
Run 2	detected AM tones	501	1535	< 0.0001	*
	NT tones	699	728	0.3517	
	Catch	-	-	-	
Run 3	AM tones	501	1045	< 0.0001	*
		1067	1336	0.1020	
	detected NT tones	520	1740	< 0.0001	*
	missed NT tones	601	1560	0.0004	*
	Catch	1142	1287	0.1634	

3.4.3 Stimulus-evoked BOLD signal

Figure 15 shows maps of the stimulus-evoked BOLD . The AM tones vs. noise contrast shows a positive BOLD response in all runs. In the first run, the activity was dominated by activity in the VAN (including AI, pSTS, and iPCS) together with AC and the cingulate cortex. During the detection of AM tones in the second run,

activity in these areas increased and extended to central and post-central sulcus, sPCS, superior frontal sulcus and larger parts of the cingulate cortex, particularly the aMCC. In the last run, AM tone activity was still stronger than in the first run, but notably reduced in some areas, like post-central sulcus, and posterior midcingulate cortex (pMCC).

The NT tones vs. noise contrast was much more influenced by task. In the first run, there was no significant activation and in the second run only small clusters in the AC and ACC. In the last run, the contrast for detected NT tones vs. noise was conceptually equal to that of detected AM tones vs. noise in the second run. The missed NT tones showed few spots of significant activation, mainly in the AI, the aMCC and the superior temporal sulcus.



FIGURE 15: Maps of stimulus-evoked BOLD signal of Experiment 3. Contrasts of stimulus vs. noise are shown for AM tones in all runs (row 1-3), and task-irrelevant, detected, and missed NT tones in the second and last run (rows 4-6, respectively). The NT tones vs. noise contrast of the first run is not shown, because there was no significant activity. For better visual comparison, all contrasts are shown with a cut-off of p=0.001. This is stricter than an FDR correction with α =0.05 for all except the last contrast.

ROI analyses were done to further investigate the task-modulation in different

areas (Figure 16). The overall pattern of increasing activity for AM/NT tones across the first two or all three runs was the same in all ROIs, but three properties differed: First, activity evoked by AM tones increased from run 2 to 3 in some ROIs, but decreased in others. Second, the missed NT tones only resulted in a significant BOLD response in AC. And lastly, some ROIs were lateralized with higher activity in one of the hemispheres. To quantify the effect of task or hemisphere, rmANOVAs were calculated for each area and the two stimulus types AM and NT tones separately. The results can be found in Table 3. For AM tones, the task modulation was only significant in AC, sPCS, SMG, and RSC. For the NT tones, all ROIs were significantly task modulated except AI, IPS, and aMCC. A significant lateralization was found in pSTS regardless of the stimulus type, in RSC for AM tones, and in AI for NT tones. The t-tests for significant activity (averaged across hemispheres) revealed two interesting points: First, activity for NT tones was already significant in the second run in AC, pSTS, and iPCS. And second, missed NT tones caused significant activation in the AC. The activation in response to detected NT tones was higher compared to undetected in all ROIs.



FIGURE 16: Analysis of the BOLD signal in cortical ROIs. Each data point represents a single subject, the mean beta value across subjects and its standard error are shown by bar height and the error bars. Two shades of one color represent data from the two hemispheres (lighter/darker shade = left/right hemisphere). All AM/NT tones vs. noise-only contrasts are shown in run order (1-3) on white/grey background, respectively. The NT tones in the last run are split up into detected and missed tones vs. noise. The beta values averaged across hemispheres were compared against 0 with two-tailed t-tests. Significant differences are marked with an asterisk; FDR-correction with the Benjamini-Hochberg procedure was applied to account for multiple comparisons (n=63).

of the ROIs and both stimulus types separately with the factors hemisphere	for multiple comparisons with the Benjamini-Hochberg procedure for all	tionally, two-tailed one-sample t-tests were calculated to test beta value	d marked with asterisk if significant. Lastly, two sets of paired t-tests were	: one for the stimulus evoked and one for the baseline activity. Here, each	rrected with n=9.
ABLE 3: Statistic results of the cortical ROIs. rmANOVAs were calculated for each	nem.; left, right) and run (1, 2, 3). The resulting p-values were FDR corrected	NOVAs together (n=54); significant effects are marked with an asterisk. Add	iveraged across hemispheres) against 0. Results are also FDR corrected (n=63) an	erformed to compare the BOLD signal evoked by detected and missed NT tones	set of p-values is FDR co

		AC	jd	STS		AI	ii	SCS	sP	CS	I	Sd	S	ИG	aM	ICC	R	SC
rmANOVA AM tu	ones																	
	щ	٩	щ	٩	щ	٩	щ	٩	щ	٩	щ	٩	щ	٩	щ	٩	щ	٩
hem.	1.7	0.358	254	*0.001	1.8	0.355	3.4	0.199	0.3	0.754	1.4	0.433	2.3	0.299	0.0	0.903	18.6	*0.003
run	5.8	*0.035	1.8	0.349	3.8	0.113	3.0	0.198	18.7	*0.001	3.8	0.113	17.4	*0.001	2.8	0.199	9.9	*0.010
hem. x run	1.3	0.457	0.3	0.755	0.3	0.808	3.0	0.199	0.8	0.653	1.2	0.471	0.6	0.754	0.1	0.856	2.6	0.224
rmANOVA NT tc	sanc																	
	щ	٩	щ	٩	ц	٩	щ	d	щ	٩	щ	٩	щ	d	щ	٩	щ	d
hem.	0.3	0.754	11.4	*0.017	8.2	*0.041	0.0	0.859	0.0	0.931	2.7	0.246	0.1	0.808	1.1	0.471	0.3	0.754
run	15.3	*0.001	5.6	*0.041	3.8	0.113	6.4	*0.031	9.3	*0.010	2.3	0.267	12.8	*0.003	4.7	0.067	9.4	*0.011
hem. x run	0.2	0.812	4.5	0.113	0.5	0.754	0.5	0.754	0.7	0.698	0.4	0.754	1.8	0.355	0.4	0.755	0.3	0.808
One-sample t-test	ts (two	-tailed)																
	t	α	t	d	t	α	t	d	t	α	t	d	t	þ	t	d	t	þ
AM tones 1	9.3	*0.000	6.0	*0.000	1.3	0.204	2.6	*0.018	2.4	*0.028	2.2	*0.037	3.3	*0.004	1.8	0.081	4.8	*0.000
det. AM tones 2	9.6	*0.000	4.6	*0.000	3.0	*0.007	3.9	*0.001	7.2	*0.000	3.2	*0.005	7.2	*0.000	3.6	*0.002	7.3	*0.000
AM tones 3	10.0	*0.000	5.9	*0.000	4.7	*0.000	5.5	*0.000	7.1	*0.000	5.0	*0.000	5.8	*0.000	5.0	*0.000	6.7	*0.000
NT tones 1	0.1	0.926	-1.7	0.115	-0.9	0.406	-1.0	0.315	-0.5	0.641	-1.7	0.101	-1.9	0.078	-1.0	0.338	-0.7	0.465
NT tones 2	4.1	*0.001	3.0	*0.008	1.2	0.235	2.1	*0.049	0.7	0.496	1.5	0.152	1.4	0.169	1.7	0.105	1.8	0.083
det. NT tones 3	7.4	*0.000	3.1	*0.006	3.7	*0.002	4.1	*0.001	5.0	*0.000	2.9	*0.009	5.6	*0.000	3.8	*0.001	6.3	*0.000
mis. NT tones 3	3.6	*0.002	0.8	0.447	0.1	0.917	0.6	0.543	0.9	0.371	-1.0	0.316	0.2	0.816	0.2	0.837	-0.1	0.941
Paired t-tests (two	o-tailec	<u>(</u>																
	t	٩	t.	٩	ب	٩	t	٩	t	٩	+	٩	+	٩	÷	٩	÷	٩
Hit vs. Miss	6.1	*0.000	2.4	*0.026	3.4	*0.004	3.9	*0.001	4.2	*0.001	4.1	*0.001	5.7	*0.000	3.5	*0.003	7.5	*0.000
Pre-stimulus acti	vity: p	vaired t-te	sts (tw	o-tailed)														
	t	d	t	đ	t	đ	t	đ	t	þ	+	α	t	þ	t	d	÷	đ
Hit vs. Miss	1.7	0.158	1.0	0.392	3.6	*0.019	3.0	*0.033	1.6	0.158	1.9	0.158	1.7	0.158	2.3	0.093	0.7	0.521

Subcortical analysis

The applied fMRI sequence was not optimized for localizing activity in subcortical structures, especially in small nuclei like the LC, which is only 1 to 2 mm wide (compared to 3x3x4 mm³ voxel size). Nevertheless, an exploratory analysis of BOLD activation in the subcortical volume was performed to receive an impression of the general activation pattern.

The overall task-dependence was similar to the cortex, although the extend of activation for AM tones was more strongly reduced from run 2 to 3 and no significant activation was found for missed NT tones (Figure 17). The major part of the activity was found in the thalamus and the midbrain, but it also expands to the pons, covering, among others, the LC area.

The corresponding ROI analysis is shown in Figure 18 and Table 4 contains the results of the rmANOVAs and t-tests. In contrast to the cortical ROIs, there was significant task modulation in all subcortical ROIs for both types of stimuli, except for LC and IC, where the task modulation for NT tones was not significant. None of the ROIs were significantly lateralized. The one-sample t-tests showed that the AM tones vs. noise contrast was significant in all runs and ROIs. In contrast, the NT tones did not evoke any activity in the first run, and in second run only in the IC and pulvinar. Detected NT tones evoked significant activity in all, the missed tones in none of the six ROIs. The comparison of activity evoked by detected and missed NT tones was significant in each ROI.

TABLE 4: Statistic results of the subcortical ROIs. rmANOVAs were calculated for each of the ROIs and both stimulus types separately with the factors hemisphere (hem.; left, right) and run (1, 2, 3). Additionally, two-tailed one-sample t-tests were calculated to test beta value (averaged across hemispheres) against 0, and two sets of paired t-tests were performed to compare the BOLD activity of detected and missed NT tones: one for the stimulus evoked and the other one for the baseline activity. None of the p-values are corrected for multiple comparisons in this exploratory analysis of the subcortical volume. Significant results (p<0.05) are marked with an asterisk.

	F	AG		LC		IC		SC	N	IGN	Pu	lvinar
rmANOVA AM to	ones											
	F	р	F	р	F	р	F	р	F	р	F	р
hem.	1.5	0.233	0.4	0.522	0.8	0.388	3.0	0.098	2.6	0.125	1.4	0.244
run	7.2	*0.003	4.6	*0.021	5.2	*0.010	5.6	*0.010	8.3	*0.002	12.0	*0.000
hem. x run	2.9	0.074	0.5	0.577	0.4	0.667	0.7	0.491	0.3	0.717	0.6	0.571
rmANOVA NT to	nes											
	F	р	F	р	F	р	F	р	F	р	F	р
hem.	0.3	0.565	2.0	0.176	0.1	0.741	0.1	0.729	0.4	0.534	0.4	0.551
run	16.0	*0.000	2.3	0.129	2.5	0.109	9.4	*0.002	5.9	*0.011	7.8	*0.005
hem. x run	2.4	0.120	0.7	0.518	0.3	0.721	1.9	0.170	0.4	0.672	1.0	0.388
One-sample t-test	s (two-	tailed)										
	t	р	t	р	t	р	t	р	t	р	t	р
AM tones 1	3.5	0.003	2.5	0.023	3.5	0.002	1.3	0.004	3.9	0.001	3.7	0.001
det. AM tones 2	6.4	0.000	4.5	0.000	7.2	0.000	1.5	0.000	5.9	0.000	4.5	0.000
AM tones 3	4.1	0.001	5.8	0.000	2.3	0.034	0.8	0.001	6.9	0.000	3.7	0.000
NT tones 1	0.1	0.926	0.1	0.944	0.4	0.676	0.8	0.936	-0.5	0.636	-0.8	0.690
NT tones 2	2.1	0.054	1.8	0.089	2.2	0.037	1.4	0.270	0.6	0.570	2.3	0.014
det. NT tones 3	6.9	0.000	3.8	0.001	3.8	0.001	-1.8	0.000	5.4	0.000	3.4	0.000
mis. NT tones 3	-0.1	0.953	0.7	0.472	0.1	0.885	-1.0	0.551	-0.1	0.913	0.4	0.516
Paired t-tests (two-tailed)												
	t	р	t	р	t	р	t	р	t	р	t	р
Hit vs. Miss	6.2	*0.000	2.7	*0.018	3.3	*0.006	6.8	*0.000	5.0	*0.000	7.1	*0.000
Pre-stimulus acti	vity: pa	ired t-tes	ts (two	-tailed)								
	t	р	t	р	t	р	t	р	t	р	t	р
Hit vs. Miss	1.5	0.149	0.4	0.678	1.1	0.291	1.6	0.127	1.1	0.269	1.1	0.287



FIGURE 17: BOLD signal in the subcortical volume for the contrasts AM tones vs. noise (run 1-3) and detected NT tones vs. noise. Other NT tones vs. noise contrasts are not shown, because there is no significant activation. Sagittal slices of the left (first row) and right (second row) are shown at x=±5 mm from the midsagittal plane. For better visual comparison, the threshold is p=0.001 for all conditions. This is stricter than the FDR-corrected threshold for all conditions (p=0.00001, 0.020, 0.005, 0.016, from left to right, respectively) except the passive AM tones in the first run, but the single voxel activated here is not influenced by this difference. In the lower row, ROIs are visualized in a selection of sagittal slices.



FIGURE 18: Analysis of BOLD signal in subcortical ROIs. Each data point represents a single subject, the mean beta value across subjects and its standard error are shown by bar height and the error bars. Two shades of one color represent data from the two hemispheres (lighter/darker shade = left/right hemisphere). All AM/NT tones vs. noise contrasts are shown in run order (1-3) on white/grey background, respectively. The NT tones in the last run are split into detected and missed tones vs. noise. The beta values averaged across hemispheres were compared against 0 with two-tailed t-tests. Significant differences are marked with an asterisk; No FDR-correction was applied because of the exploratory nature of the analysis.

3.4.4 Pre-stimulus BOLD signal and pupil size

Previous studies showed that BOLD activity before the onset of a stimulus was elevated in certain areas if the following stimulus was detected compared to missed stimuli (Sadaghiani et al., 2009; Coste and Kleinschmidt, 2016). For a replication, the pre-stimulus BOLD level was calculated with an FIR analysis and compared between hits and misses (see time courses in Figure 19, t-test results in Table 3 and Table 4). The baseline activity for hits was significantly higher in AI and iPCS, and a trend in the same direction was observed in aMCC. None of the ROIs had higher baseline activity for misses.

Baseline activity was further compared for the pupil, in form of the pre-stimulus (200 ms) pupil size and saccade rate. Both did not differ significantly between hits and misses, which can be explained for the pupil size by the symmetric, inverted-u-shaped relationship between arousal (measured as baseline pupil size) and detection rate: This leads to increased numbers of misses for both, low and high arousal, precluding a difference between hits and misses in pupil size during the baseline interval. The same explanation likely holds true for the saccade rate, which has also been related to arousal (Chen et al., 2021). However, evidence for this relationship in tasks without visual stimuli or spatial attention is rather scarce (e.g., Wang et al., 2017). These results dissociate the activity of AI and aMCC on the one hand, and pupil size and saccade rate on the other hand.



FIGURE 19: FIR-analysis of the BOLD signal in cortical and subcortical ROIs for detected and missed NT tones in the last run. Time courses are averaged across participants and hemispheres, error bars represent the standard error of the mean. The baseline activity (-2–0 s, marked with grey/white box) is compared between the two trial types. Significant differences are marked with an asterisk (p<0.05, see Table 3 and Table 4). Cortical ROIs (A) are shown on white, subcortical (B) on gray background. In Panel C, the baseline pupil size and saccade rate (each calculated as mean across the 200 ms before stimulus onset) are plotted for hits and misses. here, each data point represents one subject, bar height marks the average across subjects and error bars the standard error.

3.4.5 Co-variation of BOLD signal and pupil size

To find brain areas, where the changes in BOLD signal are correlated with changes in pupil size, the pupil size was used as regressor for the fMRI analysis. However, this regressor could not simply be convoluted with the canonical HRF, because the pupil size itself already has a considerable lag compared to the underlying neural activity (presumably LC and SC). Hence, the pupil size regressor was shifted in time to create different lags relative to the BOLD signal. In this way, a time course of BOLD signal change in response to pupil dilation was computed that is equivalent to that of a standard FIR analysis. Epochs with a 10s duration after each stimulus were excluded from the analysis to focus on the spontaneous pupil fluctuation. The resulting time courses did not show any considerable difference between the analyzed ROIs. Hence, only the time course averaged across the whole cortex is shown in Figure 20A. This time course shows that a change in pupil size at t=0s was related to an increase in BOLD signal starting up to 2s before and peaking at 2s after the pupil change. This was followed by a rapid decrease in BOLD signal from 4 to 8 s after the change in pupil size. A similar biphasic pattern was found in subcortical regions, but due the low SNR, no information on the spatial distribution of this covariation could be obtained.

The maps for the early peak and the subsequent trough are shown in Figure 20B. Areas with a significant positive change in BOLD response included the insula, SMG, central and superior frontal sulcus, occipital areas, and most parts of the cingulate cortex including ACC and aMCC. The strongest negative change was in the occipital lobe, but it also extended across somatomotor areas, the inferior frontal sulcus, superior temporal gyrus and STS. In a notable contrast to the positive peak, AI, aMCC, and ACC showed no change of BOLD activation.



FIGURE 20: Co-variation of BOLD signal and pupil size. A) Time course of the mean co-variation across the whole cortex. The time course represents the group average with the standard error of the mean. B) Maps of the significance of positive and negative correlation of BOLD response and pupil size.

Chapter 4

Discussion

4.1 Attentional modulation of brain activity

The importance of attention for perception has long been known, but the precise processes and interplay of the networks involved are complex. In this study, different aspects of this have been highlighted:

First, attention can have a differential impact depending on the stimulus. This is evident in the comparison of the changes in perception of NT tones, AM noise, and AM tones, and the corresponding evoked responses in different tasks. The AM tones and noise were presumably perceived regardless of the task. For the AM noise in Experiment 1, this was not systematically queried, but some participants reported being distracted by the AM noise during the detection of NT tones. In Experiment 3, all participants reported perceiving the AM tones after the passive condition. In contrast, the NT tones were mainly perceived when they were task relevant. The group of participants who heard NT tones without task relevance also detected them better in the previous run, which might indicate that they perceived the tones as more salient than the other group. Taken together, this suggests that the amount of attention required to perceive a stimulus decreases with its saliency. Other studies working with non-task-relevant stimuli, about which subjects were not informed in advance, used more salient stimuli than the NT tones (Pitts et al., 2012; Schlossmacher et al., 2021). This saliency difference is evident from the higher sensitivities, with an average d' between 3.5 and 4 in those studies, compared to 1.3 for the NT tones here. In line with the above proposed relation between saliency and perception, both studies found a subset of participants who were aware of these stimuli before being informed about their presence.

When considering not only the mere awareness, but also the evoked responses, even more facets of the influence of attention become apparent, as task-modulation differed not only with stimulus type but also across the different sources of the activity. In Experiment 1, the AC activity in response to AM noise was not modulated by task, but PDR and P3b were. In contrast, all three responses to the NT tones were strongly modulated, i.e. only present when task relevant. In the fMRI experiment, the pattern of task modulation was similar, with the exception that a PDR for the AM tones was also present when they were not task-relevant, even though slightly attenuated compared to the task-relevant run. This difference is likely also caused by the increased saliency of the AM tones compared to the AM noise. The distinct patterns of task-modulation across the evoked responses get sorted out on their way from early stages like the auditory activity to late stages like the P3b. This is supported by Vugt et al. (2018), who found that activity evoked by visual stimuli was only partially transmitted from visual to frontal cortex.

The addition of a passive run in Experiment 3 also revealed that the switch from

passive listening to detecting the AM tones already increased the activation level for the NT tones, which were in most cases still unperceived at this point. This suggests an increase in activation in some brain areas in preparation for the processing of (target) stimuli. Such an attentional amplification of sensory signal at an early processing stage, i.e., before the eliciting stimulus reaches awareness, could equally explain the significant AC activity for missed NT tones in all of the main experiments. This is also in agreement with a study that found activation in AC caused by auditory attention while waiting for a stimulus to occur (Voisin et al., 2006). One explanation for this could be the tuning of neurons in the AC to the target frequency, which has been demonstrated before (Natan et al., 2017). This frequency tuning could be another explanation for the missing suppression of responses to the AM tones in Experiment 3, when attention should be shifted towards the NT tones, as the AM and NT tones shared the same frequency. Hence, the similarity was possibly too high for selectively attending to only the NT tones, causing a persistent BOLD activation in response to the AM tones. Another reason for the inability to suppress this response could be that the saliency of the AM tones was too high. This would agree with the activation of regions belonging to both the VAN and CON in response to the AM tones already in the passive run. Both networks are known to be activated in response to salient and potentially relevant stimuli. The same applies to the PDR, which was also not observed for the AM noise in Experiment 1, but for the AM tones in Experiment 3.

In addition to this potentially target-specific effect, there also seems to be a general increase in activity that facilitates detection of target stimuli. The elevated prestimulus BOLD signal for hits compared to misses in the AI and iPCS (and a trend in aMCC), is an indicator of such an effect. This observation is mostly in line with the studies that found increased baseline activation in the CON for hits compared to misses (Sadaghiani et al., 2009), or fast versus slow responses (Coste and Kleinschmidt, 2016). Hence, in both cases a pre-activation of the CON facilitated performance. This is also in line with the previously suggested role of the network in maintaining a stable task performance (Dosenbach et al., 2007), and reports of AI and aMCC (or ACC) activation during sustained attention (Posner, 1994; Voisin et al., 2006; Grahn and Manly, 2012). The significant elevation of pre-stimulus activity in the iPCS in the present data was not reported in both studies, as the iPCS was not part of the networks they examined. But Sadaghiani et al. (2009) further reported increased baseline activation for hits in areas of the DMN and the opposite effect, i.e. an increased activation for missed stimuli, in the IPS and the middle temporal complex. This could not be reproduced here, a possible explanation might be that these areas are not or only partially overlapping with the ROIs chosen here. The influence of pre-stimulus activation in the CON on performance could indicate a connection between the network and the LC, which has widespread projections to the cortex, controls the arousal level, and thus influences performance (Aston-Jones and Cohen, 2005). This interaction between arousal and performance will be further discussed in the following section.

4.2 Influence of arousal

Similar to the cortical activity, the PDR evoked by the AM tones can be explained by saliency: Salient or otherwise important stimuli can evoke the so-called orienting response (Lynn, 1966). It is usually observed as a pupil dilation, signifying an

increase in arousal, accompanied by changes in heart rate, skin conductance, microsaccades, and more (Nieuwenhuis et al., 2011; Wang et al., 2017). It likely serves to rapidly respond to the original stimulus and increase sensitivity to upcoming events (Nieuwenhuis et al., 2011), which could ensure survival in critical situations. Among other things, this is achieved by lowering the sensory thresholds (Lynn, 1966). Other ways in which arousal affects performance are discussed below.

4.2.1 Pupil dilation and performance

Pre-stimulus pupil size

Arousal is known to influence different measures of performance like the detection rate or reaction times. It is typically assumed that this relationship follows an inverted U-shape, indicating peak performance during intermediate levels of arousal, i.e. when the LC fires in phasic mode (Aston-Jones and Cohen, 2005). Here, the effect of pre-stimulus pupil size on the detection rate followed the expected shape in Experiments 2 and 3, but was only linear in Experiment 1. This can most likely be attributed to overall low arousal levels during this experiment. Because no reference point of maximum arousal or pupil size has been recorded, this cannot be confirmed easily, but it seems plausible when comparing the three settings: In Experiments 2 and 3, arousal was likely higher because of the trial-based structure (Experiment 2), and the less comfortable and noisier environment of the fMRI measurement in combination with salient, startling tones (Experiment 3). Another result in favor of a quadratic effect -or some other form of symmetric relationship - is the lack of difference in prestimulus pupil size for hits compared to misses in the last experiment.

In the literature, the quadratic relationship between arousal and performance was also reported by other studies on mice (McGinley et al., 2015a) and human (Murphy et al., 2011; Smallwood et al., 2012; Unsworth and Robison, 2016). But other experiments revealed a seemingly linear relationship with optimal performance for either small (Franklin et al., 2013) or large (Mittner et al., 2014) baseline pupil sizes, and there are even reports about no consistent relationship (Martin et al., 2022). Brink et al. (2016) found a linear effect, that was dominated by the time-on-task, which influenced both performance and arousal. After correcting for this, the originally proposed inverted U-shape was discovered. These discrepancies could be attributed to the variety of tasks and measures of performance (e.g., reaction time or detection rate) which might result in different confounding factors like time-on-task, as proposed by Brink et al. (2016), or not covering the full range of arousal, as proposed here.

As already indicated above, there might be a connection between arousal and the pre-stimulus activation in some brain areas, as both influence performance. However, while the arousal-performance relationship was in the present data (and many previous reports) quadratic, the significant difference between hits and misses in pre-stimulus BOLD signal suggests a monotonic relationship between arousal and this activation. This in turn means that the pre-stimulus BOLD activity cannot be linearly related to arousal.

Task-evoked pupil dilation

Apart from the baseline pupil size, some studies investigated how phasic pupil dilation influences the behavioral outcome. It was found that the PDR scales with

surprise, encodes the perceptual content (Kloosterman et al., 2015), and the content of a decision (Gee et al., 2014). The latter effect manifested as larger PDRs for Yescompared to No-responses and the effect was more pronounced in conservative subjects, i.e. when a Yes response was more against their individual bias. This decision bias is equivalent to the decision criterion used here. Consequently, followup studies found that a larger PDR predicted a reduction in bias (Gee et al., 2017), which was also true when the bias was systematically manipulated by changing the target probabilities, and when using a memory-based task instead of a perceptual one (Gee et al., 2020). The encoding of perceptual content seems to agree well with the results presented here, especially with those of Experiment 2, where PDR amplitudes differed between ratings. But the reduction of decision bias - or criterion - for larger PDRs seems to be at odds with those results, as they showed larger amplitudes for higher criteria. However, the higher confidence ratings can be similarly interpreted as an untypical decision, i.e. a decision against the participants individual bias. In other words: participants only used the most confident signalpresent response, when exceptionally high evidence (in form of strong neural activity, as indicated by a high PDR) was available.

Nonetheless, it is important to note that the stimuli used in those studies that related PDR amplitude to bias had an important conceptual difference to the ones used here: the stimuli were presented for an extended period of time allowing for evidence accumulation before the response was made (Gee et al., 2014; Gee et al., 2017; Gee et al., 2020). This period between stimulus onset and response was responsible for the major part of the task-evoked pupil dilation und thus the underlying increase in LC activity (Gee et al., 2014; Gee et al., 2017). Therefore a longer stimulus presentation and a delayed response could increase the probability of an effect of the decision compared to the present experiments, were stimuli were much shorter. In Experiments 1 and 3, the response was also required directly after the stimulus, only in Experiment 2 the remaining noise after the tone can be considered as decision formation period. However, since the stimulus was short, there was no way to accumulate further perceptual evidence for or against a certain decision, thus this period might have no or less influence on response bias compared to the aforementioned studies.

Similar considerations are true for more studies of the same group that found a positive correlation of PDR amplitudes with uncertainty and correspondingly a negative correlation with confidence (Urai et al., 2017; Colizoli et al., 2018). This would indeed be at odds with the results of Experiment 2, but both studies used a period between response and feedback for the evaluation. Hence, both confidence and uncertainty were not evaluated with respect to stimulus presence or absence, but with respect to the correctness of the response, which involves additional metacognitive processes.

Two studies of this group also related the confidence in the current decision to behavioral parameters of the subsequent trial. According to Urai et al. (2017), a higher PDR caused by uncertainty about the previous response increases the chances of a different choice during the next trial, while Desender et al. (2019) found that low confidence on one trial can delay the response to the following trial, and vice versa. This is comparable to the transition probabilities calculated here: The lack of any significant effect in Experiment 1 might be related to the fact that no information about confidence was available for the analysis, or -as addressed in subsection 3.1.5the presence of distractors and the potentially long intervals between two targets. In Experiment 2, high confidence in signal presence or absence should usually correspond to high confidence in the correctness of the response (although there might be exceptions) and thus should not result in the urge to switch to a different response on the next trial. So the elevated probabilities for highly confident responses following each other is in line with the observations by Urai et al. (2017). The finding that confidence affects the reaction time in Experiment 2 is in turn consistent with the study by Desender et al. (2019), even though there was no prolonged stimulation for evidence accumulation.

4.2.2 Pupil dilation and brain activity

Another way to further investigate the influence of pupil-linked arousal on the various processes in the brain is to correlate pupil size and brain activity. A number of studies tried this using fMRI measurement during rest (Schneider et al., 2016), visual tasks (Gee et al., 2017; DiNuzzo et al., 2019), or both (Yellin et al., 2015; Murphy et al., 2014); the present data extends this type of analysis to auditory tasks. The results are only partially overlapping, but one common finding is a positive correlation between pupil size (or change) and brain activation in areas of the CON, i.e., insula, cingulate cortex, and thalamus. This can be also observed in the present results, and of the aforementioned studies, only Yellin et al. (2015) reported a negative rather than a positive correlation in these (and other) areas. Additionally, negative correlations in visual and sensorimotor regions were reported in a subset of these studies (Yellin et al., 2015; Schneider et al., 2016; DiNuzzo et al., 2019), whereas Murphy et al. (2014) reported a positive correlation there. While both visual and sensorimotor regions were correlated with pupil size in the present data, especially the visual areas were more pronounced in the negative peak.

Discrepancies in the results might be partially explained by the different tasks, but even more by the analysis methods. The challenge for this type of analysis is that one is typically not actually interested in a correlation of brain activity with pupil size, but the pupil is used as a proxy for changes in arousal. However, pupil dilation starts approximately 500 ms after an event (see data presented here, or Joshi et al. (2016) for recordings in monkey), but the exact timing, especially for the peak varies strongly, depending on the task or eliciting event (see for example the latency differences and different shapes for the PDR in Experiment 3). Therefore the usual fMRI analysis stream with a canonical HRF might reflect different effects compared to an analysis using other methods. Of the studies mentioned above, DiNuzzo et al. (2019) and Yellin et al. (2015) used only the canonical HRF, while Murphy et al. (2014) and Schneider et al. (2016) also included its temporal and dispersion derivatives to deal with the unknown timing. Gee et al. (2017) circumvented the problem, as they did not use the pupil size as regressor, but contrasted task-evoked BOLD responses of trials that evoked a large PDR with those that evoked a small PDR. In the present analysis, the problem was addressed by calculating the correlation for different lags between BOLD signal and the pupil size regressor. The resulting time course showed that there are strong positive correlations around the time of the pupil change (lag=0-2 s), and negative correlations shortly after (lag=4-8 s). The early peak indicates that the increase in brain activity happens simultaneously or even before the subcortical activity that causes the corresponding pupil dilation. Thus, there is either a common trigger for both, or the cortical activation can elicit a pupil dilation via subcortical pathways. The timing of the subsequent trough on the other hand is comparable to a regular event-related BOLD response, suggesting that this negative correlation could be in response to the activity that caused the pupil dilation. The low temporal resolution, which is restricted by the repetition time of the MRI sequence (2 s here), makes it difficult to determine cause and effect.

An improved temporal resolution compared to MRI can be achieved with M/EEG measurements. Pfeffer et al. (2022) searched for co-variations of pupil size and cortical activity measured with MEG. They found different types of correlation (negative, positive, and non-linear) across different frequency bands and brain regions. This again underlines the complex influence of arousal on cortical activity, and furthermore its specificity (Pfeffer et al., 2022).

A better understanding of this would help to determine at which stages of the subcortical input intervenes in the processing of auditory stimuli. One suggestion on this is that a coupling of cortical and subcortical activity is necessary for conscious processing (Aru et al., 2019). More specifically, increased dendritic activity in layer 5 pyramidal neurons of mice was found to be correlated to increased detection rates, but almost exclusively in those neurons that project to subcortical regions (Takahashi et al., 2016; Takahashi et al., 2020). Thus, the dendritic integration theory (Aru et al., 2020) proposes that the coupling of cortico-cortical and thalamo-cortical loops via these dendritic activity is essential for conscious processing. Other potential correlates of consciousness (or parts thereof) are reviewed in the following section under consideration of the evidence collected during this work.

4.3 Correlates of conscious perception

The present results provide some new evidence to reevaluate previously proposed correlates of consciousness. First, there is activity evoked in the auditory cortex both in the fMRI and the M/EEG experiments for all perceived stimuli. Even for the last run of Experiment 1, there seems to be a small negativity in the group that reported hearing NT tones, when compared to the group that did not detect any of the tones. This is not statistically significant, which may be due to the small sampling size, or - perhaps more importantly - the proportion of tones detected, which was probably much lower than in the previous run (e.g., one participant reported hearing 3-4 tones in total, another one estimated the number to be about half as many as in the previous run). In both cases, there is also activity for missed NT tones with smaller amplitudes compared to the perceived tones. This is consistent with the concept of the AAN (Eklund and Wiens, 2019), which is defined as the difference between activity evoked by perceived and unperceived stimuli. Accordingly, the present results support the AAN as a potential correlate of consciousness.

On the other hand, the P3b (which will be discussed further in subsection 4.3.1) and the PDR can be ruled out as correlates, as they could not be observed for the taskirrelevant but presumably perceived AM noise in Experiment 1. Another previously suggested correlate is the pSTS (Wiegand et al., 2018), which was therefore a central part of the research hypothesis for the fMRI experiment. In line with the hypothesis, pSTS activation was significantly higher for all perceived stimuli compared to the noise trials. But this is also true for several other ROIs: iPCS, sPCS, SMG, and RSC. This shows the challenges on the quest for the correlates of consciousness: Results have to be interpreted carefully, to make sure the correlates under considerations are truly related to consciousness instead of attention, decision making and other confounding factors (Eklund et al., 2020; Tsuchiya et al., 2015; Dembski et al., 2021; Rutiku et al., 2015). In the present case, the activation measured during the fMRI experiment could be related to task execution, including top-down attention, i.e. activation of the DAN (potential reason for the sPCS activation, Corbetta et al., 2008), decision making (P3 generation from RSC, Das et al., 2023), motor response, and more. The perception of salient AM tones in the first run should be mostly free from task-related activity, but it could still be confounded by bottom-up attentional processes, including activation in the VAN (Corbetta et al., 2008)), a P3a (a subcomponent of the P300 that can be evoked by salient but not task-relevant events, and is located more anterior compared to the P3b Polich, 2007), or more generally by an orienting response (Lynn, 1966).

The concept of contrasting perceived and unperceived stimuli, as it is done for the AAN, is a good approach to deal with this problem, because it cancels out confounding factors that are equal across trials (like task-relevance). However, in the present study, task-related processes for the unperceived tones are not (necessarily) stimulus-locked, as listeners could not know when the stimulus was presented. In Experiment 2, the noise onset served a cue, and a response was also required for unperceived tones. But there was still a substantial temporal variation of the stimulus onset, especially compared to the high temporal resolution of the M/EEG. In the future, this could be solved by introducing a visual cue time-locked to the auditory stimulus (similar to Squires et al., 1975). This allows to compare the same processes for perceived and unperceived stimuli, removing the major confounding factors while retaining the key factor awareness.

4.3.1 P3b

Another famous candidate for the neural correlates of consciousness used to be the P3b, based on its absence in unperceived trials (Sergent et al., 2005; Ye et al., 2019; Cul et al., 2007). But this view has been challenged since for different reasons: First, in some situations, stimuli are clearly perceived but no P3b is observed, e.g., for the standard tones in an oddball paradigm or when the stimuli were not task-relevant (Pitts et al., 2012; Schlossmacher et al., 2020). And second, because a number of studies suggest that the P3b more likely reflects higher-order processes like decision making, working-memory, and more (Twomey et al., 2015; Koivisto and Grassini, 2016; Andersen et al., 2016; Verleger, 2020). This is supported by a

In the present data, the P3b measured with M/EEG was -as expected - only visible after detected targets, and not for the AM noise distractor in Experiment 1. This does not only support that the P3b is not a correlate of consciousness, but it also dissociates the component from the PDR. This is in contrast to the previously suggested tight relationship (Nieuwenhuis et al., 2011), but supports other reports of a dissociation (Kamp and Donchin, 2015). In the fMRI, the RSC as presumed source of the P3b (Das et al., 2023) was activated in response to AM tones during the passive run, i.e. without task-relevance. While it is possible that participants nevertheless performed some form of task (counting the tones, or similar), it could also be attributed to a P3a or novelty P3, evoked by infrequent, task-irrelevant stimuli (Polich, 2007). A P3a could in principle also be evoked by the AM noise in Experiment 1, but the reduced saliency compared to the AM tones might prevent the emergence of a P3a or reduce its amplitude. Additionally, because of its more anterior origin, the P3a might be less detectable in the PCC/RSC ROI chosen here.

Another factor that strongly influences the detectability of a P3b, becomes apparent when looking at the P3b results of Experiment 2: The amplitudes not only decrease with confidence in signal presence, but the latencies and durations also seem to increase. Two previous studies provided evidence for a P3b even on trials with a signal absent rating, when corrected for the different latencies (Kerkhof, 1978; Kerkhof and Uhlenbroek, 1981). They showed that latencies and standard deviation of the latencies increased for unperceived versus perceived trials, and also for decreasing confidence in signal presence. Roth-Paysen et al. (2022) also found a gradual decrease in P3b amplitude with the use of the perceptual awareness scale (Ramsøy and Overgaard, 2004) and an attentional blink paradigm. They did not report if the P3b components of each rating were significant, or whether the latencies differed across ratings. But there seems to be a P3b even for the lowest rating ("no experience") and - similar to the present data - an increase in latency from highest to lowest ratings. A P3b for both perceived and unperceived stimuli would further argue against its necessity for consciousness, and rather for a connection to decision making and responding. This is supported by a study where an equated task relevance and demand for signal present and absent trials resulted in a P3b for all conditions (Schröder et al., 2021). Similar results were obtained in a study on monkeys, where frontal activation was measured not only even for signal absent ratings, once the activity was analyzed response-locked instead of stimulus-locked (Vugt et al., 2018).

4.3.2 Existence of a perceptual threshold: Implications of the SDT model for neural activity and PDR

Apart from the question what distinguishes conscious from unconscious perception, there is also the question about the different strengths of perception: Are they correlated to neural activity or measurements like the PDR, and is this the case across the whole range? In other words: Is perception graded or is there a threshold that divides perception in only two levels, perceived and unperceived? This issue was addressed with the different confidence ratings used in Experiment 2.

First, it has to be noted that the ratings were introduced to allow for a lower decision criterion. Therefore participants were asked to rate their confidence, not the strength of perception, and these variables are not necessarily interchangeable. But while other rating scales like the perceptual awareness scale (Ramsøy and Overgaard, 2004) might be superior to capture the different levels of awareness, the two scales are comparable when participants rate their confidence in perception, not in correctness of their response (Sandberg et al., 2010). Consequently, the confidence in signal presence will be used as an indication of the perceived signal strength in the following, while keeping in mind that there might be subtle differences.

The gradual decrease in amplitude of the auditory activity and the pupil dilation across ratings indicate that the strength of perception is directly coupled to neural activity. This was also recently observed in a visual experiment using the perceptual awareness scale (Roth-Paysen et al., 2022). A more subjective confirmation that the confidence ratings match the perception can be drawn from Experiment 2b, where an audibility rating scale was compared to the confidence rating. All of the participants preferred the confidence rating, and one of the most frequent explanation was that it matches their experience better. Similar reports were made in the study from which the perceptual awareness scale originates (Ramsøy and Overgaard, 2004). Another finding from Experiment 2b provides additional evidence for a correspondence between strength of perception and ratings, and thus - together with the results of Experiment 2 - for the correlation with neural activity: Participants on average estimated hearing more than 5 different levels of SNR when in fact only one type of stimulus was present (apart from the catch trials). This indicates, that not only the confidence in the perception varied from trial to trial, but also the perceived stimulus strength.

A more quantitative analysis of the correlation between behavioral data and amplitudes of the neural activity was performed with an SDT-based model. This model used the behavioral responses to calculate the relative amplitude for each criterion based on SDT, i.e. assuming one gaussian distribution each for the signal strengths of catch and target trials. The results showed a good agreement of model and data for auditory activity, first derivative of the PDR, and even the P3b.

All these findings seem to suggest that perception is gradual without a perceptual threshold. However, the data were modeled similarly well with a bimodal signal distribution from a recent publication suggesting that perception is bifurcated into perceived and unperceived (Sergent et al., 2021). That being said, a closer look at the modeling results shows that the means of both modes are very similar, leading to a barely bimodal distribution with no advantage over the unimodal model.

The controversy of a continuous or dichotomous perception has been discussed for a long time, and there is experimental evidence for both sides: A dichotomy, and thus the existence of a sensory threshold, has been mostly postulated by proponents of the global workspace theory (Dehaene et al., 1998), where exceeding a threshold causes global "ignition" and thus conscious access. Evidence was found in several attentional blink paradigms (Sergent and Dehaene, 2004a; Sergent et al., 2005), but also in the auditory study mentioned earlier (Sergent et al., 2021).

Evidence for the opposite view of a graded or continuous perception without a threshold can be found in a number of studies, most of them using the perceptual awareness scale (e.g., Overgaard et al., 2006; Andersen et al., 2016; Roth-Paysen et al., 2022). Wixted (2020) suggested that the relationship between response accuracy and confidence should be different for graded or dichotomous perception: If a threshold exists, a signal-absent rating would indicate that neural activity for this trial was below the threshold and is inaccessible to the observer. Consequently any confidence ratings for these trials would be guesses, and the accuracy should not change across ratings. In contrast, all trials above threshold result in distinguishable levels of activation on which the confidence rating can be based on. Thus, accuracy would be expected to change across ratings. In a threshold-free model, this should be similarly the case for signal-absent and signal-present ratings. This proposal was tested with the present data, and the decrease in accuracy with confidence even for unperceived trials is further evidence for graded perception.

Following the same reasoning, a threshold should also result in equal signal strengths for all ratings in the range of missed targets. This reveals a conceptual problem of the bimodal model suggested by (Sergent et al., 2021), at least for peri-threshold data like the ones used here: The bimodality is mathematically introduced, but it has no behavioral consequences, otherwise a rating with different accuracies and signal strengths would not be possible in the range of unperceived tones (i.e. the ones originating from the unperceived mode). To test the prediction of decreasing amplitudes in this range, the crucial category would be the least confident misses M1. Unfortunately, this was the least frequent outcome, resulting in a poor SNR, especially in the M/EEG data. This seems to be most harmful for the activity in the AC, where their amplitude was smaller than expected in a threshold-free model. Therefore, the indistinguishable amplitudes in the miss range would rather be in favor of a threshold. However, the PDR, which generally needs less trials for a reasonable SNR, shows that the amplitudes in fact decrease across the misses. Looking at the single subject data (Figure 10, bottom right), one outlier with an untypically high amplitude for the M1 is noticeable. But even when this participant's data set is excluded, the average PDR' for M1 is still larger than for M2 and M3 (data not shown), indicating that this not a finding is not confounded by the outlier and there

is a gradual decrease of amplitudes.

Regarding the diverging results on this topic, Overgaard et al. (2006) argued that some results in favor of perception being a continuous phenomenon are sufficient, as specific experiments (like the attentional blink) could result in only the extreme cases of perception, i.e. full or no experience of the stimulus, but no experiment would result in distinguishable levels or perception if there were none. An alternative explanation is provided by Nieuwenhuis and Kleijn (2011), who proposed that access to some levels of neural representation might be graded, while others are all-or-none (e.g., letters vs. the meaning of a word). This is also the basis of the partial awareness hypothesis (Kouider et al., 2010), that proposes different levels of awareness, varying with both stimulus strength and the confidence in having perceived something. The access to these individual levels is binary, but since perception is made of different levels, it is overall graded. The concept can be easily understood in their example of reading, where perception could vary between seeing something without being able to identify, seeing letters, whole words, and finally reading the word and thus understanding the meaning (Kouider et al., 2010). The detection of tones in noise used in this thesis is related to an early stage of perceptual processing, which might be the reason why the results are more shifted towards a gradual perception. Evidence for partial awareness can be found in a study showing that one feature of an attentional blink target can be accurately reported, while another remains unconscious (Elliott et al., 2016). Another attentional blink study showed that perception can be both graded and bifurcated, depending on the task requirements, which mainly differed in spatial attention in this study (Karabay et al., 2022).

Furthermore, it has been shown that activation evoked by weak visual stimuli is transferred from visual to frontal cortex, but may get lost at different stages for missed stimuli (Vugt et al., 2018). The authors argue that the data is in line with the global workspace theory (Dehaene et al., 1998), as ignition-like activity in the frontal cortex predicted report. But the loss of activity at different processing stages can similarly be interpreted in support of the partial awareness hypothesis (Kouider et al., 2010). They further claim that their study presents a "unification" of SDT and global workspace theory (Vugt et al., 2018). However, there is a notable difference between their nomenclature and the one by SDT: They defined the threshold for global ignition and thus perception as the quantity that was originally called -and accordingly used here- the decision criterion or bias (Green and Swets, 1966, p. 58). The criterion can be varied by the observer and does not necessarily mean that trials underneath the criterion are not perceived. This was confirmed in the present confidence-rating experiment, were five different criteria were applied simultaneously, resulting in three different categories all rated as perceived. Thus, the decision criterion could be equivalent to the ignition threshold, but this is likely not equal to a perceptual threshold. In fact, the remaining frontal cortex activation shown in Vugt et al. (2018) could be in agreement with the SDT-model presented here.

In summary, the present results support the AAN as the most probable correlate of conscious audition, showed that neural activity is linked to the perceived signal strength, and provided additional evidence for graded as opposed to bifurcated perception. This evidence is, however, not completely unambiguous, and possible experiments that could provide further insight are presented in the following section.

4.4 Limitations and future directions

The different experiments in the present thesis all have their own advantages and limitations. The drawback of Experiments 1 and 3 was that responses could only be collected for perceived targets. This increases the difference between the two conditions beyond the correlates of consciousness, including also task- and decision related processed for the perceived, but not for the unperceived trials (Tsuchiva et al., 2015). In Experiment 2, this was solved by using short intervals of noise, where the noise-offset served as response cue. However, this approach has it's own downsides, as the noise-onset caused a pupil dilation response which affected the response to the actual stimulus. While this could be solved by extending the noise interval, this would either cause an excessive increase in the total duration of the experiment, or a strongly reduced number of trials and with that would reduce the SNR. Both options would not be favorable, especially since Experiment 2 had, already with the current settings, a rather low number of trials in some categories (most importantly M1, but - by design - also correct rejections and false alarms). Using this trial-based structure for fMRI would amplify this problem, because the BOLD response is even slower, so noise- and stimulus-onset responses would almost completely overlap or the noise before stimulus-onset would have to be even longer.

A better solution could be the use of continuous noise together with a visual cue, which appears simultaneous with the auditory stimulus. With this method, stimuluslocked evoked responses can be collected to all types of trials, even for signal-absent trials. If the number of signal and catch trials is chosen appropriately, this procedure further offers the opportunity to expand the SDT model (see 3.2.5) to catch trials, where the amplitudes should show a similar decrease from highly confident false alarms to highly confident correct rejections. This would indicate that high neural activity could cause the false perception of a stimulus, as suggested in previous studies on rodents (Takahashi et al., 2016) and monkeys (Vugt et al., 2018). A disadvantage of such an experiment is that a confounding effect of the activity evoked by the visual cue cannot be excluded. This has to be considered when interpreting the evoked potentials of individual conditions. Contrasting perceived and unperceived stimuli would eliminate this problem, as both conditions would be equally affected. The fMRI measurement was further limited with respect to the spatial resolution. For the original goal of examining the influence of attention networks on detection and identifying potential correlates of consciousness, the applied sequence was sufficient. But a proper analysis of small subcortical structures like the LC requires a higher resolution, ideally with voxel sizes around 1mm^3 (compared to the 3 × $3 \times 4 \text{ mm}^3$ used here). Some increase in resolution can be achieved with different scanning protocols, for example with parallel acquisition of multiple slices. But a large factor is usually the trade-off between temporal and spatial resolution, which means that smaller voxels typically come with prolonged acquisition time. To minimize that, one could also decrease the field of view, e.g. to only the brain stem. This would however strongly depend on the research question, and which regions are of interest. In any case, a combination with cardiac gating could help to avoid artifacts and increase sensitivity, especially in areas close to the ventricles. A better knowledge of the subcortical activation related to task performance and awareness, could help to identify important subcortical-cortical networks.

Another topic that might be worth a closer look is the differential attentional modulation of distractors in Experiments 1 and 3, where the AM noise was more strongly modulated between runs than the AM tones. Exploring if this difference is caused by saliency, similarity to the target, or a mixture of both, could provide helpful guidance for the choice of stimuli in future studies.

4.5 Conclusion

The present results support the AAN as potential correlate for conscious auditory perception, and the P3b as a task- and decision-related component. The data also showed that attention can have a strong influence on the perception and processing of auditory stimuli, but that this effect differs for different types of stimuli. The results indicate that less attention is required for the perception of more salient stimuli. Additionally, the similarity between target and distractor might influence the amount of attentional modulation.

Recording the pupil size demonstrated the influence of arousal across all experiments. The analysis of pupil-related BOLD signal changes reveals the temporal relationship between the two measures, which could explain discrepancies in previous results, and highlights the widespread effect of pupil-linked arousal together with the complex interactions between cortical and subcortical structures.

Finally, it has been shown that the strength of perception (as indicated by confidence ratings) scales with neural activity and the pupil dilation response. Together with the successful modeling of the amplitudes with a threshold-free SDT model, this suggests that perception is a graded rather than an all-or-none phenomenon. Future experiments might be able to confirm this by extending the model to signal-absent trials.
Chapter 5

Summary

This thesis investigated the influence of attention and arousal on the processing of near-threshold auditory stimuli. In addition, the role of the decision criterion was examined along with the question of whether perception is graded, or an all-ornothing phenomenon. For this purpose, three experiments were conducted with different neuroimaging techniques: Two measurements with magnetoencephalography, electroencephalography, and pupillometry, and one measurement combining pupillometry and functional magnetic resonance imaging. The pupil size was recorded as a proxy for the activity of the locus coeruleus and other brainstem nuclei regulating arousal.

In Experiment 1, continuous white noise with near-threshold tones and more salient, transient amplitude-modulations of the noise were presented to the listeners. During three runs with the same stimulation, the participants had to detect the noise modulations in the first and third run, and the near-threshold tones in the middle run. They were unaware of the exact contents of the stimulation, and only informed about the respective target stimuli. The tones were perceived only in the second run, and by half of the listeners occasionally in the last run, after they got used to detecting them previously. In line with this, significant amounts of neuronal activity evoked by those tones was only present when they were task-relevant. But in this case, even the undetected tones evoked a pupil dilation response and activity in the auditory cortex. In contrast, the task had less influence on the more salient noise modulations, which were likely perceived also in passive runs and consequently evoked auditory activity in all runs. However, the pupil dilation response was not present for task-irrelevant noise modulations. In line with the expectations, the decision-related P3b was only present for detected task-relevant stimuli.

Experiment 2 used the same near-threshold tones, but with short intervals of noise that contained either one or none tone. After each interval, listeners indicated via a button press, how confident they were that a tone was present. For this, six different response options were provided, three each for signal present or absent: signal certainly/likely/uncertainly present or absent. This approach provided the opportunity to investigate, whether the auditory activity and pupil dilation for undetected targets in the first experiment was caused by wrong classification in the context of a bimodal model of perception, where tones perceived with low confidence might have been classified as miss, or whether the neuronal activity is instead coupled to the strength of perception and decreases gradually across the ratings as suggested by a unimodal model of perception. Even though the overall decision criterion was lower than in Experiment 1 (1.6 ± 0.4 vs. 0.6 ± 0.4 , mean and standard deviation across participants), the waveforms for hits and misses combined across the three ratings reproduced the previous results. But across the individual ratings, the amplitudes of the auditory cortex activity and the pupil dilation response decreased gradually. Consequently, the evoked responses for missed tones were rather

not caused by a misclassification of detected tones. The P3b appeared more bimodal, as it was mainly present for detected tones, but a large variability in latency might have influenced this. All three responses were well explained by a model based on signal detection theory, which postulates a continuous relationship between neural activity and perception.

A supplementary psychoacoustic experiment compared the confidence rating to an audibility rating used in a previous publication supporting a bifurcation of perception. The present results did not support this finding. Furthermore, listeners on average estimated the number of signal-to-noise ratios at which the tones were presented to 5-6, even though only one constant ratio was used. This indicates that for physically identical stimuli, the strength of perception varies across different levels, not only between perceived and unperceived.

Experiment 3 explored the influence of attention on auditory perception and identified related brain networks. The stimulation was similar to the first experiment, with the exception that instead of noise modulations, supra-threshold amplitudemodulated tones were used, which could be easily perceived despite the scannernoise. The tasks for the three runs changed from passive listening, to detection of the supra-threshold, and finally detection of the near-threshold tones. With the increasing amount of attention directed to the auditory stream, activity in the auditory cortex increased for the near-threshold stimuli already during the second run, even though participants did not perceive those tones yet. Overall, auditory activity was similar to those of Experiments 1 and 2, with significant activation for detected and missed targets, and the salient distractors. Apart from auditory cortex, increased activation for missed targets was also observed in the cinguloopercular network. Additionally, enhanced pre-stimulus activity for hits compared to misses was observed in this network. This effect is similar to the relationship of pupil size and performance, although the former is presumably monotonic, while the latter is inverted-U-shaped. Thus, pre-stimulus brain activation and pupil size are not directly related. A correlation of pupil size and the blood oxygenation leveldependent signal revealed a widespread interaction between arousal and cortical activity. This activity included the cingulo-opercular network, suggesting that the relationship between pupil dilation and activity within this network is more complex. A preliminary analysis of subcortical activation showed similar modulations by task and similar correlations with pupil size fluctuations as in the cortex. Future measurements with improved spatial resolution could further investigate how these activation patterns differ across the brainstem, and how the different nuclei are connected to phasic and tonic arousal.

In summary, the present work confirmed the importance of arousal and attention on the processing of different auditory stimuli, and provided evidence for a differential influence of attention on perception, depending on the type of stimuli. For near-threshold stimuli, these data showed that neural activity is directly connected to the strength of a perception, and that perception is graded rather than bifurcated.

Chapter 6

Zusammenfassung

Die vorliegende Arbeit untersuchte den Einfluss von Aufmerksamkeit und Arousal auf die Verarbeitung schwellennaher auditorischer Reize. Außerdem wurde die Rolle des Entscheidungskriteriums untersucht, zusammen mit der Frage, ob es verschiedene Abstufungen in der Wahrnehmung einfacher Reize gibt, oder ob es sich um ein alles-oder-nichts Phänomen handelt. Zu diesem Zwecke wurden drei Experimente mit unterschiedlichen Bildgebungstechniken durchgeführt: Zwei Messungen mit Magneto- und Elektroencephalographie, und eine mit funktioneller Magnetresonanztomographie, die jeweils mit Pupillometrie kombiniert wurde. Die Aufnahme der Pupille diente dabei dazu, die Aktivität des Locus Coeruleus und anderer Kerngebiete die das Arousal kontrollieren, wiederzugeben.

In Experiment 1 hörten die Studienteilnehmer kontinuierliches weißes Rauschen mit schwellennahen Tönen und salienteren Amplitudenmodulationen des Rauschens. In drei Durchläufen mit identischer Stimulation mussten die Teilnehmer im ersten und letzten Teil die Rauschmodulationen detektieren, im mittleren Teil die schwellennahen Töne. Die genauen Inhalte der Stimulation waren ihnen unbekannt, sie wurden nur über die jeweiligen Zielreize informiert. Die schwellennahen Töne wurden nur im mittleren Teil detektiert, und von der Hälfte der Probanden auch gelegentlich im letzten Teil, nachdem sie sich im vorhergehenden Abschnitt an die Detektion der Töne gewöhnt hatten. Entsprechen evozierten diese Töne nur dann signifikante neuronale Aktivität, wenn sie aufgabenrelevant waren. Dann aber evozierten auch die nicht gehörten Töne signifikante Hörkortexaktivierung und Pupillendilatation. Im Gegensatz dazu hatte die Aufgabe einen geringeren Einfluss auf die Verarbeitung der salienteren Rauschmodulationen. Sie wurden in allen Abschnitten wahrgenommen und evozierten eine entsprechende Hörkortexaktivierung. Eine Pupillendilatation wurde hingegen nur gemessen, wenn die Rauschmodulationen aufgabenrelevant waren. Erwartungsgemäß war die entscheidungsbezogene P3b-Komponente des evozierten Potenzials nur für detektierte Zielreize messbar.

In Experiment 2 wurden dieselben schwellennahen Reize in kurzen Rauschintervallen präsentiert. Nach jedem Intervall gaben die Hörer mittels sechs verschiedener Antwortoptionen an, wie sicher sie sich waren, dass ein Ton präsentiert worden war. Es gab je drei Optionen für wahrgenommene und nicht wahrgenommene Töne: Ton war sicher/ziemlich sicher/unsicher aber vermutlich enthalten bzw. nicht enthalten. Mit dieser Herangehensweise konnte überprüft werden, ob die Aktivierung im Hörkortex und die Pupillendilatation, die in Experiment 1 für nicht gehörte Töne beobachtet wurden, auf eine Fehlklassifizierung unsicher wahrgenommener Töne zurückzuführen ist, oder ob die neuronale Aktivität graduell abnimmt und somit an die Stärke der Wahrnehmung gekoppelt ist. Ersteres wäre mit einem bimodalen, letzeres mit einem unimodalen Modell der Wahrnehmung vereinbar. Obwohl das Kriterium im Mittel liberaler war als in Experiment 1 (1.6 \pm 0.4 bzw. 0.6 \pm 0.4 Mittelwert und Standardabweichung), reproduzierten die Wellenformen von gehörten und nicht gehörten Tönen gemittelt über die drei Sicherheitsstufen die vorherigen Ergebnisse. Demnach ist die Aktivität für nicht gehörte Töne nicht auf eine Fehlklassifizierung durch ein zu strenges Kriterium zurückzuführen. Die graduell abnehmenden Amplituden der Pupillen- und Hörkortexantwort sind weiterhin ein Indiz für eine ebenfalls graduelle Wahrnehmung. Die P3b erscheint hingegen eher bimodal, dies könnte aber von der Variabilität der Latenzen herrühren. Pupille, Hörkortexaktivierung und P3b konnten alle gut durch ein Modell basierend auf der "Signal Detection Theory" beschrieben werden, welches einen kontinuierlichen Zusammenhang zwischen neuronaler Aktivität und Wahrnehmung vorhersagt.

In einem ergänzenden psychoakustischen Experiment wurde die Bewertung anhand der Sicherheit mit einer Bewertung der Hörbarkeit verglichen, die laut einer anderen Studie Hinweise auf eine bimodale Wahrnehmung liefert. Die vorliegenden Ergebnisse stützen diesen Befund nicht. Außerdem schätzten die Probanden im Mittel, dass Töne in 5-6 verschiedenen Lautstärken präsentiert wurden, obwohl alle Töne identisch waren. Dies impliziert, dass die Wahrnehmung physikalisch identischer Reize nicht nur zwischen Gehörtem und Nicht-Gehörtem, sondern zwischen verschiedenen Intensitäten variiert.

In Experiment 3 wurde der Einfluss von Aufmerksamkeit auf die auditive Wahrnehmung weiter untersucht und involvierte Netzwerke des Gehirns identifiziert. Die Stimulation war ähnlich zu Experiment 1, mit dem Unterschied, dass anstelle der Rauschmodulationen saliente amplitudenmodulierte Töne als Distraktorreize verwendet wurden. In drei Durchläufen wurde durch die verschiedenen Aufgabenstellungen (passives Zuhören, Detektion der salienten Töne und Detektion der schwellennahen Töne) die Aufmerksamkeit auf die auditorische Stimulation sukzessive gesteigert. Dadurch zeigte sich im Hörkortex bereits im zweiten Durchgang eine signifikante Aktivierung durch die schwellennahen Töne, obwohl diese noch nicht bewusst wahrgenommen wurden. Insgesamt ähnelte die Hörkortexaktivierung der in den vorherigen Experimenten gemessenen, mit signifikanter Aktivierung für gehörte und nicht gehörte schwellennahe Töne sowie den salienten Distraktorreizen. Auch in Gebieten des cingulo-opercularen Netzwerks wurde Aktivierung für nicht detektierte Zieltöne gemessen. Desweiteren zeigte dieses Netzwerk höhere Aktivierung vor Tönen die anschließend detektiert wurden, als vor Tönen die nicht detektiert wurden. Dieser Effekt ähnelt dem Einfluss des Arousal auf die Detektion, der aber quadratisch ist, der Zusammenhang von Detektion und Hirnaktivität hingegen vermutlich monoton. Damit kann ein direkter Zusammenhang zwischen dem Arousal und der Hirnaktivität vor Einsetzen des Reizes in diesem Netzwerk ausgeschlossen werden. Die Korrelation von Pupillengröße und Hirnaktivität zeigte eine weitreichende Wechselwirkung zwischen Arousal und kortikaler Aktivierung, auch im cingulo-opercularen Netzwerk. Dies legt einen komplexeren Zusammenhang zwischen diesem Netzwerk und der Pupillengröße nahe. Eine explorative Auswertung der Aktivierung im Hirnstamm zeigte ähnliche Korrelationen und Aufmerksamkeitsmodulationen wie im Kortex. Zukünftige Messungen mit verbesserter räumlicher Auflösung könnten untersuchen, wie sich diese Aktivierungsmuster in den verschiedenen Kernen des Hirnstamms unterscheiden und welche der Kerne an den Modulationen des Arousal beteiligt sind.

Zusammenfassend bestätigt diese Arbeit die Bedeutung von Aufmerksamkeit und Arousal auf die Verarbeitung auditiver Reize, und liefert Hinweise auf einen differenziellen Aufmerksamkeitsffekt. Außerdem konnte gezeigt werden, dass die neuronale Aktivität in direktem Zusammenhang mit der Stärke der Wahrnehmung steht. Dies ist ein Indiz dafür, dass Wahrnehmung nicht bimodal sondern graduell ist.

Bibliography

- Andersen, Lau M., Michael N. Pedersen, Kristian Sandberg, and Morten Overgaard (2016). "Occipital MEG Activity in the Early Time Range (<300 ms) Predicts Graded Changes in Perceptual Consciousness". In: *Cerebral Cortex* 26.6, pp. 2677– 2688. DOI: 10.1093/cercor/bhv108.
- Arcaro, Michael J., Mark A. Pinsk, Janice Chen, and Sabine Kastner (2018). "Organizing principles of pulvino-cortical functional coupling in humans". In: *Nature Communications* 9.1. DOI: 10.1038/s41467-018-07725-6.
- Aru, Jaan, Mototaka Suzuki, and Matthew E. Larkum (2020). "Cellular Mechanisms of Conscious Processing". In: *Trends in Cognitive Sciences* 24.10, pp. 814–825. DOI: 10.1016/j.tics.2020.07.006.
- Aru, Jaan, Mototaka Suzuki, Renate Rutiku, Matthew E. Larkum, and Talis Bachmann (2019). "Coupling the State and Contents of Consciousness". In: *Frontiers in Systems Neuroscience* 13. DOI: 10.3389/fnsys.2019.00043.
- Aston-Jones, Gary and Jonathan D. Cohen (2005). "An Integrative Theory of Locus Coeruleus-Norepinephrine Function: Adaptive Gain and Optimal Performance". In: *Annual Review of Neuroscience* 28.1, pp. 403–450. DOI: 10.1146 [annurev. neuro.28.061604.135709.
- Auksztulewicz, Ryszard, Bernhard Spitzer, and Felix Blankenburg (2012). "Recurrent Neural Processing and Somatosensory Awareness". In: *Journal of Neuroscience* 32.3, pp. 799–805. DOI: 10.1523/JNEUROSCI.3974-11.2012.
- Baars, Bernard J. (1988). A cognitive theory of consciousness. Cambridge [u.a.]: Cambridge University Press. XXIII, 424 S.
- Berridge, Craig W and Barry D Waterhouse (2003). "The locus coeruleus–noradrenergic system: modulation of behavioral state and state-dependent cognitive processes". In: *Brain Research Reviews* 42.1, pp. 33–84. DOI: 10.1016//S0165-0173(03) 00143-7.
- Block, Ned (1995). "On a confusion about a function of consciousness". In: *Behavioral and Brain Sciences* 18.2, pp. 227–247. DOI: 10.1017/S0140525X00038188.
- Bourgeois, Alexia, Carole Guedj, Emmanuel Carrera, and Patrik Vuilleumier (2020). "Pulvino-cortical interaction: An integrative role in the control of attention". In: *Neuroscience and Biobehavioral Reviews* 111. DOI: 10.1016/j.neubiorev.2020.01. 005.
- Bouret, Sebastien and Susan J. Sara (2005). "Network reset: A simplified overarching theory of locus coeruleus noradrenaline function". In: *Trends in Neurosciences* 28.11. DOI: 10.1016/j.tins.2005.09.002.
- Brainard, David H. (1997). "The Psychophysics Toolbox". In: *Spatial Vision* 10.4, p. 433–436. DOI: 10.1163/156856897X00357.
- Branch Coslett, H (1997). "Consciousness and attention". In: *Seminars in Neurology* 17.2, pp. 137–144. DOI: 10.1055/s-2008-1040923.
- Brink, Ruud L. van den, Peter R. Murphy, and Sander Nieuwenhuis (2016). "Pupil Diameter Tracks Lapses of Attention". In: *PLOS ONE* 11.10, e0165274. DOI: 10. 1371/journal.pone.0165274.

- Burlingham, Charlie S., Saghar Mirbagheri, and David J. Heeger (2022). "A unified model of the task-evoked pupil response". In: *Science Advances* 8.16, eabi9979. DOI: 10.1126/sciadv.abi9979.
- Chen, Jui-Tai, Rachel Yep, Yu-Fan Hsu, Yih-Giun Cherng, and Chin-An Wang (2021). "Investigating Arousal, Saccade Preparation, and Global Luminance Effects on Microsaccade Behavior". In: *Frontiers in Human Neuroscience* 15.
- Cohen, David, B. Neil Cuffin, Kazutomo Yunokuchi, Roman Maniewski, Christopher Purcell, G. Rees Cosgrove, John Ives, John G. Kennedy, and Donald L. Schomer (1990). "MEG versus EEG localization test using implanted sources in the human brain". In: *Annals of Neurology* 28.6, pp. 811–817. DOI: 10.1002/[ana.410280613.
- Cohen, Michael A., Patrick Cavanagh, Marvin M. Chun, and Ken Nakayama (2012). "The attentional requirements of consciousness". In: *Trends in Cognitive Sciences* 16.8, pp. 411–417. DOI: 10.1016/j.tics.2012.06.013.
- Colizoli, Olympia, Jan Willem de Gee, Anne E. Urai, and Tobias H. Donner (2018). "Task-evoked pupil responses reflect internal belief states". In: *Scientific Reports*. DOI: 10.1038/s41598-018-31985-3.
- Corbetta, Maurizio, Gaurav Patel, and Gordon L. Shulman (2008). "The Reorienting System of the Human Brain: From Environment to Theory of Mind". In: *Neuron* 58.3. DOI: 10.1016/j.neuron.2008.04.017.
- Corbetta, Maurizio and Gordon L. Shulman (2002). "Control of goal-directed and stimulus-driven attention in the brain". In: *Nature Reviews Neuroscience* 3.3. DOI: 10.1038/nrn755.
- Coste, Clio P. and Andreas Kleinschmidt (2016). "Cingulo-opercular network activity maintains alertness". In: *NeuroImage* 128, pp. 264–272. DOI: 10//f79w6q.
- Crick, Francis and Christof Koch (1990). "Towards a neurobiological theory of consciousness". In: *Seminars in the Neurosciences* 2, pp. 263–275.
- Crick, Francis and Christof Koch (2003). "A framework for consciousness". In: *Nature Neuroscience* 6.2, pp. 119–126. DOI: 10.1038/nn0203-119.
- Cul, Antoine Del, Sylvain Baillet, and Stanislas Dehaene (2007). "Brain Dynamics Underlying the Nonlinear Threshold for Access to Consciousness". In: *PLOS Biology* 5.10, pp. 2408–2423. DOI: 10.1371/journal.pbio.
- Dale, Anders M., Bruce Fischl, and Martin I. Sereno (1999). "Cortical surface-based analysis: I. Segmentation and surface reconstruction". In: *NeuroImage* 9.2, pp. 179–194. DOI: 10.1006/nimg.1998.0395.
- Dale, Anders M., Arthur K. Liu, Bruce R. Fischl, Randy L. Buckner, John W. Belliveau, Jeffrey D. Lewine, and Eric Halgren (2000). "Dynamic Statistical Parametric Mapping: Combining fMRI and MEG for High-Resolution Imaging of Cortical Activity". In: *Neuron* 26.1, pp. 55–67. DOI: 10.1016/S0896-6273(00)81138-1.
- Das, Diptyajit, Marnie E. Shaw, Matti S. Hamalainen, Andrew R. Dykstra, Laura Doll, and Alexander Gutschalk (2023). *A role for retro-splenial cortex in the task-related P3 network*. DOI: 10.1101/2023.03.03.530970.
- Dehaene, S., M. Kerszberg, and J. P. Changeux (1998). "A neuronal model of a global workspace in effortful cognitive tasks". In: *Proceedings of the National Academy of Sciences of the United States of America* 95.24, pp. 14529–14534. DOI: 10.1073/pnas. 95.24.14529.
- Dehaene, Stanislas, Jean-Pierre Changeux, Lionel Naccache, Jérôme Sackur, and Claire Sergent (2006). "Conscious, preconscious, and subliminal processing: a testable taxonomy". In: *Trends in Cognitive Sciences* 10.5, pp. 204–211. DOI: 10.1016/j.tics.2006.03.007.

- Dehaene, Stanislas and Lionel Naccache (2001). "Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework". In: *Cognition* 79.1. DOI: 10.1016//S0010-0277(00)/00123-2.
- Dembski, Cole, Christof Koch, and Michael Pitts (2021). "Perceptual awareness negativity: a physiological correlate of sensory consciousness". In: *Trends in Cognitive Sciences* 25.8, pp. 660–670. DOI: 10.1016/j.tics.2021.05.009.
- Desender, Kobe, Annika Boldt, Tom Verguts, and Tobias H. Donner (2019). "Confidence predicts speed-accuracy tradeoff for subsequent decisions". In: *eLife*. DOI: 10.7554/eLife.43499.
- Destrieux, Christophe, Bruce Fischl, Anders Dale, and Eric Halgren (2010). "Automatic parcellation of human cortical gyri and sulci using standard anatomical nomenclature". In: *NeuroImage* 53.1, pp. 1–15. DOI: 10.1016 // J.NEUROIMAGE. 2010.06.010.
- DiNuzzo, Mauro, Daniele Mascali, Marta Moraschi, Giorgia Bussu, Laura Maugeri, Fabio Mangini, Michela Fratini, and Federico Giove (2019). "Brain Networks Underlying Eye's Pupil Dynamics". In: *Frontiers in Neuroscience* 13, p. 965. DOI: 10.3389/fnins.2019.00965.
- Dosenbach, Nico U. F., Damien A. Fair, Francis M. Miezin, Alexander L. Cohen, Kristin K. Wenger, Ronny A. T. Dosenbach, Michael D. Fox, Abraham Z. Snyder, Justin L. Vincent, Marcus E. Raichle, Bradley L. Schlaggar, and Steven E. Petersen (2007). "Distinct brain networks for adaptive and stable task control in humans". In: *Proceedings of the National Academy of Sciences of the United States of America* 104.26, pp. 11073–11078. DOI: 10.1073/pnas.0704320104.
- Dosenbach, Nico U. F., Kristina M. Visscher, Erica D. Palmer, Francis M. Miezin, Kristin K. Wenger, Hyunseon C. Kang, E. Darcy Burgund, Ansley L. Grimes, Bradley L. Schlaggar, and Steven E. Petersen (2006). "A Core System for the Implementation of Task Sets". In: *Neuron* 50.5, pp. 799–812. DOI: 10.1016/j.neuron.2006.04.031.
- Egan, James, Arthur I. Schulman, and Gordon Z. Greenberg (1959). "Operating Characteristics Determined by Binary Decisions and by Ratings". In: *The Journal of the Acoustical Society of America* 31.6, pp. 768–773. DOI: 10.1121/1.1907783.
- Eklund, Rasmus and Stefan Wiens (2019). "Auditory awareness negativity is an electrophysiological correlate of awareness in an auditory threshold task". In: *Consciousness and Cognition* 71, pp. 70–78. DOI: 10.1016/j.concog.2019.03.008.
- Eklund, Rasmus, Billy Gerdfeldter, and Stefan Wiens (2020). "Is auditory awareness negativity confounded by performance?" In: *Consciousness and Cognition* 83, p. 102954. DOI: 10.1016/j.concog.2020.102954.
- Elliott, James C., Benjamin Baird, and Barry Giesbrecht (2016). "Consciousness isn't all-or-none: Evidence for partial awareness during the attentional blink". In: *Consciousness and Cognition* 40, pp. 79–85. DOI: 10.1016/j.concog.2015.12.003.
- Fischl, Bruce (2012). "FreeSurfer". In: *NeuroImage*. 20 YEARS OF fMRI 62.2, pp. 774–781. DOI: 10.1016/j.neuroimage.2012.01.021.
- Fischl, Bruce, Martin I. Sereno, and Anders M. Dale (1999). "Cortical surface-based analysis: II. Inflation, flattening, and a surface-based coordinate system". In: *NeuroImage* 9.2, pp. 195–207. DOI: 10.1006/nimg.1998.0396.
- Fox, Michael D., Maurizio Corbetta, Abraham Z. Snyder, Justin L. Vincent, and Marcus E. Raichle (2006). "Spontaneous neuronal activity distinguishes human dorsal and ventral attention systems". In: *Proceedings of the National Academy of Sciences of the United States of America* 103.26. DOI: 10.1073/pnas.0604187103.
- Fox, Michael D., Abraham Z. Snyder, Justin L. Vincent, Maurizio Corbetta, David C. van Essen, and Marcus E. Raichle (2005). "The human brain is intrinsically

organized into dynamic, anticorrelated functional networks". In: *Proceedings of the National Academy of Sciences of the United States of America* 102.27, pp. 9673–9678. DOI: 10.1073/pnas.0504136102.

- Fox, P T and M E Raichle (1986). "Focal physiological uncoupling of cerebral blood flow and oxidative metabolism during somatosensory stimulation in human subjects." In: *Proceedings of the National Academy of Sciences* 83.4, pp. 1140–1144. DOI: 10.1073/pnas.83.4.1140.
- Franklin, Michael S., James M. Broadway, Michael D. Mrazek, Jonathan Smallwood, and Jonathan W. Schooler (2013). "Window to the wandering mind: pupillometry of spontaneous thought while reading". In: *Quarterly Journal of Experimental Psychology* 66.12, pp. 2289–2294. DOI: 10.1080/17470218.2013.858170.
- Friston, K. J., P. Fletcher, O. Josephs, A. Holmes, M. D. Rugg, and R. Turner (1998). "Event-related fMRI: characterizing differential responses". In: *NeuroImage* 7.1, pp. 30–40. DOI: 10.1006/nimg.1997.0306.
- Froesel, Mathilda, Céline Cappe, and Suliann Ben Hamed (2021). "A multisensory perspective onto primate pulvinar functions". In: *Neuroscience and Biobehavioral Reviews* 125, pp. 231–243. DOI: 10.1016/j.neubiorev.2021.02.043.
- Frässle, Stefan, Jens Sommer, Andreas Jansen, Marnix Naber, and Wolfgang Einhäuser (2014). "Behavioral/Cognitive Binocular Rivalry: Frontal Activity Relates to Introspection and Action But Not to Perception". In: DOI: 10.1523/JNEUROSCI. 4403-13.2014.
- Gee, Jan Willem de, Olympia Colizoli, Niels A Kloosterman, Tomas Knapen, Sander Nieuwenhuis, and Tobias H Donner (2017). "Dynamic modulation of decision biases by brainstem arousal systems". In: *eLife* 6. Ed. by Klaas Enno Stephan, e23232. DOI: 10.7554/eLife.23232.
- Gee, Jan Willem de, Tomas Knapen, and Tobias H. Donner (2014). "Decision-related pupil dilation reflects upcoming choice and individual bias". In: *Proceedings of the National Academy of Sciences* 111.5, E618–E625. DOI: 10.1073/pnas.1317557111.
- Gee, Jan Willem de, Konstantinos Tsetsos, Lars Schwabe, Anne E. Urai, David McCormick, Matthew J. McGinley, and Tobias H. Donner (2020). "Pupil-linked phasic arousal predicts a reduction of choice bias across species and decision domains". In: *eLife* 9. DOI: 10.7554/eLife.54014.
- Geng, Joy J. and Simone Vossel (2013). "Re-evaluating the role of TPJ in attentional control: Contextual updating?" In: *Neuroscience and Biobehavioral Reviews* 37.10, pp. 2608–2620. DOI: 10.1016/j.neubiorev.2013.08.010.
- Gilzenrat, Mark S., Sander Nieuwenhuis, Marieke Jepma, and Jonathan D. Cohen (2010). "Pupil diameter tracks changes in control state predicted by the adaptive gain theory of locus coeruleus function". In: *Cognitive, Affective and Behavioral Neuroscience* 10.2. DOI: 10.3758//CABN.10.2.252.
- Grahn, Jessica A. and Tom Manly (2012). "Common neural recruitment across diverse sustained attention tasks". In: *PLOS ONE* 7.11, e49556. DOI: 10.1371 // journal.pone.0049556.
- Gramfort, Alexandre, Martin Luessi, Eric Larson, Denis A. Engemann, Daniel Strohmeier, Christian Brodbeck, Roman Goj, Matti Hämäläinen, Samuel Garcia, Claude Bernard Lyon, France Forrest, and S. Bao (2013). "MEG and EEG data analysis with MNE-Python". In: *Frontiers in Neuroscience* 7. DOI: 10.3389//fnins.2013. 00267.
- Gray, C. M., P. König, A. K. Engel, and W. Singer (1989). "Oscillatory responses in cat visual cortex exhibit inter-columnar synchronization which reflects global stimulus properties". In: *Nature* 338.6213, pp. 334–337. DOI: 10.1038/338334a0.

- Green, David M. and John A. Swets (1966). *Signal detection theory and psychophysics*. Signal detection theory and psychophysics. Oxford, England: John Wiley. xi, 455.
- Greicius, Michael D., Ben Krasnow, Allan L. Reiss, and Vinod Menon (2003). "Functional connectivity in the resting brain: a network analysis of the default mode hypothesis". In: *Proceedings of the National Academy of Sciences of the United States of America* 100.1, pp. 253–258. DOI: 10.1073/pnas.0135058100.
- Gutschalk, Alexander, Christophe Micheyl, and Andrew J Oxenham (2008). "Neural Correlates of Auditory Perceptual Awareness under Informational Masking". In: *PLOS Biology* 6.6. Ed. by Timothy D Griffiths, e138. DOI: 10.1371/journal.pbio.0060138.
- Gutschalk, Alexander and Iris Steinmann (2014). "Stimulus dependence of contralateral dominance in human auditory cortex". In: *Human Brain Mapping* 36.3, pp. 883–896. DOI: 10.1002/hbm.22673.
- Hansen, J. C. and S. A. Hillyard (1980). "Endogenous brain potentials associated with selective auditory attention". In: *Electroencephalography and Clinical Neurophysiology* 49.3, pp. 277–290. DOI: 10.1016//0013-4694(80)90222-9.
- Hatamimajoumerd, Elaheh, N. Apurva Ratan Murty, Michael Pitts, and Michael A. Cohen (2022). "Decoding perceptual awareness across the brain with a no-report fMRI masking paradigm". In: *Current Biology* 32.19, 4139–4149.e4. DOI: 10.1016//j.cub.2022.07.068.
- Hämäläinen, Matti, Riitta Hari, Risto J. Ilmoniemi, Jukka Knuutila, and Olli V. Lounasmaa (1993). "Magnetoencephalography—theory, instrumentation, and applications to noninvasive studies of the working human brain". In: *Reviews of Modern Physics* 65.2, pp. 413–497. DOI: 10.1103/RevModPhys.65.413.
- Iglesias, Juan Eugenio, Ricardo Insausti, Garikoitz Lerma-Usabiaga, Martina Bocchetta, Koen van Leemput, Douglas N. Greve, Andre van der van der Kouwe, Bruce Fischl, César Caballero-Gaudes, and Pedro M. Paz-Alonso (2018). "A probabilistic atlas of the human thalamic nuclei combining ex vivo MRI and histology". In: *NeuroImage* 183, pp. 314–326. DOI: 10.1016/J.NEUROIMAGE.2018.08.012.
- Jas, Mainak, Denis Engemann, Federico Raimondo, Yousra Bekhti, and Alexandre Gramfort (2016). "Automated rejection and repair of bad trials in MEG/EEG". In: PRNI 2016 - 6th International Workshop on Pattern Recognition in Neuroimaging. DOI: 10.1109/PRNI.2016.7552336.
- Jas, Mainak, Denis A. Engemann, Yousra Bekhti, Federico Raimondo, and Alexandre Gramfort (2017). "Autoreject: Automated artifact rejection for MEG and EEG data". In: DOI: 10.1016/j.neuroimage.2017.06.030.
- Jones, B. E. (1991). "Noradrenergic locus coeruleus neurons: their distant connections and their relationship to neighboring (including cholinergic and GABAergic) neurons of the central gray and reticular formation". In: *Progress in Brain Research*. Ed. by C. D. Barnes and O. Pompeiano. Vol. 88. Neurobiology of the Locus Coeruleus. Elsevier, pp. 15–30. DOI: 10.1016/S0079-6123(08)63797-8.
- Joshi, Siddhartha and Joshua I. Gold (2020). "Pupil Size as a Window on Neural Substrates of Cognition". In: *Trends in Cognitive Sciences* 24.6, pp. 466–480. DOI: 10.1016/j.tics.2020.03.005.
- Joshi, Siddhartha, Yin Li, Rishi M. Kalwani, and Joshua I. Gold (2016). "Relationships between Pupil Diameter and Neuronal Activity in the Locus Coeruleus, Colliculi, and Cingulate Cortex". In: *Neuron* 89.1, pp. 221–234. DOI: 10.1016/j.neuron. 2015.11.028.
- Kamp, Siri Maria and Emanuel Donchin (2015). "ERP and pupil responses to deviance in an oddball paradigm". In: *Psychophysiology* 52.4, pp. 460–471. DOI: 10. 1111/psyp.12378.

- Karabay, Aytaç, Sophia A. Wilhelm, Joost de Jong, Jing Wang, Sander Martens, and Elkan G. Akyürek (2022). "Two faces of perceptual awareness during the attentional blink: Gradual and discrete". In: *Journal of Experimental Psychology. General* 151.7, pp. 1520–1541. DOI: 10.1037//xge0001156.
- Keren, Noam I., Carl T. Lozar, Kelly C. Harris, Paul S. Morgan, and Mark A. Eckert (2009). "In vivo mapping of the human locus coeruleus". In: *NeuroImage* 47.4. DOI: 10.1016/j.neuroimage.2009.06.012.
- Kerkhof, G. A. (1978). "Decision latency: The P3 component in auditory signal detection". In: *Neuroscience Letters* 8.4, pp. 289–294. DOI: 10.1016/0304-3940(78) 90138-6.
- Kerkhof, Gerard A. and José Uhlenbroek (1981). "P3 latency in threshold signal detection". In: *Biological Psychology* 13 (C), pp. 89–105. DOI: 10.1016 0301 0511(81)90029-6.
- Kloosterman, Niels A., Thomas Meindertsma, Anouk M. van Loon, Victor A. F. Lamme, Yoram S. Bonneh, and Tobias H. Donner (2015). "Pupil size tracks perceptual content and surprise". In: *European Journal of Neuroscience* 41, pp. 1068– 1078. DOI: 10.1111//ejn.12859.
- Koch, Christof, Marcello Massimini, Melanie Boly, and Giulio Tononi (2016). "Neural correlates of consciousness: progress and problems". In: *Nature Reviews Neuroscience* 17.5, pp. 307–321. DOI: 10.1038/nrn.2016.22.
- Koivisto, Mika and Simone Grassini (2016). "Neural processing around 200ms after stimulus-onset correlates with subjective visual awareness". In: *Neuropsychologia* 84, pp. 235–243. DOI: 10.1016/j.neuropsychologia.2016.02.024.
- Kouider, Sid, Vincent de Gardelle, Jérôme Sackur, and Emmanuel Dupoux (2010). "How rich is consciousness? The partial awareness hypothesis". In: *Trends in Cognitive Sciences* 14.7, pp. 301–307. DOI: 10.1016/j.tics.2010.04.006.
- Krauzlis, Richard J., Lee P. Lovejoy, and Alexandre Zénon (2013). "Superior colliculus and visual spatial attention". In: *Annual Review of Neuroscience* 36, pp. 165–182. DOI: 10.1146//annurev-neuro-062012-170249.
- Kwong, K K, J W Belliveau, D A Chesler, I E Goldberg, R M Weisskoff, B P Poncelet, D N Kennedy, B E Hoppel, M S Cohen, and R Turner (1992). "Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation." In: *Proceedings of the National Academy of Sciences of the United States of America* 89.12, pp. 5675–5679.
- Lamme, Victor A. F. and Pieter R. Roelfsema (2000). "The distinct modes of vision offered by feedforward and recurrent processing". In: *Trends in Neurosciences* 23.11. DOI: 10.1016/S0166-2236(00)01657-X.
- Lau, Hakwan and David Rosenthal (2011). "Empirical support for higher-order theories of conscious awareness". In: *Trends in Cognitive Sciences* 15.8. DOI: 10.1016// j.tics.2011.05.009.
- Lecluyse, Wendy and Ray Meddis (2009). "A simple single-interval adaptive procedure for estimating thresholds in normal and impaired listeners". In: *The Journal of the Acoustical Society of America* 126, pp. 2570–2570. DOI: 10.1121/1.3238248ÍŤ.
- Lynn, Richard (1966). *Attention, Arousal and the Orientation Reaction*. Oxford: Pergamon Press. 118 pp.
- Maness, Eden B., Joshua A. Burk, James T. McKenna, Felipe L. Schiffino, Robert E. Strecker, and John G. McCoy (2022). "Role of the locus coeruleus and basal forebrain in arousal and attention". In: *Brain Research Bulletin* 188, pp. 47–58. DOI: 10.1016/j.brainresbull.2022.07.014.

- Maris, Eric and Robert Oostenveld (2007). "Nonparametric statistical testing of EEGand MEG-data". In: *Journal of Neuroscience Methods* 164, pp. 177–190. DOI: 10. 1016/j.jneumeth.2007.03.024.
- Martin, Joel T., Annalise H. Whittaker, and Stephen J. Johnston (2022). "Pupillometry and the vigilance decrement: Task-evoked but not baseline pupil measures reflect declining performance in visual vigilance tasks". In: *European Journal of Neuroscience* 55.3, pp. 778–799. DOI: 10.1111/jejn.15585.
- McGinley, Matthew J., Stephen V. David, and David A. McCormick (2015a). "Cortical Membrane Potential Signature of Optimal States for Sensory Signal Detection". In: *Neuron* 87, pp. 179–192. DOI: 10.1016/j.neuron.2015.05.038.
- McGinley, Matthew J., Martin Vinck, Jacob Reimer, Renata Batista-Brito, Edward Zagha, Cathryn R. Cadwell, Andreas S. Tolias, Jessica A. Cardin, and David A. McCormick (2015b). "Waking State: Rapid Variations Modulate Neural and Behavioral Responses". In: *Neuron* 87.6. DOI: 10.1016/j.neuron.2015.09.012.
- Menon, Vinod and Lucina Q. Uddin (2010). "Saliency, switching, attention and control: a network model of insula function." In: *Brain structure & function* 214.5. DOI: 10.1007//s00429-010-0262-0.
- Meter, D. van and D. Middleton (1954). "Modern statistical approaches to reception in communication theory". In: *Transactions of the IRE Professional Group on Information Theory* 4.4, pp. 119–145. DOI: 10.1109/TIT.1954.1057471.
- Mittner, Matthias, Wouter Boekel, Adrienne M. Tucker, Brandon M. Turner, Andrew Heathcote, and Birte U. Forstmann (2014). "When the Brain Takes a Break: A Model-Based Analysis of Mind Wandering". In: *Journal of Neuroscience* 34.49, pp. 16286–16295. DOI: 10.1523/JNEURDSCI.2062-14.2014.
- Molins, A., S. M. Stufflebeam, E. N. Brown, and M. S. Hämäläinen (2008). "Quantification of the benefit from integrating MEG and EEG data in minimum l2-norm estimation". In: *NeuroImage* 42.3, pp. 1069–1077. DOI: 10.1016/j.neuroimage. 2008.05.064.
- Murphy, Peter R., Redmond G. O 'connell, Michael O. ' Sullivan, Ian H. Robertson, and Joshua H. Balsters (2014). "Pupil diameter covaries with BOLD activity in human locus coeruleus". In: *Human Brain Mapping* 35.8, pp. 4140–4154. DOI: 10. 1002/hbm.22466.
- Murphy, Peter R., Ian H. Robertson, Joshua H. Balsters, and Redmond G. O 'connell (2011). "Pupillometry and P3 index the locus coeruleus– noradrenergic arousal function in humans". In: *Psychophysiology* 48, pp. 1531–1542. DOI: 10.1111/j. 1469-8986.2011.01226.x.
- Nani, Andrea, Jordi Manuello, Lorenzo Mancuso, Donato Liloia, Tommaso Costa, and Franco Cauda (2019). "The neural correlates of consciousness and attention: Two sister processes of the brain". In: *Frontiers in Neuroscience* 13 (OCT). DOI: 10.3389/fnins.2019.01169.
- Natan, Ryan G., Winnie Rao, and Maria N. Geffen (2017). "Cortical Interneurons Differentially Shape Frequency Tuning following Adaptation". In: *Cell Reports* 21.4, pp. 878–890. DOI: 10.1016/j.celrep.2017.10.012.
- Nieuwenhuis, Sander, Eco J. de Geus, and Gary Aston-Jones (2011). "The anatomical and functional relationship between the P3 and autonomic components of the orienting response". In: *Psychophysiology*. DOI: 10.1111/j.1469-8986.2010.01057.x.
- Nieuwenhuis, Sander, Gary Aston-Jones, and Jonathan D. Cohen (2005). "Decision making, the P3, and the locus coeruleus-norepinephrine system". In: *Psychological Bulletin* 131.4, pp. 510–532. DOI: 10.1037/0033-2909.131.4.510.

- Nieuwenhuis, Sander and Roy de Kleijn (2011). "Consciousness of targets during the attentional blink: a gradual or all-or-none dimension?" In: *Attention, Perception, & Psychophysics* 73.2, pp. 364–373. DOI: 10.3758/s13414-010-0026-1.
- Ogawa, S, T M Lee, A R Kay, and D W Tank (1990). "Brain magnetic resonance imaging with contrast dependent on blood oxygenation." In: *Proceedings of the National Academy of Sciences* 87.24, pp. 9868–9872. DOI: 10.1073/pnas.87.24.9868.
- Overgaard, Morten, Julian Rote, Kim Mouridsen, and Thomas Zoëga Ramsøy (2006). "Is conscious perception gradual or dichotomous? A comparison of report methodologies during a visual task". In: *Consciousness and Cognition*. Special Issue on Introspection 15.4, pp. 700–708. DOI: 10.1016/j.concog.2006.04.002.
- Paul, Dina Doré and Samuel Sutton (1972). "Evoked potential correlates of response criterion in auditory signal detection". In: Science. DOI: 10.1126//science.177. 4046.362.
- Paxinos, George, Xu-Feng Huang, Gulgun Sengul, and Charles Watson (2012). "Organization of brainstem nuclei". In: *The Human Nervous System*. Amsterdam: Elsevier Academic Press, pp. 260–327.
- Peterson, W., T. Birdsall, and W. Fox (1954). "The theory of signal detectability". In: *Transactions of the IRE Professional Group on Information Theory* 4.4, pp. 171–212. DOI: 10.1109/TIT.1954.1057460.
- Pfeffer, Thomas, Christian Keitel, Daniel S Kluger, Anne Keitel, Alena Russmann, Gregor Thut, Tobias H Donner, and Joachim Gross (2022). "Coupling of pupiland neuronal population dynamics reveals diverse influences of arousal on cortical processing". In: *eLife* 11, e71890. DOI: 10.7554/eLife.71890.
- Pitts, Michael A., Lydia A. Lutsyshyna, and Steven A. Hillyard (2018). "The relationship between attention and consciousness: an expanded taxonomy and implications for 'no-report' paradigms". In: *Philosophical Transactions of the Royal Society B: Biological Sciences* 373.1755, p. 20170348. DOI: 10.1098/rstb.2017.0348.
- Pitts, Michael A., Antígona Martínez, and Steven A. Hillyard (2012). "Visual processing of contour patterns under conditions of inattentional blindness". In: *Journal* of Cognitive Neuroscience 24.2, pp. 287–303. DOI: 10.1162/jocn_a_00111.
- Pitts, Michael A., Stephen Metzler, and Steven A. Hillyard (2014). "Isolating neural correlates of conscious perception from neural correlates of reporting one's perception". In: *Frontiers in Psychology* 5.
- Polich, John (2007). "Updating P300: An integrative theory of P3a and P3b". In: *Clinical Neurophysiology* 118.10, pp. 2128–2148. DOI: 10.1016/j.clinph.2007.04.019.
- Posner, M. I. (1994). "Attention: the mechanisms of consciousness". In: Proceedings of the National Academy of Sciences of the United States of America 91.16, pp. 7398–7403. DOI: 10.1073/pnas.91.16.7398.
- Ramsøy, Thomas Zoëga and Morten Overgaard (2004). "Introspection and subliminal perception". In: *Phenomenology and the Cognitive Sciences* 3.1, pp. 1–23. DOI: 10.1023/B:PHEN.0000041900.30172.e8.
- Reimer, Jacob, Matthew J. McGinley, Yang Liu, Charles Rodenkirch, Qi Wang, David A. McCormick, and Andreas S. Tolias (2016). "Pupil fluctuations track rapid changes in adrenergic and cholinergic activity in cortex". In: *Nature Communications* 7.1, p. 13289. DOI: 10.1038/ncomms13289.
- Roth-Paysen, Marie-Luise, Anne Bröcker, Maximilian Bruchmann, and Thomas Straube (2022). "Early and late electrophysiological correlates of gradual perceptual awareness in- and outside the Attentional Blink window". In: *NeuroImage* 263, p. 119652. DOI: 10.1016/j.neuroimage.2022.119652.

- Rutiku, R., M. Martin, T. Bachmann, and J. Aru (2015). "Does the P300 reflect conscious perception or its consequences?" In: *Neuroscience* 298, pp. 180–189. DOI: 10.1016/j.neuroscience.2015.04.029.
- Saalmann, Yuri B. and Sabine Kastner (2011). "Cognitive and perceptual functions of the visual thalamus". In: *Neuron* 71.2, pp. 209–223. DOI: 10.1016/j.neuron. 2011.06.027.
- Sadaghiani, Sepideh, Guido Hesselmann, and Andreas Kleinschmidt (2009). "Distributed and antagonistic contributions of ongoing activity fluctuations to auditory stimulus detection". In: *Journal of Neuroscience* 29.42, pp. 13410–13417. DOI: 10.1523/JNEUROSCI.2592-09.2009.
- Samuelsson, John G., Noam Peled, Fahimeh Mamashli, Jyrki Ahveninen, and Matti S. Hämäläinen (2021). "Spatial fidelity of MEG/EEG source estimates: A general evaluation approach". In: *NeuroImage* 224, p. 117430. DOI: 10.1016/j.neuroimage. 2020.117430.
- Sandberg, Kristian, Bert Timmermans, Morten Overgaard, and Axel Cleeremans (2010). "Measuring consciousness: Is one measure better than the other?" In: *Consciousness and Cognition* 19.4, pp. 1069–1078. DOI: 10.1016/j.concog.2009. 12.013.
- Scammell, Thomas E., Elda Arrigoni, and Jonathan O. Lipton (2017). "Neural Circuitry of Wakefulness and Sleep". In: *Neuron* 93.4, pp. 747–765. DOI: 10.1016//j.neuron.2017.01.014.
- Schlossmacher, Insa, Torge Dellert, Maximilian Bruchmann, and Thomas Straube (2021). "Dissociating neural correlates of consciousness and task relevance during auditory processing". In: *NeuroImage* 228, p. 117712. DOI: 10/ghrmhh.
- Schlossmacher, Insa, Torge Dellert, Michael Pitts, Maximilian Bruchmann, and Thomas Straube (2020). "Differential Effects of Awareness and Task Relevance on Early and Late ERPs in a No-Report Visual Oddball Paradigm". In: *Journal of Neuroscience* 40.14, pp. 2906–2913. DOI: 10.1523/JNEUROSCI.2077-19.2020.
- Schneider, Max, Pamela Hathway, Laura Leuchs, Philipp G. Sämann, Michael Czisch, and Victor I. Spoormaker (2016). "Spontaneous pupil dilations during the resting state are associated with activation of the salience network". In: *NeuroImage*. DOI: 10.1016/j.neuroimage.2016.06.011.
- Schröder, Pia, Till Nierhaus, and Felix Blankenburg (2021). "Dissociating Perceptual Awareness and Postperceptual Processing: The P300 Is Not a Reliable Marker of Somatosensory Target Detection". In: *Journal of Neuroscience* 41.21, pp. 4686–4696. DOI: 10.1523/JNEURDSCI.2950-20.2021.
- Schubert, Ruth, Felix Blankenburg, Steven Lemm, Arno Villringer, and Gabriel Curio (2006). "Now you feel it–now you don't: ERP correlates of somatosensory awareness". In: *Psychophysiology* 43.1, pp. 31–40. DOI: 10.1111/j.1469-8986.2006. 00379.x.
- Sergent, Claire, Sylvain Baillet, and Stanislas Dehaene (2005). "Timing of the brain events underlying access to consciousness during the attentional blink". In: *Nature Neuroscience* 8.10. DOI: 10.1038/nn1549.
- Sergent, Claire, Martina Corazzol, Ghislaine Labouret, François Stockart, Mark Wexler, Jean Rémi King, Florent Meyniel, and Daniel Pressnitzer (2021). "Bifurcation in brain dynamics reveals a signature of conscious processing independent of report". In: *Nature Communications* 12.1. DOI: 10.1038/s41467-021-21393-z.
- Sergent, Claire and Stanislas Dehaene (2004a). "Is consciousness a gradual phenomenon? Evidence for an all-or-none bifurcation during the attentional blink". In: *Psychological Science* 15, pp. 720–728. DOI: 10.1111/j.0956-7976.2004.00748.x.

- Sergent, Claire and Stanislas Dehaene (2004b). "Neural processes underlying conscious perception: Experimental findings and a global neuronal workspace framework". In: *Journal of Physiology Paris* 98.4. DOI: 10.1016/j.jphysparis.2005.09. 006.
- Shulman, G. L., J. A. Fiez, M. Corbetta, R. L. Buckner, F. M. Miezin, M. E. Raichle, and S. E. Petersen (1997). "Common Blood Flow Changes across Visual Tasks: II. Decreases in Cerebral Cortex". In: *Journal of Cognitive Neuroscience* 9.5, pp. 648– 663. DOI: 10.1162/jocn.1997.9.5.648.
- Silva, Fernando H. Lopes da (2010). "Electrophysiological basis of MEG signals". In: *MEG: An introduction to methods*. New York, NY, US: Oxford University Press, pp. 1–23. DOI: 10.1093/acprof:0s0/9780195307238.003.0001.
- Smallwood, Jonathan, Kevin S. Brown, Benjamin Baird, Michael D. Mrazek, Michael S. Franklin, and Jonathan W. Schooler (2012). "Insulation for Daydreams: A Role for Tonic Norepinephrine in the Facilitation of Internally Guided Thought". In: *PLOS ONE* 7.4, e33706. DOI: 10.1371/journal.pone.0033706.
- Sommer, Tobias (2011). "Neuroimaging: neuro-bildgebende Verfahren". In: *Der Expe4rimentator: Neurowissenschaften*. Experimentator. Heidelberg: Spektrum Akademischer Verlag, pp. 209–263. DOI: 10.1007/978-3-8274-2369-6_10.
- Squires, Kenneth C., Nancy K. Squires, and Steven A. Hillyard (1975). "Decisionrelated cortical potentials during an auditory signal detection task with cued observation intervals". In: *Journal of Experimental Psychology: Human Perception and Performance*. DOI: 10.1037///0096-1523.1.3.268.
- Stanislaw, Harold and Natasha Todorov (1999). "Calculation of signal detection theory measures". In: *Behavior Research Methods, Instruments, and Computers* 31.1. DOI: 10.3758/BF03207704.
- Sutton, Samuel, Magery Braren, Joseph Zubin, and E. R. John (1965). "Evoked-potential correlates of stimulus uncertainty". In: *Science* 150.3700, pp. 1187–1188. DOI: 10.1126/science.150.3700.1187.
- Takahashi, Naoya, Christian Ebner, Johanna Sigl-Glöckner, Sara Moberg, Svenja Nierwetberg, and Matthew E. Larkum (2020). "Active dendritic currents gate descending cortical outputs in perception". In: *Nature Neuroscience* 23.10, pp. 1277–1285. DOI: 10.1038//s41593-020-0677-8.
- Takahashi, Naoya, Thomas G. Oertner, Peter Hegemann, and Matthew E. Larkum (2016). "Active cortical dendrites modulate perception". In: *Science (New York, N.Y.)* 354.6319, pp. 1587–1590. DOI: 10.1126/science.aah6066.
- Tanner Jr., Wilson P. and John A. Swets (1954). "A decision-making theory of visual detection". In: *Psychological Review* 61, pp. 401–409. DOI: 10.1037/h0058700.
- Tsuchiya, Naotsugu, Ned Block, and Christof Koch (2012). "Top-down attention and consciousness: comment on Cohen et al." In: *Trends in Cognitive Sciences* 16.11, p. 527. DOI: 10.1016/j.tics.2012.09.004.
- Tsuchiya, Naotsugu, Melanie Wilke, Stefan Frässle, and Victor A.F. Lamme (2015). "No-Report Paradigms: Extracting the True Neural Correlates of Consciousness". In: *Trends in Cognitive Sciences*. DOI: 10.1016 / j.tics.2015.10.002. arXiv: 1011.1669v3.
- Turker, Hamid B., Elizabeth Riley, Wen-Ming Luh, Stan J. Colcombe, and Khena M. Swallow (2021). "Estimates of locus coeruleus function with functional magnetic resonance imaging are influenced by localization approaches and the use of multi-echo data". In: *NeuroImage* 236, p. 118047. DOI: 10.1016/j.neuroimage.2021. 118047.

- Twomey, Deirdre M., Peter R. Murphy, Simon P. Kelly, and Redmond G. O'Connell (2015). "The classic P300 encodes a build-to-threshold decision variable". In: *European Journal of Neuroscience*. DOI: 10.1111/Jejn.12936.
- Unsworth, Nash and Matthew K. Robison (2016). "Pupillary correlates of lapses of sustained attention". In: *Cognitive, Affective, & Behavioral Neuroscience* 16.4, pp. 601–615. DOI: 10.3758/s13415-016-0417-4.
- Urai, Anne E., Anke Braun, and Tobias H. Donner (2017). "Pupil-linked arousal is driven by decision uncertainty and alters serial choice bias". In: *Nature Communications* 8.1, p. 14637. DOI: 10.1038/ncomms14637.
- Uusitalo, M. A. and R. J. Ilmoniemi (1997). "Signal-space projection method for separating MEG or EEG into components". In: *Medical and Biological Engineering and Computing* 35.2, pp. 135–140. DOI: 10.1007//BF02534144.
- Verleger, Rolf (2020). "Effects of relevance and response frequency on P3b amplitudes: Review of findings and comparison of hypotheses about the process reflected by P3b". In: *Psychophysiology* 57.7, e13542. DOI: 10.1111/psyp.13542.
- Vittek, Anne-Laure, Cécile Juan, Lionel G. Nowak, Pascal Girard, and Céline Cappe (2022). "Multisensory integration in neurons of the medial pulvinar of macaque monkey". In: Cerebral Cortex (New York, N.Y.: 1991), bhac337. DOI: 10.1093 cercor/bhac337.
- Voisin, Julien, Aurélie Bidet-Caulet, Olivier Bertrand, and Pierre Fonlupt (2006). "Listening in Silence Activates Auditory Areas: A Functional Magnetic Resonance Imaging Study". In: *Journal of Neuroscience* 26.1, pp. 273–278. DOI: 10.1523 JNEUROSCI.2967-05.2006.
- Vugt, Bram van, Bruno Dagnino, Devavrat Vartak, Houman Safaai, Stefano Panzeri, Stanislas Dehaene, and Pieter R. Roelfsema (2018). "The threshold for conscious report: Signal loss and response bias in visual and frontal cortex". In: Science. DOI: 10.1126/science.aar7186.
- Wang, Chin-An, Gunnar Blohm, Jeff Huang, Susan E. Boehnke, and Douglas P. Munoz (2017). "Multisensory integration in orienting behavior: Pupil size, microsaccades, and saccades". In: *Biological Psychology* 129, pp. 36–44. DOI: 10.1016/j. biopsycho.2017.07.024.
- Wang, Chin-An and Douglas P. Munoz (2015). "A circuit for pupil orienting responses: implications for cognitive modulation of pupil size". In: *Current Opinion in Neurobiology* 33, pp. 134–140. DOI: 10.1016/j.conb.2015.03.018.
- Wen, Xiaotong, Li Yao, Yijun Liu, and Mingzhou Ding (2012). "Causal interactions in attention networks predict behavioral performance". In: *Journal of Neuroscience* 32.4, pp. 1284–1292. DOI: 10.1523/JNEUROSCI.2817-11.2012.
- Wiegand, Katrin, Sabine Heiland, Christian H. Uhlig, Andrew R. Dykstra, and Alexander Gutschalk (2018). "Cortical networks for auditory detection with and without informational masking: Task effects and implications for conscious perception". In: *NeuroImage* 167, pp. 178–190. DOI: 10.1016/j.neuroimage.2017.11. 036.
- Wixted, John T. (2020). "The Forgotten History of Signal Detection Theory". In: *Journal of Experimental Psychology: Learning Memory and Cognition* 46.2, pp. 201–233. DOI: 10.1037/x1m0000732.
- Wyart, Valentin and Catherine Tallon-Baudry (2008). "Neural Dissociation between Visual Awareness and Spatial Attention". In: *Journal of Neuroscience* 28.10, pp. 2667–2679. DOI: 10.1523/JNEUROSCI.4748-07.2008.
- Ye, Muwang, Yong Lyu, Ben Sclodnick, and Hong Jin Sun (2019). "The P3 reflects awareness and can be modulated by confidence". In: *Frontiers in Neuroscience* 13 (MAY). DOI: 10.3389/fnins.2019.00510.

Yellin, Dov, Aviva Berkovich-Ohana, and Rafael Malach (2015). "Coupling between pupil fluctuations and resting-state fMRI uncovers a slow build-up of antagonistic responses in the human cortex". In: *NeuroImage* 106, pp. 414–427. DOI: 10.1016/j.neuroimage.2014.11.034.

Personal publications

Preliminary results of Experiment 1 (section 3.1) have been presented at the annual meeting of the Society for Neuroscience (SfN) in 2019:

Doll, L., Dykstra, A.R., Gutschalk, A. (2019). "Effects of task and arousal level on the processing of peri-threshold tones investigated with MEG, EEG, and pupillometry". In: *SfN Abstr.*, URL: https://www.abstractsonline.com/pp8/#!/7883// presentation/71164

My personal contribution consisted of the data collection and analysis, and the preparation of the abstract and the poster, which were revised by Prof. Gutschalk and Prof. Dykstra.

The results of the M/EEG Experiments (section 3.1 and 3.2) are currently prepared for a publication together with Prof. Andrew Dykstra and Prof. Alexander Gutschalk. A second publication in preparation together with Prof. Gutschalk will cover the fMRI Experiment (section 3.4). The discussion in the present dissertation (chapter 4) was written in an effort to combine the results of all experiment, but naturally there is thematic overlap with the discussions of the manuscripts in preparation.

For both future publications, my personal contribution consisted of the data recording and analysis, as well as writing the first draft of the manuscripts.

Danksagung

An erster Stelle geht mein Dank an meinen Doktorvater Herrn Prof. Dr. Alexander Gutschalk für das Thema dieser Arbeit und die hervorragende Betreuung. Den damit verbundenen Einstieg in die Neurowissenschaften hatte ich nach dem Studium zwar nicht vorhergesehen, bin aber sehr dankbar dafür und würde mich jederzeit wieder so entscheiden.

Danke auch an Herrn Prof. Andrew Dykstra für die Einarbeitung und die gute Zusammenarbeit und an Herrn PD Dr. André Rupp für die zahlreichen Ratschläge und die interessanten und lehrreichen Unterhaltungen.

Ein großes Dankeschön auch an alle anderen Kollegen der Sektion Biomagnetismus und des Auditory Cognition Lab für die Unterstützung im Laufe meiner Arbeit und die gute und herzliche Zusammenarbeit im MEG Labor.

Ein besonderer Dank gebührt dabei natürlich Frau Barbara Burghardt und Frau Esther Tauberschmidt für die Hilfe bei der Durchführung der M/EEG Messungen, sowie die Unterstützung bei zahlreichen anderen, größeren und kleineren Problemen.

Ebenso möchte ich mich bei Frau Prof. Dr. Sabine Heiland und dem Team des Forschungs-MRT, insbesondere Herrn Dr. Marcel Prager und Frau Dorothea Willich für die Unterstützung bei den MRT Messungen bedanken.

Zu guter Letzt geht ein riesiges Dankeschön an meine Familie und Freunde, für den Rückhalt und die Unterstützung, nicht nur im Laufe dieser Doktorarbeit. Danke für die Ermutigungen, das Zuhören, Bestärken, Beratschlagen und so vieles mehr.

Eidesstattliche Erklärung

- 1. Bei der eingereichten Dissertation zu dem Thema *"Influence of arousal and attention on the perception of auditory near-threshold stimuli"* handelt es sich um meine eigenständig erbrachte Leistung.
- 2. Ich habe nur die angegebenen Quellen und Hilfsmittel benutzt und mich keiner unzulässigen Hilfe Dritter bedient. Insbesondere habe ich wörtlich oder sinngemäß aus anderen Werken übernommene Inhalte als solche kenntlich gemacht.
- 3. Die Arbeit oder Teile davon habe ich bislang nicht an einer Hochschule des In- oder Auslands als Bestandteil einer Prüfungs- oder Qualifikationsleistung vorgelegt.
- 4. Die Richtigkeit der vorstehenden Erklärungen bestätige ich.
- 5. Die Bedeutung der eidesstattlichen Versicherung und die strafrechtlichen Folgen einer unrichtigen oder unvollständigen eidesstattlichen Versicherung sind mir bekannt. Ich versichere an Eides statt, dass ich nach bestem Wissen die reine Wahrheit erklärt und nichts verschwiegen habe.

Ort und Datum

Unterschrift