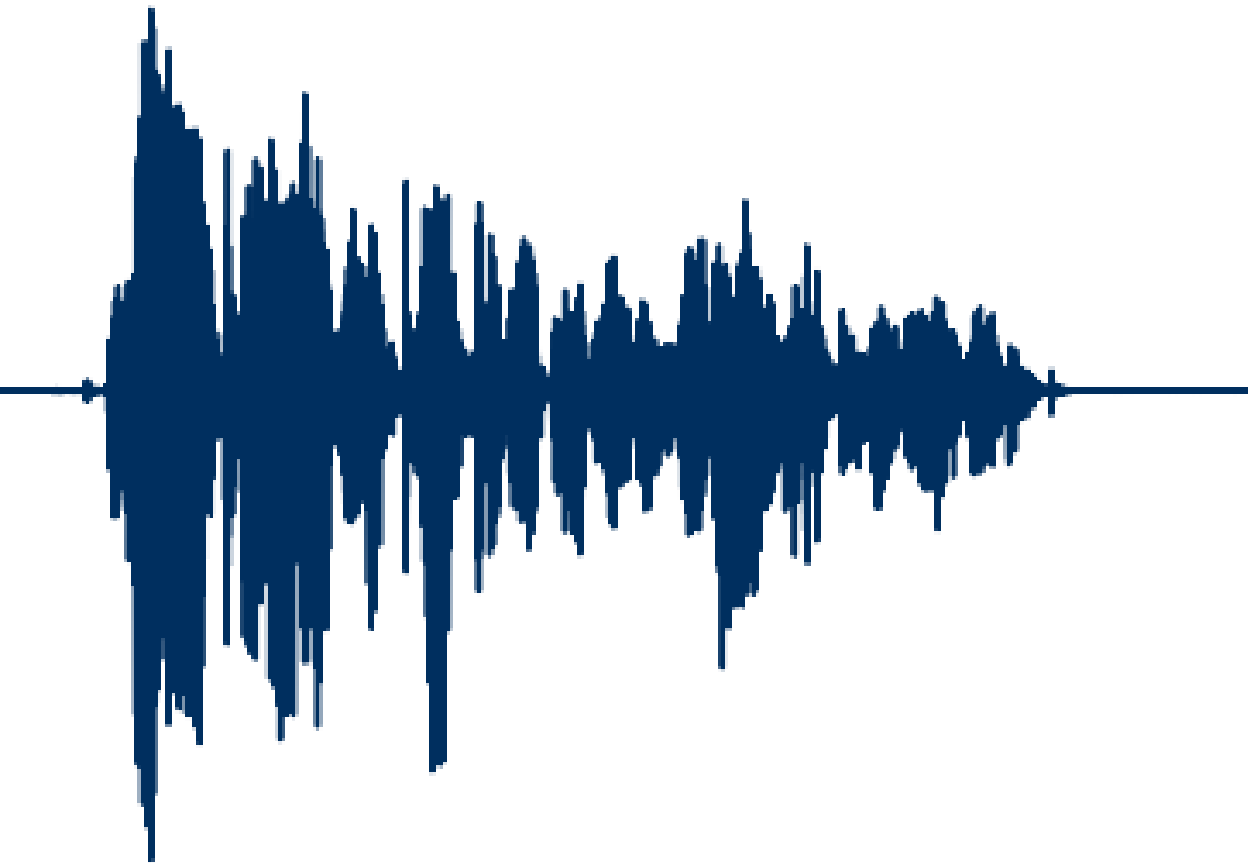


# Neural Correlates of Consciousness in Sound Localization

Billy Gerdfeldter





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Billy Gerdfeldter

Academic dissertation for the Degree of Doctor of Philosophy in Psychology at Stockholm University to be publicly defended on Friday 23 May 2025 at 13.00 in Lärosal 31, hus 4, våning 2, Albanovägen 12.

## Abstract

Within neuroscience, biological markers of consciousness are known as the neural correlates of consciousness (NCCs). Electrophysiological data have suggested two candidate NCCs in hearing: the auditory awareness negativity (AAN), and late positivity (LP). The AAN is linked to phenomenal awareness of sound, and the LP to post-perceptual behavioral response and executive control. Earlier research on the analogs of the AAN in both vision and touch found topographical mapping onto the cerebral hemisphere that is contralateral to stimulus source. Similar research has not been conducted on the AAN. Sound localization is the ability to perceive spatial locations of sound sources. Localization of sound in the horizontal dimension utilizes binaural cues of time and intensity differences. Sound is typically perceived from outside the head and is localized to a physical space (sound localization). When sound is perceived within the head, by using headphones, sound is instead lateralized to the left or right along an intracranial axis (sound lateralization). The thesis comprised three studies of threshold-level identification tasks, where listeners were tasked to localize laterally displaced sounds. The first study tested the NCCs to sound lateralization using a binaural click stimulus that was lateralized randomly toward either ear, presented through headphones. Then, the second study tested the NCCs to sound localization using a square pulse stimulus played from random positions in a semicircular array of thirteen horizontally displaced equidistant loudspeakers. In the third study, the NCCs to different binaural cues in sound lateralization were tested, specifically manipulating differences in time and intensity with the same stimulus and equipment used in the first study. The overall results showed that the AAN contralaterally changes in relation to experienced sound source only in sound lateralization, and only in the tested condition where binaural cues of time and intensity differences were combined. The LP showed a hemispheric contralateral effect in relation to experienced sound source, but only to sound localization. This contralateral effect may be an attentional artifact of audiovisual integration, as the loudspeakers were seen by the listeners. The thesis suggests that the NCCs to sound localization and sound lateralization differ in expression based on hearing medium.

**Keywords:** *neural correlates of consciousness, NCC, auditory awareness negativity, AAN, hearing, sound localization, electroencephalography, EEG, event-related potential, ERP.*

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Department of Psychology

Stockholm University, 106 91 Stockholm





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# Abstract

Within neuroscience, biological markers of consciousness are known as the neural correlates of consciousness (NCCs). Electrophysiological data have suggested two candidate NCCs in hearing: the auditory awareness negativity (AAN), and late positivity (LP). The AAN is linked to phenomenal awareness of sound, and the LP to post-perceptual behavioral response and executive control. Earlier research on the analogs of the AAN in both vision and touch found topographical mapping onto the cerebral hemisphere that is contralateral to stimulus source. Similar research has not been conducted on the AAN. Sound localization is the ability to perceive spatial locations of sound sources. Localization of sound in the horizontal dimension utilizes binaural cues of time and intensity differences. Sound is typically perceived from outside the head and is localized to a physical space (sound localization). When sound is perceived within the head, by using headphones, sound is instead lateralized to the left or right along an intracranial axis (sound lateralization). The thesis comprised three studies of threshold-level identification tasks, where listeners were tasked to localize laterally displaced sounds. The first study tested the NCCs to sound lateralization using a binaural click stimulus that was lateralized randomly toward either ear, presented through headphones. Then, the second study tested the NCCs to sound localization using a square pulse stimulus played from random positions in a semicircular array of thirteen horizontally displaced equidistant loudspeakers. In the third study, the NCCs to different binaural cues in sound lateralization were tested, specifically manipulating differences in time and intensity with the same stimulus and equipment used in the first study. The overall results showed that the AAN contralaterally changes in relation to experienced sound source only in sound lateralization, and only in the tested condition where binaural cues of time and intensity differences were combined. The LP showed a hemispheric contralateral effect in relation to experienced sound source, but only to sound localization. This contralateral effect may be an attentional artifact of audiovisual integration, as the loudspeakers were seen by the listeners. The thesis suggests that the NCCs to sound localization and sound lateralization differ in expression based on hearing medium.

# Sammanfattning på svenska

Inom neurovetenskap kallas de biologiska markörerna för mänskligt medvetande för de neurala korrelaten av medvetande (NCC). Elektrofysiologiska data har antytt två kandidater till NCC inom hörsel: AAN och LP. AAN är länkat till fenomenal varseblivning av ljud, och LP till postperceptuella beteenderesponser och exekutiv kontroll. Tidigare forskning inom analoger av AAN i både syn och känsel fann topografisk kartläggning på den cerebrala hemisfären som är kontralateral till stimuluskällan. Liknande forskning har inte bedrivits på AAN. Ljudlokalisering är förmågan att kunna uppfatta den spatiala platsen för ljudkällor. Lokalisering av ljud i den horisontella dimensionen utnyttjar binaurala ledtrådar av tids- och nivåskillnader. Ljud upplevs typiskt utanför huvudet, och lokaliseras till en fysisk plats (ljudlokalisering). När ljud upplevs från inom huvudet, med hörlurar, lateraliseras ljudet istället till vänster eller höger längst en intrakranial axel (ljudlateralisering). Avhandlingen består av tre studier med identifikationsuppgifter vid tröskelnivå, där lyssnare ombads lokalisera lateralt förskjutna ljud. I första studien testades NCC till ljudlateralisering med ett binauralt klickstimulus som lateralisades slumpmässigt till någotdera öra genom hörlurar. I andra studien testades NCC till ljudlokalisering med en kvadratpulsstimulus som spelades från en slumpmässig position i en semicirkulär uppsättning av tretton horisontellt förskjutna ekvidistanta högtalare. I tredje studien testades NCC till olika binaurala ledtrådar inom ljudlateralisering, specifikt genom att manipulera tids- och nivåskillnader med samma stimulus och utrustning som första studien. De övergripande resultaten visar att AAN skiftar kontralateralt i relation till upplevd ljudkälla endast vid ljudlateralisering, och endast i den testade betingelsen när binaurala ledtrådar av tids- och nivåskillnader kombineras. LP uppvisar en hemisfäriskt kontralateral effekt i relation till upplevd ljudkälla, men endast vid ljudlokalisering. Denna kontralaterala effekt kan vara en artefakt från uppmärksamhet vid audiovisuell integration, eftersom högtalarna kunde ses av lyssnaren. Avhandlingen föreslår att NCC till ljudlokalisering och ljudlateralisering skiljer sig i uttryck baserat på hörselmedium.

# Acknowledgments

Nine years ago, my journey at Stockholm University began, when I became eligible for the master's program. I was uncertain of what I wanted to do as a vocation, and I never believed that I had the qualities, nor the merits, to be employed as a scientist. Nevertheless, throughout adolescence I've pondered regularly on the nature of human consciousness and its complexities. When getting to my master's thesis, I was introduced to Gösta Ekmans Laboratory, opening my eyes to research into the neural correlates of consciousness. GEL never ceased to amaze me in how wonderful the people working there were, never failing to support me in my learning or my research. After graduation, I applied as a research assistant at GEL, where I then worked for a year, before getting accepted as a PhD-student. However, that's when the troubles began in hindsight. COVID-19 hit just months afterward, and the pandemic was a vast social upheaval for us all. When society recovered, and when everyone eventually was back at campus, I was falling behind schedule. The following years saw intermittent hardships and delayed deadlines, that slowed down my overarching thesis work, but not my fondness for my day-to-day work. This understanding has convinced me to pursue a career in academia. This thesis is unironically the end of a chapter, but hopefully just the beginning, for the next page of my life.

None of it would be possible without the support of my colleagues. I extend specific recognition to my supervisor Stefan for his kindness and patience with me, and for being a good friend. I thank my co-supervisor Mats, always helpful in discussing ideas and pushing me in the right direction when needed, and to Maria who has always been very supportive of me. I thank Annika and Mingailè for our collaborative research and discussions on the nature of consciousness. I thank Malina and Ronald for great discussions and your technical expertise. I thank William and Teodor for the sidetracked discussions as office-mates. I thank Marta and Raver for our time in the PhD-council.

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Well, here it is. I hope you enjoy.

# List of Studies

**Study 1:** Eklund, R., Gerdfeldter, B., & Wiens, S. (2021). The early but not the late neural correlate of auditory awareness reflects lateralized experiences. *Neuropsychologia*, *158*, 107910. <https://doi.org/10.1016/j.neuropsychologia.2021.107910>

**Study 2:** Gerdfeldter, B., Andersson, A., & Wiens, S. (2024). Examining the lateralization of electrophysiological correlates of auditory awareness. *Psychophysiology*, *61*(11), e14656. <https://doi.org/10.1111/psyp.14656>

**Study 3:** Gerdfeldter, B., Greičiūtė, M., & Wiens, S. (2025). Examining experienced lateralization of sounds over headphones with electroencephalography. *Neuropsychologia*, *207*, 109064. <https://doi.org/10.1016/j.neuropsychologia.2024.109064>

# Glossary

**AAN:** Auditory awareness negativity

**BF:** Bayes factor

**Binaural:** Between both ears.

**CI:** Credibility interval

**EEG:** Electroencephalography

**ERP:** Event-related potential

**GNWT:** Global neuronal workspace theory

**ILD:** Interaural level difference

**ITD:** Interaural time difference

**LP:** Late positivity

**LPCpc:** Posterior contralateral late positive component.

**N2ac:** Anterior contralateral component of the N2-wave.

**NCC:** Neural correlates of consciousness

**PAN:** Perceptual awareness negativity

**pd:** Probability of direction

**RPT:** Recurrent processing theory

**SAN:** Somatosensory awareness negativity

**SDT:** Signal detection theory

**Sound Lateralization:** Ability to localize sound internally, via e.g. headphones.

**Sound Localization:** Ability to localize sound in real space, via e.g. loudspeakers.

**VAN:** Visual awareness negativity

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# 1 Introduction

In the search for the physical substrate of consciousness, scientists measure the neural correlates of consciousness (NCCs). The NCCs represent the neural processes associated with conscious activity, measured by neuroimaging. However, fundamental to the research field is the idea of correlation and not causation: Neuroimaging cannot provide causal proof of neural mechanisms, only measure what brain activity correlates with behavioral function of consciousness. While lacking causal evidence, NCCs provide insight into which neural processes are integral for maintaining conscious awareness. A common definition of NCCs as proposed by Koch et al. (2016, pg. 308) reads: “*the minimum neuronal mechanisms jointly sufficient for any one specific conscious percept.*”

Furthermore, there is a difference between content-specific and full NCCs (Koch et al., 2016). Content-specific NCCs concern ephemeral and transient experiences, such as the thoughts you experience, which cease to exist after you stop thinking about them. Full NCCs concern the neural architecture that powers consciousness, and which differs in states such as wakefulness, sleep, or anesthesia. The NCCs covered by this thesis are all content-specific NCCs. To define what constitutes content-specific consciousness itself is difficult, as it needs to be disambiguated from concurrent processes such as attention, working memory, introspection, and metacognition (Searle, 1998). However, the general definition used in this thesis is: the experience caused by perceptual input of an outward existence. In this sense, conscious experience is closely linked to perception, as perceptual experience is maintained in mind. Conscious experience and perceptual awareness are thus synonymous in this endeavor.

To elaborate on the definition of consciousness are the distinctions between phenomenal and access consciousness (Block, 2005). Phenomenal consciousness reflects the raw experience of an event, synonymous to qualia: the irreducible qualities of an experience, such as color. The neural areas that process these qualities send information upstream to trigger access consciousness. Access consciousness reflects the information of the event available within mind for decision-making and subsequent action.

The accessibility of conscious content may thus be construed as the strength of representation from perceptual input, whether exogenous (outward experience) or endogenous (memory recall). However, perception is not static,

as sensory stimuli vary in strength (Millidge et al., 2021). Sensory uncertainty affects perception, which biases conscious experience. The brain can reduce sensory uncertainty in two ways. One is through a bottom-up process, allocating more attentional resources to the stimulus and enhancing sensory signal strength for a clearer perception. The other is by leveraging prior knowledge to predict the most likely experience based on available sensory cues, essentially 'filling in the blanks' of an unclear picture, forming a top-down representation. This prediction of experience is explained by the theory of predictive coding (Mumford, 1992; Kok & de Lange, 2015; Walsh et al., 2020); that the brain's primary function is 1) maintaining an internal probabilistic model of the world, and 2) actively minimizing the prediction errors between perceptual input and the predicted experience by continuously updating the internal model.

Given the perceptual nature of conscious awareness, NCCs have been studied within the different sensory modalities. Vision is the most studied sense, and research into the neural correlates of visual awareness has found candidate neural processes and substrates along the neural visual pathway (Koivisto & Revonsuo, 2010). The neural correlates of awareness to touch (Auksztulewicz & Blankenburg, 2013) and hearing (Eklund & Wiens, 2019) have similarly been found along their respective sensory pathway. Further, research into visual and somatosensory correlates of consciousness found that lateral stimuli elicited stronger contralateral hemispheric responses within respective sensory cortex (Koivisto & Grassini, 2016; Auksztulewicz & Blankenburg, 2013). These findings suggest a mapping effect from stimulus to experience, in relation to stimulus source. In other words, that the neural correlate to an experience changes in tandem with the spatial location of the experience. Similar mapping effects have not been investigated in hearing.

Further, the neural functions of the auditory system are not fully understood, and the research into neural correlates of auditory consciousness is still in its relative nascency. An aspect of auditory perception subject to much research is the ability to localize sounds. Additionally, the brain processes sound differently if it is experienced from outside (re: loudspeakers) or inside (re: headphones) the head. To make this distinction, experiencing lateral sound outside the head is known as *sound localization*, and within the head as *sound lateralization*. To elaborate on this distinction: When sound is experienced from outside the head, it is experienced as originating from a physical location around you. When a sound is experienced within the head, it is experienced as originating along a continuum of lateralization from the left to the right along the inside of the head, without any depth.

The neural auditory pathway from ear to auditory cortex has been extensively studied over the past decades, yet the neural correlates to sound localization and sound lateralization remain difficult to pinpoint (Middlebrooks, 2021; Dietz et al., 2018). Combining knowledge of the neural correlates of auditory consciousness with the neural correlates of sound localization and

sound lateralization can give insight into how the experience of different sound sources is generated.

## 1.1 General Aim

The general aim of the thesis is to expand the knowledge of how auditory conscious experience may be generated within the brain, with a focus on how candidate NCCs of auditory awareness change based on perceived location of sound using electroencephalography (EEG). Earlier research investigated binaural stimuli presented via headphones (Eklund & Wiens, 2019; Eklund et al., 2019; Eklund et al., 2020). In these experiments, subjects listened for weak sounds and reported whether they were aware of the sound or not. The EEG data to trials rated as aware were then contrasted against data to trials rated as unaware, to produce a difference wave of neural activity correlating to awareness. This difference wave contains the auditory awareness negativity (AAN) as an electrophysiological signature of auditory consciousness.

The AAN has counterparts in the visual and somatosensory domains, and these counterparts have shown a contralateral activation to perceived lateral stimuli (Koivisto & Grassini, 2016; Auksztulewicz & Blankenburg, 2013). If AAN follows a similar pattern, it would provide important evidence supporting a supramodal mechanism of perceptual awareness (Dembski et al., 2021). To investigate whether the AAN exhibits a contralateral activation to lateral auditory stimulation, this thesis explores lateral auditory NCCs, a topic that has not been systematically examined in previous auditory research.

### 1.1.1 Specific Aims

To achieve the general aims outlined above, three experimental studies were designed with the following specific aims (with respective studies in parentheses):

- 1) The hemispheric lateralization of AAN in response to auditory lateralization of sounds presented in headphones (Sound lateralization; Study 1).
- 2) The hemispheric lateralization of AAN in response to auditory localization of sounds presented in loudspeakers (Sound localization; Study 2).
- 3) The hemispheric lateralization of AAN in response to manipulation of binaural cues to auditory lateralization of sounds presented in headphones (Sound lateralization; Study 3).

## 1.2 Theories of Consciousness

There are many neural processes involved in generating conscious experience (Koch et al., 2016). Several plausible theories have emerged, and a curated selection of two leading theories most relevant to the thesis are covered below (Pitts et al., 2018).

### 1.2.1 Recurrent Processing Theory

Recurrent processing theory (RPT) is a theory of consciousness as a series of recurrent, reciprocal, neural activities between cortical areas (Lamme, 2006; 2010; 2018). RPT stipulates that most information that reaches the brain is processed unconsciously, and only a fraction of that information reaches conscious awareness: The body constantly and passively records sensory input, and when the input is deemed salient due to some internal trigger, consciousness is recruited to monitor the input and decide how to act upon it.

According to RPT, perceptual processing begins with feedforward sweeps of sensory information. When sensory organs are stimulated, they send the signal toward the sensory cortices and higher brain areas. This neural feedforward sweep is completed roughly 200 ms post-stimulus (Lamme & Roelfsema, 2000). During the feedforward sweep, the information processing is not available for conscious experience, but the neural signal is unconsciously decoded for basic sensory features, and carries forward into the motor cortex. Hardwired instincts unconsciously act upon this information, and can execute intelligent reflexes, such as blinking in response to strong light, flinching at a loud noise, or even catching a drinking glass that is knocked off a table, even though you do not intentionally commit to these actions (Lamme, 2018). This feedforward sweep of information is mechanically processed by your brain, even when you are otherwise unconscious, such as during sleep.

As the feedforward sweep reaches a neural area in its path, horizontal connections are made to adjacent neurons. These horizontal connections then feed information back toward lower areas. Higher areas in the sensory hierarchy are generally tasked with more abstract interpretation of stimuli, meaning that these areas send feedback to lower areas regarding salience of feature processing and sensory detail. For example, one lower level of the visual system is responsible for detecting color, and another for detecting contours. When the feedforward sweep from these areas reaches a higher visual area pertaining to object recognition, the higher area sends feedback to lower areas that the processed colors and contours actually belong to the same object. This feedback loop constitutes recurrent processing, and is satisfactory to achieve phenomenal consciousness (Lamme, 2010).

Lamme (2010) argues the distinction between phenomenal and access consciousness is actually a matter of levels of awareness. Phenomenal awareness is the true inception of conscious perception, and when attention is recruited,

the awareness is enhanced and reaches a detailed, access awareness. When attention is recruited, the recurrent processing is pushed further, reaching fronto-parietal executive areas of the brain. When the horizontal connections in executive areas begin recurrent processing, full access consciousness is achieved. At this stage of global recurrent processing, executive control can manage and manipulate sensory information to evaluate the best course of action to the stimulus.

To summarize, RPT stipulates that recurrent loops of neural areas interconnect to provide feedback and unity to a given experience. The recurrent activity becomes deeper and more widespread as more attention is allocated to a given stimulus. The wider the recurrent activity is, the higher level of consciousness is reached (for neuroanatomical modeling of RPT, see Lamme, 2010).

### 1.2.2 Global Neuronal Workspace Theory

Global neuronal workspace theory (GNWT) is a competing theory of consciousness. GNWT represents a framework of decentralized processes within the brain converging on a central stage where all conscious thought is conducted. Consciousness and subsequent intentional action are a product of multiple cognitive systems cooperating as a central information exchange (Baars, 2005). Cognitive functions such as sensory input and memory recall remain outside of conscious awareness, yet they are necessary for awareness to continue. Conscious thought is thus an emergent function of multiple brain functions working together.

GNWT stipulates that endogenous (memory recall) or exogenous (external stimulation) activation of sensory cortices place a sensory stimulus in the attentional spotlight (Dehaene et al., 2011). This stimulus is then distributed among other brain areas to recruit specialist functions toward the spotlight (such as object recognition and memories of the object) in order to process the stimulus for future action. To facilitate the number of simultaneous processes recruited, working memory is theorized to form the actual stage that accommodates the attentional spotlight and recruited information processing.

GNWT primarily functions bottom-up, i.e., sensory information is fed upstream to higher areas for consciousness (Mashour et al., 2020; Dehaene et al., 2011). However, upon reaching higher areas reciprocal recurrent loops feed back to lower areas to amplify salient information until a singular percept is achieved. Top-down modulation then focuses on sustaining the percept and keeps it available in consciousness. Any other simultaneous percepts are blocked out by forced neural inhibition, effectively pushed out of the spotlight of attention.

To summarize, GNWT takes sensory information and recruits multiple systems to process the input and subsequently causes conscious experience. Consciousness is thus a consequence of perception (for neuroanatomical modeling of GNWT, see Dehaene et al., 2011).

### 1.2.3 Comparison of Theories

RPT and GNWT have their differences, predominantly in how they define the inception of conscious awareness. RPT argues that phenomenal experience is the inception point, whereas GNWT argues that it is but a prerequisite to achieve true experience at the level of access consciousness. To elaborate, GNWT perceives consciousness as a product of cognitive function after recurrent sensory processing, while RPT perceives consciousness as recurrent sensory processing per se. GNWT and RPT are both reconcilable with predictive coding, and both agree on the reciprocity of top-down & bottom-up modulation of conscious experience (Lamme, 2010; Dehaene et al., 2011). Other theories attempt to establish a position between the temporally early model of RPT and late model of GNWT, stipulating that consciousness arises after sensory processing, but before access consciousness (see Brown et al., 2019 for a review), or view consciousness as a product of unique configurations of neural states (e.g., information integration theory; Tononi et al., 2016). While these other theories do exist, they have not achieved the same empirical credence as RPT and GNWT (Pitts et al., 2018).

## 1.3 Measuring Consciousness

Regardless of what theory best explains consciousness, they base their assumptions on empirical data of brain function. To collect real-time data from a living brain, special tools and methods need to be used to correctly assess neural activity of interest.

### 1.3.1 Neuroimaging

Neurological phenomena are commonly studied using neuroimaging methods. These methods track changes in brain activity via different media, such as blood oxygen consumption, or electromagnetic fields. Different neuroimaging methods confer their respective advantages and disadvantages to research, primarily concerning resolution of neural activity in time and space. Because consciousness is generated on a very rapid timescale from stimulus exposure to conscious experience, a neuroimaging method with high temporal resolution is preferred.

### **1.3.1.1 Electroencephalography**

Electroencephalography (EEG) is a method that uses sensitive electrodes applied to a person's scalp to measure fluctuations in local electric field potentials (Buzsáki et al., 2012; Luck, 2014). These fluctuations can be tracked to follow neural signals from beginning to end, and be compared to the simultaneous behavioral output the person provides. EEG has good temporal resolution, but is limited by poor spatial resolution of neural phenomena, as it measures summated electric fields across the scalp.

### **1.3.1.2 Event-related Potentials**

Event-related potentials (ERPs) are a specific application of EEG used to measure neural responses to discrete events, such as sensory stimuli or cognitive processes. By analyzing voltage changes in the EEG signal that are time-locked to these events, ERPs provide insights into the timing and sequence of neural processing. The basic premise of the ERP technique is to amplify the neural activity of interest, in lieu of minimizing irrelevant concurrent neural activity (Luck, 2014; Sur & Sinha, 2009). When a test subject is exposed to a stimulus or performs a behavior, there will be a neural response of interest. Experiments can be constructed to take a snapshot of the brain's neural activity time-locked to stimulus exposure or behavior execution of interest. The snapshot recording will contain the neural activity of interest, alongside irrelevant, concurrent, background activity (re: noise). This snapshot can be repeated multiple times, and each snapshot should contain identical activity of interest, surrounded by noise. When these snapshots are averaged together into a single measurement, the activity of interest will be unchanged (because the average of multiple instances of a single value will always equal itself), while the noise will be reduced (because random deviations of voltage can be positive or negative, and will eventually average each other out).

Further, the ERPs between individuals may differ in expression of amplitude or latency, even if they represent the same underlying neural response (Luck, 2014). This effect can partly be explained by contextual factors such as sleep and age, but is largely due to the unique cortical structure of each individual's brain: In general, brains are organized similarly, but there are local differences in where processes are implemented. Also, the pattern of cortical folds of gyri and sulci differ uniquely among individuals. These folds change the distribution of aligned neurons, and thus electric dipoles measured by EEG. In modern EEG studies, grand-averaged ERPs across subjects are typically reported. These grand averages show the ERP as typical across a sample of subjects, although each individual differs from the average in a normally distributed fashion. Importantly, the ERPs presented in this thesis are all grand-averaged ERPs, unless otherwise noted.

### 1.3.1.3 Contrastive Analysis

To measure specific conscious experiences using EEG, experimental design needs to accommodate the ERP technique. Conventionally, psychophysical experiments expose test subjects to varying perceptual stimuli, followed by prompting the subject for behavioral performance, by for example, indicating the location of a sound, or what color an image was. By time-locking the ERP to specific events (e.g., the stimulus presentation) in the experimental task, researchers can detect brain responses to these events. This method provides neural correlates to different aspects of sensory processing, but does not exclude all confounding factors that may overlap this processing (Aru et al., 2012; de Graaf et al., 2012). To clarify, when measuring consciousness, there will also be systematic effects present that do not relate to consciousness, such as processes regarding motor skills, memory, or even homeostasis. For example, if participants are instructed to press a particular key on trials when they had a conscious experience, it is ambiguous whether the activity revealed by the ERP reflects conscious awareness of the stimulus or motor processes related to pressing a key. To disentangle these from the neural signature of consciousness, it is also necessary to compare ERPs that lack conscious awareness.

The method of contrastive analysis is used to extract activity specific to conscious processes from other concurrent effects (Aru et al., 2012). When measuring ERPs, it is thus necessary that there are samples from the same subject, performing the same task, when they are aware (conscious) of a stimulus, and when they are unaware (unconscious) of the same stimulus. If these two conditions are subtracted from each other (trials rated as aware minus trials rated as unaware), background activities will be canceled out, and the difference remaining will be the activity between being aware and unaware. This method effectively isolates the neural activity of consciousness.

To achieve a functional contrastive analysis, two issues must be addressed: First, that the task is equal in all ways regardless of conscious awareness (e.g., that a button be pushed even if unaware of the stimulus), and second, that the stimulus of interest can both be sometimes perceived and sometimes not, at the same intensity level. The counterintuitive notion of being aware and unaware of the same level stimulus is achieved via a threshold-level stimulus paradigm. The stimulus of the experiment is calibrated to the subject's individual perceptual threshold, that is, a level of intensity where the subject will experience the stimulus roughly half of the time (imagine a sound that is very difficult to hear, or an image that is almost the same color as its background). Using the thresholding procedure eliminates any stimulus confound, as the stimulus is always presented to the subject at the same level. Fluctuations between perceiving or not perceiving a stable stimulus is due to internal noise within the brain, e.g., from events preceding a stimulus (Aru et al., 2012; de Graaf, 2012).



#### 1.3.1.4 Perceptual Threshold

The perceptual threshold can be viewed through the lens of signal detection theory (SDT; Hautus et al., 2022), where the detection of a stimulus is modeled as a probability function based on sensitivity to the stimulus and an internal response criterion (the minimum stimulus level where an individual will respond to it as detected). However, SDT may not be suitable to measure consciousness, as it is unclear in how to model awareness (Macmillan, 1986; Hautus et al., 2022). Macmillan (1986) argues that stimuli below the response criterion can still be consciously perceived, albeit at a lower probability than stimuli above the criterion. In other words, SDT takes no stance on whether a signal is consciously perceived or not. If the criterion were a measure of conscious awareness, stimuli below the criterion should not be consciously perceived. If stimuli below the criterion can be perceived (as hits), their incidence rate should match that of false alarms, meaning that the response criterion and perceptual awareness threshold are separated (Macmillan, 1986). In support of this notion, ERPs to false alarms have been found identical to hits in NCC research (Faramarzi et al., 2021), suggesting that endogenous (hallucinatory) awareness to the stimulus is similar to exogenous awareness, and thus consciousness is not suitably measured by SDT. Further, instructions or strategies may change a subject's criterion through response bias, but not necessarily change their underlying threshold of awareness (Hautus et al., 2022).

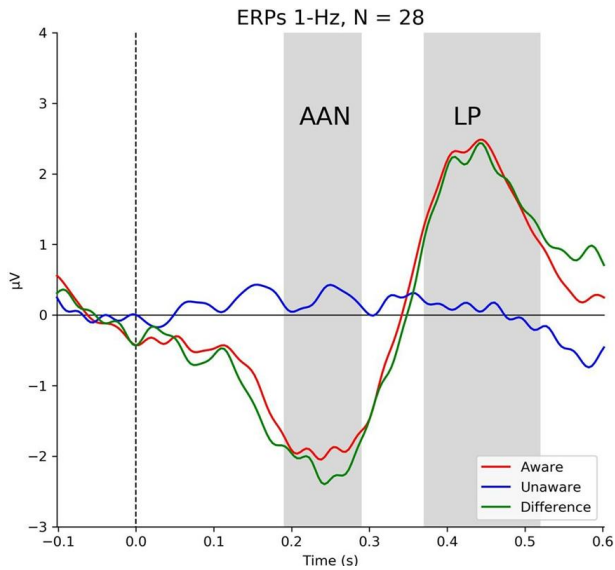
When presented with a choice of reporting whether a stimulus was experienced, low confidence can pose a problem: Test subjects may exhibit liberal or conservative response biases (Hautus et al., 2022). A subject with a liberal response bias will respond being aware of stimuli even at low awareness levels. Conversely, a subject with a conservative response bias will only respond being aware at high awareness levels. These biases effectively shift the decision criterion of the subjects to require an individually stronger or weaker stimulus in relation to their awareness threshold. The problem with response bias in ERP studies is that the relatively higher stimulus level required for the conservative bias will create a stronger neural response and a greater amplitude in the ERP (Fahrenfort et al., 2024). The converse is true of liberal bias, with a weaker amplitude in the ERP. To ameliorate response biasing, the perceptual awareness scale (PAS) has been designed to provide a graded response scale for measuring perceptual phenomena (Sandberg et al., 2010). The PAS allows for responses that are meaningfully different to the perceiver, such as "I experienced the stimulus weakly" and "I experienced the stimulus strongly". This small change can lessen response biases in perceptual experiments where confidence is low, by allowing gradients to subjective experience. Thus, the threshold prescribed in this thesis follows the perceptual threshold of awareness, which in turn may be slightly over- or underestimated depending on the subject's response bias (Fahrenfort et al., 2024). See section 4.4.2 for further discussion.

### 1.3.2 Neuroimaging Evidence of Neural Correlates of Consciousness

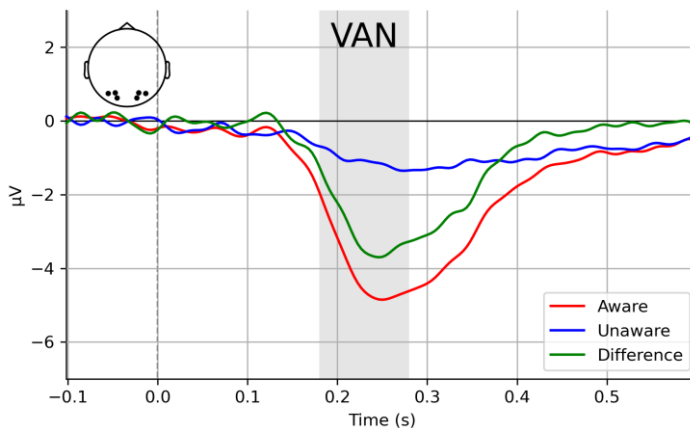
Electrophysiological data, such as ERPs, provide the majority of evidence of NCCs given the necessity of temporal resolution. Common ERPs to sensory mechanisms have been documented (Luck, 2014; Sur & Sinha, 2009) and these align with discovered NCCs. For hearing, a common ERP called the N100 wave has been discovered over vertex areas of the scalp, which infers a central location (coinciding with dipoles from the auditory cortex). N100 is a naming convention meaning a negative deflection (in polarity) occurring around 100 ms post-stimulus. This ERP is correlated with sensory processing in the auditory cortex. In perspective to theories of consciousness, this would translate to a feedforward sweep of sensory information. An ERP that follows the N100 is the N2b, a negative deflection around 200-300 ms post-stimulus over frontocentral areas, that reflects sensitivity to change detection in perception. Finally, there is the P300, a strong positive deflection at ~300-600 ms post-stimulus occurring over a widespread frontoparietal area. A subcomponent of the P300, the P3b, is localized over parietal areas and correlates with behavioral executive control and decision making. These ERPs, and their analogs in the other senses, are central to sensory processing. They are correlated with processing a perceptual stimulus and behaviorally responding to it.

When applying the contrastive analysis method of subtracting awareness from unawareness, NCCs to perceptual stimuli have been discovered, as the contrastive analysis removes concurrent neural activity (Aru et al., 2012). In vision, the visual awareness negativity (VAN) represents the post-contrast neural activity to awareness of visual stimuli (Koivisto & Revonsuo, 2010; Eklund & Wiens, 2018). The VAN is a negative deflection ~200 ms post-stimulus concentrated over occipital areas (location of visual cortex). The VAN is often accompanied by the Late Positivity (LP): a large centro-parietal positive deflection ~300 ms post-stimulus. Similarly, contrastive analyses have discovered the auditory counterpart: the auditory awareness negativity (AAN). The AAN is similarly a negative deflection ~200 ms post-stimulus concentrated to centro-temporal areas (location of auditory cortex), and is often accompanied by a similar LP as found with VAN (Eklund & Wiens, 2019). See figures 1 and 2 for example ERPs of VAN and AAN. Note the similar polarity and interval for AAN and VAN. Lastly, similar results have been found with the sense of touch, the somatosensory awareness negativity (SAN): a negative deflection ~150 ms around parietal areas (location of motor cortex), with an accompanying LP (Auksztulewicz & Blankenburg, 2013; Dembski et al., 2021). The commonalities of the NCCs have led to a theory of a supramodal perceptual awareness negativity (PAN), stating that the sensory processing underlying consciousness may be a common mechanism even if per-

formed at different cortical locations (Dembski et al., 2021). The PAN is analogous to the N2b, and the LP is analogous to the P3b, as they share respective neural activation patterns.



*Figure 1* Example ERPs of auditory awareness at the awareness threshold, over central electrode sites (C3, C1, Cz, C2, C4, CP3, CP1, CPz, CP2, CP4, P3, P1, Pz, P2, and P4). Red line shows ERP to awareness of auditory stimulus, and blue line shows ERP to unawareness. The contrastive ERP is shown in green. Intervals for AAN and LP are marked in gray. The y-axis shows amplitude in  $\mu\text{V}$ . The x-axis shows time in seconds. Figure taken from Eklund et al. (2020).



*Figure 2* Example ERPs of visual awareness at the awareness threshold, over occipital electrode sites (O1, O2, PO3, PO4, PO7, and PO8). Red line shows ERP to awareness of visual stimulus, and blue line shows ERP to unawareness. The contrastive ERP is shown in green. The interval for VAN is shown in gray. The y-axis shows amplitude in  $\mu\text{V}$ . The x-axis shows time in seconds. Figure taken from Wiens et al. (2023).

Notably, the LP is excluded as an NCC in the theory of PAN. The LP is contentious within NCC research because it can be excluded as an NCC depending on the definition of consciousness ascribed by the scientist. Central to research into NCCs is the disambiguation of consciousness from its antecedents and successors (Aru et al., 2012; de Graaf et al., 2012). In other words, the prerequisites and consequences of consciousness. Aru et al. (2012) make the taxonomical distinction by classifying them as NCC-pr (prerequisite) and NCC-co (consequence). To give an example: When light reaches your eye, the cone cells within your eye are stimulated and send signals toward your brain to form the experience of vision. The activity in your eyes is causally necessary for the experience to occur, but your eyes are not causally necessary for consciousness to exist, otherwise closing your eyes would render you devoid of visual consciousness. In other words, if you were to close your eyes, you will still be able to imagine visual input. Your eyes are thus an NCC-pr, and must be separated from the true NCC. Conversely, after seeing an image, you may think about what the image meant to you, recalling memories to introspectively form judgment of the image. This recollection is not intrinsic to experiencing the image, it is a consequence of experiencing the image, and thus an NCC-co.

PAN can be measured to conscious activity without the corresponding LP, and these paradigms typically lack behavioral responses to stimuli (Pitts et al., 2014; Cohen et al., 2020; Schlossmacher et al., 2020). This would logically conclude that LP is consistent with behavioral response patterns and executive control, but not conscious awareness per se. According to this view, LP would be an NCC-co, a consequence of behavior given an experience. The designation of LP as an NCC-co is contentious because the definition of consciousness varies between the theories of consciousness. RPT would align with the concept of LP as an NCC-co, because it stipulates that awareness begins with recurrent processing in sensory cortices, in alignment with PAN. Conversely, GNWT stipulates that PAN is only an NCC-pr, the sensory processing that facilitates the existence of consciousness, in the form of LP as the true NCC (Pitts et al., 2018).

## 1.4 Auditory perception

Auditory perception, or hearing, is the ability to perceive disturbances (re: sounds) in the surrounding medium by detecting changes in atmospheric pressure (Middlebrooks & Green, 1991). These changes in pressure are typically caused by movement, which causes soundwaves, which cause experience of sound. When soundwaves interact with the ears, they compose auditory cues that allow localization of a sound in physical space. Sound can be perceived in three dimensions (horizontal, vertical, and depth), and likewise, be localized in these three dimensions using different auditory cues. Horizontal sound

localization can also be divided as externalized perceptions (sound perceived outside the head) using loudspeakers, and internalized perceptions (sound perceived inside the head) using headphones. This thesis focuses on horizontal sound localization (for further reading on all types of sound localization, see Carlini et al., 2024; Middlebrooks & Green, 1991; Ahveninen et al., 2014).

### 1.4.1 Horizontal Sound Localization

In acoustics, the horizontal plane is commonly referred to as the azimuth. The azimuth is equidistant; a horizontal radius, or circle, centered around the listener. The ability to localize azimuthal sounds is primarily through binaural cues, which rely on differences in the timing and intensity of sounds reaching each ear (Carlini et al., 2024; Middlebrooks & Green, 1991).

#### 1.4.1.1 Interaural Time Differences

When a soundwave reaches your head from your left side, it will first reach your left ear, before moving around your head to reach your right ear through acoustic diffraction (the property of soundwaves moving around corners). Because the soundwave reaches your left ear before your right ear, there is a small difference in time between when your ears register the sound, known as the interaural time difference (ITD). Given the speed of sound, this difference is typically on the scale of microseconds ( $\mu\text{s}$ ). These small differences are registered, and if the sound in each ear shares the same properties, they are inferred to belong to the same source (Carlini et al., 2024; Middlebrooks & Green, 1991). The sound is inferred to originate from the direction of the first stimulated ear. The difference in time also directly relates to what angular direction the sound is experienced. A smaller time difference shifts the experience to be more toward the center of the body, and a larger time difference shifts the experience outward to the side. ITDs are temporally sensitive: If the ITD were to exceed around 0.7 ms (700  $\mu\text{s}$ ) the stimuli tend to be perceived as two similar, yet distinct sounds from separate directions instead (Mills & Tobias, 1972; Carlini et al., 2024).

#### 1.4.1.2 Interaural Level Differences

As a soundwave propagates, it loses energy. The amount of energy that the wave has at any single point is expressed as the wave's amplitude, and affects the intensity of the experienced sound. The intensity is referred to as the sound pressure level (or simply *level* for short), measured in decibels (dB). Therefore, the farther a soundwave travels, the lower the level of the sound will become. The level also affects sound localization. In the example above, where the soundwave approaches your head from the left, the soundwave must travel farther to reach your right ear, also traversing the head. The head itself plays a role in sound localization, because its mass can be an obstacle to soundwaves, effectively casting an acoustic shadow over one ear. When the

sound comes from the left, the head casts a shadow over (blocking) the right ear. This acoustic shadow causes an interaural level difference (ILD). Acoustic diffraction can overcome this limitation, but it still results in noticeable ILDs, as the soundwave loses more energy from the collision with the head than from traveling the physical distance between the ears. A combination of ILD and ITD are used to infer directionality of incoming soundwaves. However, this only works in the azimuthal plane, because the ears are in horizontal separation on the head.

### 1.4.1.3 Effect of Frequency

A feature of wave mechanics is frequency: the rate of oscillation measured in Hertz (Hz), or oscillations per second. Different sounds have different frequencies, affecting their pitch (higher frequencies sound shrill, and lower frequencies sound dull). As the soundwave frequency denotes the oscillations per second, lower frequencies have longer intervals between reaching their crests and troughs. The speed of sound in air (at 20 °C) is ~343 m/s. Assuming that the average head is ~20 cm wide from ear to ear, it follows that sound can travel through 1715 adjacent heads per second, or conversely, that a soundwave at 1715 Hz will collide once with each of the 1715 heads along its path. Halving the frequency, to ~857 Hz would have the soundwave collide with every second head, but miss the others due to oscillations around the heads. The fact that soundwaves at lower frequencies (< 1 kHz) have oscillatory crests and troughs that are larger than a human head means that they may sometimes not collide with the head, and thus avoid the acoustic shadow of the head. When the acoustic shadow is avoided, there is no collision with the head, and thus no tangible loss of energy to cause a meaningful ILD. In this case, ILD loses explanatory power for sound localization, because there is no information to extract (Carlini et al., 2024; Middlebrooks & Green, 1991). For these lower frequency sounds, when the sound is unobstructed by the head, extracted ITDs are prioritized for localization cues.

In the opposite direction, when frequency is high, there is difficulty matching the ITD between the ears (Carlini et al., 2024; Middlebrooks & Green, 1991). This difficulty happens because the quick oscillations (or phases) of higher frequencies are too fast to parse and subsequently match together to calculate the time difference. However, these higher frequencies are adequately blocked by the acoustic shadow, amplifying their ILD. Processing of ILDs is prioritized as localization cues for higher frequency sounds (> 3 kHz). In the span between 1-3 kHz, both localization cues are processed.

As a soundwave oscillates, a pattern can be traced along its crests and troughs. This pattern is called the wave's envelope. The envelope oscillates based on the soundwave's amplitude, creating a slower waveform in tandem with changing amplitudes. Even at high-frequency sounds, the envelope may carry information that can be extracted as ITDs, as the envelope itself acts as a lower frequency soundwave (Bernstein & Trahiotis, 1985).

The exact quantities of ILD and ITD can be present along two opposing points along the azimuthal axis, such as  $45^\circ$  to the left both in front of a listener and to their back, as these two spots are the same distance from the ears. Because of this ambiguity, alternative cues such as from the pinnae must be used to infer if a sound is localized to the front or back of a listener (Carlini et al., 2024; Middlebrooks & Green, 1991).

### 1.4.2 Internalized Sound Localization

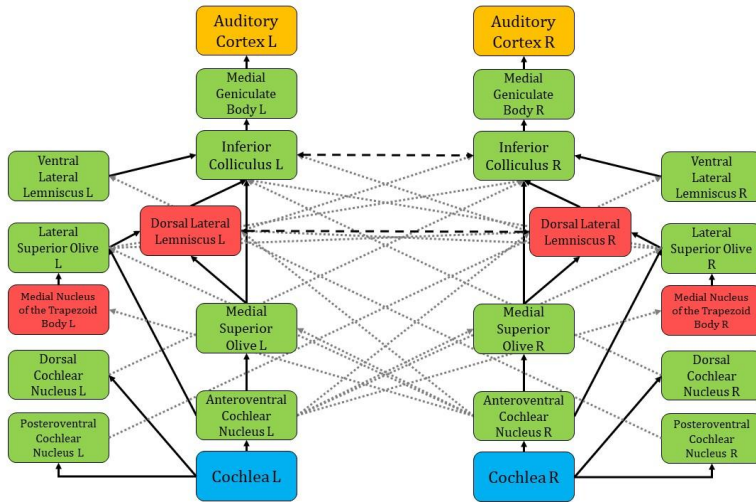
When sound is experienced within the head from headphones, the ability to discriminate from leftward and rightward sounds is often called sound lateralization ability, compared to sound localization ability when sound is presented externally to the head. It is possible to recreate simulated sound localization cues using static emitters such as headphones. Using stereophonic headphones, it is possible to manipulate ILD and ITD with great precision, by programming discrepancies in time or level in the outputs presented to the left and right ear. This simulated reality is meant to mimic naturalistic sound cues to trick the auditory system into experiencing these different qualities of sound. Sounds from headphones are experienced as originating within the head, with e.g. sounds heard from the left perceptually experienced to the left along an internal axis (Middlebrooks & Green, 1991). This intracranial axis only extends to various lateral degrees along the inside of the head, and does not localize any distal sound outside the head, meaning that this function is known as sound lateralization, as the sound can only be experienced as lateralizing more or less toward the left and right ear.

Normally, ILDs are not useful for sound localization at low frequencies due to the lack of acoustic shadow of the head (see example in section 1.4.1.3.). However, when using headphones, the binaural sound is presented directly to each ear, completely bypassing the shadowing effect of the head, giving the ability to process ILDs as sound lateralization cues even at low frequencies.

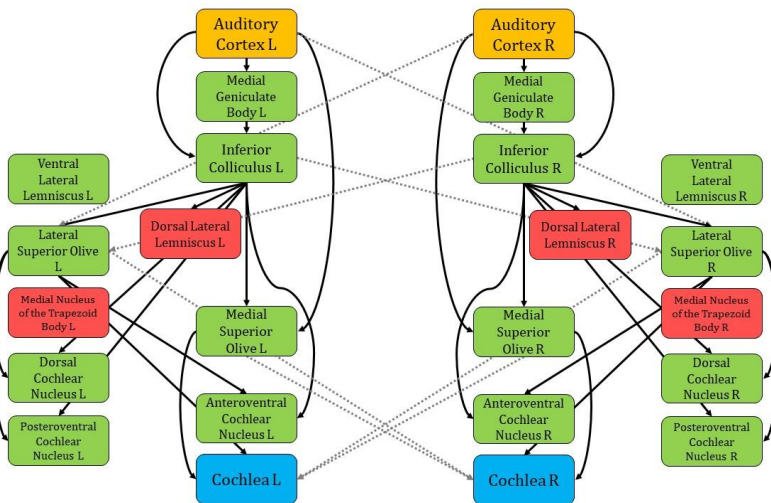
### 1.4.3 Neural Auditory Pathway

The neural pathway from ear to conscious experience is not yet fully understood (Dietz et al., 2018; Middlebrooks, 2021). Much of the current knowledge is learned from non-human mammalian brains, and results from studies on human brains are not always consistent (Pickles, 2015). The full auditory pathway is a complex web of interconnected neural structures from ear, to brain stem, to midbrain, to auditory cortex. The auditory pathway is reciprocal and also feeds information downward from the auditory cortex, in alignment with recurrent processing and predictive coding (Heilbron & Chait, 2018). EEG data suggest that the most likely main generator of the AAN is the auditory cortex (Eklund et al., 2020), so in the interest of space, only the

auditory cortex will be covered in detail. The full auditory pathway(s) is depicted in figures 3 and 4 (for exhaustive reviews see: Pickles, 2015; Dietz et al., 2018).



*Figure 3* Schematic of the ascending auditory pathway. Nodes ending with L indicate structures in the left hemisphere, and R indicate the right hemisphere. The pathway begins at the cochlea (blue) and ends at the auditory cortex (yellow). Green nodes are excitatory pathways, and red nodes are inhibitory. Bold arrows are ipsilateral connections, and dotted arrows are contralateral connections. The dashed arrows are bilateral connections. Note the multiple levels of bifurcation and decussation in the pathway.



*Figure 4* Schematic of the descending auditory pathway. Nodes are the same as figure 3. The descending pathway begins at the auditory cortex and ends at the cochlea. Bold arrows are ipsilateral connections, and dotted arrows contralateral connections.



### 1.4.3.1 Auditory Cortex

The auditory cortex is the final destination of the ascending (afferent) auditory pathway. The auditory cortex is situated in the temporal lobe of the cerebral cortex, specifically in the superior temporal gyrus of the lateral sulcus (Pickles, 2015). The auditory cortex is divided into several areas, which differ between species. For primates (homologous to humans), the core areas of the auditory cortex are: the primary auditory area (A1), the rostral cortical field (R), and the rostrotemporal cortical field. Each core area is highly tonotopically organized, and reciprocally connected. The core areas receive direct input from the ventral medial geniculate body of the thalamus, which projects qualities of sound. The core areas are surrounded by the belt areas, which in turn are surrounded by the parabelt. The belt areas receive input from the medial and dorsal divisions of the medial geniculate body, which project cross-modal information, and also heavy input from the core areas of the auditory cortex. The parabelt only connects to the belt areas, as well as connections to the frontal lobes of the cerebral cortex.

The cortical surfaces of the core areas are tonotopically organized, where strips along the cortical surface are activated in response to different frequency bands. The three core areas are functionally divided by the reversal of tonotopic organization within (e.g., A1 may map frequencies ascendingly: from anteriorly low to posteriorly high, and upon reaching the neighboring R, the mapping switches to descend from anteriorly high to posteriorly low). Thus, although there are three core areas, they all map tonotopically. In the core areas, different cells are found to react to monaural sounds from binaural sounds, suggesting highly specific interpretation of the auditory soundscape. The multiple parts of the auditory cortex are necessary to consciously process complex sounds, including frequency shifts and temporal shifts present in stimuli such as speech.

Moreover, the auditory cortex is important for sound localization ability. Early lesion studies on animals showed unilateral lesions interfering with localizing sound in the contralateral hemifield, suggesting a contralateral processing in sound localization (Pickles, 2015). However, this effect has been unclear in human lesion studies: Lesions to the left auditory cortex caused deficits to localizing sounds in the contralateral hemifield, while lesions to the right auditory cortex caused deeper deficits to sound localization in both hemifields, suggesting a more integrative role of sound localization ability in the right auditory cortex (Spierer et al., 2009). The cortical processing of binaural localization cues in humans are unclear, but in macaques the A1 and the caudolateral belt area most strongly signal sound localization (Miller & Recanzone, 2009).

The auditory pathway is reciprocal and also feeds information downward from the auditory cortex (Pickles, 2015). The descending (efferent) pathway does not take the exact same path as the ascending pathway (see figure 2). The

auditory cortex has strong projecting connections to the medial geniculate body and inferior colliculus. These connections are found to modulate representations of sound from the lower areas, effectively enhancing aspects of stimuli that are of interest, which are then fed back up to the auditory cortex. The inferior colliculus projects down to the superior olivary complex and the cochlear nucleus, where the mechanistic processing of sound features can be inhibited or otherwise modulated as directed by higher areas in the auditory pathway.

#### 1.4.4 Neural Correlates of Sound Localization

The auditory system is seemingly unique in its processing speed; it is able to process ITDs on a scale of microseconds, an order of magnitude faster than other senses. It remains unclear how the brain actually manages this phenomenon, although cross-correlation models of matching neurons between ears have been suggested (Pickles, 2015; Ahveninen et al., 2014; Dietz et al., 2018). ERPs can track neural correlates along the auditory pathway, from auditory brainstem responses to thalamic mid-latency responses, to late-latency responses in the auditory cortex. ILDs and ITDs appear to ultimately be processed in the auditory cortices, as measured by experiments that manipulate them, but the exact model or pathway as to how, when, or where they are combined into a single perceptual localization cue is still not understood (Palomäki et al., 2005; Woldorff et al., 1999; Ahveninen et al., 2014; Middlebrooks, 2021). Early areas in the ventral auditory pathway that process ILDs and ITDs, such as the superior olivary complex (where ILDs and ITDs from each ear are combined), and the inferior colliculus (where all sound properties are combined), have an identified function (Pickles, 2015), but not their degree of contribution toward an integrated conscious percept. As such, the auditory cortex remains the prime candidate for discovering the NCC of auditory consciousness.

Other senses, mainly vision and touch, follow a topological mapping. For example, the visual field directly maps onto the visual cortex. Vision and touch are both afferently wired contralaterally, meaning that their sensory input is processed by the contralateral cerebral hemisphere (Koivistio & Grassini, 2016; Eklund & Wiens, 2018; Aukstulewicz & Blankenburg, 2013). In contrast, the afferent auditory system bifurcates and decussates at multiple junctions both ipsilaterally and contralaterally, meaning signals from each ear reach both cerebral hemispheres (as seen in figure 3; Pickles, 2015).

Hearing operates with a contralateral bias to lateral stimuli (Ahveninen et al., 2014; Gutschalk & Steinmann, 2015). This means that hearing a sound to the left will more strongly activate the right auditory cortex. However, the auditory cortices also specialize in certain functions, such as the left auditory cortex being more involved in complex pitch processing (such as language), while the right auditory cortex is more involved in slow modulatory changes

in sound (such as musical melodies). This results in an added level of unilateral processing that adds on top of sound localization mapping, and the specific quality of a sound that is being localized will change the neural activity in processing it (Sininger & Bhatara, 2012; Ahveninen et al., 2014). On top of this, there is an activation in the right auditory cortex that appears specific to spatial localization of sounds regardless of the stimulus location (Palomäki et al., 2005; Pickles, 2015). Regardless of function in the auditory pathway, it thus remains unclear what degree of the signal is processed contralaterally, ipsilaterally, or bilaterally.

The current understanding of how sound localization processing in auditory cortex works is by broadly-tuned populations of neurons in each cerebral hemisphere (Middlebrooks, 2021; Dietz et al., 2018; Ahveninen et al., 2014; Woldorff et al., 1999). These neurons fire excitatory signals in response to sounds in the contralateral hemispace, and fire inhibitory signals in response to sounds in the ipsilateral hemispace. This results in a net contralateral excitatory effect, but it is unclear if this neural processing is due to dominance of the excitatory or inhibitory signals.

#### **1.4.4.1 Neural Correlates of Auditory Attention**

Gamble & Luck (2011) studied lateralized attentional effects in hearing. They discovered an ERP to attending toward a lateralized percept in concurrent noise. This ERP was an anterocentrally located negativity at ~200 ms, and named the N2ac. Moreover, Gamble & Luck (2011) found that the N2ac was often followed by a lateralizing P300-wave. This ERP would lateralize contralaterally to the attended location, and was named the late positive component (LPC). The LPC was theorized to be a reorientation effect post-stimulus. Specifically, they found that before participants were told which of two locations they would need to attend to on a trial, they would direct their attention to the mid-point between the two locations. After attending to e.g., the left location to hear a sound, the listener will prepare for the next sound, and need to effectively reset the position of their attention toward the middle of possible locations. This reorientation of attention back toward the baseline is theorized to reflect the LPC.

Upon further studies into the N2ac and LPC, Lewald et al. (2016) examined effects of attention with concurrent distractors from multiple locations, using a free-field sound environment with loudspeakers. They also found the N2ac and corresponding LPC, and coined the posterior-contralateral late positive component (LPCpc). This new effect was similar to the LPC, but attributes specifically to the contralateral effect of spatial reorientation of attention, whereas the LPC has multiple hypothesized functions, due to overlapping areas with the P3b (Lewald et al., 2016).

## 2 Methods

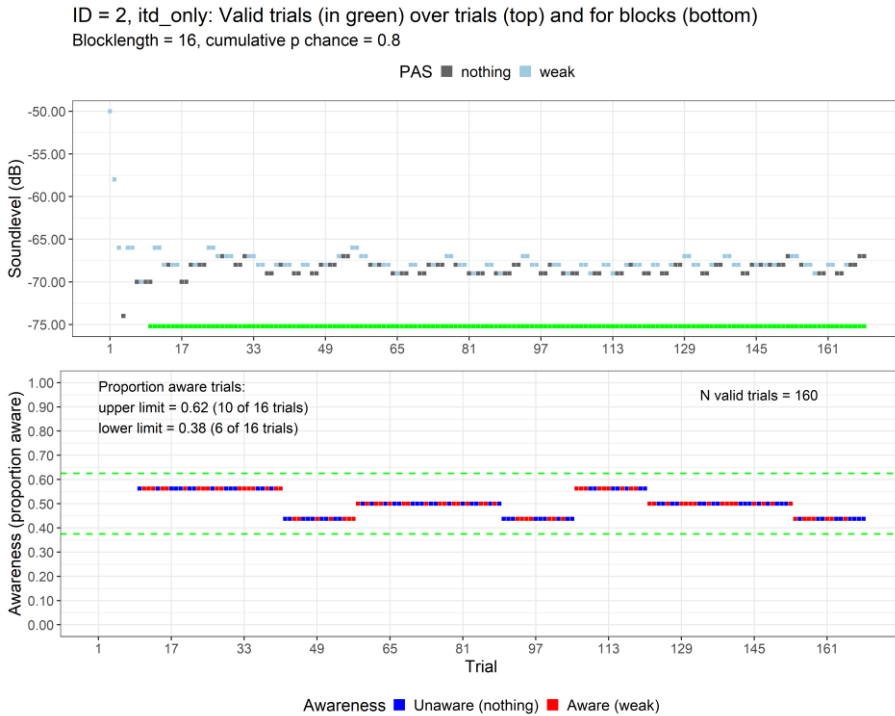
The NCCs have a good candidate in the perceptual awareness negativity (PAN), which is theorized to reflect processes of awareness within respective sensory cortices (Dembski et al., 2021). Because vision and touch have found lateral conscious experience to accurately map onto these NCCs contralaterally, the AAN should prospectively follow suit. However, as hearing has a more complicated pathway that is comparatively poorly understood, this notion may be premature. The aim of this thesis was to investigate the AAN in response to lateral auditory stimuli. Hypothetically, the AAN either mirrors the supramodal function of PAN with clear contralateral effects, or the AAN follows more convoluted localization features of the auditory pathway. The thesis aimed to study these phenomena using experimental paradigms conventionally suited for study of NCCs, namely contrastive analyses of ERPs using EEG. The following subsections describe methods common to all studies contained in the thesis.

### 2.1 Experimental Methods

The thesis consists of three studies, each testing an experiment with psychophysical tasks. All experiments were programmed and run using PsychoPy 3.0 (Peirce et al., 2019). EEG data were recorded using a 64-channel BioSemi ActiveTwo EEG system (BioSemi, Amsterdam, Netherlands), and ERPs were time-locked to stimulus presentation. Experiments were conducted in sound-dampened laboratories at Stockholm University campuses, with either in-ear headphones or loudspeakers. The samples of each experiment comprised between 26-40 test subjects, drawn from a population of healthy adults, aged 18-43. Each subject completed hundreds of trials per experiment. See each individual study for details.

The auditory stimuli were presented at threshold level for contrastive analysis. To calibrate threshold-level stimuli for the experiments, psychophysical staircasing procedures were used (Kingdom & Prins, 2016). A staircase method entails playing a stimulus to a subject at a set level, and given the subject's response, the stimulus level is either increased (if the subject did not hear it), or decreased (if the subject did hear it). This way, the stimulus level will home in toward the subject's hearing threshold. A staircase from a typical

subject can be seen in figure 5. Note the stabilizing hearing threshold (at around  $-68$  dB). Each study in the thesis used differing staircasing methods, see each study for details.



*Figure 5* Visualization of staircasing data from a single subject in Study 3 (ID = 2, condition = ITD-only). **Top:** Each dot shows a trial, with the stimulus level (dB) on the y-axis, and trial number on the x-axis. Light-blue dots indicate a weak awareness to the stimulus, and dark-blue indicate no awareness to the stimulus. Each reversal halves the preceding step size, until it reaches  $\pm 1$  dB. The first reversal is a 1 up/1 down staircase, after which it becomes a 2 up/2 down staircase (i.e., two identical responses in a row are required to change the stimulus level). The solid green line shows acceptable blocks according to rule from the bottom figure. **Bottom:** Counting backwards, trials are binned into blocks of sixteen. Each block is inspected for ratio of trials rated as aware (red) and unaware (blue). The y-axis shows the total proportion of trials rated as aware within each block. The x-axis shows trial numbers (matching the top figure). The green dotted lines show acceptable limits of proportion of awareness for inclusion into the analysis model.

## 2.2 Analysis Methods

After collection, EEG data were processed and filtered using MNE-python (Gramfort et al., 2014; Gramfort, 2013). The statistical analyses were then computed using either Bayesian t-tests (Study 1), or Bayesian mixed effects regression modeling (Study 2 & 3). The statistical analyses were conducted using R Statistical Software (R Core Team, 2021), using Aladins Bayes Factor in R for Bayesian t-tests (Wiens, 2017), and brms for Bayesian mixed effects regression modeling (Bürkner, 2017, 2018).

The thesis used Bayesian indices to quantify evidence with regard to presence or absence of laterality of the AAN. Bayesian analyses compute the likelihood of an effect given the observed data and prior belief, and provide this likelihood as a distribution of posterior beliefs (Makowski et al., 2019). The prior belief can be informed by earlier theory, providing differing biases (or weights) toward the posterior distribution, as the likelihood distribution shifts upon adding more evidence. Conversely, the prior can be uninformed, providing an unbiased distribution for the data to inform the posterior distribution.

The Bayesian approach to statistical inference provides quantifiable evidence of the alternative and the null hypothesis (Makowski et al., 2019). In hypothesis-testing, Bayes factors (BF) compare different models, and provide evidence for or against a given model. The BF is a continuous measure of relative evidence for one model in comparison to another (Tendeiro et al., 2024; Dienes, 2016; Wagenmakers et al., 2016; Wiens & Nilsson, 2017). A common interpretation scheme states that  $1 < BF < 3$  is regarded as anecdotal evidence, and recommends a minimum of  $3 < BF < 10$  to be regarded as moderate evidence for a given model compared to its competing model, although a higher number ( $> 10$ ) provides more evidence (Wagenmakers et al., 2018).

Beside BFs, Bayesian indices of 95% credible intervals (CIs) and probability of direction (pd) were examined (Makowski et al., 2019). CIs provide a reasonable range for the true parameter value. The pd is a hypothesis-testing index that is computed as the proportion of the posterior distribution that crosses zero on the side that contains the median. If  $pd = 0.95$ , then 95% of the posterior distribution does not cross zero, suggesting a non-zero effect in the direction of side that contains the median.

## 2.3 Ethics Statement

All experiments contained herein adhere to the ethical principles outlined in the Declaration of Helsinki. Ethical review and approval were not required for studying human subjects in accordance with local law and institutional requirements, as we did not collect personal or biological data that can be traced back to the subject. Study 3 was part of a larger project that was ethically reviewed and approved by the Swedish Ethical Review Authority (2022-

06409-01). All test subjects provided written consent before participation, agreeing that their raw data were to be shared as open data in anonymized form. See each individual paper in the appendix for more details on each study.

## 2.4 Open Science Practices

Science should be transparent in its practices and open to the public (Munafò et al., 2017). All research conducted as part of this thesis follows open science practices to the extent possible. All studies contained herein have been preregistered at the Open Science Framework (<https://osf.io>), meaning that the hypotheses, methodology, and analysis pipelines were constructed in advance of testing. Preregistration as a practice reduces researcher degrees of freedom, indicating that the researcher cannot pick and choose analyses and hypotheses after seeing their data to best fit their narrative (Nosek et al., 2018). The studies in this thesis are also freely accessible online, and all data with respective analysis scripts are freely available at public online repositories (see the individual publications for links to data repositories and preregistrations).

# 3 Thesis: Neural Correlates of Consciousness in Sound Localization

The following subsections summarize the findings of the studies that comprise the thesis. For full details, see each paper in the appendix.

## 3.1 Study 1: Lateralization of AAN with Headphones

Previous research into the AAN found its properties and its similarities to other NCCs, such as the VAN (Eklund & Wiens, 2019; Eklund et al., 2019; Eklund et al., 2020). The VAN and its somatosensory counterpart, the SAN, were found to be spatially topographically organized contralaterally, meaning that NCCs to lateralized experiences are observed in the sensory cortex of the contralateral cerebral hemisphere (Koivisto & Grassini, 2016; Auksztulewicz & Blankenburg, 2013). Notably, the contralateral effects were unique to the early awareness negativity, and did not appear for the later LP.

Because existence of the AAN had not been tested for lateralized processing or sound localization features, a research design was constructed to test whether lateralized sounds played via headphones would elicit lateralized AAN and whether the corresponding LP would be lateralized or not. The hypotheses were: 1) AAN is elicited to awareness of sound and is lateralized, and 2) LP is elicited to awareness of sound, but is not lateralized.

### 3.1.1 Method

The preregistered study design was composed of a stimulus played via in-ear headphones specifically designed for audiological research (ER2; Etymotic Research Inc., IL; [www.etymotic.com](http://www.etymotic.com)). The stimulus played was a simulated sound based on multiple recordings of click-noises made by an expert echolocator, chosen for its naturalistic sound and broadband frequency properties. The stimulus was dominated by higher frequencies at 3-7 kHz (recording provided by Thaler et al., 2017). A broadband sound covers a wide range of frequencies, and due to the auditory cortex' tonotopic organization, a broadband sound will activate multiple areas of the cortex simultaneously. Broadband signals, as compared to narrowband signals, allows for better lateralization of sound due to utilizing both ILDs and ITDs, and a larger activation will



in turn produce a larger electrical field potential, making the ERP more accentuated.

The monaural click was then transformed into a binaural click, and manipulated to produce an ILD of 8 dB and an ITD of 0.25 ms. These values were chosen to produce a naturalistic combination of both ILD and ITD, as expected in a free-field sound environment. The ILD and ITD were flipped along channels to provide lateralization toward the opposite ear. The experience of the sound varied individually, but was clearly lateralized to the left and right according to pilot testing at threshold level of awareness.

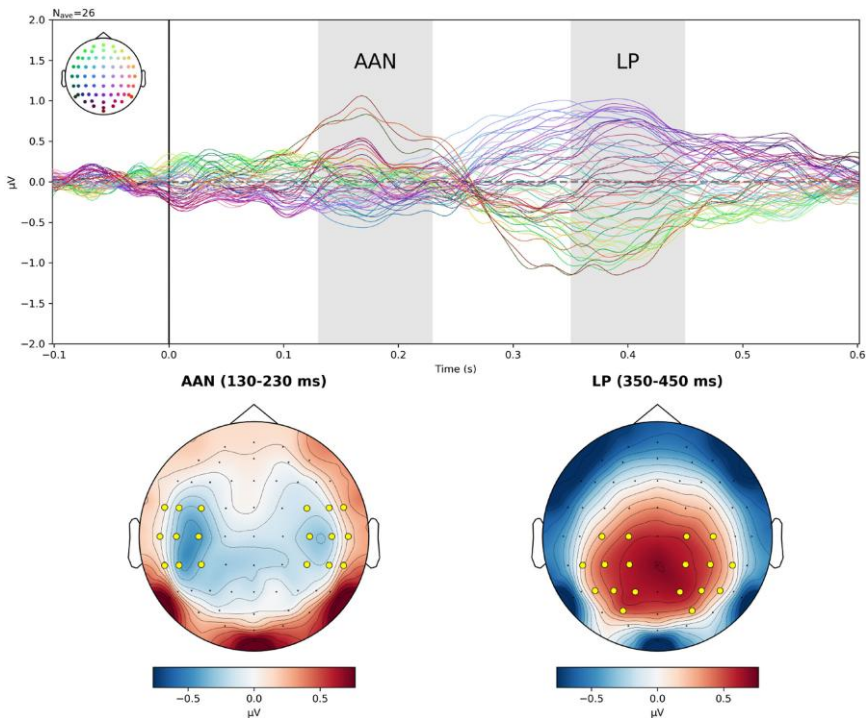
The study sample consisted of 26 test subjects. They performed a task where they were asked to listen for a total of 720 clicks each, lateralized randomly to the left or right. After playing a click, they were prompted for information first regarding what direction they heard the click from (leftward or rightward), then what experience they had of the click, using a modified version of PAS with three possible choices (“heard nothing”, “heard something weakly”, “heard something clearly”). If the subject responded that they heard the stimulus, the proceeding stimulus was presented at a lower level. Conversely, if the subject responded that they did not hear the stimulus, the proceeding stimulus was presented at a higher level. This pattern would repeat until a stable individual threshold of perception was achieved, where the stimulus is experienced roughly half of the time, allowing for contrastive analysis between awareness and unawareness of the stimulus. The specific staircase procedure used in the study was a 1 up/1 down staircase (Kingdom & Prins, 2016), with decreasing reversal steps at 8, 8, 4, 4, 2, and 2 dB for the first six reversals and 1 dB for subsequent reversals.

During the experiment, 64-channel EEG was recorded using the standard international 10-20 system (Luck, 2014). EEG data were recorded from all channels with an additional reference electrode on the nose, and put through a 30-Hz low-pass filter. Specific channels and intervals were picked to construct ERPs of AAN and LP, on the basis of previous research (Eklund et al., 2020). However, upon analysis, a drift was discovered from the reference electrode (nose). Upon realization, the experiment deviated from preregistration: Data were reprocessed with an average-referencing of all 64 channels, and intervals and electrode sites of interest were slightly adjusted. For AAN, the new interval was between 130 and 230 ms; left electrodes were CP3, CP5, TP7, C3, C5, T7, FC3, FC5, and FT7; and right electrodes were CP4, CP6, TP8, C4, C6, T8, FC4, FC6, and FT8. For LP, the new interval was between 350 and 450 ms; left electrodes were C1, C3, PO3, P1, P3, P5, CP1, CP3, and CP5; and right electrodes were C2, C4, PO4, P2, P4, P6, CP2, CP4, and CP6. These electrodes and intervals, along with the contrastive ERP from all channels (the grand mean average) can be seen in figure 6.

For each stimulus side, difference waves were calculated from correctly lateralized trials rated as aware, minus correctly and incorrectly lateralized trials rated as unaware. From these difference waves, ERPs were extracted

based on a division of click lateralization and cerebral hemisphere. In other words, there were four possible ERPs of interest: 1) “left click & left hemisphere”, 2) “left click & right hemisphere”, 3) “right click & left hemisphere”, 4) “right click & right hemisphere.” These were later pooled into ipsilateral and contralateral ERPs. “Left click & left hemisphere”, and “right click & right hemisphere” were categorized as ipsilateral ERPs. “Left click & right hemisphere”, and “right click & left hemisphere” were categorized as contralateral ERPs. Finally, the mean between both contralateral ERPs was computed, along with the mean between both ipsilateral ERPs.

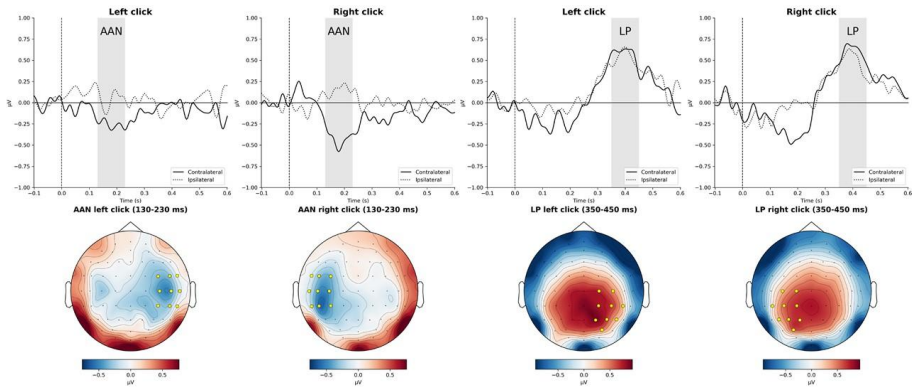
To calculate any contralateral effect, the mean ipsilateral ERP was subtracted from the mean contralateral ERP in their respective interval. In this experiment, the Bayesian null hypothesis was no lateralization of the ERP, and the Bayesian alternative hypothesis was a lateralization of the ERP. The data were analyzed using Bayesian one-sample t-tests with an uninformed prior (uniform distribution from  $-1 \mu\text{V}$  to  $+1 \mu\text{V}$ ).



**Figure 6 Top:** Butterfly plot of the grand mean ( $N = 26$ ) difference wave between aware trials and unaware trials across left and right clicks. Auditory awareness negativity (AAN) was measured between 130 and 230 ms post-stimulus, and late positivity (LP) was measured between 350 and 450 ms post-stimulus. These intervals are marked in gray. **Bottom:** Topographies of mean amplitudes for AAN and LP across left and right clicks. See text for chosen electrode sites (marked here in yellow). The data were average referenced. In the plots, the data were low-pass filtered at 30 Hz.

### 3.1.2 Results

The study found  $BF_{10} = 268$  for a lateral effect of AAN, suggesting extreme evidence that the data were much more compatible with the notion of AAN being lateralized, compared to not being lateralized at all. For LP,  $BF_{10} = 0.3$ , or conversely,  $BF_{01} = 3.33$ , suggesting moderate evidence that the data were more compatible with the absence of lateralization of LP than with a lateralization. The AAN and LP divided by hemisphere and sound source are illustrated in figure 7 (note the differing blue spots of the topology of AAN to lateralized clicks, compared to the widespread red area of the LP).



**Figure 7 Left Top:** Grand mean ( $N = 26$ ) difference waves between aware (correct) trials and unaware (correct and incorrect) trials for electrodes relevant for auditory awareness negativity (AAN), separately for each click side and electrode laterality. AAN was measured between 130 and 230 ms post-stimulus. These intervals are marked in gray. **Left Bottom:** Topographies of mean amplitudes for AAN, separately for left and right clicks (contralateral electrodes are marked in yellow). **Right Top:** Grand mean ( $N = 26$ ) difference waves between aware (correct) trials and unaware (correct and incorrect) trials for electrodes relevant for late positivity (LP), separately for each click side and electrode laterality. LP was measured between 350 and 450 ms post-stimulus. These intervals are marked in gray. **Right Bottom:** Topographies of mean amplitudes for LP, separately for left and right clicks (contralateral electrodes are marked in yellow). The data were average referenced. In the plots, the data were low-pass filtered at 30 Hz.

### 3.1.3 Discussion

The study provided evidence for lateralization of AAN, but not the LP. This finding agrees with theories of consciousness proposing that awareness is generated at recurrent processing in sensory areas, such as RPT (Lamme, 2006).

The fact that the AAN changed in response to differently lateralized stimuli suggests that processes related to awareness follow veridical differences in stimuli. The finding that LP does not change suggests that LP is not contingent on becoming aware of differing stimuli, instead relating to post-perceptual processing of awareness (an NCC-co). The findings also strengthened the notion that a supramodal general perceptual awareness negativity (PAN) exists, because the AAN followed the same pattern as VAN and SAN. Shortly after publication of this study, Dembski et al. (2021) published their theory on PAN, directly citing this study as contributory evidence of the PAN.

However, this study was limited in scope, only comparing two angular sound sources, and headphones to deliver stimuli, resulting in sound lateralization, not localization. The AAN was thus only tested dichotomously, over artificially manipulated sound.

## 3.2 Study 2: Lateralization of AAN with Loudspeakers

With the success of Study 1, Study 2 aimed to push the boundaries of the lateralization of AAN in several aspects. First, the study employed a free-field sound environment by using physical loudspeakers in a sound-proofed laboratory. Secondly, the study used 13 different stimulus locations for sound localization (13 loudspeakers). The main purpose of the study was to investigate the nuances of AAN: No earlier study on AAN had been conducted with the use of loudspeakers, and the extent of lateralization patterns of AAN beyond Study 1 were unknown.

The primary hypotheses of the study were that: AAN, but not LP, is lateralized as a function of azimuthal sound source (loudspeaker location). Accordingly, in the AAN-relevant time frame, a left sound location was predicted to be associated with larger negative amplitudes over right than left electrodes (and vice versa). Secondary hypotheses were that AAN and LP would be present overall at the central (non-lateralized) sound source. The second hypothesis was necessary as a manipulation check, as AAN had yet to be tested using free-field sound (re: loudspeakers).

### 3.2.1 Method

The experiment was conducted in a sound-proofed laboratory using a custom-built rig to house multiple loudspeakers for surround sound. The 13 loudspeakers were positioned at ear-level height, 150 cm away from the listener, and oriented in a 180° semicircular array in front of the listener, equidistantly separated by 15°. The subject was placed in a chair with a chin rest to affix head position toward the central loudspeaker, and was provided with a wire-

less mouse to respond to the task on a computer screen below the loudspeakers. The subject was connected to EEG during testing, applying the same electrode placement as in Study 1.

The stimulus used in the experiment was changed from the recorded mouth-click to an artificial computer generated 4 ms square pulse. The change in stimulus was to create a minimalistic sound that still perceptively sounded like a click. The reason for change of stimulus was twofold: First, to have a fully neutral stimulus (not created by a person) that would not bias listeners. Second, to test whether the AAN still occurs under a new stimulus. The study sample was composed of 37 subjects, who were instructed to perform a threshold task similar to that of Study 1: Stimuli would be played from randomized loudspeakers, and the subject was prompted for their experience of the stimulus, and their perceived location of the stimulus.

To calibrate a baseline for the threshold paradigm, a short calibration period was used: When a subject reported hearing a sound (or not), the proceeding sound would be lower (or higher) in level, regardless of loudspeaker, until a threshold of ~50% experience was achieved, using an identical staircasing procedure as described in Study 1. During the actual experiment, each loudspeaker position would vary in level by increments of  $\pm 1$  dB if the subject reported hearing the sound or not. This adaptive roving staircase was used as it confers several benefits (Wiens et al., 2023). First, the procedure should avoid miscalibrations. Second, it should avoid unequal proportions of aware and unaware trials for each subject. Third, it allows for change of awareness threshold during testing, in case of subject fatigue or faltering attentiveness.

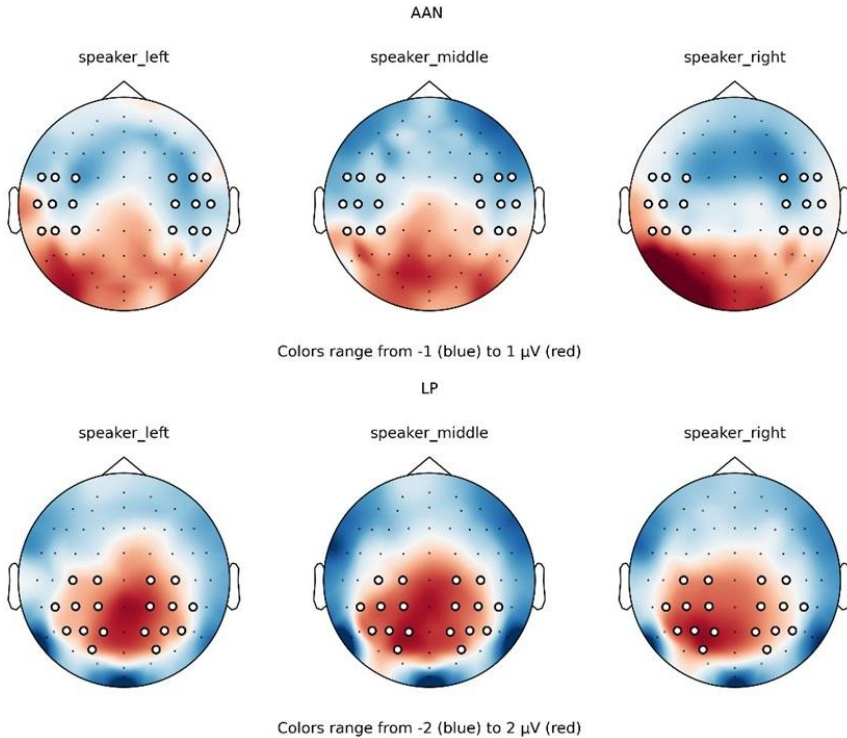
Each subject completed 780 trials, distributed as 60 trials per loudspeaker location, and consequently ~30 aware and unaware trials per loudspeaker location for the purpose of contrastive analysis. The ~30 contrastive trials per condition are far fewer than the ~180 of Study 1. However, time constraints and concerns regarding subject fatigue limited the number of trials.

The electrode sites and intervals of interest for AAN and LP were the same as in Study 1. Due to the multilevel design of the study, Bayesian linear mixed effects regression modeling was used for analysis (Alday & van Paridon, 2021; Brown, 2021; Franke & Roettger, 2019; Makowski et al., 2019; Winter, 2019). This regression modeling allows for detection of statistical trends with consideration of effects within and across participants. The regression model contained awareness, loudspeaker position, and sound level as predictors. Evidence for lateralization effects was determined by the BF related to the interaction of all predictors. The prior distribution was modeled as a normal distribution ( $\mu = 0$ ,  $\sigma = 2$ ). Beside BF, Bayesian 95% CIs and pd were examined. See the paper for full regression formulae.

### 3.2.2 Results

Initial analyses showed very strong evidence that AAN was not lateralized as a function of sound source ( $BF_{01} = 68$ ), and strong evidence that LP instead was lateralized as a function of sound source ( $BF_{10} = 23$ ). These results were the complete opposite of the first hypothesis. For the second hypothesis, there was moderate evidence against AAN to the central loudspeaker ( $BF_{01} = 6.7$ ), and extreme evidence of LP ( $BF_{10} = 859$ ). Concerns were raised regarding data quantity, as different ERP effects measured via EEG have different signal strength (Luck, 2014). The LP for example, is a widely distributed activity all across the parietal area of the scalp, which makes LP a naturally strong ERP. The AAN is a smaller ERP than the LP, and the suggested generators of AAN are deeper in the brain, as the auditory cortex is folded on the superior surface of the temporal lobe by the lateral sulcus (for source localization of AAN, see Eklund et al., 2020). This makes the AAN more difficult to detect via EEG. The measurement of  $\sim 30$  contrastive trials per loudspeaker did not capture any evidence of the AAN (compare to the  $\sim 180$  contrastive trials per stimulus in Study 1). To further check for any evidence of AAN, the pd was examined (Makowski et al., 2019). The pd = 0.91 showed that AAN was present with 91% of the posterior distribution in the predicted direction.

An exploratory analysis served to aggregate data from loudspeaker positions into bigger groups. The three leftmost loudspeakers were combined into an aggregate left, the three rightmost loudspeakers were combined into an aggregate right, and the three central loudspeakers were combined into an aggregate center. From this procedure, each aggregated loudspeaker now had  $\sim 90$  contrastive trials. These three aggregate loudspeakers were used for the exploratory analysis. In the exploratory analysis, AAN was detected with moderate evidence as an overall effect at the central aggregate loudspeaker ( $BF_{10} = 3.7$ ), and LP was detected with very strong evidence ( $BF_{10} = 75$ ). For lateralization hypotheses, there was still strong evidence against lateralization of AAN to loudspeaker location ( $BF_{01} = 10$ ), and extreme evidence of a lateralized LP to loudspeaker location ( $BF_{10} = 123$ ). Topographical results from the exploratory analyses can be seen in figure 8.



*Figure 8* Topographic maps of the exploratory results of Study 2. **Top row:** Topographies for AAN. **Bottom row:** Topographies for LP. **Left Column:** The left aggregate loudspeaker. **Middle column:** The middle aggregate loudspeaker. **Right column:** The right aggregate loudspeaker. Measured electrodes are marked with white dots. Note the difference in scale between top and bottom rows.

### 3.2.3 Discussion

Study 2 found no lateralized AAN, but did find a contralateral LP, to lateral sound from loudspeakers. The results were contrary to expectations based on results from Study 1. For the opposing results from Study 1, the notion that AAN does not lateralize, yet LP does lateralize in response to lateralized stimuli, disagrees with the supramodal mechanism of lateral experiences, suggested by PAN. Alternatively, Study 2 may have measured a different process than Study 1. In Study 2, the free-field sound localization has a natural ILD and ITD to the stimulus. In Study 1, the stereo channels of the headphones manipulated ILD and ITD to create lateralized percepts. Manipulation of the ILD caused the signal in the weaker ear to be 8 dB below the signal in the other ear. Using a threshold-level paradigm, this means that the weaker ear would in fact be 8 dB below the empirical detection threshold (re: hearing threshold) of the listener. When this happens, the binaural signal may be heard, and thus processed, by only one ear. Monaural processing in the brain

has been found to be different from binaural processing (from both ears), specifically by strong activation in the contralateral auditory cortex (Ahveninen et al., 2014; Gutschalk & Steinmann, 2015). Thus, the results of Study 1 may indeed be a measure of monaural hearing, and not binaural lateralization, as was previously assumed. Study 1 also manipulated ITD, but if the listener cannot hear a signal in both ears, there is no second channel to extract a time difference from, meaning there were no binaural cues (ILD/ITD) at all. Finally, to detect AAN, ~90 contrastive trials with the same data were sufficient. The results suggest that the number of trials is an important consideration.

The LPCpc was the most likely contender of a lateralized LP. Earlier research that found LPCpc used similar experimental setups: localizing sound from a selection of loudspeakers (Lewald et al., 2016; Gamble & Woldorff, 2015). One of the main, yet subtle, differences in Study 2 compared to Study 1 is the inclusion of vision. When allowed to see the loudspeakers, attention could be focused on them and the sound bound to the objects with higher precision. Vision, with higher spatial acuity than hearing, drives attention and thus perception of stimuli in intermodal spatial localization tasks (Chen & Vroomen, 2013). This implies that vision will bias attention more than hearing, and visually fixating on the sound source and then back again could cause the strong reorienting effect of the LPCpc (Gamble & Luck, 2011).

### 3.3 Study 3: Effects of Sound Lateralization Cues on AAN

One important difference between Studies 1 and 2 is that: in the former the sound may have been perceived by only one ear (monaurally; see explanation above), while in the latter they were always perceived by both ears (binaurally). Study 3 was aimed at assessing whether this difference could resolve the apparent contradiction in results between the two studies. To investigate if it could cause the perception of a lateralized sound, only manipulating the ITD of the stimulus was also tested. If possible, only manipulating ITD would once again enable a threshold-level paradigm without running the risk of ILD causing a monaural perception.

The experiment tested several conditions, all reminiscent of Study 1: First, it included a direct replication of the condition from Study 1. This ILD+ITD condition was the control condition. Second, it included a condition that only manipulated ITD. Third, it included a condition that was purely monaural, to examine how it compared to the ILD+ITD condition. These findings would be juxtaposed to evaluate their contributions toward AAN and LP.

In Study 1, subjects responded with a dichotomous forced choice between left and right lateralization of the stimulus, regardless if the stimulus was heard or not. This forced choice leads to a problem regarding veracity of experience



to the stimuli, as the listener may be aware of the stimulus but unsure of what direction it is lateralized toward. In this case, the objectively correct responses to trials (e.g., answering left to a leftward stimulus) will be lumped together regardless of the listener's experience. In other words, the analysis cannot differentiate between trials that were heard, but not experienced laterally, and trials that were heard and experienced laterally. These trials should be treated as misses, but are instead treated as hits. Veridical experience is paramount to research into NCCs, and while hits and false alarms share similar NCC-related ERPs, misses and correct rejections do not (Faramarzi et al., 2021). To ameliorate this issue in Study 3, the subject was allowed to respond with an option that they did not know which direction the sound was lateralized toward. In this way, the listener's true experience is better captured, instead of inferring their experience from behavioral responses. This ensures that when a subject reports hearing the sound from the left, it is verified, instead of erroneously processing a lucky guess from a forced choice as a correct experience of the sound. Conversely, this strategy may change the subject's response bias by shifting their response criterion to what stimulus strength classifies as e.g., "leftward," compared to Study 1. However, a shift in criterion should ultimately not affect the awareness threshold of the subject (Hautus et al., 2022).

Further, the sensitivity of AAN to number of trials was investigated. The results from Study 1 were reanalyzed in different increments of included trials, to track any emergence or divergence of the lateralization effect of AAN, as well as any level of data saturation, where adding more trials does not alter the effect. Specifically, this analysis was included to test if the disparity between 90 trials in Study 2, and 180 trials in Study 1, had any bearing on lateralization of AAN. Note that this analysis is not fully discussed in the published study, yet accessible through the supplementary materials. However, the results of the analysis are fully presented here (see table 1).

The hypotheses for Study 3 were: First, that the AAN in the ILD+ITD condition would be lateralized. Second, that the AAN in the ITD-only condition would not be lateralized. Third, that the AAN in the monaural condition would be lateralized. Fourth, that there is an AAN overall in all conditions (as a manipulation check). Fifth, that there is an LP overall in all conditions (as a manipulation check).

### 3.3.1 Method

The study was split into two different samples, to minimize subject fatigue, as the task was quite demanding. The first sample ( $n = 31$ ) performed the ILD+ITD and ITD-only tasks. The second sample ( $n = 40$ ) performed the monaural task. The same equipment and stimulus as Study 1 was used, with two exceptions. First, a response option was added, allowing for the subject to respond that they cannot discern the lateralization of the stimulus. Secondly, an adaptive roving staircase procedure was applied throughout the experiment.

In Study 1, the stimuli were presented at a fixed stimulus level after careful calibration. In this study, as in Study 2, each stimulus level varied depending on the awareness of the preceding stimulus, because it retains a higher amount of data (Wiens et al., 2023).

The number of trials in this study were also variable, using a time limit instead to gather as many trials as possible within the allotted time. This method works thanks to the multi-level modeling, allowing weighting of subject data depending on contributory amount of data. Study 3 computed ERPs similarly to Study 2, and used similar Bayesian linear mixed effects regression modeling to Study 2, reporting BF, CI, and pd. The regression model contained awareness, sound lateralization (leftward/rightward), and sound level as predictors. Evidence for lateralization effects was determined by the BF related to the interaction of all predictors. The prior distribution was modeled as a normal distribution ( $\mu = 0$ ,  $\sigma = 2$ ). See the appended paper for the regression formulae.

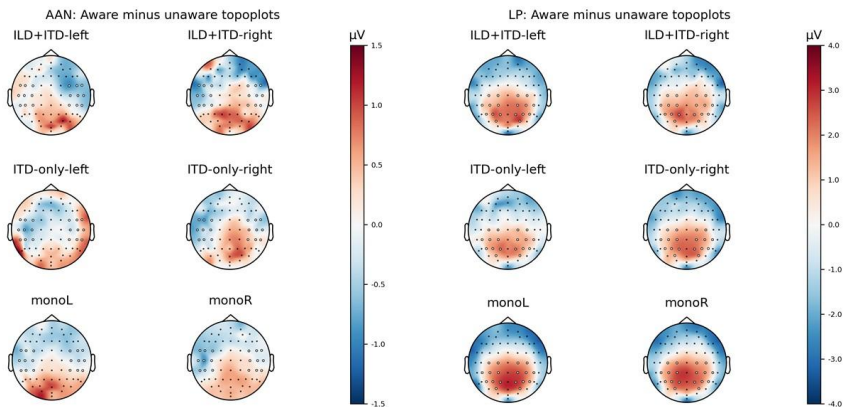
### 3.3.2 Results

First, the results of the ILD+ITD condition closely resembled the results of Study 1. There was extreme evidence ( $BF_{10} = 161$ ) for an overall AAN, and moderate evidence ( $BF_{10} = 6.75$ ) for a contralateral AAN to lateralized stimuli. There was extreme evidence ( $BF_{10} > 1000$ ) for an overall LP, but anecdotal evidence ( $BF_{01} = 2.48$ ) of a lateralizing effect. The ITD-only condition found moderate evidence against any lateralization effect to both AAN ( $BF_{01} = 7.16$ ) and LP ( $BF_{01} = 6.21$ ). This condition found no evidence ( $BF_{10} = 1.04$ ) of AAN overall, although it did find extreme evidence ( $BF_{10} > 1000$ ) for the LP overall. The monaural condition found anecdotal evidence for any lateralization effect of AAN ( $BF_{10} = 1.92$ ) and LP ( $BF_{10} = 2.01$ ), yet the median effect and pd suggest both a contralateral AAN (median =  $0.41 \mu V$ ; pd = 0.99) and an ipsilateral LP (median =  $-0.51$ ; pd = 0.99). For the monaural condition, there was extreme evidence for an overall AAN ( $BF_{10} = 212$ ) and LP ( $BF_{10} > 1000$ ). See figure 9 for topographical plots of the AAN and LP for each condition. See table 1 for a summary of the results.

Lastly, a separate Bayesian mixed effects linear regression model was run to compare the three conditions. The model for AAN suggests there is moderate evidence against any difference between the monaural and ILD+ITD condition ( $BF_{01} = 3.9$ ), or between the monaural and ITD-only condition ( $BF_{01} = 3.83$ ), and anecdotal evidence against any difference between ILD+ITD and ITD-only condition ( $BF_{01} = 1.34$ ). However, these findings need to be interpreted cautiously, because these higher-order interactions have lower statistical power (Luck, 2014), and the Bayes factors tend to favor the null hypothesis (Makowski et al., 2019).

*Table 1* Results divided by stimulus conditions (experiment 1: ILD+ITD and ITD-only; experiment 2: monaural). The table shows the median ERP-voltage and 95% credible intervals, the Bayes Factor, and pd-index, separately for AAN and LP. AAN/LP Lateralization shows the effect of lateralization of the ERP, via an interaction effect between stimulus side, awareness, and electrode side. In the lateralization analysis, a positive value indicates a contralateral lateralization effect, and a negative value an ipsilateral effect. AAN/LP Overall shows the strength of the overall ERP. Results with  $BF_{10} > 3$  marked in bold. Table taken from Study 3.

	<b>ILD+ITD</b>	<b>ITD-Only</b>	<b>Monaural</b>
<b>AAN Lateralization</b>			
Median $\mu V$ [CI]	<b>0.76 [0.21, 1.31]</b>	0.11 [-0.4, 0.61]	0.41 [0.09, 0.72]
BF <sub>10</sub> [BF <sub>01</sub> ]	<b>6.75 [0.15]</b>	0.14 [7.16]	1.92 [0.52]
pd	<b>0.99</b>	0.67	0.99
<b>LP Lateralization</b>			
Median $\mu V$ [CI]	-0.44 [-1.15, 0.26]	-0.06 [-0.68, 0.57]	-0.51 [-0.94, -0.09]
BF <sub>10</sub> [BF <sub>01</sub> ]	0.4 [2.48]	0.16 [6.21]	2.01 [0.5]
pd	0.9	0.58	0.99
<b>AAN Overall</b>			
Median $\mu V$ [CI]	<b>-0.28 [-0.38, -0.17]</b>	-0.16 [-0.27, -0.04]	<b>-0.16 [-0.23, -0.1]</b>
BF <sub>10</sub> [BF <sub>01</sub> ]	<b>161 [&lt; 0.01]</b>	1.04 [0.96]	<b>212 [&lt; 0.01]</b>
pd	<b>1</b>	0.99	<b>1</b>
<b>LP Overall</b>			
Median $\mu V$ [CI]	<b>1.5 [1.15, 1.86]</b>	<b>1.27 [0.97, 1.57]</b>	<b>1.54 [1.27, 1.81]</b>
BF <sub>10</sub> [BF <sub>01</sub> ]	<b>&gt; 1000 [&lt; 0.01]</b>	<b>&gt; 1000 [&lt; 0.01]</b>	<b>&gt; 1000 [&lt; 0.01]</b>
pd	<b>1</b>	<b>1</b>	<b>1</b>



*Figure 9* Topographic maps of the AAN and LP from conditions in Study 3. **Left:** Topographies of AAN showing ILD+ITD, ITD-only, and monaural conditions, divided by stimulus type (rows) and stimulus direction (columns). **Right:** Topography of LP divided by stimulus type (rows) and stimulus direction (columns). Note the different scales for AAN and LP.

### 3.3.2.1 Reanalysis of Study 1

The data of Study 1 were reanalyzed using the same data with the current mixed regression model approach. Further, to test the robustness of the effect, the model was tested with different trial increments, to see if, and at what point, a saturation of data for investigating AAN could be satisfactorily reached. The model was tested using samples comprising the first 100, 200, 400, 600, and all (720) trials, per subject, as they had been collected. The results are reported in table 2.

For the full model, there is extreme evidence for a lateralized AAN ( $BF_{10} = 814$ ), and the positive median ( $0.7 \mu V$ ) indicates a contralateral effect. When reduced to 600 trials per subject, the effect size remains similar ( $0.7 \mu V$ ), and the BF drops, although retaining extreme evidence for the lateralization ( $BF_{10} = 271$ ). When reduced to 400 trials per subject, the effect size drops to  $0.52 \mu V$ , and drops to strong evidence for a lateralization effect of the AAN ( $BF_{10} = 10.54$ ). When dropped to 200 trials per subject, the effect size increases again, to  $0.61 \mu V$ , but the degree of evidence drops to moderate ( $BF_{10} = 5.08$ ). Finally, at 100 trials per subject, the effect size drops yet again, to  $0.29 \mu V$ , and the evidence is reversed to moderate evidence toward the null ( $BF_{01} = 4.22$ ).

For the full model, there is anecdotal evidence against lateralization of the LP ( $BF_{01} = 2.66$ ), with an effect size of  $-0.21 \mu V$ , indicating a trend toward an ipsilateral lateralization effect, if any. When dropping to 600 trials per subject, the effect size increases slightly ( $-0.24 \mu V$ ), yet the evidence remains anecdotal ( $BF_{01} = 1.87$ ). When dropping to 400 trials per subject, the effect size increases again to  $-0.38 \mu V$ , however the evidence remains anecdotal, even if the more likely hypothesis is reversed, meaning evidence toward lateralization ( $BF_{10} = 2.32$ ). When dropped to 200 trials per subject, the effect size drops to a similar level of the full model ( $-0.25 \mu V$ ), and the model provides moderate evidence toward the null hypothesis of no lateralization effect ( $BF_{01} = 4.55$ ). Finally, with 100 trials per subject, the effect size increases somewhat to  $-0.3 \mu V$ , and the BF evidence is still moderate in favor of the null hypothesis ( $BF_{01} = 3.95$ ).

### 3.3.3 Discussion

The replication of Study 1 through the ILD+ITD condition showed similar results. The reanalysis of data from Study 1 also suggested that there is a data saturation for AAN using this analysis method around 200 trials. This notion strengthens the results of the exploratory analysis in Study 2, as the 90 contrastive trials per condition exceeds the 50 trials per condition suggested by the reanalysis (200 trials over four conditions: left/right stimulus, and aware/unaware).

The results of the ITD-only condition did not suggest an overall AAN, and found strong evidence against any lateralization. Unfortunately, the stimulus used in the experiment consisted primarily of frequency bands above 3 kHz, rendering ITDs inefficient as a lateralization cue (Middlebrooks & Green, 1991). This effect could be seen in the behavioral data, as subjects had difficulty in correctly lateralizing stimuli in the ITD-only condition (56% correctly lateralized), as compared to ILD+ITD (91%) and monaural (94%) conditions.

The monaural condition was expected to exhibit similar results as the ILD+ITD condition. The idea was that the threshold-level paradigm would cause binaural stimuli with ILDs to become monaural. However, the results for the monaural condition did not reach sufficient evidence for a lateralized AAN ( $BF_{10} = 1.92$ ) as did the ILD+ITD condition ( $BF_{10} = 6.75$ ). This suggests that the lateral effect of the ERP in the ILD+ITD condition is not driven by monaural perception.

Lateralized AAN was only found with sufficient evidence in the ILD+ITD condition. A possible explanation for the requisite of both ILD and ITD to effectively capture a lateralized AAN may be due to stronger neural stimulation from concurrent lateralization cues. In other words, when both ILD and ITD are processed, they are done so in parallel, which may create an amplified or otherwise different pattern of activation in auditory cortex (Su & Recanzone, 2001). These results cast doubt on the premise of 8 ILD causing a monaural perception in our experiments. In sum, the study reinforced the findings from Study 1, yet could not fully disentangle what lateralization cue was driving the lateralized effect of AAN. Given the results, a combination of ILD and ITD is the most plausible explanation for a lateralized AAN.

*Table 2* Reanalyzed data from Study 1, using a Bayesian mixed effects regression model. The table shows the median ERP-voltage and 95% credible intervals for AAN & LP, the Bayes Factor, and pd-index. All shown effects are measures of lateralization, via an interaction effect between stimulus side, awareness, and electrode side. By computing left-to-right, a positive value indicates a contralateral lateralization effect, and a negative value an ipsilateral effect. The analysis was split into different increments to track data saturation (columns). The full sample consisted of 720 trials. Also tested were 600 trials, 400 trials, 200 trials, and 100 trials.

	720 Trials (Full Sample)	600 Trials	400 Trials	200 Trials	100 Trials
<b>AAN Lateralization</b>					
Median $\mu V$ [CI]	0.7 [0.42, 0.97]	0.7 [0.42, 0.98]	0.52 [0.21, 0.85]	0.01 [0.18, 1.04]	0.29 [-0.36, 0.94]
BF <sub>10</sub> [BF <sub>01</sub> ]	814 [0]	271 [0]	10.54 [0.09]	5.08 [0.2]	0.24 [4.22]
pd	1	1	0.99	0.99	0.82
<b>LP Lateralization</b>					
Median $\mu V$ [CI]	-0.21 [-0.42, 0]	-0.24 [-0.47, -0.01]	-0.38 [-0.66, -0.1]	-0.25 [-0.66, 0.14]	-0.3 [-0.84, 0.24]
BF <sub>10</sub> [BF <sub>01</sub> ]	0.38 [2.66]	0.54 [1.87]	2.32 [0.43]	0.22 [4.55]	0.25 [3.95]
pd	0.97	0.98	0.99	0.9	0.87

## 4 General Discussion

The thesis investigated the expression of AAN in regard to experiences of lateralized sound. The thesis investigated both sound lateralization and sound localization, and found differing results. In response to sounds over headphones, AAN exhibited a contralateral pattern to the experience of lateralized percepts, when the binaural cues of ILD and ITD are combined. Using loudspeakers, there was no evidence for lateralization of AAN, yet evidence for a contralateral LP. The findings of the specific studies are discussed below in relation to the thesis, followed by general lessons and limitations from all the studies.

### 4.1 Lateralization of AAN with Headphones (Studies 1 & 3)

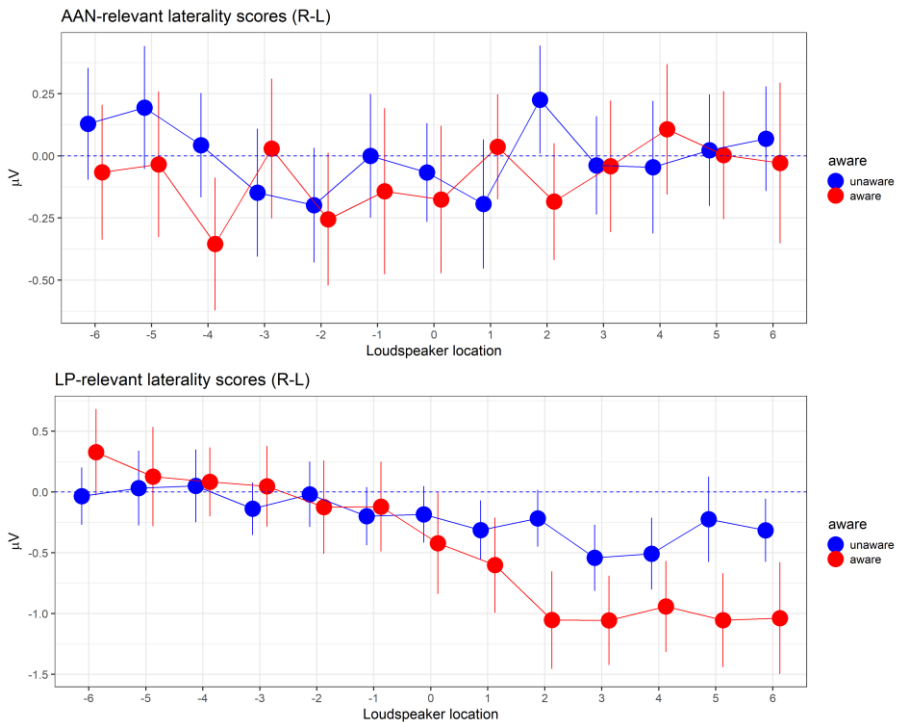
Study 1 was designed to examine the properties of AAN to sound lateralization. Lateral stimulation has been shown to activate differently, depending on stimulus used (Ahveninen et al., 2014; Gutschalk & Steinmann, 2015; Pickles, 2015; Middlebrooks, 2021). However, given the theory of PAN (Dembski et al., 2021), a lateralized binaural signal was tested to investigate any contralateral effect.

With regard to the lateralization of AAN, Study 1 showed a clear-cut pattern of a contralateral AAN to lateral stimuli. Study 3 again provided evidence of a contralateral AAN, although the degree of which differed depending on individual stimulus lateralization cues (more on this in section 4.3).

### 4.2 Lateralization of AAN with Loudspeakers (Study 2)

Study 2 aimed to further the notion of a lateralized AAN with free-field sound. The hypothesis was that AAN would show similar contralateral effects as to sound lateralization. The study found opposite results however, as the AAN was found to not lateralize in response to different sound locations. In fact, the overall AAN was initially not found in the data. The number of trials in the study were insufficient to detect the AAN, as its small effect is sensitive

to noise (Luck, 2014). In support, when similarly lateralized trials were aggregated, the overall AAN was detected. In this respect, the data at each given loudspeaker position may not have the resolution required to adequately estimate it. To visualize this effect, see figure 10. In the figure, the confidence intervals around the amplitudes of the AAN-relevant data largely overlap, and any linear lateral trend cannot be found. The results suggest that there is no linear trend of a contralateral effect to AAN, or that the trend is nonlinear, or that the data lack the resolution to discover it. If a true trend exists, it is indistinguishable from noise, but with more data confidence intervals contract, and a more accurate amplitude at each loudspeaker position can be discerned.



*Figure 10* Raw mean amplitudes of the data across all subjects from Study 2. The x-axis shows the thirteen loudspeaker locations, centered on 0. The y-axis shows mean amplitude in microvolts ( $\mu\text{V}$ ). **Top:** Raw mean amplitudes with 95% confidence intervals in the AAN-relevant interval (130-230 ms), with a laterality score computed by subtracting right-hemispheric electrodes by left-hemispheric electrodes. Red dots indicate trials rated as aware, and blue dots indicate trials rated as unaware. The laterality score implies that if a contralateral AAN were to exist, a positive linear trend for aware-trials should exist, while the unaware-trials should hover around the zero-line. **Bottom:** Raw mean amplitudes with 95% confidence intervals in the LP-relevant interval (350-450 ms). Laterality scores computed identically to AAN, with LP-specific electrodes. A contralateral LP would imply a negative linear trend from the aware-trials, as can be seen in the data. The unaware-trials should hover around the zero-line. Notice, on the y-axis, the greater amplitudes of the LP.

However, the LP exhibited a contralateral pattern to the lateralized sounds, as can also be seen in figure 10. The current plausible theory for these findings is the visual integration of the sound-emitting objects (the loudspeakers) causing the attentional reorientation effect LPCpc. Tentatively, it can be construed that if there is any lateral AAN in a free-field soundscape, it is drowned out by audiovisual integration (of the LPCpc). This notion is based on findings that attention is driven visually (Lewald et al., 2016), because when auditory targets can be seen, vision supersedes hearing in localization function (Chen & Vroomen, 2013). Further, the n2ac (the neural correlate of auditory attention), does not occur when single stimuli are played from visible loudspeakers, only when multiple sounds are played simultaneously (Gamble & Luck, 2011).

While the visual component may be a confounding factor, it is also diligent to contend with the other factors that separate free-field sound from headphones. Specifically, headphones produce stimulation to each ear separately, bypassing the acoustic shadow of the head, the reverberation of the room, and the role of the pinnae. Performance in Study 2 was generally good (see figure 2 in Study 2 in the appendix), and because performance was good, the acoustic shadow is likely not to blame. Likewise, the experiment was conducted in a sound-dampened laboratory, so reverberations are unlikely to have interfered (see Study 2 in appendix for specifics on laboratory acoustics). Finally, the pinnae filter sound in different patterns dependent on the direction of the soundwave, picking up spectral cues that assist in sound localization (Carlini et al., 2024; Middlebrooks & Green, 1991). These spectral cues primarily aid in localization in elevation, and not in azimuth. In sum, it is unlikely that these factors would influence the (non)lateralization of AAN to sound localization.

### 4.3 Effect of Sound Lateralization Cues on AAN (Study 3)

Because a contralateral mapping effect of AAN was found to sound lateralization (Study 1), Study 3 aimed to examine the specific lateralization cues in an attempt to isolate the cause of a lateralized AAN. Because headphones can manipulate sound presentation with precision, it is possible to deliver sounds that include or omit specific lateralization cues. The idea was that monaural stimulation drives the contralateral AAN, given that 1) earlier research into neural correlates of sound localization suggest that monaural stimulation produce the greatest contralateral effect (Gutschalk & Steinmann, 2015; Ahveninen et al., 2014), and 2) monaural stimulation would not be naturally achievable in free-field conditions, which could explain the lack of a lateralized AAN to loudspeakers.



The results of Study 3 showed that the only condition that provided a clear contralateral effect of AAN was a combination of ILD and ITD, mimicking natural sound. The reason for only a combination of ILD and ITD causing a lateralized AAN may speak for a joint coding of lateralization cues in the auditory cortex. Whether this is due to ipsilateral inhibition or contralateral excitation remains unclear.

In all conditions, an AAN overall (nonlateralized) was tested for as a manipulation check. A complication for interpretation in Study 3 was the evidence against any AAN at all in the ITD-only condition. A possible explanation is that the ITD-only stimulus was insufficient to properly create a lateral percept (as ~50% of trials were reported as ambiguously lateralized), which in turn causes a lack of trials for computing the ERP. In Study 3, each subject completed ~40 trials per condition of stimulus type, stimulus lateralization (left/right), and awareness (aware/unaware). This number is close to the ~50 trials per condition that the reanalysis of Study 1 suggests (see Study 3 in appendix for more details on number of trials). However, it is unknown what the effect was from the large amount of trials that were not perceived as lateralized.

Another interesting finding is the unclear evidence of contralateral AAN to monaural stimulation, specifically because monaural stimulation has relatively consistently shown predominantly contralateral activation of auditory cortex (Ahveninen et al., 2014; Gutschalk & Steinmann, 2015). To understand these results, the models of the study were compared. The comparison suggested no difference in AAN between the monaural and ILD+ITD condition ( $BF_{01} = 3.9$ ), nor monaural and ITD-only condition ( $BF_{01} = 3.83$ ). These findings need to be interpreted cautiously. Because these model comparisons test higher-order interactions between conditions, they may lack statistical power (Luck, 2014). In analyses with small numbers of trials, Bayes factors tend to favor the null hypothesis (Makowski et al., 2019). However, at face value, if the models do not differ from each other, it begs the question whether the lateralization of AAN in only one condition holds merit.

It is also important to note that an ILD-only condition was not tested in the study. The premise for the study was that an ILD of 8 dB at threshold level would effectively be perceived monaurally. Therefore, a monaural condition was included in lieu of an ILD-only condition, and the hypothesis was that the monaural condition would match the ILD+ITD condition to show the monaural perception driving the lateralized AAN. Yet, the conclusion that only the ILD+ITD condition shows a contralateral AAN may be somewhat premature. Because the ITD-only condition shows no lateralization of AAN, and the ILD+ITD does show lateralization, it is possible that only the ILD of 8 dB drives the lateralization effect. It would be diligent to test this possibility in future research of the lateralization of AAN to binaural cues.

## 4.4 Lessons and Limitations

The following subsections continue the discussion of the results from the thesis, outside the scope of the specific studies.

### 4.4.1 Neural Pathways and Contralateral Mapping of AAN

According to PAN (Dembski et al., 2021), the visual (VAN) and somatosensory (SAN) counterparts to AAN are mapped to experiences contralaterally onto the respective sensory cortex. In comparison, the contralateral pattern of the AAN is not as clearly defined.

In the sense of touch, the somatosensory dorsal column-medial lemniscus pathway travels afferently from the body to the dorsal column of the spinal cord, then passes contralaterally through the medial lemniscus, to the thalamus, and finally the somatosensory cortex, giving it a single transference to the contralateral hemisphere. In the visual neural pathway, the optic nerves from both eyes feed afferently bilaterally toward the lateral geniculate nuclei of the thalamus, but the nerves split along the optic chiasma to only feed information from the contralateral visual hemifield to the visual cortex. As seen in figure 2, even though the auditory system is biased with excitatory signals from the contralateral ear, the multiple levels of decussation, bifurcation, and integration make it less clear what happens to the afferent signal (Pickles et al., 2015). Even if an auditory percept is strongly lateralized, the AAN is not consistently matching the percept with a complimentary lateralized effect. The implication is that some of the intricacies of the auditory system are undiscovered.

Perhaps nuances of the auditory cortex cannot be accurately captured using EEG (Middlebrooks, 2021), given its position in the lateral sulcus, compared to more superficial areas of the visual and somatosensory cortex. Middlebrooks (2021) argues that relatively blunt instruments like EEG are unsuitable for measuring the nuances of neural sound localization, because EEG can only measure summated differences in electric field potentials. In other words, EEG can miss the nuances of inhibitory ipsilateral neuronal populations because the effect will be averaged out in the computation of the ERP. However, the interplay between excitatory and inhibitory nerves confound the measurement, and thus whether a lateral AAN is caused by excitatory or inhibitory responses is unclear. Invasive single-cell recordings may be a pathway forward to investigate the fine-grained details in the auditory system, but it may become difficult to learn about the integrative, multilineal process of consciousness from single neurons. EEG avoids this problem as a global measure, and as EEG has been used to measure AAN and comparable NCCs in the past, EEG was used in the experiments of this thesis for comparability.

Overall, the AAN can exhibit a contralateral activation to lateral sounds, in agreement with the theory of PAN. However, it is unresolved whether the lateralizing effect of AAN only happens to sound lateralization, and not sound localization. Given the different responses of AAN from different lateral stimuli, and between lateralized and localized sounds, future research should investigate different approaches to stimuli and lateralization cues, and even combinations of crossmodal auditory stimuli in the search for the NCC of auditory consciousness.

#### 4.4.2 Methodological Considerations and Limitations

Two major findings across studies that separate the research from earlier neural correlates of sound localization ability are that 1) the AAN as a contrastive effect eliminates concurrent activity extraneous to consciousness, and 2) the findings are not only based on behavioral performance, but on subjective judgment of experience. However, a limitation of all consciousness-related research is the accurate measurement of consciousness. Qualia, and different states of mind, are unverifiable by means other than conventional communication (barring physiological reflex, e.g. pupil dilation; Aru et al., 2012), and the researcher resorts to trusting the subject in their report.

Further, because perceptual stimuli vary in intensity, not all stimuli will be interpreted as discrete experiences. Predictive coding stipulates that there will always be a quotient of uncertainty to experience (Millidge et al., 2021; Aru et al., 2012), and thus it is desirable to control for this uncertainty. The current best practice to gather report of experience is to provide a response schema of alternatives that are meaningful to the subject (let the subject dictate what response options are meaningful). For this thesis, a modified version of the PAS was used, as PAS is a validated method for precisely this method (Sandberg et al., 2010). It was modified in the studies herein (as advised by Sandberg & Overgaard, 2015) by removing a response option, and was thus locally streamlined for our research. Specifically, the gradients of interest for the contrastive analysis require the threshold of awareness, which would result in dichotomous response alternatives of having an experience (above threshold) and not having an experience (below threshold). However, to validate that the experience was close to the perceptual threshold, as well as to reduce response bias, a third alternative was added to indicate having a stronger experience than threshold-level.

The PAS has come under recent criticism because it does not always defend against response bias (Fahrenfort et al., 2024). By manipulating instruction or strategy, subjects can shift their response criterion to become more liberal or conservative. When analyzing neural data (such as EEG data), the effect sizes become over- or underestimated depending on subject response bias. For example, if a subject adopts a conservative response bias, they require a stronger stimulus level before responding being aware of the stimulus. The stronger

stimulus (compared to their true awareness threshold) elicits a (relatively) stronger neural response, and thus provides a stronger effect. Fahrenfort et al. (2024) challenge the construct validity of PAS, but nevertheless admit that the problem of an arbitrary response criterion is intrinsic to decision making, and practically unavoidable. The studies in the thesis provided as neutral instructions as possible to test subjects, and asked them to accurately report their true experience without emphasizing correct performance, in an effort to minimize response biases. However, the studies herein did not control for whether subjects exhibited specific response biases.

Regardless, this modified version of PAS is not a complete tool for an awareness study with an identification task such as sound lateralization/localization. To elaborate, in Study 1 and 2, PAS allowed the subjects to report their awareness to detecting the stimuli, but were then forced to identify the sound source, irrespective if the sound is experienced as lateral. If the stimulus was experienced, but the laterality of the stimulus was ambiguous to the listener, a forced guessing would occur. Even though subjects did not have a lateralized experience (miss), the forced choice response would be analyzed as if they had a lateralized experience (hit), leading to NCCs that are not representative of a veridical experience (Faramarzi et al., 2021).

In Study 3, the experimental method was changed by providing the option of responding with “?”, which indicated an ambiguous or uncertain experience of laterality of sound. This small change allowed for verifying experience of the signal in both the domains of detection (hearing sound) and identification (lateralizing sound). Study 3 included a replicative condition of Study 1, and even with the updated method allowing for indication of ambiguous laterality, the aggregate percentage of correctly experienced lateral sounds matched with the performance of Study 1, at ~80% of trials (see Study 3 in appendix). Further, a potential tool for stimuli that are difficult to lateralize, such as the ITD-only condition of Study 3, is to increase the possible responses in a gradient of lateralization to each side (e.g., “slightly to left”, “extremely to the left”). A multidimensional awareness scale should be refined and validated, for increased precision in prompting experience. However, because EEG requires a large amount of trials to compute reliable ERPs, a balance is needed between number of possible conditions and statistical power.

The stimulus used in Study 1 and 3 was a recording of a mouth-click produced by an expert echolocator. The stimulus was chosen based on two factors: First, preliminary pilot testing of the stimulus indicated a clear lateralization of both ILD and ITD independently, ascertained from earlier work in our lab (Tirado et al., 2021). Tirado et al. (2021) performed behavioral piloting (with the same stimulus as Study 1 and 3), where 6 dB ILD and 0.25 ms ITD were matched to produce an equally lateralized percept (i.e., matching perceived lateral angle). Using these values as a baseline, Study 1 was piloted,

but piloting showed that the values required tweaking to produce a consistently natural lateralization. Therefore, the ILD was adjusted slightly to 8 dB and achieved much better behavioral results.

Second, the spectral broadband properties of the recorded click mean that several of the tonotopically organized bands in the auditory cortex will activate in response to the stimulus. Given the cortically deep location of the auditory cortex, its activity is difficult to detect using EEG. However, by eliciting a stronger response from broadband stimuli, the activity is stronger and the signal theoretically easier to detect. However, the dominant frequency bands of the signal ( $>3$  kHz) were not optimal for the investigated individual effects of ITD in Study 3, as ITD favors lower frequencies (for full spectral analysis, see stimulus EE1 in Thaler et al., 2017). Therefore, a different stimulus such as white noise could have been used, with equal distribution across the frequency bands. However, because one of the main objectives of Study 3 was to corroborate and expand upon the findings of Study 1, the original stimulus was kept.

In Study 2, the stimulus was changed from the recorded click to a computer-generated square pulse. It remains unknown whether the change of stimulus has had any influence on the results of Study 2, however, there is currently no strong argument for it. To add to this point, the changes between Study 1 and 2 were many. In hindsight, it may have been more prudent to only change one variable at first, such as presentation medium. By changing presentation mode, stimulus, and complexity (re: number of conditions) of the experiment, it is difficult to ascertain the source of the discrepant results from Study 1. By changing one variable at a time, the differences in results could have been studied better. For example, it may be worthwhile to study AAN to sound localization using only two laterally displaced loudspeakers playing the same stimulus as Study 1 and Study 3.

An important factor in ERP studies is an adequate number of trials to detect the effect of interest. Certain ERPs require more trials due to an effect located deeper in the brain or generated in a smaller area than others (Luck, 2014). This means that the recorded effect is weak in relation to concurrent recorded noise, and requires more trials to detect the effect of interest. The AAN may require many trials to sufficiently be detected. To test this premise, the data from Study 1 were reanalyzed in increments, and suggested a sufficiency at 200 trials (averaging to 50 trials per contrastive condition; see table 1). More trials will always add more evidence, so there is no tangible upper limit to testing. However, the large number of conditions present in these studies puts pressure on data collection, as time is limited and subject fatigue a ubiquitous risk.

It is customary to conduct audiometric screening of listeners in auditory experiments. This entails gauging listeners' hearing levels at different frequencies in each ear, to discover potential hearing deficits to certain stimuli. In psychophysical tasks, a threshold task measures ability to perform correctly

at different stimulus levels. Research into NCCs is less concerned with performative ability, and more with the experience of a stimulus, regardless of performance. Stimuli are calibrated to each individual threshold level based on awareness ratings, and not performance. Because audiometric screening is more concerned with performance than the subjects' experience of the stimulus, it was not conducted in the studies of this thesis.

#### 4.4.3 Implications for Consciousness Research and Future Studies

Research on consciousness is primarily basic research. In other words, research with the express intent of furthering understanding of the subject matter, without any predetermined application. This builds a foundation for the next generation of research to create practically applied value. The human brain is still relatively poorly understood, and understanding the mechanisms by how it integrates functions such as consciousness, can cascade into technological innovations.

More immediately however, the research on NCCs can help classify consciousness in response to various stimuli. More specifically, if, for example, the AAN is expressed differently to different stimuli, these different expressions can be used as a marker of conscious response. When treating patients with disorders of consciousness, such as comatose or locked-in syndrome, EEG is often used as a diagnostic tool to infer brain activity (Bai et al., 2021). A step in another direction would be to embrace technological advancements of neural decoding in hopes of discovering patterns within the data of auditory perception that cannot be discerned manually (Glaser et al., 2020). Neural decoding allows for machine learning algorithms to sort through staggering amounts of neuroimaging data to find patterns that may be too small for humans to find.

Recent developments in the research of consciousness place focus on the role of attention, and whether it can be separated from consciousness (Pitts et al., 2018). The relationship between conscious awareness and attention is nebulous, but the increasing separation of early and late NCCs (e.g., AAN and LP), with the dissociation of LP as a true NCC, has been pushing the idea that these two mental phenomena are separable, and possibly construed as the early awareness correlate, and the late attention correlate. This separation is not without criticism, as attention may likewise be a part of the function of, or may even replace awareness itself as the early correlate, leaving the late correlate as ulterior post-perceptual functions, and thus no consciousness-related activity is represented in the candidate NCCs of PAN or LP (Bola & Doradzińska, 2021). Furthermore, the LP is also analogous to the centroparietal positivity (CPP; O'Connell & Kelly, 2021). The CPP is described as the ERP representing encoding of evidence accumulation, which rises in strength

until a decision is made, whereupon it quickly dissipates. The LP may thus represent building internal evidence toward decision making extraneous to consciousness.

An immediate path forward for future research into the NCCs in hearing is to continue testing the effects of auditory cues on AAN. For example, more research is needed to understand the relationships between ILD, ITD, and AAN. To understand whether the ILD of 8 dB in Study 3 caused a monaural perception, it would be prudent to test an ILD-only condition, to gauge whether the ILD alone drives the contralateral AAN observed in Study 1 and Study 3. Likewise, it would be diligent to test both ILDs and ITDs with stimuli that are equally suited for them in frequency, such as white noise.

Further, it would be informative to investigate AAN to free-field sound over loudspeakers, and to record the experimental stimulus using an artificial head to recreate its spectral properties and head-related transfer functions (Carlini et al., 2024). As a second condition, to investigate AAN to the recorded stimulus using headphones. This experimental paradigm can minimize the differences between free-field and simulated soundscapes.

## 4.5 Conclusion

The three studies contained in the thesis further the understanding of AAN, and by extension, the auditory NCCs. AAN to sound lateralization matches the supramodal contralateral mapping pattern of PAN (Dembski et al., 2021). However, AAN to sound localization does not appear to follow the mapping pattern of PAN. The reason for this difference remains unclear. The findings of AAN are consistent with RPT and GNWT, with an early sensory component, and a late widespread component. The LP documented in this thesis follows earlier research into NCCs (Pitts et al., 2018), with the exception of the contralateral LP in Study 2. This ERP is presumed to be the LPCpc, which may overlap in area with the underlying LP, or reflect an aspect of the same component. The thesis demonstrates the differences between sound localization and sound lateralization in the expression of candidate auditory NCCs.

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