Electrophysiological correlates of consciousness

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Abstract
How does the brain enable us to experience seeing or hearing a stimulus? If a stimulus is repeatedly presented at the awareness threshold, subjects will report that they are aware of the stimulus on half of the presentations. Electroencephalography (EEG) can be used to non-invasively record neural activity as event-related potentials (ERPs). The contrastive analysis of neural activity to trials rated as aware minus neural activity to trials rated as unaware reveals the neural correlates of consciousness (NCC). Research on the NCC in vision has resulted in two ERPs: an early negative difference wave (visual awareness negativity, VAN) and a subsequent late positivity (LP). Visual awareness may be reflected by one or both of these ERPs. However, the contrastive analysis (aware minus unaware) may not isolate the NCC because it arguably compares aware processing with a combination of unaware processing and no processing. In support, previous research that tried to isolate a comparison between aware processing and unaware processing found that LP was the only NCC. However, subsequent replications suggested VAN and LP as NCC. Because of these mixed results, we followed up on these studies in Study I with a preregistered design that manipulated stimulus size. Results showed VAN and LP as NCC. The findings provide evidence for VAN as an early NCC.

Another main goal of this thesis was to investigate auditory awareness. In Study II, an auditory threshold task was used, and the contrastive analysis revealed an early negative difference wave (auditory awareness negativity, AAN) and LP. These ERPs are comparable to VAN and LP in vision. Because post-perceptual processes related to responding may confound the NCC in contrastive analysis, no-response tasks can be used to isolate awareness-related activity. In vision, a previous study in which the manual response requirement was manipulated showed effects on LP but not on VAN. In Study III, we used a similar task with auditory stimuli at the awareness threshold. Results suggested that AAN and LP are unaffected by the response manipulation. However, the present no-response task may not be optimal for removing post-perceptual processing because subjects need to reflect on their experience even if they do not need to respond manually. Additional analyses that attempted source localization of the AAN suggested that it is generated in auditory cortex.

From a theoretical perspective, one view of these results is that VAN and AAN reflect local recurrent processing and that this is the neural signature of awareness, whereas LP reflects global recurrent processing that enables reporting. Other views suggest that VAN and AAN merely reflect preconscious processes, whereas LP and global recurrent processing reflect consciousness. The studies described in this thesis do not support one theory over the other but provide robust evidence for early neural correlates of visual and auditory awareness.

Keywords: neural correlates of consciousness, electroencephalography, event-related potentials, visual awareness negativity, auditory awareness negativity, recurrent processing, phenomenal consciousness, access consciousness.
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"Seek the truth, hear the truth, learn the truth, love the truth, speak the truth, hold the truth and defend the truth until death"

- Jan Hus
List of studies

This doctoral thesis is based on the following three studies:


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Abbreviations

Auditory awareness negativity (AAN)
Bayes factor (BF)
Electroencephalography (EEG)
Event-related potential (ERP)
Functional magnetic resonance imaging (fMRI)
Late positivity (LP)
Neural correlates of consciousness (NCC)
Signal detection theory (SDT)
Visual awareness negativity (VAN)
Primary visual cortex (V1)
Transcranial magnetic stimulation (TMS)
1. Introduction

How does the brain enable us to experience the bright yellow color of the sun, or the rumble and crack of thunder? Nowadays, most people would agree that the inner workings of the brain create our sensory experiences. This common understanding probably comes partly from the fact that most people directly or indirectly know someone who has suffered from brain-related health problems (e.g., dementia, stroke, other forms of brain damage) and know what it does to the mental life of a person. As humans, we also have close contact with hospitals and mental healthcare and can clearly see how the mind is affected by damage to the brain. But how can this lump of fat in our heads create the seemingly magical experience of seeing and hearing? This problem is referred to as the mind-body problem, or the hard problem (Farthing, 1992; Searle, 2000).

In philosophy, there are two dominant theories regarding how the body is related to the mind. Dualism suggests that two substances exist: the physical and the mental. These are two separate constituents of the world. In contrast, monism suggests that only one thing makes up the world. This one thing encompasses both the physical and the mental. Biological realism is one monistic theory, suggesting that the mental can be fully explained by biology and neuroscience: “Subjective phenomenal consciousness is a real, natural biological phenomenon that literally resides within the confines of the brain” (Revonsuo, 2009, p. 10). Accordingly, the brain has to be investigated to understand the emergence of mental phenomena. In this thesis, I will review philosophical discussions only briefly and adopt the perspective of biological realism to try to understand how the brain generates our visual and auditory experiences.

1.1. Consciousness

Consciousness can be divided into states and contents of consciousness (Aru, Bachmann, Singer, & Melloni, 2012; Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006). States of consciousness refer to different sustained levels of arousal or wakefulness such as sleep, meditation, coma, and other altered states of consciousness (Farthing, 1992). In contrast, the contents of consciousness refer to moment-to-moment experiences such as that of a briefly presented red square on a computer screen, or the sudden sound of someone sneezing. Contents of consciousness can also be stretched out over time, for example, when one looks at a painted piece of art for a prolonged period. The painting as a whole is part of the experience as different parts of the painting are
attended to. From this perspective, being asleep but dreaming could be considered a state of consciousness that contains awareness of the content but maybe without the capacity to reflect on the content (Frith, Perry, & Lumer, 1999).

In this thesis, only transient contents of consciousness will be investigated, such as that of a briefly presented red square or of a soft tone. To understand how the brain generates experiences, it is necessary to identify “the minimal set of neural processes that are together sufficient for the conscious experience of a particular content” (Aru et al., 2012, p. 738). These neural processes are commonly referred to as neural correlates of consciousness (NCC).

When searching for the NCC, it is important to avoid confounding these correlates with prerequisites and consequences of consciousness (de Graaf, Hsieh, & Sack, 2012). The prerequisites of consciousness are what is required to create conscious experiences. Our eyes are essential to processing any visual stimuli at all. Similarly, the thalamus is essential for the normal functioning of consciousness, but its activity is more related to the current state of consciousness than to the content of consciousness (Llinás, Ribary, Contreras, & Pedroarena, 1998). Attention is a cognitive prerequisite of consciousness (de Graaf et al., 2012; Dehaene & Naccache, 2001). For example, spatial attention is a prerequisite for visual stimuli to reach consciousness (Koivisto, Kainulainen, & Revonsuo, 2009; Koivisto & Revonsuo, 2010). Another prerequisite is the neural activity occurring just before stimulus onset. Research has shown that the rate and phase of neuronal firing predicts whether a stimulus reaches consciousness (Mathewson, Gratton, Fabiani, Beck, & Ro, 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006).

The consequences of consciousness are what happens after the experience of some content of consciousness. They are secondary and thus not necessary for the emergence of consciousness. Examples of these consequences include evoked memories connected to the experience (de Graaf et al., 2012) and the planning of a response after a stimulus is presented (Tsuchiya, Wilke, Frässle, & Lamme, 2015). In experiments that require subjects to make a physical response to categorize their level of awareness evoked by the stimulus, responses are usually perfectly correlated with the emergence of consciousness. Therefore, it is important to experimentally separate these consequences from the proper correlates of consciousness (Tsuchiya et al., 2015).

Philosophers tackle consciousness by refining definitions of consciousness. According to Block (2005), phenomenal consciousness refers to the experience of the contents of consciousness. Access consciousness refers to the later cognitive operations performed on the experience, what above is referred to as the consequences of consciousness. Whereas some adopt this split between phenomenal and access consciousness (Lamme, 2018), others argue that without access, there is
no consciousness (Naccache, 2018). Dehaene and Changeux (2011), for example, defined consciousness as a reportable subjective experience. Thus, theories of consciousness disagree on how to define consciousness.

Neuroscientists tackle consciousness from another angle by using experiments to understand consciousness empirically. Crick and Koch (1990) suggested that we stop trying to define consciousness and instead focus on experimentation. However, neuroscience and philosophy complement each other in understanding consciousness. Neuroscience affects philosophers’ definitions, and philosophy affects neuroscientists’ design of their experiments. The distinction between phenomenal and access consciousness is probably such a case, in which philosophy used findings from neuroscience to come up with new definitions of consciousness. In this thesis, I use the terms consciousness and awareness interchangeably to refer to phenomenal consciousness, that is, what it is like to have an experience (Revonsuo, 2009).

1.2. Outline of this thesis

The ultimate goal of research on consciousness is to solve the mind-body problem or the hard problem of how the physical brain creates the seemingly non-physical, subjective experiences that we have. So far, there is no answer to this question, and no theory has been able to address it without resorting to dualism, that the mind is something non-physical. Therefore, one line of research towards solving the hard problem is to map brain activity that is correlated with subjective experiences, that is, to find the neuronal firing that is correlated with subjective reports of sensory experiences. Because no one has any viable theory on how neurons create experiences, mapping neural activity related to experiences is the first step towards addressing this question.

This thesis is organized as follows: The first part focuses on vision and contains a theoretical background of how consciousness can be measured behaviorally, how the brain processes visual information (that may or may not lead to awareness), how this brain activity can be measured electrophysiologically, and results from electrophysiological experiments on visual awareness. This is followed by a description of my first study on visual awareness (Study I) together with an alternative interpretation of the results (beyond the published paper) and a discussion of the problems with measuring consciousness electrophysiologically. This discussion goes beyond that of the published version of the study. The next part focuses on hearing. A theoretical background is provided on how the brain processes auditory information, together with a review of previous results of electrophysiological experiments on auditory awareness. This is followed by a description of my second study (Study II), in which the findings in vision are expanded to hearing, and a
description of my third study (Study III), in which I tried to control for the consequences of consciousness in an auditory experiment. Finally, I summarize the main findings, address the main aims of the thesis, suggest future research, and give a final thought on what processes I think give rise to consciousness. Below is a short summary of the main aims of this thesis.
2. Aims

The overall goal of the three experiments in this thesis was to investigate the neural correlates of visual and auditory awareness by using electroencephalography. Four specific questions were addressed:

1. Is visual awareness negativity an early correlate of visual awareness? (Study I)
2. Are the electrophysiological correlates of auditory awareness similar to those of visual awareness? (Study II)
3. If the task has a manual response requirement, does this requirement affect the electrophysiological correlates of auditory awareness? (Study III)
4. Is auditory awareness negativity generated in auditory cortex? (Study III)
3. Measuring consciousness behaviorally

To measure consciousness behaviorally, subjects are usually asked about their contents of consciousness after a stimulus is presented. The stimulus is often ambiguous in that it can be perceived in more than one way (e.g., the rabbit-duck illusion). There are several ways in which stimuli can be manipulated so that they are perceptually ambiguous (Kim & Blake, 2005; Koivisto & Revonsuo, 2010). For example, in binocular rivalry, one image is displayed to the right eye and another image is displayed to the left eye. The contents of consciousness will vary between the two different images. Conveniently, neural activity to the image that is perceived can be compared to the one not perceived.

Another example is threshold tasks. In threshold tasks, a physical property of a stimulus is adjusted so that the stimulus is just at the threshold of detection (Goldstein, 2009). For example, a red square is presented repeatedly on a computer screen for a progressively shorter duration until the subject reports it as present approximately 50% of the time. Similarly, the loudness of a tone can be adjusted to the 50% threshold of detection. If the 50% detection threshold is found, the stimulus can be kept physically the same, but perception changes from trial to trial. Threshold tasks were used in all the experiments conducted for this thesis. That is, stimuli were adjusted so that subjects reported being aware of the stimulus 50% of the time. Brain activity was measured with electroencephalography (EEG) and compared between detected stimuli (i.e., stimuli accompanied by awareness) and undetected stimuli (i.e., accompanied by unawareness).

To measure detection, manual responses are usually collected after a stimulus is presented. Objective measures are used to quantify the subject’s performance; responses can be categorized as either correct or incorrect and labeled in terms of signal detection theory (SDT; Macmillan & Creelman, 2005). For example, a red square is briefly flashed on the screen, followed by the question: “Was a red square displayed?” Two response options are typically allowed: yes and no. If a red square was displayed and the response is yes, it is a correct response (hit). If a red square was displayed and the response was no, it is an incorrect response (miss). If a red square was not displayed and the response is no, it is a correct response (correct rejection). If a red square was not displayed and the response is yes, it is an incorrect response (false alarm). If the 50% threshold was defined on the basis of performance, I will refer to it as the detection threshold.

Subjective measures try to capture the subjective quality of the detection. In research on awareness, it is interesting to know whether subjects responded yes because they had an experience of the stimulus, or whether they responded yes despite being unsure about the experience. To know this, confidence in detection can be measured (Squires, Hillyard, & Lindsay, 1973). For example,
the question “How sure are you about having seen a red square?” can be asked, and subjects provide a rating between 1 and 8 to indicate their degree of confidence in detection. Another way of measuring confidence is to make the subject bet money on their decision. This is called post-decision wagering (Sandberg, Timmermans, Overgaard, & Cleeremans, 2010).

However, it can be argued that these measures of confidence only indirectly measure awareness (Ramsøy & Overgaard, 2004). To measure awareness more directly, an alternative scale can be used. Because awareness can have different degrees of clarity, the perceptual-awareness scale was developed to capture different levels of awareness experienced during normal experimental settings (Ramsøy & Overgaard, 2004). For example, the question “How did you experience the stimulus?” is asked, and four response options are provided: clear experience, almost clear experience, brief glimpse, and no experience. These answers were created by the participants themselves in a detection experiment (Ramsøy & Overgaard, 2004). If a 50% threshold was defined on the basis of a scale that captures levels of awareness (such as the perceptual awareness scale), I will refer to it as the awareness threshold.

A good measure of awareness should correlate strongly with performance. For example, the more the subject claimed to be aware of a red square, the more likely the subject should have been correct in that a red square was actually presented. To find out which measure best correlates with performance, Sandberg et al. (2010) compared the perceptual awareness scale, a confidence rating, and post-decision wagering. They found that the perceptual awareness scale correlated most strongly with performance in general.

An important difference between the subjective rating and the objective rating is that the subjective rating attempts to be exhaustive regarding levels of awareness (Sandberg et al., 2010). If a nonexhaustive subjective scale is used, trials may be incorrectly classified because the subject is given limited options for reporting degrees of awareness. For example, imagine a forced choice task with a stimulus presented either to the right or to the left visual field, with a two-choice objective response and a two-choice subjective scale (seen or not seen). It is possible that a subject has a brief glimpse of the stimulus but chooses to report “not seen” because there were only two response options and the subject reserved the “seen” response only for stimuli that were clearly seen. In signal detection terms, this hypothetical subject has a conservative criterion and is unwilling to report having seen the stimulus if the subject is less than certain about having seen it (Macmillan, 1986). If the stimulus was correctly localized but reported as not seen, this trial would be incorrectly categorized as the subject having processed the stimulus unconsciously. Specifically, the processing was not unconscious because the subject experienced a brief glimpse of the stimulus.
However, there might be no difference between using objective or subjective measures. In one study with two experiments (Cul, Dehaene, & Leboyer, 2006), target numbers were flashed, followed by a backward mask (reducing the visibility of the target number). In the first experiment, the task was to determine whether the target number was larger or smaller than 5, and subjects provided an objective response (left hand for smaller and right hand for larger). In a second experiment, subjects also provided subjective ratings of their perception of the number. As the stimulus-onset asynchrony between the target and the mask was varied, the detection threshold and individual awareness threshold could be calculated from psychometric response functions. Importantly, the objective and subjective thresholds were almost perfectly correlated within subjects. Depending on the task, the results might be similar for objective and subjective ratings.

In sum, perception can be affected by manipulating a stimulus. Awareness of the stimulus can be assessed with objective and subjective measures. Objective and subjective measures may provide different but sometimes the same information about the detection of a stimulus.
4. Neural mechanisms of visual processing

To investigate how the brain enables visual awareness, the neural mechanisms of visual processing have to be understood. It is important to know where in the brain sensory stimuli are processed and how they are processed. This information can be used so that electrophysiological recordings can be planned and understood. Three modes of visual processing are important for understanding visual awareness: the feedforward sweep, localized recurrent processing, and global recurrent processing.

4.1. Feedforward sweep

The most posterior part of the human and monkey brain is the occipital cortex, which is primarily concerned with processing visual information (Felleman & Van Essen, 1991). If a visual stimulus is presented to the eye, the information will travel through the brain in a predetermined way because of how the neurons are interconnected. The visual information received by the retina of the eye is sent through the optic tract, the lateral geniculate nucleus in the thalamus, and the occipital cortex (Lamme & Roelfsema, 2000). The occipital cortex is divided into more than 25 areas on the basis of their connectivity, anatomy, and hierarchical structure within the visual stream (Felleman & Van Essen, 1991). The rapid, automatic, sequential activation of the visual areas within the hierarchy of the occipital cortex is called the feedforward sweep.

The primary visual cortex (V1) is considered to be at the bottom of the hierarchy within the cortex (Lamme & Roelfsema, 2000). V1 is divided into six layers, of which the fourth layer is called the granular layer because of its granule cells (Kalloniatis & Luu, 1995). The higher layers (1-3) are referred to as supragranular layers, and the lower layers (5-6) are referred to as infragranular layers. Feedforward connections to V1 mainly terminate in the fourth, granular layer (Felleman & Van Essen, 1991).

The receptive field of a neuron refers to the type of information that activates it. When the feedforward sweep reaches V1, cells with receptive fields to the specific visual space where the visual stimulus was presented will activate (Gattass, Gross, & Sandell, 1981). V1 is activated as early as 40 ms after stimulus onset in macaque monkeys (Nowak & Bullier, 1997). Cells in V1 are specifically receptive to details of visual information such as edges, the orientation of those edges, length, direction, and spatial frequency (Hubel & Wiesel, 1968). Higher visual areas in the visual hierarchy have different receptive fields and can react to more complex information such as color or the direction of motion (Felleman & Van Essen, 1991). The ventral temporal cortex is at the top of the visual hierarchy and processes faces and objects (Haushofer, Livingstone, & Kanwisher,
2008; Haxby et al., 2001); it is activated much later than V1, at around 120 ms after stimulus onset in macaque monkeys (Nowak & Bullier, 1997).

The visual cortex in general and V1 in particular are mapped in correspondence with the visual field. V1 is spatially coded according to the cells of the retina. This is called retinotopic organization and has been invasively studied in monkeys (Gattass et al., 1981). The retinotopic organization of more extended visual areas, including V1, has been mapped non-invasively with functional magnetic resonance imaging (fMRI) in humans (Sereno et al., 1995). Specifically, the right visual field is mapped to the left visual cortex, and the left visual field is mapped to the right visual cortex. The upper visual field is mapped to the ventral part of the calcarine sulcus, which extends out laterally around the occipital pole of both cortical hemispheres. The lower visual field is mapped to the rostral part of the calcarine sulcus, which also extends out laterally around the occipital pole. These retinotopic maps are mirrored for adjacent visual areas. For example, neurons in the medial and anterior part of V1 map the periphery of the visual field, whereas the neurons in the posterior lateral edge of V1 map the fovea. In the adjacent area V2, neurons bordering V1 map the fovea and reverse towards the periphery as it connects to the next visual area (Sereno et al., 1995).

The feedforward sweep is considered not to be experienced consciously because “no matter what area of the brain is reached by the feedforward sweep, this in itself is not producing (reportable) conscious experience” (Lamme, 2006, p. 497).

4.2. Localized recurrent processing

During and after the fast feedforward sweep, feedback and horizontal connections influence neurons that remain active as their receptive fields are changed (Lamme & Roelfsema, 2000). Feedback and horizontal connections mostly terminate in the supragranular and infragranular layers of the cortex (Felleman & Van Essen, 1991). Horizontal connections interconnect neurons within visual areas that have similar receptive fields, grouping them into functional networks, whereas feedback connections descend from hierarchically higher visual areas back to lower areas (Lamme, Supère, & Spekreijse, 1998).

Within the visual cortex, almost all areas have feedback connections that run parallel to the feedforward connections (Felleman & Van Essen, 1991). Feedback connections from higher areas modulate activity in lower areas, changing their receptive fields. For example, if a square is displayed to the eye, initially neurons in V1 respond according to their receptive fields during the feedforward sweep. The cells that respond to the orientation of the edge of the square will fire more than cells that are not responsive to that orientation. After about 40 ms, feedback from higher
areas changes the receptive field of the neurons depending on whether their receptive fields are within the boundaries of the square (Lamme, 1995) or at the edge of the square (Lamme & Roelfsema, 2000). This contextual modulation of neuronal activity also occurs in higher visual areas. For example, in the ventral temporal cortex of macaque monkeys, cells are first receptive to the type of object (e.g., if it is a human, a monkey, or another object) and subsequently (after 51 ms) code identity and facial expressions (Sugase, Yamane, Ueno, & Kawano, 1999).

Loops of forward activations and feedback continuously tune the neurons and change their activity. Importantly, the feedforward activity is considered automatic and unconscious, whereas localized recurrent processing largely reflects higher cognitive functions such as grouping objects on the basis of attentional selection, figure-ground segregation, and object recognition (Lamme & Roelfsema, 2000). These cognitive processes are tightly linked with awareness.

In a classic monkey study on figure-ground segregation, Supèr, Spekreijse, and Lamme (2001) recorded multiunit activity of V1 neurons from macaque monkeys in a visual detection task. The figure stimulus was a peripheral square made up of diagonal lines against a background made up of orthogonal lines. The monkeys had their eyes fixed on a fixation dot, and they were waiting for the square to appear at different peripheral positions. Monkeys indicated detection of a square by making a saccade to the location of the square. Because monkeys looked at the square if they detected it, the authors argued that this behavior presumes awareness of the squares. If fixation was kept at the fixation cross as a square was presented, the square was treated as undetected. Neural activity was recorded from two sets of neurons. One set of neurons had their receptive field in the location of the square and were tuned to the orientation of the lines making up the square. The other set of neurons had their receptive field on the background and were tuned to the orientation of the lines making up the background. Activity to detected squares was compared with that to undetected squares. Undetected squares showed feedforward activity for both square and background but no modulatory activity separating the two. In contrast, around 100 ms after stimulus onset, detected squares elicited additional modulatory activity in the neurons with receptive field of the square compared to the neurons with receptive field of the background. Thus, neural activity differed between figure and background only for detected squares, not for undetected squares. This modulation of neural activity is thought to come from feedback and horizontal connections and to index localized recurrent processing (Lamme et al., 1998). The authors concluded that recurrent processing correlates with awareness in the monkeys (Supèr et al., 2001).

The correlation between localized recurrent processing within early visual areas and awareness has also been demonstrated in human subjects. Subjects performed a visual detection task as neural activity was measured with magnetoencephalography (MEG; Boehler, Schoenfeld, Heinze,
In this task, four circles that were half black and half white were presented for a short duration in either the upper or the lower right visual field. The four circles had different orientations. One of the circles was the target and was surrounded by smaller, all-white circles (the mask). The task was to identify the orientation of the target. On some trials, the mask had its offset together with the circles, and on some trials, the mask remained for 250 ms after the offset of the circles. When the mask remained, task performance was decreased. Activity to all stimuli could be tracked in that the feedforward sweep reached V1 around 70 ms after stimulus onset, followed by activity in the ventral visual areas at around 110 ms. Feedback activity could be seen in that V1 was activated again at around 130 ms. The difference in neural activity between correctly discriminated targets and masked targets was the feedback activity that reached V1 around 100 ms after stimulus onset. This additional feedback activity for correct detections was also specific to the upper and lower visual field. Specifically, correctly identified targets displayed in the upper visual field produced feedback activity at the ventral bank of the calcarine sulcus, and correctly identified targets displayed in the lower visual field produced feedback activity at the dorsal bank of the calcarine sulcus.

Evidence that feedback activity plays a causal role in awareness has come from research involving transcranial magnetic stimulation (TMS), a non-invasive method of manipulating neuronal activity. If recurrent processing in the visual cortex of humans is disrupted during a visual detection task, awareness of the visual stimuli will be degraded or abolished (Amassian et al., 1989). Critically, the TMS stimulation needs to target neurons that have receptive fields corresponding to the retinal location where the stimulus is presented. Also, disruptive effects occur only between 60 and 120 ms when recurrent processing is thought to occur within lower visual areas (Koivisto, Railo, & Salminen-Vaparanta, 2011). One goal of the study by Koivisto et al. (2011) was to separately interrupt feedforward and recurrent processing, but they were unsuccessful in doing so. They argued that because recurrent processing has been shown to start as early as 10 ms after the initial feedforward sweep, it was not possible to separately disrupt them. TMS has also been used to selectively impair the higher-order motion area (middle temporal, MT) as it feeds back information to V1, resulting in degraded motion perception (Silvanto, Lavie, & Walsh, 2005). The task was to determine whether dots on the screen were moving as TMS was applied to either V1 or V5/MT at different time intervals. TMS to V5/MT decreased performance only when applied at an interval between 60 and 80 ms. In contrast, TMS to V1 decreased performance when applied at an interval between 80 and 100 ms. Because motion detection was impaired when TMS was applied to V1 at a later interval than to V5/MT, these findings suggest that V5/MT needs to send feedback to V1 to enable awareness of motion.
Reversed hierarchy models propose that complex information is rapidly extracted from higher visual areas such as ventral temporal cortex during the feedforward sweep and that this information is then sent back to the lower areas with feedback connections that enable the high resolution of vision (Bullier, 2001). Supporting these models is the perception-action model (Goodale, 2011). This model suggests that there are two streams of information processing in the brain: the rapid, action-oriented dorsal stream, and the slow, perception-oriented ventral stream. Acting on visual information has to be quick. For example, if a ball is thrown at us, the trajectory of the ball has to be calculated within milliseconds, and we have to put our hand in the path of the calculated trajectory and grip the ball at the right time. This is a very complex calculation that we do without awareness of how it is done. The experience of catching the ball seems to come after it happens. The perception-action model fits well with the idea that information is rapidly extracted largely unconsciously (Goodale & Milner, 1992) and, if necessary, quickly acted upon, followed by the slower ventral processing resulting in perception (Kanwisher, 2001).

To summarize, localized recurrent processing between hierarchically high and low visual areas changes the receptive fields of neurons within early visual areas. Findings suggest that this process is critical for the emergence of visual awareness.

### 4.3. Widespread global recurrent processing

After the rapid local recurrent processes have started between ventral visual areas, they spread to include frontal and motor areas (Lamme, 2006). The widespread activation involves “a distributed neural system or ‘workspace’ with long-distance connectivity that can potentially interconnect multiple specialized brain areas in a coordinated, though variable manner” (Dehaene & Naccache, 2001, p. 13). Hierarchically lower sensory areas are seen as modules, specialized in processing specific information, and attention is top-down, selecting these modules to include them in the workspace. Dehaene and Naccache (2001) suggested that the selected modules included in the workspace and the specific information that they process make up the current content of consciousness. Without the global integration, there will be only preconscious processing (Dehaene et al., 2006). Proponents of the global workspace theory (Dehaene & Changeux, 2011; Dehaene et al., 2006) emphasize that global activations are critical for consciousness.

In most studies that are described as supporting the global workspace theory (Dehaene & Changeux, 2011), activity in early sensory areas precedes widespread global activity, and both are related to awareness. Proponents of the global workspace theory suggest that the early activity reflects only preconscious activity, whereas the global widespread activity reflects awareness (Dehaene & Changeux, 2011; Dehaene et al., 2006; Dehaene & Naccache, 2001). For example, in
one study (Sadaghiani, Hesselmann, & Kleinschmidt, 2009), fMRI was used to measure neural activity in an auditory detection task. The task was to detect a rare white-noise burst masked by the MRI scanner noise. Event-related activity in auditory cortex was stronger before and after a hit than a miss. Also, undetected targets elicited event-related activity in the auditory cortex. According to Dehaene and Changeux (2011), the activity to undetected targets suggests that activity in auditory cortex does not reflect auditory awareness but only physical properties of the stimulus. However, it is unclear whether this activity reflects feedforward activity that does not enable awareness, or local recurrent processing that could potentially enable awareness (Lamme, 2006). Furthermore, Sadaghiani et al. (2009) compared activity between hits and misses in several areas of distributed networks. The networks were defined with resting-state functional connectivity. For the default mode system, baseline activity and activity after stimulus onset in the precuneus was higher before hits than before misses. Only after stimulus onset was activity in the medial prefrontal cortex and the lateral parietal cortex higher to hits than to misses. Activity in most areas of the dorsal attention system (intraparietal sulcus, medial temporal, and frontal eye field) showed a peak after stimulus onset to hits. But activity to misses was generally higher than activity to hits before and after stimulus onset. Activity in the intrinsic alertness system (dorsal anterior cingulate cortex, anterior thalamus, and anterior insula) was higher to hits than to misses before and after stimulus onset and showed a peak to hits. According to Dehaene and Changeux (2011), the widespread activity to hits supports the global workspace theory. However, because of the low temporal resolution of fMRI and because post-perceptual processes should come after perception, activity in the auditory cortex may be related to perception, and the widespread activity may be related to other, post-perceptual cognitive processes.

In another study (Haynes, Driver, & Rees, 2005), fMRI was used to measure event-related activity to a brightness change that was masked. Stimuli were filled white hexagons with black borders in a honeycomb pattern. Sometimes, the central hexagon was gray (target). The mask was white hexagons fit into the black background of the white-filled hexagons. This kind of mask, which does not overlap with the location of the target image, is called a metacontrast mask. Hexagon patterns were presented in the four quadrants, and on each trial, subjects were cued to attend to the two quadrants on one of the diagonals (i.e., lower left and upper right, or upper left and lower right). As the stimulus-onset asynchrony between mask and target was varied from short to long latency, changes in visibility followed a U-function: high visibility at short stimulus-onset asynchrony, low visibility at intermediate stimulus-onset asynchrony, and high visibility at long stimulus-onset asynchrony. The patch of V1 cortex (region of interest, ROI) that processes the hexagon patterns was located with a retinotopic mapping procedure. Results showed that activity correlating with the U-shaped visibility function was maximal at the immediate surrounding area.
(center-surround) of the ROI and in the lateral visual area fusiform gyrus. Visibility was strongly associated with neural coupling (measured by effective coupling analysis) between the center-surround of the ROI and the fusiform gyrus. Undetected targets lacked this neural coupling between V1 and fusiform gyrus. Furthermore, medial and inferior frontal gyrus activity correlated with visibility. According to Dehaene and Changeux (2011), the frontal activity suggests that more widespread activity is needed for awareness to emerge. An alternative explanation is that the close coupling between fusiform gyrus and V1 could reflect local recurrent processes that enable awareness of the brightness change (Haynes et al., 2005; Lamme, 2006).

According to the global workspace theory, global recurrent processing is critical for consciousness. A contrasting view is that global recurrent processing reflects only post-perceptual processes (de Graaf et al., 2012; Koivisto & Grassini, 2016). Accordingly, local processing in the sensory cortices reflects awareness (Lamme, 2006), and the subsequent widespread activity has to do with task-related responding (Koivisto, Salminen-Vaparanta, Grassini, & Revonsuo, 2016; Snyder, Yerkes, & Pitts, 2015; Verleger, Jaśkowski, & Wascher, 2005), working memory (Polich, 2007), decision making (Parasuraman & Beatty, 1980; Squires et al., 1973), and other cognitive processes (Block, 2005; Lamme, 2010) that are only consequences of consciousness (Aru et al., 2012; de Graaf et al., 2012). Because many of the studies that are interpreted as supporting the global workspace theory (Dehaene & Changeux, 2011) show activity in sensory areas that correlates with awareness, these findings are also consistent with the alternative view that local processing reflects awareness and is not just simply a preconscious process.

In sum, opinions about the neural mechanisms of consciousness differ. One view is that a local sensory process enables the moment-to-moment experiences referred to as phenomenal consciousness, separate from subsequent cognitive processes such as working memory or introspection (Koivisto & Grassini, 2016; Lamme, 2006). Another view is that consciousness is a global process referred to as access consciousness. It occurs only if the sensory information is accessed and reflected upon cognitively (Dehaene & Changeux, 2011; Dehaene et al., 2006).
5. Measuring neural activity with electroencephalography

5.1. Event-related potentials

EEG is a non-invasive electrophysiological brain imaging method that can continuously record the combined electrical activity produced by the brain; because this activity reaches the scalp almost instantaneously, EEG can separate different neuronal computations with high temporal resolution (in milliseconds) (Oostenveld, 2003). Therefore, EEG is an excellent tool to separate neural correlates of consciousness from post-perceptual consequences such as making a motor response measure (de Graaf et al., 2012).

However, not all neural activity (such as that of single cells) can be picked up by EEG. Synchronized communication between neurons generates measurable electrical fields that can be detected by sensitive electrodes placed on the scalp (Luck, 2014). A sending neuron has its axon connected to the dendrites of a receiving neuron by the synaptic cleft. Action potentials travel through the axon and initiate the release of chemicals in the synaptic cleft. Because the synaptic cleft and the soma have different charges, an extracellular current is created between the synapse and the soma (Niedermeyer & Lopes da Silva, 2005). Because the dendrites of the most common pyramidal neurons are long (making the distance between the synapse on the dendrites and the soma long), a strong electric dipole between the two will be generated. If hundreds of parallel pyramidal neurons are activated simultaneously, their electric dipoles will spatially summate, resulting in a larger electric dipole moment that is measurable from the scalp (Buzsáki, Anastassiou, & Koch, 2012).

In the continuous EEG recording, a mark can be made at the onset of the stimulus. The time interval after this mark contains activity related to the processing of the stimulus. Such a time interval together with a short baseline interval before the stimulus onset is called an epoch (Luck, 2014). For example, in the studies described in this thesis, the typical epoch ranged between 100 ms before stimulus onset to 600 ms after stimulus onset. Within the epoch, the signal of interest occurs together with irrelevant activity and noise. This is because the whole brain is active and processes other information simultaneously. Also, the signal of interest is usually not visible in a single epoch unless the response is very strong. To extract the signal of interest that is hidden in irrelevant activity and noise, the stimulus is typically presented repeatedly on many trials. The resulting epochs can be overlaid and averaged to obtain an event-related potential (ERP). Because the stimulus onset is marked at the start of every epoch, the signal will perfectly overlap if epochs are averaged. As a result, only the signal remains, and any activity that is not part of the signal disappears. Critically, to obtain an ERP, the signal has to have a constant phase across epochs.
Unrelated activity or activity that is random and not synchronized in phase will average out and thus disappear. In sum, an ERP is an average of phase-locked electrical activity averaged across many trials, and it looks like a wave (Luck, 2014).

A superficial cortical neural generator will create an electric dipole throughout the conductive medium of the brain, skull, and scalp. To measure the voltage of this dipole, the potential between two electrodes has to be measured. For example, for a dipole that is oriented perpendicular to the scalp, if one electrode is put on the scalp closest to the dipole and another electrode is put on the opposite side of the head (at the other pole of the dipole), the voltage difference will be maximal. The difference in voltage between these two electrodes will capture the strength of the dipole moment (Luck, 2014). Electrodes that are not optimally positioned in relation to the dipole will result in a smaller voltage difference. For some superficial, single sources, the difference in voltage among spatially distributed electrodes can give us some information about the location of the source. This voltage distribution can be visualized with a topographic image (topography) that shows the distribution of voltage of many electrodes on the scalp at a particular time point (or an average of time points). However, because there is an infinite number of neural generators that can generate the same electrical activity on the scalp, one can never use the voltage measured from the scalp to locate a source with certainty. This is called the inverse problem (Luck, 2014).

To compute descriptive statistics from ERP data, the ERPs need to be quantified. The ERP is typically analyzed at a particular interval after stimulus onset. For example, to test whether an ERP recorded between 160 and 260 ms after stimulus onset differs between two behavioral conditions (e.g., stimulus was perceived vs. not perceived), the most common way of quantifying a component would be to compute the mean amplitude across this interval (Luck, 2014). If the mean amplitudes for the two conditions (perceived vs. not perceived) are extracted for each subject, inferential statistical analysis can be conducted on the mean amplitude differences between the two conditions.

5.2. Source localization

To estimate the neural generators or sources of an ERP, the ERP’s topography must be used to estimate the most likely sources that generated the electrical field recorded by the electrodes (Jatoi, Kamel, Malik, Faye, & Begum, 2014; Niedermeyer & Lopes da Silva, 2005). Although the inverse problem implies that there is an infinite number of neural generators that can generate the same electrical activity on the scalp (Luck, 2014), the number of inverse solutions can be reduced with some restrictions and assumptions. For example, one can spatially restrict potential generators (source space) to be located only in the gray matter of the cortex. Also, the conductivity within
different head tissues can be assumed to be homogenous, so that only the boundaries between them (brain, skull, and skin) need to be modelled. This is called the boundary element model (Hamalainen & Sarvas, 1989; Oostenveld, 2003), and the boundaries can be modelled from a structural MRI scan (Niedermeyer & Lopes da Silva, 2005). Furthermore, the source space can be modelled with thousands of equally spaced dipoles distributed in the gray matter volume. From these sources and how their neural activity is conducted through the different elements of the head, the forward model can be defined. The forward model defines the relationship between the location of each dipole in the source space and its corresponding electric field as measured by the electrodes on the scalp. From the forward model, multiple solutions can be simulated to explain the ERP’s topography. The generators that have the best fit in explaining the activity are suggested as sources.

To obtain the most accurate inverse solution, the forward model should be generated with a unique boundary element model for each subject on the basis of that subject’s MRI scans (Henson, Mattout, Phillips, & Friston, 2009). Also, the electrode positions should be digitally located on each subject’s head so that their positions can be coregistered in the head model (Dalal, Rampp, Willomitzer, & Ettl, 2014). However, because source localization with EEG is relatively coarse, a structural MRI template can be used as the model for all subjects, with a template electrode montage that approximates the electrode positions of the actual recording. Although using a template can reduce the accuracy of the source localization and can move the apparent location of the sources by several centimeters (Akalin Acar & Makeig, 2013), it can provide suggestive evidence for the neural sources of the ERP. Also, if the electrodes are positioned well on each subject’s head, the difference in electrode positions between actual and template montages can be minimized.

In sum, neural activity to stimulus events can be non-invasively recorded with EEG. If repeated presentations (epochs) are averaged, the average wave is the ERP. If the ERP is plotted as a topography at a particular interval after stimulus onset, the topography may provide some information about the neural sources. With source localization, the topography is used to estimate the most likely neural generators. However, because of the inverse problem, localization with EEG is not as accurate and precise as localization with fMRI or MEG.
6. Electrophysiological correlates of visual awareness

In research on awareness, tasks have been used in which some stimuli are perceived whereas others are not (Kim & Blake, 2005). If neural activity is also recorded during stimulus presentation, the contrastive analysis of the difference in neural activity between a perceived stimulus and a stimulus that is not perceived reflects the NCC (Aru et al., 2012). The logic of this contrastive analysis is that if the stimulus is physically identical across repeated stimulations, the differences in neural activity between perceived and unperceived stimuli should reflect only conscious processing (Frith et al., 1999).

This contrastive analysis has been mainly used in vision. From EEG recordings, two ERPs have been discovered. The earlier of these is the visual awareness negativity (VAN), a negative difference wave (aware minus unaware) about 200 ms after visual onset (Ojanen, Revonsuo, & Sams, 2003). The topography of VAN has its negative peak at occipital electrodes, and source localization suggests primary visual cortex and ventral occipital cortex (Koivisto & Revonsuo, 2010). The later ERP is the late positivity (LP), a positive difference wave about 300 ms after visual onset that has a positive peak at parietal electrodes (Wilenius & Revonsuo, 2007), with widespread sources in occipital and fronto-parietal areas (Koivisto & Revonsuo, 2010). These two ERPs have been repeatedly found in studies of visual awareness (Koivisto & Revonsuo, 2010).

However, there is a potential problem with the contrastive analysis used in most of these studies. According to Lamy et al. (2009), the contrastive analysis may not isolate awareness because it compares aware processing with a combination of unaware processing and no processing. To isolate awareness, stimuli that are processed and aware should be compared to stimuli that are processed and unaware.

The argument of Lamy et al. (2009) is captured by the high threshold model (see Figure 6.1). As described by Morales et al. (2015), the high threshold model includes two thresholds: A processing (or detection) threshold and an awareness threshold. Only stimuli above the detection threshold are processed, and stimuli above the detection threshold can fall either between the detection threshold and the awareness threshold, or above the awareness threshold. Thus, stimuli below the detection threshold are not processed at all, whereas stimuli above the detection threshold are processed either consciously or unconsciously. Supporting the possibility of unconscious processing (i.e., processing above the detection threshold but below the awareness threshold), previous research suggests that stimuli below the awareness threshold can be correctly responded to without awareness (Dehaene & Changeux, 2011). Critically, according to the model, stimuli rated
as unaware mix together two different types of processing: stimuli that were processed unconsciously, and stimuli that were not processed at all. As a consequence, the contrastive analysis of neural activity to stimuli rated as aware minus neural activity to stimuli rated as unaware captures not only the difference between conscious and unconscious processing but also the difference between conscious processing and a combination of unconscious and no processing (Lamy et al., 2009).

![Figure 6.1. The high threshold model. A stimulus can fall above or below two thresholds. The processing threshold determines whether a stimulus was processed at all by the brain. The awareness threshold determines whether a stimulus reached awareness. Adapted from Morales, Chiang, & Lau (2015).](image)

According to Lamy et al. (2009), awareness can be isolated if stimuli that are processed and aware are compared to stimuli that are processed and unaware. Importantly, this comparison should not include stimuli that are not processed at all (i.e., stimuli below the detection threshold). Only then can the contrast reveal proper NCC. To achieve this goal, Lamy et al. used a detection task with backward-masked stimuli presented in the four visual quadrants. Subjects indicated in which quadrant the stimulus appeared and then rated their awareness of the stimulus. The delay between the target and the mask was adjusted so that targets were reported as aware on 50% of trials. Neural activity to stimuli that were correctly localized and reported as aware were compared with neural activity to stimuli that were correctly localized and reported as unaware. Critically, task performance across all trials rated as unaware was well above chance, presumably indicating unconscious processing (i.e., the stimuli had fallen above the detection threshold but below the awareness threshold).
In their analyzes, Lamy et al. (2009) proposed an additional adjustment. They argued that some trials in the unaware correct condition were correct simply by chance. These trials were not guided by unaware processes because they fell below the detection threshold. The influence of these correct-by-chance trials was mathematically removed, leaving only chance-free trials in the unaware correct condition (i.e., trials that were localized correctly, presumably because of unconscious processing). With this adjustment, the difference between aware correct trials and unaware correct (chance-free) trials should properly isolate aware processes (Lamy et al., 2009).

Critically, when the authors used this new contrastive analysis, there was no statistically significant effect for VAN, but there was one for LP. Therefore, Lamy et al. (2009) argued that VAN reflects preconscious processing and that LP is the proper NCC.

6.1. Study I: Controlling for unconscious processing

6.1.1. Background

In a previous study, contrasting awareness with unawareness by controlling for unconscious processing did not yield a statistically significant effect for VAN (Lamy et al., 2009). Instead, LP was found to be the earliest neural correlate of visual awareness. On the basis of these findings, Lamy et al. argued that LP reflects visual awareness. In response, Koivisto and Grassini (2016) conducted a replication of the study by Lamy et al. with some modifications to increase the sensitivity to detect the early visual responses. Three main improvements were made: First, larger stimuli were used. Second, neural activity was analyzed contralateral to the visual stimulus location. For example, the left occipital electrodes were analyzed for stimuli presented in the right visual field, because the left hemisphere processes visual information presented in the right hemifield (and vice versa). Third, a detection task with a single stimulus was used to avoid any influence of the visual stimulation of the mask, which was used in the backward masking task by Lamy et al. Stimuli were calibrated to the awareness threshold. Unlike the results by Lamy et al., results showed that the contrast between aware correct and unaware correct trials resulted in VAN as the earliest neural correlate of visual awareness.

Because these two studies found mixed results despite their similar experimental settings, the main goal of Study I was to replicate and extend these studies. In addition, we wanted to see whether VAN varies with stimulus size. Because the difference between the results of the two previous studies might have been due to the small stimuli used in the Lamy et al. study, which may not have elicited a detectable VAN, we compared large and small stimuli. These stimulus sizes were comparable to the ones used in the previous studies. If VAN is an indirect measure of local recurrent processing or feedback activity that enables vision with high resolution (Bullier,
2001), then a large stimulus that covers a large area of the visual cortex should generate a larger VAN than a small stimulus.

Before any data collection, we preregistered our hypotheses, sampling plan, and methods, and the statistical analyzes that we planned to conduct, in as much detail as possible. To establish the predictive value of a theory, the theory should be first constructed and then tested, not the other way around. If the theory is constructed on the basis of the data, this is known as hypothesizing after the results are known (Kerr, 1998). In fact, any story can be construed after picking out any significant effects from a data set (Gelman & Loken, 2013). Note that hypothesizing after the results are known is different from exploring the data and coming up with new hypotheses to test by collecting new data. This explorative approach is as important as hypothesis testing because it can generate new ideas that can be tested in future research. However, for hypothesis testing, it is important to preregister the hypotheses and the statistical analyzes because the more variables and tests conducted, the higher the probability of a statistically significant result by chance. In EEG research, there are almost endless possibilities to find and select statistically significant effects (Luck & Gaspelin, 2017). The huge data sets (channels and intervals) and analytic flexibility post a substantial risk for false positives. Because this risk can be reduced with preregistration (Nosek, Ebersole, DeHaven, & Mellor, 2018), it is important to preregister research before data collection. In all the studies conducted in this thesis, electrodes and time intervals, as well as hypotheses, were preregistered to minimize this risk.

In all studies in this thesis, the Bayesian statistical approach was used, because there are several problems with the classical statistics approach. From observed data, null hypothesis significance testing (NHST) cannot distinguish among evidence for the null hypothesis, evidence for the alternative hypothesis, and the lack of evidence for either hypothesis (Dienes & McLatchie, 2018). Instead, only a two-way distinction can be made. A significant result provides evidence for the alternative hypothesis (in terms of the probability of the data given the null), but a nonsignificant result does not tell whether there is a lack of evidence for either hypothesis or evidence for the null. To know how much the data support one theory over some other theory, Bayesian statistics can be used. In Bayesian statistics, two models are needed, plus the model of the data (Dienes, 2008). One model models the prior probability of the effect: what we expect to see based on our a priori theory. For example, a normal distribution around an expected effect could be used. Half of a normal distribution can be used if the effect is expected to only go in one direction and to be more likely close to zero than large. Flat priors can also be used, where all effects are modelled to be equally likely. However, in psychology, all effect sizes are rarely equally likely. For example, it is unrealistic to have ERP amplitudes above a few µV. The second model models what we would
expect to see if our theory were wrong: usually a stick function at zero to model the null hypothesis of an effect size of zero. Last, the data are modelled as a normal distribution because data are usually normally distributed (Dienes & McLatchie, 2018).

6.1.2. Method
Thirty-five subjects participated in the study. Stimuli were low-contrast sinusoidal Gabor patches: one large Gabor with the same size and properties as the one used by Koivisto and Grassini (2016), and one small Gabor with a similar size to the stimuli used by Lamy et al. (2009). Subjects participated in two separate sessions: one session with the large Gabor size, and one with the small Gabor size (counterbalanced order). At the beginning of each session, a staircase procedure was used to calibrate the duration of the Gabor to be reported as aware on about 50% of trials (individual awareness threshold). In the experiment, there were three trial types: critical, control, and catch trials. In critical trials, the Gabor was presented at the individual awareness threshold; in control trials, a longer-duration Gabor was presented; and in catch trials, there was no stimulus. In every trial (see Figure 6.2), a fixation cross was displayed for 1200 ms, followed by no stimulus or a Gabor that was displayed in one of the four visual quadrants. After stimulus presentation, subjects provided two responses. First, they responded about the stimulus location with four buttons corresponding to the visual quadrants. Second, they rated their awareness on a modified perceptual awareness scale with three responses: (1) I saw the stimulus clearly, (2) I saw the stimulus weakly, or (3) I did not see the stimulus.

![Figure 6.2. The time course of a trial.](image-url)
Throughout the experiment, high-density EEG was recorded from 64 electrodes. Trials were categorized depending on subjects’ responses into four categories: aware correct, unaware correct, aware incorrect, and unaware incorrect. The aware category contained trials rated as clearly or weakly seen; the unaware category contained trials rated as not seen.

6.1.3. Results
The behavioral results suggested that performance on the unaware correct trials was at chance (i.e., 25%). Therefore, computing ERPs for chance-free unaware correct trials was not feasible. As shown in Figure 6.3, VAN was found as a negative difference wave between aware and unaware correct for large and small Gabors between 180 and 280 ms after stimulus onset. The topography of VAN revealed that the voltages were maximal at contralateral occipital electrodes in relation to the stimulated visual hemifield (Figure 6.4). As shown in Figure 6.5, LP was found as a positive difference wave between aware and unaware correct for large and small Gabors between 350 and 550 ms after stimulus onset. For the topography of LP, the voltages were maximal at parietal electrodes (Figure 6.6).

![Figure 6.3](image-url) Figure 6.3. ERPs for contralateral occipital electrodes (O1 and O2). The upper panel shows VAN for large and small Gabors. The lower panels show ERPs for aware-correct, unaware-correct, and unaware-incorrect trials for large Gabors (left) and small Gabors (right). Gray areas indicate the preregistered interval from 180 to 280 ms after stimulus onset.
Priors were modeled as a Cauchy distribution (distribution \( r = 0.707 \)). Bayesian \( t \) tests for each Gabor size supported the presence of VAN for large \((n = 24, BF_{10} > 70)\) and small \((n = 15, BF_{10} > 110)\) Gabors, and LP for large \((n = 24, BF_{10} > 62,000)\) and small \((n = 15, BF_{10} > 40)\) Gabors. Because of our strict but reasonable exclusion criteria, only 13 subjects completed both sessions with each Gabor size, so only their data were used in a paired-samples Bayesian \( t \) test. We also explored results from a larger sample \((n = 39)\) that included as many subjects as possible and tested the difference between the Gabor sizes with an independent-samples Bayesian \( t \) test. Results suggested that there was no difference between large and small \((n = 13, BF_{10} > 3)\) Gabors for VAN.

**Figure 6.4.** Topographies of VAN for left and right visual fields (columns) and large and small Gabors (rows) from 180 to 280 ms after Gabor onset. The scale ranged from −1.5 (blue) to 1.5 µV (red).
= 13 and 39, BF$_{01} > 3$) and LP ($n = 13$, BF$_{01} > 3$). The difference between large and small Gabors for LP with the larger sample ($n = 39$) was inconclusive (BF$_{01} = 1.85$).

**Figure 6.5.** ERPs for parietal electrodes (P1, Pz, and P2). The upper panel shows LP for large and small Gabors. The lower panels show ERPs for aware-correct, unaware-correct, and unaware-incorrect trials for large Gabors (left) and small Gabors (right). Gray areas indicate the preregistered interval from 350 to 550 ms after stimulus onset.
6.1.4. Discussion

The main results were that for both Gabor sizes, VAN, as well as LP, was found to correlate with visual awareness. Thus, possible reasons why Lamy et al. (2009) did not find VAN are that their stimuli were presented at a more peripheral location in the visual field and that their stimuli had lower spatial frequency. These are physical properties known to reduce the size of the N1 (Capilla et al., 2016; Mihaylova, Hristov, Racheva, Totev, & Mitov, 2015). Another possible reason is that Lamy et al. used masking to manipulate awareness (Koivisto & Grassini, 2016).

Results provided some evidence that there was no effect of Gabor size on VAN and LP. However, because the mean duration of the small Gabor (51.6 ms) was longer than the mean duration of the large Gabor (25.9 ms), the present data do not resolve the question of whether size per se would have an effect on the VAN (as differences in duration are a potential confound of stimulus size). In the present study, Gabor size may not have had an effect on VAN if the neural summation needed for the small, 52-ms Gabor to reach awareness approximately equalled the neural summation needed for the large, 26-ms Gabor to reach awareness. Another explanation is that because the effect size of Gabor size may be very small, it was not possible to detect any differences between the Gabor sizes with EEG and with the number of trials that we used.

The VAN had lateral occipital topography corresponding to the retinotopic organization of early visual areas. As seen in Figure 6.4, Gabors shown in the left visual field resulted in negativity...
at the right occipital electrodes, and Gabors shown in the right visual field resulted in negativity at the left occipital electrodes. The timing and location of VAN fits well with local recurrent processing (Lamme & Roelfsema, 2000). LP showed a large positivity distributed across the posterior part of the head. The timing and spatial distribution of LP fits well with widespread global recurrent processing (Dehaene & Changeux, 2011; Lamme, 2006).

6.2. Insights after publication

In the publication (Eklund & Wiens, 2018), we did not mathematically control for performance because unaware performance was apparently at chance (i.e., mean performance was about 25%). However, we subsequently discovered that we had incorrectly calculated unaware performance as the percentage of unaware-correct trials among all trials. Instead, it should be expressed as a percentage of all trials rated as unaware. Accordingly, unaware performance (in percent) is the number of unaware-correct trials divided by the sum of the number of unaware-correct trials and the number of unaware-incorrect trials, and this number is multiplied by 100. If calculated correctly, unaware performance (see Figure 6.7) was above 25% for both small Gabors, \( M = 42.05\% \), 95% CI [36.38, 37.72] and large Gabors, \( M = 46.15\% \), 95% CI [40.0, 52.30]. Because performance was well above chance, the mathematical correction could have been performed according to Lamy et al. (2009).

However, there is a theoretical problem with the correction proposed by Lamy et al. (2009) that is captured by the high threshold model (Morales et al., 2015), as discussed in section 6 and shown in Figure 6.1. According to SDT (Macmillan & Creelman, 2005), processing of a stimulus is not binary (i.e., either processed or not processed above the detection threshold). Instead, the repeated presentation of a physically identical stimulus elicits internal responses that vary in strength on a normal distribution. The internal responses vary because on every trial, the internal processing of the stimulus is combined with internal noise. A strong internal response reflects a strong percept, and a weak internal response reflects a weak percept. If the internal response does not reach the subject’s criterion for awareness, the subject will report unawareness (Macmillan, 1986). Accordingly, a stimulus could theoretically get processed with a fairly strong internal perceptual response but not reach the awareness criterion.

In contrast, the correction by Lamy et al. (2009) assumes that stimuli fall above or below a strict binary detection threshold. Because SDT implies that this assumption is incorrect, the correction by Lamy et al. will not remove the influence of trials with no processing. Another difficulty with the high threshold models is that stimuli are frequently (2 to 3%) incorrectly localized but still rated as aware (Eklund & Wiens, 2018; Lamy et al., 2009), something that does not make
sense according to the high threshold model: If a stimulus is incorrectly localized, it must have been processed below the detection threshold and also below the awareness threshold. Thus, stimuli that are incorrectly localized should be reported as unaware rather than as aware. According to SDT, however, these trials can be explained with noise that results in a strong enough internal perceptual response that the stimuli are rated as aware. Notably, when the Lamy et al. correction was applied to simulated ERP data, it did not perform as intended and is thus incorrect in threshold tasks (Morales et al., 2015).

In contrast to the correction by Lamy et al. (2009), Morales et al. (2015) applied an SDT perspective to correct for unconscious processing. Under the assumption that “[neural] activation intensity is linearly determined by the internal response” (Morales et al., 2015, p. 7), the weak internal responses to unaware-correct trials can be scaled to the same level as the strong internal.

Figure 6.7. Percent unaware-correct for individual subjects for small Gabors (closed circles) and large Gabors (open circles). Mean unaware performance was above chance (>25%) for small (dashed) and large (dotted) Gabors.
responses to aware-correct trials. The scaling factor can be calculated from the behavioral data by using SDT. If applied, this correction may equate unconscious processing in the unaware-correct trials to that in the aware-correct trials. The difference between aware-correct trials and unaware-correct (adjusted) trials should therefore isolate processes related to awareness.

To apply the correction by Morales et al. (2015), sensitivity ($d'$) and awareness criteria need to be estimated from the behavioral data for each quadrant. In a four-alternative forced-choice task, sensitivity can be easily calculated if one assumes that there was no response bias (Macmillan & Creelman, 2005). However, in our data (Study I), the distribution of responses for the individual quadrants for each subject shows that many subjects had a strong bias towards certain quadrants (even if we explicitly told them not to). For example, some subjects responded the same quadrant whenever they reported not seeing the Gabor. This resulted in no correct trials in any of the other quadrants. Calculating sensitivity and response bias for each quadrant can be done, but it is more complicated (DeCarlo, 2012). Because the correction by Morales et al. does not take response bias into account, it is unclear how the model could be applied to our data.

Critically, I argue that the correction suffers from two general problems besides this practical problem. First, the correction by Morales et al. (2015) (and the correction developed by Lamy et al. 2009) assumes that unconsciously processed information can affect performance. An alternative explanation is that a conservative awareness criterion (Macmillan, 1986; Macmillan & Creelman, 2005) can result in a weak experience being misclassified as no experience. In this case, the internal perceptual responses should, on average, be stronger for trials that are localized correctly but reported as unaware than for trials that are localized incorrectly but reported as unaware. As can be seen for our data in Figure 6.3, correct trials rated as unaware showed a substantial early negativity compared to incorrect trials rated as unaware. This negativity had the same timing as the negativity in correct trials rated as aware. The same pattern can be seen for the P3 in Figure 6.5. Accordingly, subjects may have had information about the stimulus but did not report this information because of a conservative awareness criterion. Because subtracting trials reported as unaware (diluted by some trials accompanied by awareness) from trials reported as aware would reduce the difference of the contrastive analysis, our estimate of the ERP correlate of visual awareness would be conservative.

Second, Morales et al. (2015) assume that the internal perceptual response reflects processing of the physical stimulus properties, not awareness. Also, processing reflecting awareness is considered qualitatively different from the low-level processing of sensory information. However, if the internal perceptual response actually reflects awareness, the correction will not isolate
awareness but, rather, will completely remove processing related to awareness. Accordingly, isolating awareness by matching the internal perceptual response of aware trials and unaware trials only works if awareness-related processing is different from sensory processing.

Critically, this assumption that the internal perceptual response reflects only unaware processing is questionable. It has been suggested that awareness is a gradual phenomenon (Sandberg et al., 2010) and that awareness is indexed by local recurrent processing in sensory areas (Lamme, 2006). If so, it is possible that local recurrent processing is perfectly correlated with the internal perceptual response so that the level of recurrent processing matches the strength of the internal perceptual response.

Furthermore, if awareness or unawareness is decided upon depending on whether the internal perceptual response is above the awareness criterion, then what is the awareness criterion, and what is the difference between trials just above the awareness criterion and trials just below it? The awareness criterion may reflect the level of the internal perceptual response at which the percepts reaches reportability. This implies that a stimulus presentation can result in awareness without being reportable. This is the “neural argument” put forward by Lamme (2010): The level of localized recurrent processing indexes the level of awareness, and local recurrent processing in visual areas can occur without the percept reaching the level of reportability. Indeed, early activity in visual cortex is associated with the reported strength of perception if measured with a perceptual awareness scale (Andersen, Pedersen, Sandberg, & Overgaard, 2016). Also, activity already in V1 closely matches perception (Lamme, Supér, Landman, Roelfsema, & Spekreijse, 2000; Michel, Chen, Geisler, & Seidemann, 2013; Schwarzkopf, Song, & Rees, 2011; Silvanto et al., 2005).

Accordingly, if local recurrent processing is perfectly correlated with the internal perceptual response, mathematically scaling the internal perceptual response of percepts below the awareness criterion to the level of percepts above the awareness criterion would isolate processing related to reportability. Thus, the correction would remove processing related to awareness to isolate post-perceptual processes. Post-perceptual processing involves activity that is different from awareness-related activity but perfectly correlated with awareness, such as planning a report of the experience (Pitts, Metzler, & Hillyard, 2014; Tsuchiya et al., 2015). Indeed, the Morales correction assumes that awareness is something extra, beyond sensory processing: “When controlling for performance capacity in imaging studies, researchers should focus on controlling for the internal response strength . . . . In imaging studies of consciousness, this means isolating some kind of further processing which only happens during trials crossing the awareness criteria.” (Morales et al., 2015, p. 9). The correction by Morales assumes that awareness is something different from sensory processing, an assumption that is questionable.
In general, the argument is reasonable that unconscious processing needs to be controlled for (irrespective of whether it affects performance). Not all activity related to the processing of a stimulus reaches awareness (Lamme & Roelfsema, 2000). However, how this should be done is not clear. Maybe the normal contrastive analysis is enough to isolate awareness (Aru et al., 2012; Crick & Koch, 1990).

To conclude, if local recurrent processing in respective primary sensory areas is an index of awareness, the contrastive analysis will isolate neural activity to percepts strong enough to be reported as aware and thus will be a conservative estimate of the NCC together with any post-perceptual processes. We replicated the studies of Lamy et al. (2009) and Koivisto et al. (2016), and our results suggested that VAN and LP are NCC. However, it is unclear whether VAN or LP is confounded by potential unconscious processing and whether LP is related to awareness, post-perceptual processing, or both. Also, whether corrections for performance should be used depends on how aware processing is defined. If awareness is related to the internal perceptual response, as implied by the recurrent processing theory (Lamme, 2006), the use of a signal detection correction (Morales et al., 2015) may remove awareness-related activity altogether.
7. Neural mechanisms of auditory processing

The second aim of this thesis was to investigate whether the electrophysiological correlates of auditory awareness are similar to those found in vision. To determine whether the processes in hearing are similar to those in vision, it is important to understand how auditory information is processed by the brain.

On top of the human temporal lobe are the transverse temporal gyri (or Heschl's gyri), the location of the primary auditory cortex (A1) in humans (Formisano et al., 2003; Kaas & Hackett, 2000). For a sound to reach the primary auditory cortex and result in awareness, it has to be converted from pressure waves into electrical and chemical signals by the nervous system. As described by Goldstein (2009), this is first done by the outer hair cells inside the liquid-filled cochlea. The vibrations of the air are amplified in the middle ear and transferred to the liquid of the cochlea. When the liquid is vibrating, the outer hair cells bend and transduce the vibrations into electrical signals that are passed on by the auditory nerve to the cochlear nucleus, superior olivary complex, inferior colliculus, auditory thalamus, and finally to the auditory cortex.

The monkey auditory cortex is also located on the superior temporal cortex and can be divided into 13 areas on the basis of cytoarchitectonics, connectivity patterns, and invasive cell recordings (Hackett et al., 2014; Kaas & Hackett, 2000). The auditory cortex can be separated into three main divisions: the core, belt, and parabelt areas. These are further divided into smaller areas. The core receives most of its input from the thalamus and then outputs the information to the hierarchically higher belt and parabelt areas (Hackett et al., 2014).

Neurons in most of the auditory cortex have unclear receptive fields that respond to many types of auditory input. Neurons that preferably respond to sound frequency, duration, and amplitude are found in lower auditory areas such as the inferior colliculus (King & Nelken, 2009). The inferior colliculus is a major processing station between the cochlea and the thalamus and is thought to process information at a comparable level to the information processed by V1 in vision. Because the auditory cortex is much higher up in the hierarchy, its receptive fields are more complex, making it hard to map (King & Nelken, 2009). However, general frequency gradients (tonotopic maps) have been found within most areas of the auditory cortex. Similar to retinotopic maps in visual cortex, the tonotopic maps in auditory cortex show frequency gradients that are reversed from one auditory area to the next connecting at the same frequency. That is, one area is mapped from high to low frequency in one direction and connects to the neighboring area by the low frequency. The neighboring area is mapped from low to high frequency. This tonotopic organization has been studied invasively in monkeys (Kaas & Hackett, 1998) and with fMRI in humans.
(Formisano et al., 2003). Besides tonotopic maps and amplitopic maps (sound intensity gradients), other receptive fields of the auditory cortex have not been located (Schreiner & Winer, 2007).

Neuronal communication within auditory cortex is very similar to communication within visual cortex. Feedforward connections mainly terminate in layer 4, and feedback and horizontal connections mainly terminate in the supragranular and infragranular layers (Kral & Eggermont, 2007). Basic features are processed in lower areas, and this information is output to higher areas that process object type information (Kral, Yusuf, & Land, 2017). Higher auditory areas (belt and parabelt) send feedback to lower auditory areas, thereby reshaping their receptive fields (Fritz, Shamma, Elhilali, & Klein, 2003; Kral et al., 2017).

Not much evidence exists of the specific neural activity correlated with auditory awareness in early auditory areas. Brosch, Schulz, & Scheich (1998) measured multiunit and local field potentials from primary auditory cortex in macaque monkeys as two tones were played in rapid succession. The goal was to find the neural correlates of the backward masking effect (i.e., the second tone masks the first tone). To vary the masking effect, the interstimulus interval between the two tones was varied. Single tones resulted in a strong early response followed by a later response. If the second tone overlapped with the late response of the first tone, the late response was suppressed. Unfortunately, the monkeys did not do any active task that allowed responses to indicate detection of the second tone. Therefore, we cannot know whether suppression of the later response resulted in unawareness of the first tone. One interpretation of the data is that the early response corresponds to the early feedforward activity and the later response corresponds to feedback. If feedback activity is suppressed, awareness of the tone should be affected, just as in vision (Supèr et al., 2001).
8. Electrophysiological correlates of auditory awareness

In electrophysiological research on awareness, more has been done in vision than in hearing. An early, classical study in hearing used a detection task in which subjects detected tones at their detection threshold (Hillyard, Squires, Bauer, & Lindsay, 1971). Three subjects were asked to detect tones (50% probability of presence) that were played with white noise in the background. EEG was recorded from a central electrode (vertex) referred to the right mastoid electrode (the mastoid is the bone behind the ear). Two ERPs were averaged from tone-present trials: one for detected tones (hits) and one for undetected tones (misses). The ERP to detected tones showed an N1 for one subject and a P3 for all three subjects. Undetected tones were essentially flat. These results were replicated and extended with more subjects in three subsequent studies (Parasuraman & Beatty, 1980; Paul & Sutton, 1972; Squires et al., 1973).

In the first of these studies (Paul & Sutton, 1972), EEG was recorded from vertex as tones at the detection threshold were played, and the response criterion was varied either with payoffs or by changing the number of catch trials. Results suggested that the N1 was unaffected by the criterion. For both manipulations, the P3 to hits was smaller if a liberal criterion was adopted than if a conservative criterion was used. If subjects adopt a conservative criterion, the detection of a tone will be reported only if they are very confident that they heard a tone. Thus, the P3 amplitude correlated positively with confidence of detection.

In the second study (Squires et al., 1973), EEG was recorded from vertex as tones at the detection threshold were played. In addition, confidence of detection was measured with a rating scale. Results suggested that N1 and P3 were larger and had shorter latency to tones that were detected with high versus low confidence. The authors suggested that the N1 is related to signal strength in line with SDT (Macmillan & Creelman, 2005). Accordingly, although the signal is physically the same on every repetition of a signal, the perceived signal strength varies (and this internal perceptual strength is normally distributed). Some tones are perceived as louder than other tones, and the N1 amplitude and latency is related to tone level (Picton, Woods, Braun, & Healey, 1977). To investigate whether the N1 level increases with signal strength, Squires et al. (1973) included a passive task in which the tone level was varied. Results confirmed that the N1 became larger and had an earlier latency as the tone level was increased. Interestingly, the tones detected with highest confidence in the active task elicited an N1 amplitude and latency that were equal to those elicited by an 8-dB louder tone in the passive task, suggesting that internal perceptual signal strength may be reflected by the N1 amplitude and latency.
In the third study (Parasuraman & Beatty, 1980), EEG was recorded from central electrodes as tones with different frequencies at the detection threshold were played. Subjects performed a detection and discrimination task. They first provided confidence ratings and then had to identify the pitch of the tone. Results suggested that irrespective of pitch, the N1 and P3 were larger to tones detected with high confidence than to those detected with low confidence. Tones that were detected and correctly identified showed larger P3 than detected tones that were incorrectly identified. By measuring confidence, the same relationship between confidence and the P3 was found as in previous studies (Paul & Sutton, 1972; Squires et al., 1973). Because N1 was unaffected by identification performance, the N1 may be related to the perceived signal strength.

More recently, an informational masking task was used to study the neural correlates of auditory awareness (Gutschalk, Micheyl, & Oxenham, 2008). In this task, a stream of target tones is played among multiple non-target tones with random frequency in the background. This background cloud of tones induces informational masking, rendering the stream of target tones hard to detect (multitone masking). The target tones are separated in frequency from the non-target tones to prevent physical masking. In the study, subjects were instructed to press a button as soon as they detected the stream of target tones. Concurrently, neural activity was measured with MEG. Detected target tones elicited an awareness-related negativity 50 to 250 ms after tone onset, starting about two tone repetitions before the stream of target tones was detected.

In another study, a similar multitone masking task was used as invasive electrocorticography was recorded from presurgical epilepsy patients (Dykstra, Halgren, Gutschalk, Eskandar, & Cash, 2016). Target tones elicited an awareness-related negativity 50 to 250 ms after tone onset in auditory cortex and a P3-like positivity 300 to 600 ms after tone onset in frontal and temporal cortex. A negativity related to detection was replicated in another study (Dykstra & Gutschalk, 2015), which investigated the effect of awareness on mismatch negativity. To obtain the mismatch negativity with EEG, the ERP to frequent standard tones is subtracted from the ERP to rare deviant tones (Szychowska, Eklund, Nilsson, & Wiens, 2017; Wiens, Szychowska, Eklund, & Berlekom, 2019; Wiens, van Berlekom, Szychowska, & Eklund, 2019). To manipulate awareness, a multitone masked stream of target tones was played that contained standard and deviant tones (Dykstra & Gutschalk, 2015). Subjects were instructed to press a button when the stream of target tones was detected. As a result, detected target tones elicited an awareness-related negativity, whereas undetected target tones did not. Deviant target tones resulted in a larger negativity than standard target tones, and this mismatch negativity was only observed to tones that were detected.
8.1. Study II: Awareness negativity in hearing

8.1.1. Background
Because there is a lack of EEG studies on auditory awareness, the main goal of Study II was to replicate the very early studies that used signal detection tasks with tones at the detection threshold (Hillyard et al., 1971; Parasuraman & Beatty, 1980; Paul & Sutton, 1972; Squires et al., 1973). In these early studies, yes or no answers or confidence ratings were used, but no contrastive analysis (aware minus unaware) was conducted to isolate awareness. In our study, we wanted to conduct the contrastive analysis to isolate the effects of awareness (Aru et al., 2012). Also, we used the subjective perceptual awareness scale to find the individual awareness threshold (Sandberg et al., 2010). Thus, we wanted to make the experimental design comparable to that of previous studies in vision that used perceptual awareness ratings (Eklund & Wiens, 2018; Koivisto & Grassini, 2016).

As in previous experiments on visual awareness, we expected to find a negative difference between trials rated as aware and trials rated as unaware. Our best guess was that this negativity would overlap the N1 component in time and space (topography). Therefore, we preregistered to expect a negativity at central electrodes (Squires et al., 1973) at an interval at which the peak of the N1 to control trials would be at its maximum.

8.1.2. Method
The final sample from two separate experiments consisted of 49 subjects (24 in experiment 1 and 25 in experiment 2). Stimuli were 100-ms, 1000-Hz pure tones. There were three trial types: critical, control, and catch trials. In critical trials, the tone was played at the individual awareness threshold; in control trials, tones were 10 dB above this threshold; and in catch trials, there was no tone. In each trial, a fixation cross was presented for 1000 ms with a tone played (or no tone) at 500 ms after fixation onset. Subjects rated their experience with three buttons corresponding to “I did not hear any stimulus,” “I heard the stimulus weakly,” and “I heard the stimulus clearly.” Before the experiment, a staircase procedure was used to calibrate the level of the tone to be heard weakly or clearly on about 50% of trials (individual awareness threshold).

Throughout the experiment, EEG was recorded from six central and parietal electrodes. Trials were categorized depending on responses into two categories: aware (clearly or weakly heard) and unaware (not heard).
8.1.3. Results and discussion

For the first experiment, as seen in Figure 8.1A, no negativity was observed in the preregistered interval between 94 and 194 ms (see gray area in figure). A Bayesian $t$ test suggested no difference between trials rated as aware and trials rated as unaware for this preregistered interval ($BF_{10} = 2.70$). However, as seen in Figure 8.1B, a late positivity (LP) was observed at the parietal electrode, as supported by a Bayesian $t$ test ($BF_{10} > 45,000$) for the preregistered interval (see gray area in figure).

Because there was some support for no negativity in the preregistered interval (between 94 and 194 ms), we stopped the experiment. However, an apparent negativity was visible at a later interval between 140 and 240 ms after stimulus onset (see Figure 8.1A). In retrospect, this finding is not surprising because the latency of the N1 is affected by tone intensity (Picton et al., 1977; Squires et al., 1973). Because critical trials were 10 dB lower than control trials, the N1 to critical tones was likely to occur later than the N1 to control tones. Because the preregistered interval was too early, we preregistered the later interval and conducted a second experiment.

For the second experiment, as seen in Figure 8.1C, a negativity (auditory awareness negativity, AAN) was observed in the preregistered interval and was supported by a Bayesian $t$ test ($BF_{10} = 5.90$). As seen in Figure 8.1D, the LP was also observed and was supported by a Bayesian $t$ test ($BF_{10} > 80$).

The main finding of Study II was that the electrophysiological correlates of auditory awareness are strikingly similar to the electrophysiological correlates of visual awareness. Just as low-contrast visual stimuli elicit an early negativity (VAN) and a late positivity (LP), low-intensity auditory stimuli elicit an early negativity (AAN) and a late positivity (LP). These electrophysiological correlates of awareness fit very well in time with local and global recurrent processing.
8.2. Study III: Manipulating the response requirement and localizing AAN

8.2.1. Background

Introspection and manual responding are almost always required from subjects in tasks in which stimuli have to be detected or discriminated. If these tasks are used to conduct a contrastive analysis, decision making and motor preparation could be potential confounds. For example, if a stimulus has been consciously perceived, the nature of the task requires that the content be kept in working memory and that decisions be made about this content. Such post-perceptual processes would be added on top of perception in trials rated as aware compared to trials rated as unaware (Pitts, Metzler, et al., 2014). Notably, some argue that there is no division between perception and
reflection upon the percept, as the reflection upon the experience defines consciousness (Dehaene & Changeux, 2011; Dehaene & Naccache, 2001). Nonetheless, if perception is separate from cognition (Block, 2005), manipulating the manual response requirement should make it possible to dissociate perception from the post-perceptual processing steps of responding manually to the stimuli.

Recently, new no-response tasks were introduced in which subjects must attend to visual stimuli without having to make overt manual responses to indicate their contents of consciousness. Instead, subjects’ perception is measured indirectly (Tsuchiya et al., 2015). For example, in a binocular rivalry task (Frässle, Sommer, Jansen, Naber, & Einhäuser, 2014), stimuli were either dynamic, inducing tiny involuntary eye movements, or static, with changes in luminance inducing changes in pupil size. As the two stimuli were presented, one to each eye, perception switched between the left and the right stimulus. Before the main experiment, subjects reported their fluctuating percept with a button press. This was done to verify and validate the robustness of the eye measures. In the main experiment, only eye measures were used to track perception. Findings suggested occipital and parietal activation related to perception in the passive viewing task and additional frontal activation in the active response task. Several studies with no-response paradigms suggest that activity in the posterior cortical areas rather than the prefrontal cortex correlates with visual awareness (for a review, see Koch, Tononi, Massimini, & Boly, 2016), consistent with recurrent processing theory (Lamme, 2006).

Koivisto, Salminen-Vaparanta, Grassini, & Revonsuo (2016) devised a task to separate the neural activity of responding manually from that of awareness in vision. On each trial, a Gabor patch was presented at the individual awareness threshold, and subjects reported their awareness of the Gabor in two different response conditions. In one condition, subjects pushed a button if they were aware of the Gabor and withheld responding if they were unaware of the Gabor. The other condition was reversed: Subjects pushed a button if they were unaware of the Gabor and withheld responding if they were aware of the Gabor. From these conditions, two difference ERPs were calculated: the response ERP and the no-response ERP. The response ERP was computed from trials in which subjects pressed a button to indicate either awareness or unawareness, and the no-response ERP was computed from trials in which subjects did not press a button to indicate either awareness or unawareness. Thus, the contrastive analysis could be conducted for the response and no-response conditions separately.

Kovisto et al. (2016) argued that if the requirement to press a button confounds the NCC, then there should be a difference between the response ERP and the no-response ERP. Results suggested that the LP was larger to response trials than to no-response trials, whereas the response
manipulation had no (statistically significant) effect on VAN. Because LP was affected whereas VAN was apparently unaffected, the authors suggested that VAN reflects visual awareness whereas LP is not a pure measure of awareness and reflects post-perceptual processes (Koivisto et al., 2016).

In hearing, the N1 has been found in passive tasks, whereas P3 appears when the stimuli have to be responded to (Hillyard et al., 1971; Squires et al., 1973). However, in these passive tasks, subjects did not attend the sounds, and awareness was not measured. In one study (Shucard, Abara, McCabe, Benedict, & Shucard, 2004), EEG was recorded, and the task was to detect auditory target syllables among non-target syllables, either with a manual response or by mentally noting them without any manual response. The P3 to targets detected by a manual response was larger than the P3 to targets detected by mentally noting them. Non-targets did not show any P3. The N1 was the same in all conditions because the syllables were presumably well above the awareness threshold. Accordingly, the P3 should differ between manual responding and withholding of manual responding for auditory stimuli, just as was found in vision.

The main goal of Study III was to investigate whether the effects in vision can be replicated with auditory stimuli. We used a tone-detection task and manipulated the response requirement of reporting awareness in two conditions, similar to the design by Koivisto et al. (2016). Tones were presented at each subject’s individual awareness threshold, and neural activity related to awareness was measured. Trials with manual responses were compared with trials in which no manual responses were required. We expected AAN to be unaffected by the response manipulation, whereas we expected the LP to be larger to response trials than no-response trials. To explore the neural generators of AAN, we recorded high-density electroencephalography with 64 electrodes, rather than only a few electrodes.

8.2.2. Method

The final sample consisted of 52 subjects. Stimuli were 100-ms, 1000-Hz pure tones. There were three trial types: critical, control, and catch trials. In critical trials, the tone was played at the individual awareness threshold; in control trials, tones were 10 dB above this threshold; and in catch trials, there was no tone. In each trial, a fixation cross was presented for 500 ms with a tone played (or no tone) at the fixation offset. Subjects were required to respond in two different conditions: In one condition, subjects pressed the spacebar on a keyboard if they heard the tone weakly and did not press the spacebar if they did not hear the tone. In the other condition, subjects pressed the spacebar if they did not hear the tone and did not press the spacebar if they heard the tone. Before the experiment, a staircase procedure was used to calibrate the level of the tone to be reported as
heard on about 50% of trials (individual awareness threshold). In this staircase, subjects pressed two buttons, one to indicate awareness and the other to indicate unawareness. Throughout the experiment, EEG was recorded from 64 electrodes. Trials were categorized according to the subjects’ responses into four categories: aware response, unaware response, aware no-response, and unaware no-response. The contrastive analysis (aware minus unaware) was calculated separately from trials in which subjects pressed a button and from trials in which subjects did not press a button.

8.2.3. Results and discussion

As can be seen in Figure 8.2, the green line shows AAN peaking around 210 ms after stimulus onset followed by LP peaking at around 400 ms. AAN and LP look almost identical for response and no-response trials. Bayesian t tests supported the presence of AAN in response (BF$_{10}$ > 10,000) and no-response (BF$_{10}$ > 9,000) trials. A difference in AAN between response and no-response trials was inconclusive (BF$_{01}$ = 2.0). Thus, for the preregistered prior (−1 to 1 µV), more data would be needed. Bayesian t tests supported the presence of LP for response (BF$_{10}$ > 700) and no-response

![Figure 8.2. Mean ERPs across 15 central parietal electrodes. (A) ERPs to critical tones for response trials: aware (red), unaware (blue), and aware minus unaware (green). The gray intervals mark the preregistered intervals for AAN (160 to 260 ms) and LP (350 to 550 ms). (B) ERPs to critical tones for no-response trials. (C) Catch trials that subjects rated as unaware by responding (solid) or not responding (dashed). (D) Control tones that subjects rated as aware by responding (solid) or not responding (dashed).](image)
(BFₐ > 40,000) trials but inconclusive evidence for no difference between response conditions (BF₀₁ = 2.8). **Figure 8.3** shows the topographies of AAN as a central negativity and LP as a parietal positivity for both response conditions. As can be seen in **Figure 8.4**, source localization suggested bilateral auditory cortices for AAN and the N1 to control trials rated as aware. The early negative peak at about 150 ms after stimulus onset in **Figure 8.2** is probably a visual response to the offset of the fixation cross because it had a bilateral occipital component, as can be seen in **Figure 8.5**.

Before stopping recruitment, we ran simulations that sampled from our data to approximate how many subjects would be needed to support no difference for AAN and LP with our preregistered prior (assuming that our sample was representative of the population). The simulations suggested that for AAN, more than 300 subjects would be needed. For LP, about 230 would be needed. We therefore stopped our data collection because further increasing our already large sample size (n = 52) would not be worth the effort because of how many more subjects the simulation suggested that we would need to obtain a sufficient strength of evidence.

**Figure 8.3** Topographies of the mean amplitude difference between aware and unaware for response (top) and no-response trials (bottom). (A) AAN, from 160 to 260 ms after tone onset. (B) LP, from 350 to 550 ms after tone onset. The electrodes used for analysis are highlighted. The scale ranged from −1.9 (blue) to 1.2 µV (red).
We also ran exploratory analyzes of the difference between response and no-response trials for AAN and LP with the default prior used in JASP (Cauchy = 0.707). Results provided moderate support for no difference for AAN ($BF_{10} = 5.9$) and LP ($BF_{10} = 6.2$).

Results for LP suggest that contrary to our hypothesis, there is apparently no difference between responding and not responding. We expected LP to be affected by varying the response condition because such an effect was found in vision (Koivisto et al., 2016). As the tone is detected by the brain and reaches awareness, local recurrent processing starts in the auditory cortex. This could be reflected in the negativity in the aware condition around 200 ms after tone onset (N1). This information is then processed in working memory, and a decision is made on the basis of this information (Polich, 2007). Local recurrent processes develop into global recurrent processes involving the fronto-parietal network, and this activity is probably reflected by the positivity starting

![Figure 8.4. Source localization for AAN at 210 ms after stimulus onset (top row) and N1 to control trials rated as aware at 150 ms after stimulus onset (bottom row).](image)
about 300 ms after stimulus onset (P3). If the tone is not detected and does not reach awareness, no N1 is seen and a much weaker P3 is seen because there is no content for working memory (Pitts, Padwal, Fennelly, Martinez, & Hillyard, 2014). Because these same processing steps have to occur in both the response and the no-response conditions, there may not be much of a difference in the P3 between the aware response condition and the aware no-response condition. In support, Figure 8.6 shows that the ERPs were similar for response and no-response conditions. Further, as can be seen in Figure 8.2, the P3-like positivity in catch trials, which did not contain a tone at all, looks very similar to the P3 in unaware trials. This is true for response trials and no-response trials. Accordingly, the P3 was similar when there was no tone (in catch trials) and when the tone was not perceived (in unaware trials).

To conclude, AAN and LP were found but were apparently not affected by manipulating the response requirements. These results could be interpreted such that both AAN and LP are correlates of awareness and that they are not confounded by manual responding. However, it is possible that tasks in which stimuli have to be reflected upon are not optimal for dissociating awareness-related activity from post-perceptual processes. If the subject has to reflect upon the experience even if no response is required, the sensory information has to be transferred to working memory, which may be reflected by the LP. Finally, as an accidental demonstration of how the contrastive analysis isolates processing related to awareness, only VAN and the LP remained, and the activity associated with the fixation cross (see Figure 8.5) was removed.

![Figure 8.5](image-url)

**Figure 8.5.** Mean topographies of the visual component to the offset of the fixation cross between 120 and 180 ms. A bilateral occipital negativity can be seen in all conditions except for control trials in which it is covered by the strong auditory component. Note that the small square in the scale is the color range for critical and catch trials, whereas the full scale is for control trials.
Figure 8.6. Mean ERPs for response trials (A), no-response trials (B), the difference between aware minus unaware response trials and aware minus unaware no-response trials (C), aware response and aware no-response trials (D), unaware response and unaware no-response trials (E), and the difference between aware response trials minus aware no-response trials and unaware response trials minus unaware no-response trials (F).
9. General discussion

9.1. The electrophysiological correlates of visual awareness

If the visibility of a visual stimulus is calibrated to be at the awareness threshold, it will be reported as aware in half of the trials and reported as unaware in the other half of the trials (Kim & Blake, 2005). The contrastive analysis (Aru et al., 2012) of the neural activity to trials rated as aware minus the neural activity to trials rated as unaware results in an early negative difference wave (VAN) with its peak around 200 ms after stimulus onset and a late positive difference wave (LP) with its peak around 400 ms after stimulus onset (Koivisto & Revonsuo, 2010). Visual awareness may be reflected by one of these ERPs, or both.

However, the contrastive analysis may not isolate awareness because it compares aware processing with a combination of unaware processing and no processing. To control for no processing and to isolate awareness, Lamy et al. (2009) devised a procedure in which consciously processed visual information was presumably contrasted only with unconsciously processed visual information. Results suggested that only LP is a neural correlate of visual awareness. In response, Koivisto and Grassini (2016) conducted a modified replication of the study by Lamy et al. In their study, Koivisto and Grassini controlled for performance and used larger stimuli to have a higher sensitivity for early visual ERPs. Results suggested that VAN as well as LP were neural correlates of visual awareness.

Because the difference in stimulus size between the two studies could potentially explain the mixed results (Koivisto & Grassini, 2016; Lamy et al., 2009), we replicated these studies in Study I (Eklund & Wiens, 2018) with the addition of comparing large and small stimuli. The results of Study I suggested that VAN and LP can be obtained for both large and small stimuli. However, small visual stimuli had to have a longer duration than large stimuli to be at the awareness threshold. Because the duration of the stimuli differed for the two sizes and thus may act as a physical confound, the study could not determine whether stimulus size explains the mixed results in previous studies.

Notably, after Study I was published, we realized that we did not control for unconscious processing (as suggested by Lamy et al., 2009) in the published version of our study because of a calculation error of the behavioral data. However, this error and the lack of a correction does not challenge our results because the correction is inherently problematic, being based on an incorrect understanding of thresholds in visual processing (Morales et al., 2015). In theory, a proposed correction method derived from SDT (Morales et al., 2015) could have been used in an attempt to
isolate awareness. However, because of problems with response bias and how response bias is modeled by the SDT correction, it was not feasible to apply this correction to our data. Critically, I argue that there is a problem with the idea of unconscious processing and how it is calculated from behavioral data. It assumes that unconscious processing can be measured by accurate performance in combination with unawareness. However, from an SDT perspective, this performance can be explained in terms of a conservative awareness criterion (Macmillan, 1986). Further, I argue that if processes related to awareness are reflected by the internal perceptual response, the SDT correction might eliminate awareness-related processes altogether and isolate only post-perceptual processes.

To conclude, VAN and LP were found as neural correlates of visual awareness. If local recurrent processing is the key ingredient for the emergence of awareness and VAN is an index of local recurrent processing, then VAN is the electrophysiological correlate of visual awareness. Although Study I did not solve whether the contrastive analysis is problematic, it does provide high-quality data that could be revisited in the future. Critically, in the discussion after publication of Study I, I provided new arguments for why the idea of correcting for performance is inherently problematic.

9.2. Similarities between visual and auditory correlates of awareness

The contrastive analysis of neural activity to tones at the awareness threshold reported as heard minus neural activity to physically identical tones reported as not heard revealed two neural correlates of auditory awareness: an early negativity at central electrodes about 200 ms after stimulus onset (AAN), and a late positivity at parietal electrodes about 400 ms after stimulus onset (LP). As suggested by the results of Study II (Eklund & Wiens, 2019), the correlates of auditory awareness closely match correlates of visual awareness. Previous studies (which did not use the contrastive analysis) reported an early negativity (N1) to detected stimuli (Dykstra, Cariani, & Gutschalk, 2017). A reasonable assumption is that these early and late ERPs reflect similar processes related to perception (and possibly post-perceptual processes).

According to recurrent processing theory (Koivisto & Grassini, 2016; Lamme, 2006, 2010), the local recurrent processing in the early sensory processing areas reflects visual awareness (VAN) and auditory awareness (AAN). The subsequent late activity (LP) reflects post-perceptual processes related to introspection and reporting about perception.
9.3. Effects of response requirements on correlates of auditory awareness

Research attempting to separate the neural correlates of visual awareness from post-perceptual processes has suggested that neural activity in the back of the brain is related to visual awareness whereas activity in the front of the brain is related to post-perceptual processes (Koch et al., 2016). Koivisto et al. (2016) showed that the requirements for manual responses in a visual detection task affected the LP whereas the VAN was apparently unaffected. This provides further evidence that parts of the LP are related to post-perceptual processes whereas VAN is related to visual awareness.

To extend these findings to auditory awareness, we attempted to replicate these results in Study III (Eklund, Gerdfeldter, & Wiens, 2019) by using an auditory detection task and manipulating the response requirements. However, the results suggested that there was no difference between response trials and no-response trials for either AAN or LP. One interpretation of the results is that AAN corresponds to the experience of hearing a tone and LP corresponds to the information being transferred into working memory and reflected upon to make either a response or no response. To isolate awareness in a no-response task, the task must not require either active or passive reporting about the stimuli (Pitts, Metzler, et al., 2014).

9.4. Auditory awareness negativity is generated by auditory cortex

Knowing the source of the neural activity that correlates with auditory awareness is informative because according to local recurrent processing theories, sensory areas mediate awareness. Thus, these theories predict auditory cortex as the main generator. In support, previous research with MEG found that early activity related to auditory awareness can be localized to the auditory cortex (Dykstra et al., 2016; Gutschalk et al., 2008). In Study III (Eklund et al., 2019), we used high-density EEG recordings in an auditory detection task to localize the potential neural generators of AAN. Although source localization with EEG has its theoretical limits (inverse problem), source localization suggested bilateral auditory cortices as generators, suggesting that AAN is comparable to the awareness-related activity found previously. In sum, AAN is probably generated in the auditory cortex and may reflect local recurrent processing.

9.5. Limitations and future research

9.5.1 General

All studies conducted in this thesis have the major limitation of being merely correlational. To further investigate the mechanism of visual and auditory awareness, neural activity should be manipulated directly to establish the causality of the correlates. For example, TMS can be used to
disrupt recurrent processing selectively to inhibit awareness of the contents of consciousness (Silvanto et al., 2005). Additionally, the contrastive analysis (aware minus unaware) may include post-perceptual processes that confound the awareness-related activity (Aru et al., 2012). The present studies do not adequately address the problem with post-perceptual processes. This potential confound may be present in all the experiments conducted in this thesis. However, in Study III, we tried to capture processes related to a manual response requirement. The next step in this line of research should be to measure auditory awareness by using a task in which no responses have to be made to indicate awareness (Tsuchiya et al., 2015). From a recurrent processing perspective, the ideal result would be that LP disappears and AAN remains as the only correlate of awareness. This would support the idea that the early activity in the sensory areas enables awareness of stimuli and provides arguments against the global workspace theory and other theories that propose late activity as the neural correlate of awareness or access.

Because source localization with EEG has limited validity (inverse problem), the present EEG findings for AAN should be replicated with better source localization methods, such as MEG. Also, a different way of analysing EEG data is to extract the frequency and time-frequency information at the moment of awareness. A popular hypothesis is that awareness is associated with neuronal activity that is synchronized at 40 Hz (Gold, 1999). In a future study, the combined data could be used to explore whether the current data for hearing support the 40-Hz thesis.

9.5.1 Study I: Limitations

Many subjects had to be excluded because of a limitation of our study design. From the total of 35 subjects, only 24 were retained for the large Gabors and 15 for the small Gabors. The main reason was that we used the same duration for the control trials for all subjects. However, subjects varied in their visual acuity, and some subjects had problems seeing the Gabor stimulus even in the control trials. Ideally, control trials should be clear compared to the critical trials. Because our calibration of the critical trials did not allow for stimulus durations longer than those in the control trials, the duration of Gabor stimuli could not be calibrated to the 50% awareness threshold for some subjects. As a consequence, many subjects had to be excluded even though they could have been included if a better calibration procedure had been used—for example, if the critical trials had been calibrated freely and the control trials were 100 ms longer than the critical trials.

Another limitation was the manipulation of Gabor size. In retrospect, it is obvious that small stimuli had to be displayed for a longer duration than large stimuli to reach the same level of visibility. Thus, the duration confound could have been anticipated.
Finally, because we failed to calculate the percent correct for unaware trials correctly, we did not perform the proposed correction for unconscious processing. However, because from an SDT perspective the proposed correction for unconscious processing has been shown to be theoretically flawed, the correction does not seem useful anyway.

9.5.2 Study II: Limitations
We collected two samples of data because for the first sample, we preregistered an incorrect time interval for the AAN. We preregistered to look for AAN where the N1 peak was observed to control trials. We could have predicted that softer tones would generate an earlier N1 already for the first sample of subjects. This would have made it unnecessary to collect a second sample. However, this limitation of collecting a second sample is also a strength, because it proves that we adhered strictly to our preregistration rather than deciding about data analyzes after peeking at the data. Thus, our research minimizes false positives and provides unbiased estimates of the effects.

9.6. Final thoughts
I have spent some time thinking about what theory I would wholeheartedly subscribe to regarding how the brain generates experiences, or if I have my own idea. One starting point is to consider the definition of consciousness. Is there such a thing as phenomenal consciousness that is disconnected from access consciousness? When using introspection to think about the current moment and the experience that I have in this moment, it seems like it is a mix of both phenomenal and access consciousness. For example, when looking at a green apple, is it possible to completely turn off the thoughts and just have this green color in the mind, without any meaning or context? Because the experience is subsequently reflected upon, cognition and mental operations have to be involved. So, was it pure phenomenology, phenomenal experience followed by access, or only access all along? Accordingly, if it was only access, the pure experience of the color was only access of some unconscious processing of the color. Also, if phenomenology and access are separate, access itself may generate phenomenology. That is, it feels like something to reflect upon my experience. Because of this phenomenological experience of doing a mental operation on the sensory experience, phenomenology and access are intertwined and seem impossible to separate. It is also possible to reflect further upon the experience of reflecting upon the experience (meta-cognition), until the working memory runs out. But these secondary experiences are very different from the first sensory experience. Although introspective reports have been used throughout the history of humanity, apparently, they have not been very helpful in understanding how the mind works.

From a third-person (objective) perspective on the brain, my own interpretation of the results is that there are pure phenomenal experiences that are generated by local recurrent loops in our
sensory areas, as suggested by Lamme (2006). Different retinotopic and tonotopic maps communicate with each other to create the full experience, as suggested by Edelman (2001). For us to experience fine textures in vision and connect them to abstract objects, the higher areas need to feed the information back to the lower areas, as suggested by Bullier (2001). Maybe recurrent loops are the key process, and all experiences are driven by these loops. Whatever area that the loops incorporate, that is what you experience. Local recurrent processing in sensory areas reflects the experience of sensory information, and global recurrent processing reflects the experience of putting the information into working memory and the experience of deciding what to do with the information. The neural argument put forward by Lamme is very interesting because our own mind may have limits with regard to understanding consciousness. Accordingly, we need to look at the data and figure out how they can explain how the brain creates awareness, even if the result is not in line with our intuitions. I also lean towards the idea that consciousness is not really this one unity, that I am one mind. Why do split-brain patients behave like they do? For example, one hand does one thing and the other hand another, sometimes contradictory thing. Maybe every module of the brain has its own consciousness (Zeki, 2003), supported by recurrent processing. I guess this would be a restricted version of panpsychism, which states that everything is conscious. As far as I know, there are no recurrent loops in stones. It is, however, a complete mystery to me how a loop of activity can create any experience.

9.7. Ethics

All studies in this thesis were carried out in agreement with Swedish legislation. The Ethical Review Act regulates research involving humans. It does not require explicit ethical approvals unless the law applies to a study. In these studies, subjects performed visual or auditory detection tasks as electroencephalograms were recorded. No sensitive personal information was collected. Therefore, no ethics approval was required according to the national regulations. All subjects gave written informed consent in accordance with the Declaration of Helsinki.
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Sammanfattning på svenska


I forskning på synupplevelser så har detektionsuppgifter använts där försökspersoner indikerar sina upplevelser med knapptryckningar. Denna forskning har visat att tidig aktivitet i synhjärnan och sen hjärnaktivitet i frontal- och temporalloben efter en visuell retning korrelerar med synupplevelser. En teori menar att den tidiga aktiviteten är kopplad till synupplevelsen medan den sena aktiviteten har med andra processer att göra, så som knapptryckningarna. En annan teori säger att den tidiga aktiviteten endast reflekterar omedvetna processer och att den sena aktiviteten är kopplad till synupplevelser.


En annan fråga är om hjärnaktiviteten som skapar synupplevelser liknar den som skapar ljudupplevelser. Kanske liknar tidig aktivitet i hörselhjärnan tidig aktivitet i synhjärnan. Om främre sen aktivitet reflekterar andra processer, såsom beslutsfattande, bör aktiviteten påverkas av att man förändrar sättet att svara på i ett experiment. Om man inte behöver svara med en knapptryckning så kanske det påverkar den sena men inte den tidiga aktiviteten.

I Studie I jämfördes omedvetna visuella processer med medvetna visuella processer. Studien replikerade och utökade de tidigare studierna som funnit blandade resultat i liknande experiment.
Resultaten visade att både tidig aktivitet i synhjärnan och sen aktivitet i frontal- och temporalloben korrelerade med visuella upplevelser. Detta tyder på att både den tidiga och den sena aktiviteten är viktig för synupplevelser.

**I Studie II** testades om neurala korrelat för ljudupplevelser liknar de för synupplevelser. Resultaten visade att både tidig aktivitet i hörselhjärnan och sen aktivitet i frontal- och temporalloben korrelerade med ljudupplevelser. Detta tyder på att det finns ett mönster av aktivitet som möjliggör både ljud- och synupplevelser på ett liknande sätt.


Sammanfattningsvis undersöktes hjärnaktiviteten kopplad till syn- och ljudupplevelser i tre experimentella studier (N = 136). Resultaten visade att de neurala korrelaten för synupplevelser liknar de för ljudupplevelser och att både tidig aktivitet i synhjärnan och sen aktivitet i frontal- och temporalloben är viktiga för skapandet av upplevelser.
“Thou shalt not rest or be content, no matter what thy accomplishments. Thou must strive all the days of thy life. Thou must discover all things, know all things, master all things.”

— William Pierce
10. References


