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Attention in the Hierarchy of Predictions and Prediction Errors

An EEG Study of Attentional Effects on Predictive Processing of Auditory Patterns

Vegard Volehaugen

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Abstract

Author: Vegard Volehaugen

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Supervisors: Sabine Leske and Alejandro Blenkmann

Auditory perception depends critically on predictive models. These models can be formed at different time-scales, as statistical regularities are extracted from the acoustic input at progressively higher levels of a predictive hierarchy. It is well-known that simple regularities are extracted automatically at a relatively low level of the auditory system; however, less is known about the attentional involvement in extraction of temporally extended auditory patterns, or global regularities in sound. This thesis explores the interplay of attention and predictive processing through a set of analyses of EEG data acquired from a sample of healthy adults ($n = 20$) in two conditions (attended and unattended) of an auditory oddball paradigm which involved the presentation and violation of global auditory regularities. Analyses of ERPs revealed that the early global deviance response is independent of attentional engagement, whereas a later global deviance response is emitted contingent on attention to towards the auditory stream. Source localization of these ERP effects implicate neuronal networks distributed over temporal, frontal, and parietal areas. Finally, time-frequency analyses revealed attention-dependent modulations in the theta and beta bands during global deviance processing.

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Introduction

Decades of thinking about neuronal function converges on a view of the brain as an inference machine that continuously deploy predictions to explain away the noisy barrage of signals impinging on its sensors (Clark, 2013b; Friston, 2005, 2010; Dayan, Hinton, Neal, & Zemel, 1995; Mumford, 1992; Rao & Ballard, 1999). By this view, errors of prediction are used to fine-tune a hierarchically distributed model that specifies how sensory signals relate across time and space, and, which, implicitly, anchors perception in the likely causes of sensations.

The auditory system is probably exquisitely reliant on predictive processes to efficiently segregate, identify, and track auditory objects, and, thereby, give rise to structured perception of the acoustic environment (Bendixen, 2014; Bregman, 1990; Denham & Winkler, 2020)¹. In brief, this is because sounds are superimposed in a dynamic pressure field that evolves rapidly over time. Neurophysiological research suggests that the auditory system deals adaptively with this challenge by extracting statistical regularities to prospectively model the likely continuation of acoustic signals (e.g. Barascud et al, 2016). Moreover, evidence suggests that the modeling occurs recursively, such that patterns unfolding over longer time-scales constrain expectations about faster acoustic variations (e.g. Wacongne, et al., 2011).

The formation predictions based on temporally extended auditory patterns (i.e. global auditory regularities, or auditory Gestalts²) is critically dependent on the regularity encoding process, which may be state-dependent. In other words, a pattern must be learnt to influence expectations about upcoming sounds, and learning may vary with endogenous factors such as arousal and attention. To the extent that the auditory system learns by propagating error signals through a hierarchy, the formation such predictions rely on the accumulation of error signals at hierarchical levels that have the requisite temporal resolution to extract the long-term pattern.

Attention is a critical factor in shaping the magnitude and trajectory of neuronal signaling. Classically construed as an adaptation to the inherent capacity limitations of the neural information processing architecture, selective attention can be seen as the process by

¹ This computational challenge is variably referred to as auditory scene analysis, the cocktail party problem, or blind source separation, and there is currently massive interest in developing neuronally inspired solutions to this problem for digital signal processing applications.

² A Gestalt refers to a perceptual “whole” composed by integration of component parts that are extended in space and/or time (Köhler, 1947).

which incoming signals are enhanced or dampened in accordance with centrally maintained goal sets (van Boxtel, Tsuchiya, & Koch, 2010). As a computational process governing information weighting and gating, attention may therefore influence the encoding of statistical regularities from the sensory stream. Indeed, focal attention has been suggested to be necessary for the encoding statistical regularities defined over longer time intervals (e.g. Bekinschtein et al., 2009). Nevertheless, it has been shown that even unattended patterns can be extracted during auditory processing and used to constrain prior expectations (e.g. Kompus, Volehaugen, Todd, & Westerhausen, 2020).

Although the relation between attention and prediction has attracted substantial research interest over the past decade (Chennu et al., 2013; Foldal et al., 2019; Garrido et al., 2018; Kok et al., 2012; Kompus et al., 2020; Summerfield & de Lange, 2014; Summerfield & Egner, 2016), their interplay remains underdetermined. The main aim of this thesis is to address the question of how attention influences predictive processing of global auditory patterns across levels of the auditory predictive hierarchy. To this end, electroencephalography (EEG) data acquired during a novel auditory oddball paradigm involving complex auditory patterns were analyzed. EEG provides a direct measure of neuronal activity with temporal precision in the millisecond range, which is ideally suited to discern modulations at distinct hierarchical stages of processing.

Furthering the understanding of hierarchical predictive processing and how it interacts with attentional mechanisms is an important research endeavor. Delivering on this research goal would provide a better understanding of the operations of the healthy brain, that, by extension, could be applied to understand the computational foundations of perceptual and cognitive abnormalities (see Smith, Badcock, & Friston, 2021 for a recent review of clinical neuroscientific research applying the predictive processing framework). There is indeed a growing literature around the proposal that deficits affecting predictive message-passing may lie at the core of neurodevelopmental- and/or psychiatric disorders, such as autism and schizophrenia (e.g. Baldeweg et al., 2004; Friston, Brown, Siemerikus, & Stephan, 2016; Goris et al., 2018; Hohwy, 2013; Light & Näätänen, 2013; Sauer et al., 2017). In brief, the idea is that the debilitating mental symptoms of these disorders are caused by aberrant attentional mechanisms operating on the hierarchical propagation of error signals (e.g. Adams et al., 2013; Lawson, Rees, & Friston, 2014). This highlights the need to better characterize the interplay of predictive and attentive mechanisms in the healthy human brain.

This thesis will present results that indicates that the interplay of attention and prediction are expressed differently across hierarchical levels during predictive processing of auditory patterns. Briefly, the results indicates that early processing levels are not dependent on selective attention to respond to predictive deviations from global auditory structures, while the response at later stages of processing is highly attention-dependent. These findings challenge currently held ideas about the necessity of attention for the extraction of long-term patterns from the acoustic stream (e.g. Bekinschtein et al., 2009) and raise questions about an influential view about electrophysiological markers as indexing successive stages of hierarchical predictive processing (e.g. Chennu et al., 2013). Further, source reconstruction results are presented to give information about the neuroanatomical loci of these effects. Finally, results from time-frequency analyses performed to test oscillatory modulations by attention and predictability are presented, motivated by the hypothesis that distinct frequency-bands subserve channeling of predictive signals.

Before the presentation and discussion of the results, the thesis will present the hierarchical predictive processing framework, which forms the theoretical background of the current work and review the literature on electrophysiological signatures of predictive processing relevant for the analyses that were performed.

Hierarchical Predictive Processing

The notion that the brain is inherently predictive has gained momentum across neuroscientific disciplines over the past decades. Although predictive mechanisms have been tacitly invoked in influential frameworks of perception, cognition, and action over the last century, it is not until recently that these ideas have been formally developed under a unified framework of predictive processing. The basic idea in this framework - that neural computations incorporate prior information to anticipate and interpret input - may represent fundamental principle of neurocognitive function (see Bubic, von Cramon, & Schubotz, 2010; Clark, 2013b, 2016; Friston, 2005, 2010; Howhy, 2013; Teufel & Fletcher, 2020 for integrative treatments).

The impetus for this line of thinking is tightly interwoven with the idea of neuronal predictive coding³. Predictive coding, in essence, encapsulates the idea that a neural circuit

³ In neuroscience, predictive coding was originally proposed as a sparse coding scheme utilized by retinal ganglion cells to restrict forward signal transmission to useful information (i.e. useful in the sense of being statistically surprising, or informative) while maintaining high dynamical signal range (Srinivasan et al., 1982). These ideas were adapted to visual cortical function (Rao & Ballard, 1999) to explain receptive field properties that were hard to reconcile with a strict feedforward feature integration view (e.g. end-stopping, or the fact that the response rate of a cell reduces when a bar at preferred orientation extends beyond the receptive field of the

compares its input with a prediction derived from prior information, and signals the prediction error – defined as the residual after subtracting the prediction – forwards to the next stage of processing to update the representations that gave rise to the prior estimate. Thus, predictive coding falls squarely within the view of neural function put forward as the Bayesian brain hypothesis (c.f. Knill & Pouget, 2004), as predictive coding can be seen as an instantiation of empirical Bayes in the sense that sensory causes are approximated by the integration of sensory data with prior estimates which are updated based on actual data. By recapitulating this prediction error minimization algorithm across a deep hierarchical architecture, a multi-level model of sensory causes emerges.

This formulation of predictive processing in terms of hierarchical Bayesian model optimization⁴ is attractive as an explanation of perception because it solves a problem articulated by Herman von Helmholtz (1867). Helmholtz realized that the brain faces an ill-posed problem in identifying the causes of sensations, because its access to these causes are necessarily restricted to transduced electrical potentials generated at sensory epithelia (e.g. phototransduction at the retina or mechanotransduction at the cochlear basilar membrane). Sensory transduction is an inherently noisy process and the transduced signals themselves may be consistent with a multitude of distinct causes.

Helmholtz suggested that the brain solves the inverse problem of perception by engaging in “unconscious inference”, which can be understood as low-level abduction of sensorial causes facilitated by prior knowledge, or, in simpler terms, an automatized best-guess of what is causing the observed sensory data given what the system already knows about regularities in the sensory stream (Dayan et al., 1995). The notion of perception as fundamentally inferential has had a major impact on cognitive psychological theorizing about the nature of the perceptual process. For example, the analysis-by-synthesis framework (Neisser, 1967) and Gregory’s (1980) conceptualization of perception as hypothesis-testing both recourse to probabilistic inference mediated through interactions between top-down priors and bottom-up data in explaining how perception arises. The predictive processing framework incorporates and expands this view by suggesting how perceptual inference and learning can be implemented neuronally.

cell; Hubel & Wiesel, 1968). Later, this hierarchical prediction scheme was proposed as a fundamental principle of cortical function (Friston, 2005).

⁴ Model optimization is equivalent to minimization of prediction error.

Under the predictive processing view, a percept is a hypothesis about the causes of sensory data generated from a model. The basic idea is that the perceptual hierarchy (i.e. all hierarchically connected neuronal circuits involved in perceptual processing) embodies a generative model, i.e. a parameterization of how causes conspire to produce sensory data. This model is updated according to how derived predictions fit the incoming sensory data, and perception emerges from the inversion of the model as sensory input is “explained away” (Clark, 2013b)⁵. That is, when prediction error transmission is suppressed due to a successful mapping from cause to sensation (i.e. a successful prediction), the percept corresponds to the reverse mapping from sensation to cause (i.e. the hypothesis which generated the prediction). Thus, prediction error signaling represents a means to arbitrate between mutually exclusive model-derived hypotheses and thereby facilitate perceptual inference. On longer time-scales, prediction errors shape model parameters through changes in connectivity among the hierarchically distributed circuits embodying the model, thus facilitating perceptual learning. This view has the phenomenological implication that organisms perceive their successful predictions – an implication which seems especially fruitful not only for explaining the reliability of perception (e.g. invariant recognition of perceptual objects despite changes in luminance, size, etc.) but also perceptual biases (i.e. illusions) and aberrancies (i.e. hallucinations).

There are multiple ideas about how the predictive processing may be realized algorithmically (see Spratling, 2017 for a review), but common to all is the assumption of separate neural populations dedicated to representing probabilistic estimates (i.e. prediction units) and signaling predictive residue (i.e. prediction error units). The most influential of these perspectives is the one originally proposed by Rao and Ballard (1999), which assumes that predictive feedback is conveyed along descending feedback connections from higher to lower levels, while prediction error is signaled along ascending connections in the opposite direction.

A Hierarchical Computation: Prediction Error Minimization Across the Hierarchy

Predictive processing assumes that an elementary or canonical computation is realized across recurrently connected hierarchical levels to minimize prediction error across the hierarchy. As indicated above, the computation is construed as a form of Bayesian model fitting implemented between immediately adjacent levels, in which the relatively higher level

⁵ To “explain away” refers to a state in which a set of predictions across hierarchical levels suppresses bottom-up transmission of error signals.

communicates a model-derived prior estimate (i.e. a prediction) to the subordinate level. The prediction is compared to the input arriving at that level, and, in case of a mis-fit, the residue is communicated back up to adjust the model held by the higher-level, leading to a new prior estimate to be compared with the next input sample. Thus, each level of the hierarchy tries to model the activity patterns occurring at the level below, and is, in a sense, supervised by their prediction errors such that an optimal multi-level model of the environment emerges from hierarchical message-passing.

The focus on deep hierarchical structure in predictive processing corresponds well with neuroanatomical knowledge about sensory system organization. Indeed, all major exteroceptive cortical systems have more or less well-defined hierarchical structure (e.g. Felleman & van Essen, 1991), that involves a bifurcation at the level of early sensory cortex into parallel streams (e.g. Alain et al., 2001; Rauschecker & Tian, 2000; Ungerleider & Mishkin, 1982)⁶. Along the hierarchical progression of areas, neuronal responsivity differ markedly; from sharply tuned receptive fields in early sensory cortex to more diffuse, spatiotemporally expansive fields towards hierarchical apex areas (e.g. Hubel & Wiesel, 1962, 1965). This points at integration into more sparse and invariant representations when moving up the hierarchy. Critically, connectivity among areas is massively recurrent with feedback outnumbering feedforward connections⁷. This neuroanatomical observation holds across sensory modalities and is hard to reconcile with the traditional feedforward model of perception as progressive feature extraction and integration.

Hierarchical cortical organization may have emerged as an adaptation to nested sensory regularities (Kiebel, Daunizeau, & Friston, 2008). Sensory regularities occur at different time-scales, from rapid millisecond fluctuations to slower dynamics expressed in the order of seconds, minutes, hours, and beyond. Regularities are often nested such that slower dynamics predict faster fluctuations, as when sentence structure predicts words which, in turn, predict phonological variations, or when recurrent melodic phrases predict individual tones. Hence, the cortical hierarchy may have evolved to recapitulate the time-scales of the

⁶ The tendency for cortical information streams to segregate into a dorsal “where/how” pathway and a ventral “what” pathway has been interpreted to reflect the conditional independence of location and identity information (Friston & Buzsáki, 2016). The idea is that it may be efficient, in terms of degrees of freedom in the generative model, to process location and identity information in separate hierarchical streams, as location does not usually predict identity and vice versa.

⁷ At early levels of auditory processing, it is estimated that feedback connections from A1 to medial geniculate nucleus outnumber the thalamocortical feedforward projections by a factor of 10 (Malmierca, Anderson, & Antunes, 2015).

environment: primary sensory cortex process fast variations in the input stream while downstream cortical areas extract progressively slower regularities under which the faster variations unfold, and backpropagate predictions to constrain early cortical processing according to these regularities. Neuroanatomically, the hierarchical progression abides to a rostrocaudal axis of organization, which has been described for both frontocortical control systems (Badre & D'Esposito, 2009) and posterocortical sensory systems (Huntenburg, Bazin, & Margulies, 2017), in which more caudal areas deal with concrete and immediate representations while more rostral areas encode progressively more abstract and temporally invariant representations. It has been shown that cortical areas have intrinsic activity patterns consistent with integration windows tuned to different environmental time-scales (Murray et al., 2014), and there is evidence that early cortical processing is shaped by patterns extracted over longer time-scales (e.g. Kompus et al., 2020; Wacongne et al., 2011).

The prediction error computation recapitulated across this hierarchy of time-scales may be carried out at the level of the cortical column, within a hypothesized canonical microcircuit housing the requisite computational machinery to integrate thalamocortical and corticocortical feedforward and feedback streams (e.g. Bastos et al., 2012; Shipp, 2016). A cortical column refers to a recurring arrangement of cells that spans the six horizontal layers of cortex. These columns are recapitulated across the cortical mantle, which is the basis for the idea that the cerebral cortex performs a stereotyped computation, implemented with minor variations across cortical areas (Mountcastle, 1997).

While the organization of cell types across cortical laminae remains relatively similar across cortex, there is marked cytoarchitectonic differences between areas (e.g. in cell density and connectivity), which corresponds to the degree laminar differentiation of these areas. In brief, the primary sensory areas (i.e. koniocortices) are maximally laminarly differentiated while higher-level association areas in prefrontal, temporal, and parietal areas are only loosely differentiated. Intermediate areas (i.e. downstream from sensory but upstream from higher-level association areas, such as secondary and tertiary sensory cortical areas) lie somewhere in between on this continuum of laminar differentiation. These anatomical considerations has led to the proposal that prediction errors flow from laminarly differentiated to less differentiated areas while predictions are communicated in the opposite direction (Chanes & Barrett, 2016), i.e. from less laminarly differentiated towards more differentiated areas. Thus, the hierarchy postulated by predictive processing may be defined by neuroanatomical characteristics such

as cytoarchitecture and laminar differentiation at the microscale, in addition to the rostrocaudal axis of processing at the macroscale.

The idea of the canonical microcircuit of predictive processing specifies the intracolumnar origins and terminations of prediction errors and predictions. The feedforward driving input to a cortical column consistently arrives in layer 4, also known as the granular layer due to the preponderance of small-sized pyramidal neurons or granule cells. Descending feedback, on the other hand, preferentially target the infragranular or deep layers (5/6) and supragranular or superficial layers (1-3). There is currently no consensus on how feedback information is maintained within the cortical column, but proposals include recurrent interactions among excitatory cells within the column and/or synaptic plasticity changes instigated by N-methyl-d-aspartate receptor (NMDAR) mediated signaling⁸. Regardless, the predictive template conveyed along the descending connections is proposed to be compared with the feedforward sweep arriving in layer 4 to give rise to prediction error signals transmitted from excitatory projection neurons residing in the superficial layers 2/3, which restarts the cycle in the next column. This is necessarily an oversimplified view, but crucially, there is evidence that the feedforward and feedback populations intrinsic to a cortical column are distinct, as neurons involved in feedforward or feedback signaling do not give rise to axonal bifurcations that project in the opposite direction (Markov et al., 2014; Shipp, 2016). Thus, one of the essential postulates of the predictive processing framework – the presence of distinct error and prediction units – does have empirical support.

The Conceptualization of Attention in Predictive Processing

From the predictive processing framework, attention has been equated with the adjustment of the gain on cortical pyramidal neurons reporting error signals (Feldman & Friston, 2010). This operation, which is proposed to reflect optimization of expected precision during hierarchical inference, can supposedly explain both exogenous and endogenous attention. Optimization of expected precision refers to adjustments of expectations about sensory reliability. According to the predictive processing framework, the degree of influence of forward-propagated error signals on model parameters are adjusted in accordance with the

⁸ Pharmacological blockade of NMDARs, for example by ketamine, disrupts evoked responses to unpredicted stimuli, suggestive of reduced prediction error generation (Umbricht et al., 2000). This is consistent with a state in which backpropagated predictions are not encoded properly by the microcircuitry performing the prediction error computation. Likewise, schizophrenia, a condition for which there is now converging evidence for NMDAR dysfunction, is characterized by reduced sensory-evoked responses to unpredicted input (Friston et al., 2016).

expected reliability of the error, i.e. prediction errors are precision-weighted (Clark, 2013a; Howhy, 2013; Feldman & Friston, 2010; Friston, 2009).

The underlying rationale is that sensory signals differ in their degree of noise and uncertainty. Hence, the cortical hierarchy is seen as inferring two quantities: (i) the content of the sensory signal and (ii) the reliability of the sensory stream. The latter determines whether inferences related to the former should be updated in light of mismatching sensory data. By analogy to statistical testing, this can be seen as equivalent to taking the sample variance (here equated with the expected precision) into account when computing the test statistic from the difference in sample means (here equated with the predictive residue). Thus, dynamic adjustments to precision expectations are proposed to balance the influence of prior estimates and sensory evidence on inference and learning. Failures to take sensory reliability into account can, therefore, be expected to produce disordered perception, which is a central idea in predictive processing-based explanations of neuropsychiatric phenomena (e.g. Smith et al., 2021).

The idea that precision-weighting of prediction errors underlie attentional effects is similar to classical ideas of attentional gain (e.g. Hillyard, Hink, Schwent, & Picton., 1973), since precision-weighting is equivalent to multiplying the prediction error with a scalar or gain factor. Neurophysiologically, this is believed to be implemented by adjusting the post-synaptic sensitivity - that is, the excitability - of superficial pyramidal cells (i.e. the hypothesized error projecting neurons). A proof-of-concept simulation study has given support to the idea expected precision can account for both electrophysiological and psychophysical responses during the Posner paradigm (Posner, 1980), a classical paradigm used to evaluate attention effects (see Feldman & Friston, 2010).

On the Relation Between Prediction and Attention

The effects of prediction and attention have often been confounded in the literature (see Schröger, Marzecová, & SanMiguel, 2015; Summerfield & de Lange, 2014 for discussions). However, prediction and attention are clearly based on distinct computations. Prediction is based on prior probability, while attention operates according to relevance. As such, prediction and attention should have dissociable effects on neuronal processing.

Indeed, prediction and attention are typically found to have diametrically opposed effects on neuronal responses. Predicted inputs tend to be attenuated, whereas attended inputs are accentuated (Schröger et al., 2015). These effects are consistent with the above-mentioned

ideas of expectation suppression (e.g. Todorovic, van Ede, Maris, & de Lange, 2011) and attentional gain (e.g. Hillyard et al., 1973).

Yet, when operating simultaneously, prediction and attention may have interactive effects on the neuronal response. Both probabilistic and attentional effects are mediated through feedback connections. Moreover, probabilistic information does guide attentional selection in many circumstances (e.g. Chun & Jiang, 1998), and, attentional selection may, in turn, shape the encoding of statistical regularities (e.g. Marti, Thibault, & Dehaene, 2014). Besides, according to the predictive processing framework, attention is a computational process intrinsic to hierarchically predictive message-passing (i.e. the process of estimating the weighting factor applied to feedforward error signals based on expected sensory reliability; Feldman & Friston, 2010).

Two mutually exclusive models on the interplay of prediction and attention have been formulated (e.g. Garrido et al., 2018; Kok et al., 2012). An opponent-process view prescribes that ascending information is equally weighted by attentional selection regardless of predictability (e.g. Garrido et al., 2018). In other words, both predicted and unpredicted input are prioritized during attentional allocation towards the input stream and are thus amplified by the same gain factor. In contrast, an interaction model suggest that attentional selection is biased by the level of predictability. Multiple forms of interaction can be conceived. For example, attention may be favorably biased towards unpredicted inputs, hence amplifying the difference in the neuronal response to unpredicted and predicted inputs (e.g. Auksztulewicz & Friston, 2015; Woldorff, Hackley, & Hillyard, 1991). Alternatively, attention may reverse the effect of expectation suppression on the neuronal response by selectively amplifying responses to predicted input (e.g. Kok et al., 2012).

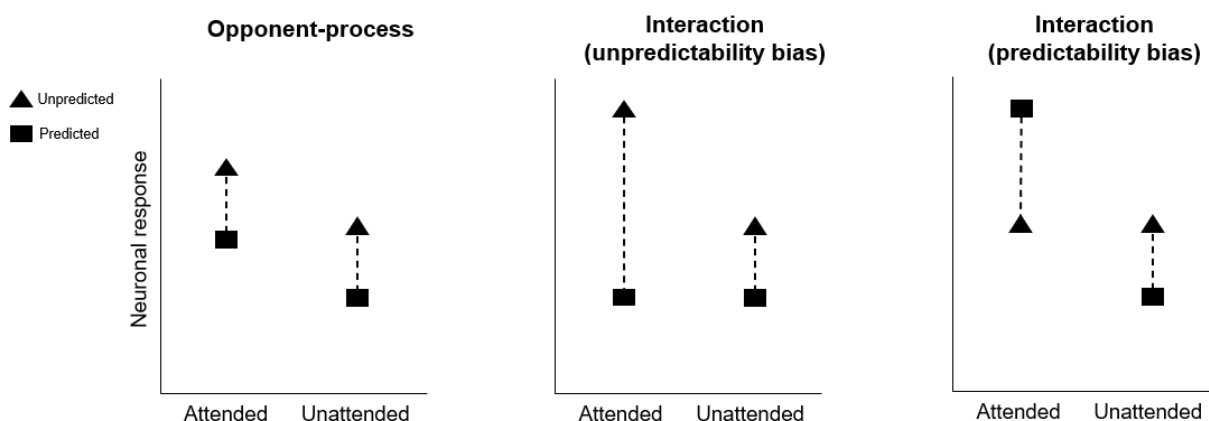


Figure 1. Theoretical Models of the Interplay Between Attention and Prediction. The figure visualizes different suggestions about the interplay of attention and prediction proposed in the literature (Aukstulewicz & Friston, 2015; Garrido et al., 2018; Kok et al., 2012). (Left) A non-interactive, opponent-process model, in which attention and prediction exert independent effects on the neuronal response (e.g. Garrido et al., 2018). (Middle) An interaction model in which attention selectively amplifies the response to unpredicted input (Aukstulewicz & Friston, 2015). (Right) An interaction model in which attention reverses the effect of expectation suppression (Kok et al., 2012).

There are few studies that have manipulated predictability and attention independently to adjudicate between these models (but see Aukstulewicz & Friston, 2015; Chennu et al., 2013; Foldal et al., 2019; Garrido et al., 2018; Hsu et al., 2014; Kok et al., 2012; Kompus et al., 2020). Moreover, the studies that do exist have yielded diverging findings. In brief, some studies show that attention interacts with prediction to enhance the response to predictable input (Hsu et al., 2014; Kok et al., 2012). This is in stark contrast to findings which show either no interaction (Foldal et al., 2019; Garrido et al., 2018) or that reveal different patterns across levels of processing, with responses at early processing levels being attention-independent and later levels showing an interaction effect expressed as an attention-dependent enhanced response to unpredictable stimuli (e.g. Bekinschtein et al., 2009; Chennu et al., 2013; Kompus et al., 2020). These studies are, furthermore, in conflict with studies which show that, even at early levels of processing, the neuronal response is a multiplicative function of predictability and attention, such that the difference between unpredictable and predictable input is amplified (Aukstulewicz & Friston, 2015; Woldorff et al., 1991).

Electrophysiological Indices of Predictive Processing

Evoked Potentials

An interpretation of evoked potentials as indices of prediction errors emerges naturally from the predictive processing framework (Carbajal & Malmierca, 2018; Garrido, Kilner, Kiebel, & Friston, 2007; Heilbron & Chait, 2018). ERPs generated by auditory stimuli, or auditory evoked potentials, can therefore be a useful means to evaluate the effects of attention on hierarchical predictive processing. Auditory stimuli elicit a sequence of evoked potentials, which can be classified according to a progression from stimulus-obligatory (i.e. exogenous) to endogenous components – the latter of which are elicited critical on internal dynamics, such as actively maintained representations that anticipate incoming information. As such, it is the endogenous components that have received most attention as potential reflections of

internal generative models⁹. The mismatch negativity (MMN) and P300 ERP components are particularly interesting in this regard, as these components have been suggested to reflect prediction errors elicited at successive stages of the predictive hierarchy (e.g. Chennu et al., 2013). The following gives a brief overview of the MMN and P300, funneling into a review of studies that have used these components to probe hierarchical predictive processing and its modulation by attention.

The MMN is a frontocentral negative deflection evoked 100-250 ms relative to a discriminable change in auditory stimulation (Näätänen, Gailard, & Mäntysalo, 1978). MMN is now widely regarded as an expression of lower-level prediction error (e.g. Garrido et al., 2008; Garrido, Kilner, Stephan, & Friston, 2009; Lieder, Stephan, Daunizeau, & Friston, 2013; Schmidt et al., 2013; Wacongne, Changeux, & Dehaene, 2012; Winkler & Czigler, 2012), with converging evidence implicating generator sources in a frontotemporal network that includes the superior temporal and inferior frontal cortices (e.g. Alho, 1995; Deouell, 2007; Hari et al., 1984; Opitz, Rinne, Mecklinger, von Cramon, & Schröger, 2002; Schonwiesner et al., 2007; Tse & Penney, 2007). The changes that elicit the MMN range from basic feature deviations (e.g. in pitch, duration, intensity, or location) to violations of abstract relationships or contingencies in the stimulus stream (Paavilainen, Arajärvi, & Takegata., 2007; Tervaniemi, Maury, & Näätänen, 1994; Xiao et al., 2018). For example, an unexpected reversal of pitch-scaling direction or a repetition in the context regularly ascending or descending pitch-scaling has been shown to elicit the MMN (e.g. Tervaniemi et al., 1994). Even the omission of an expected stimulus can elicit the MMN (e.g. Yabe, Tervaniemi, Reinkainen, & Näätänen, 1997), highlighting the endogenous nature of the generator process.

Speaking to its low-level nature, the MMN is highly resistant to changes in cortical arousal, as indicated by the fact that it is elicited across conscious states. The MMN has been reported to occur during sleep (e.g. Strauss et al., 2015) as well as in disorders of consciousness (Bekinschtein et al., 2009; Faugeras et al., 2011; Morlet & Fischer, 2014). The persistence of the MMN in unconscious states, along with the reports of robustness to attentional manipulations (e.g. Näätänen, Paavilainen, Tiitinen, Jiang, & Alho, 1993; Winkler, Karmos, & Näätänen, 1996; but see Aukstulewicz & Friston, 2015 and Woldorff et al.,

⁹ It should be noted, however, that there is a growing literature on the modulations of exogenous components by predictability (Grimm & Escera, 2012; Grimm, Escera, Slabu, & Costa-Faidella., 2011; Recasens, Grimm, Wollbrink, Pantev & Escera, 2014). For example, late components of the middle-latency response (MLR) occurring ~40 ms post-stimulus have been shown to be sensitive to simple pitch violations (e.g. Grimm & Escera, 2012).

1991), led to the notion of the MMN as reflecting a pre-attentive process. However, studies have shown that attention can modulate MMN expression, likely reflecting attentional effects on auditory grouping and segregation processes (e.g. Sussman, 2007, 2013; Sussman, Winkler, Huotilainen, Ritter, & Winkler, 2002; Sussman, Chen, Sussman-Fort, & Dinces, 2014). Hence, the MMN is responsive to top-down factors, and, thus, it may not be useful to view the underlying process as operating prior to attentional selection in any strict sense.

A later ERP component, the P300 (Sutton, Braren, Zubin, & John, 1965), can follow the MMN as a sustained positivity in the 250-600 ms time-frame if attention is allocated towards the auditory stream. Akin to the MMN, the P300 is sensitive to stimulus probability and deviance (Squires, Wickens, Squires, & Donchin, 1976; Mars et al., 2008). Accordingly, the P300 has been interpreted as reflecting prediction error arising downstream from the frontotemporal network underlying the MMN (e.g. Chennu et al., 2013; Wacongne et al., 2011).

The P300 has been distinguished into the P3a and P3b subcomponents (Polich, 2007). The former expressed frontocentrally around 250 ms relative to stimulus-onset, while the latter is characterized by parietocentral maximum beyond 300 ms relative to the eliciting stimulus. Functionally, the P3a is typically interpreted as reflecting an involuntary attentional reorienting process (Escera & Corral, 2007), which may relate to the operations of the ventral attention network (Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002; Nieuwenhuis, Aston-Jones, & Cohen, 2005). The P3b, on the other hand, is traditionally linked to updating of behaviorally relevant information in working memory (Donchin, 1981; Polich, 2007). P3b has also been interpreted to reflect the ignition of a fronto-parietally distributed global neuronal workspace which serves to broadcast relevant information to modular or encapsulated subsystems – a function that, from this view, equates to conscious access (Dehaene & Changeaux, 2011; Dehaene & Naccache, 2001; Dehaene, Sergent, & Changeaux, 2003).

Dissociating Levels of Predictive Processing and Their Modulation by Attention.

Evidence from studies of evoked potentials and their magnetic counterparts (i.e. evoked fields) have given support to the view that probabilistically deviant events elicit a cascade of responses arising as a function of predictive feedback (e.g. Chennu et al., 2013; Wacongne et al., 2011). Over the last decade, important evidence for hierarchical stages in auditory predictive processing, linked to the MMN and P300, has been derived from studies using a

paradigm that dissociates neuronal responses elicited at hierarchically nested levels of temporal regularity – the local/global auditory oddball paradigm (Bekinschtein et al., 2009).

In the local/global paradigm, tone-sequences are presented to build and violate regularities at two time-scales simultaneously. At the local level, the regularity is determined by the transition probability between tones within sequences. For example, a five-tone sequence composed of equal-pitched tones constitutes a local standard (e.g. xxxxx), while a pitch-deviating last tone constitutes a local deviant (e.g. xxxxy). The global level reflects the pattern of auditory sequences as they unfold over a longer time-frame; thus, the global regularity is established between sequences at a time-scale of several seconds. This takes the form of repeated presentation of either the local standard or deviant sequence, such that a global violation occurs upon presentation of a sequence that is improbable given the context established in a block (e.g. an xxxxx sequence presented in a block in which the xxxxy sequence is frequent). Thus, the paradigm has a factorial (2x2) structure, as local and global regularities, and violations therein, are orthogonally manipulated across blocks. As such, four sequence types can be distinguished: (i) global standard/local standard, (ii) global deviant/local deviant, (iii) global standard/local deviant, and (iv) global deviant/local standard. This 2x2 design feature allows for isolation of local and global processing dynamics from concurrently obtained neural measures (e.g. ERPs), as well as assessment of the interaction between processing levels.

The classical finding from MEEG research with the local/global paradigm is that the local effect (i.e. the contrast between local deviant and standard responses collapsed over global status) is characterized by an early MMN-like response irrespective of attentional allocation. The global effect (i.e. the contrast between rare and frequent sequences collapsed over local status), on the other hand, is expressed later as a sustained response in the P300 time-frame contingent on attentional allocation to the sound stream (e.g. Bekinschtein et al., 2009; Chennu et al., 2013; Strauss et al., 2015; Wacongne et al., 2011). These findings are typically interpreted to suggest that the brain tracks local transitional probabilities among tones automatically, whereas regularities that are expressed over extended temporal intervals require focused attention to be encoded.

Functional neuroimaging have been used to localize the networks underlying deviance signaling at the local and global levels. These studies converge with work on identifying the generators of the auditory MMN and P300 responses by showing that the local effect is associated with an activation pattern restricted to perisylvian auditory cortical areas while the

global effect is associated with recruitment of distributed frontoparietal and temporal areas (e.g. Bekinschtein et al., 2009; Uhrig, Dehaene, & Jarraya, 2014; Wang, Uhrig, Jarraya, & Dehaene, 2015). Hence, the local effect can be interpreted to arise from an encapsulated and highly modular system that integrates sensory information over relatively short time-intervals, and which is thus relatively blind to context. Output from this lower-level system can be integrated at higher levels with longer temporal tuning curves to detect long-term contextual regularities if attention is engaged. Violation of detected global regularities then engages a widespread network involved in updating probabilistic representations of the long-term structure of the auditory environment.

The notion that responses elicited by local/global paradigm reflect the operations of a hierarchical architecture with recurrent connectivity and top-down flow of predictions is directly supported by the observation that the global regularity shapes responses at early levels (e.g. Kompus et al., 2020; Wacongne et al., 2011). For example, Wacongne and colleagues showed that responses to predictable local deviants were attenuated relative to globally unexpected local deviants. Moreover, the same study showed that unexpected omission of the last tone led to a larger response when a local deviant was expected compared to when a standard was expected under the global regularity. In other words, when several predictions were concurrently violated (i.e. an expectation of another tone and a top-down prediction of its deviancy) the ensuing prediction error was larger in magnitude.

The study by Wacongne et al. (2011) shows that hierarchical levels interact; however, they did not address the role of attention. The role of attention and conscious expectation on hierarchical error processing during the local/global paradigm was addressed by Chennu and colleagues (2013). They manipulated expectation by having participants either attend to tones (i.e. count local deviants) or to sequences (i.e. count global deviants) while the effect of modality-specific attention was assessed by including a visual distraction condition. Interestingly, it was found that attention modulated prediction error signaling at the early stage, indicated by larger deviant-standard difference in the attend sequences relative to the visual distraction condition. In contrast, conscious expectation reduced the early level response, evident by an attenuation of the MMN when tones were attended (i.e. in the condition which subjects was consciously expecting local deviants) relative to when participants focused on the sequence-level regularity. Higher-level prediction error reflected in the P300 was found to be attention-dependent, in agreement with previous studies, as it was absent in visual distraction; and, in contrast to the MMN, the P300 was sharpened by

conscious expectation, evident in a more protracted response in attend sequences relative to attend tones.

The question of whether attention modulates the interaction among hierarchical levels was addressed directly in a recent study by Kompus and colleagues (2020). In this study, attention was manipulated in two conditions during presentation of the local/global paradigm: participants either listened attentively to the presented sounds or performed a demanding visual working memory task. Interestingly, it was found that the global regularity influenced the MMN independently of attention, which suggests that long-term regularities are extracted and used as priors for early auditory cortical processing even when attention is directed towards a cognitively taxing task. Moreover, since P300 elicitation by global rule violations were highly attention-dependent, these findings suggest that P300 generation is not a unique marker of global rule encoding, as the global rule influenced early cortical responses regardless of whether global deviants elicited the P300.

Neuronal Oscillations

A large part of neural activity is rhythmic, reflecting fluctuations in the excitatory-inhibitory balance within neuronal assemblies. By employing time-frequency analysis techniques, evidence for event-related modulations of neuronal oscillations can be obtained (e.g. modulations of oscillatory power; e.g. Cohen, 2014). In cognitive electrophysiological research, neuronal oscillations are traditionally divided into a set of discrete frequency-bands: delta (.5-3 Hz), theta, (4-7 Hz), alpha (8-12 Hz), beta (13-25 Hz), and gamma (> 30 Hz). Studying the event-related modulation of these frequency-bands is important, as the rhythmicity of neuronal activity is increasingly viewed as a functionally significant property that impacts on and organizes neuronal computations across time and space (Buzsáki, 2006, 2019; Buzsáki & Draguhn, 2004).

A prevailing idea is that neuronal oscillations facilitate communication within and between assemblies through the impact that patterns of synchronization and desynchronization of oscillatory populations have on information flow (Fries, 2005; Jensen & Mazaheri, 2010). By this view, oscillations influence the formation and dissipation of signaling pathways, and thereby determine the shifting patterns of effective connectivity during neurocognitive processing.

Due to their potential relevance of rhythmic neuronal activity in shaping feedforward and feedback signaling, neuronal oscillations represents a candidate mechanism for the

neurophysiological implementation of predictive processing across the perceptual hierarchy (Bastos et al., 2012; Engel, Fries, & Singer, 2001; Arnal & Giraud, 2012). Moreover, the attentional impact on predictive processing may similarly rely on oscillatory mechanisms, in part due to its dependence on top-down signals from the frontoparietal control network (Buschman & Kastner, 2015; Clayton, Yeung, & Cohen Kadosh, 2015; Helfrich et al., 2018).

An Oscillatory Asymmetry of Feedforward and Feedback Signaling. The predictive processing framework holds that perception is implemented as a bi-directional cascade of message-passing involving feedforward signaling of prediction errors and feedback signaling of predictions. Recent evidence supports a model in which these distinct signaling vectors are mediated by separate frequency-bands (e.g. Bastos et al., 2012; Chao et al., 2018). The gamma-band is implicated in feedforward transmission from lower to higher levels, whereas lower frequencies, especially the beta-band, is implicated in channeling feedback predictions in the opposite direction. Thus, the functional asymmetry of feedforward and feedback signaling may be mirrored by an oscillatory asymmetry at the implementational level.

The gamma-band is traditionally linked to local cortical computations, generally, and encoding of incoming stimuli, in particular (Donner & Siegel, 2011; Tallon-Baudry & Bertrand, 1999). Its role as a vector of prediction error propagation is supported by studies showing increased gamma-band power under conditions of predictive mismatching akin to those eliciting the MMN as well as relative suppression of gamma-band activity when incoming information matches a predictive template (e.g. Crone et al., 2001; Dürschmid et al., 2016; Edwards et al., 2005; Todorovic et al., 2011).

In addition to the gamma-band, the theta-band may also be involved in feedforward processing. This is indicated by studies linking theta modulations to the processes underlying the MMN (e.g. Choi, Lee, Ko, Lee, Jung, & Kim, 2013; Fuentemilla, Marco-Pallares, Munte, & Grau, 2008; Hsiao, Wu, Ho, & Lin, 2009; Ko et al., 2012). Moreover, recent studies have shown theta-band modulation in sensory cortices during presentation of regularity-deviating stimuli. For example, Bastos and colleagues (2015) observed increased feedforward theta- and gamma-band connectivity among visual cortical areas of macaques during presentation of visual oddball stimuli. Furthermore, a recent MEG study demonstrated increased theta power and phase-locking in auditory cortex, hippocampus, and prefrontal cortex during auditory predictive violations, coincident with increased theta-band feedforward connectivity from auditory cortex to ventromedial prefrontal cortex (Recasens, Gross, & Uhlhaas, 2018). In

sum, a growing body of evidence implicates theta in addition to gamma in feedforward transmission in the cortical hierarchy.

On the other hand, beta oscillations may be a rhythmic substrate of feedback predictions. The beta-band is enigmatic with respect to functional associations, but consistent a role in predictive signaling, it has long been linked to integrative and top-down functions that involve long-range cortical interactions (Bressler & Richter, 2015; Donner & Siegel, 2011). Its involvement in inter-regional communication have been proposed to reflect synchronization properties that can tolerate long conduction delays, which contrasts with the predominantly local nature of gamma-band synchrony (Kopell, Ermentrout, Whittington, & Traub, 2000). In addition, beta is the characteristic rhythm of sensorimotor cortex and associated subcortical motor circuits (Baker, 2007). Here, beta synchrony is typically maintained at a high-level during passive states, whereas movement or sensory stimulation, including preparatory activity, associates with a stereotypical desynchronization followed by resynchronization – the so-called beta rebound (Bauer, Oostenweld, Peeters, & Fries, 2006; Hari & Salmelin, 1997).

The role of beta oscillatory mechanisms in predictive functions is supported by studies linking beta-band power modulations to error processing. However, the direction of observed beta oscillatory power modulation during error processing has been inconsistent across studies. For example, in the context of an isochronous beat, beta oscillatory power has been observed to fluctuate in tandem with the stimulation rate, such that the beta power peaks at expected stimulus onset before becoming suppressed (Fujioka, Trainor, Large, & Ross, 2009). This is consistent with beta oscillatory power reflecting mobilization of neuronal populations under a prediction of the upcoming sound. If the expected stimulus is omitted, however, the ensuing power-decrease time-locked to stimulus onset is absent. Instead, there is an increase gamma-band power along with a further increase in beta-band power. This may be interpreted as a cascade of error processing, in which gamma oscillatory power increases as a function of the unexpected silence, signaling prediction error, while the beta oscillatory power increase reflect a downstream updating process.

Consistent with this, Chang and colleagues (2016) observed a beta power increase following deviant pitch tones in the context of an isochronous tone sequence. These findings were extended in a follow-up study focusing on the predictive mechanisms operating prior to stimulus onset, which showed that the extent of beta power suppression prior to a globally predictable pitch deviation (i.e every fifth tone was a deviation) determined the magnitude of

the associated P300 (Chang, Bosnyak, & Trainor, 2018). This can be interpreted to suggest that beta power suppression reflects the degree of predictive activity and hence the capacity to quench prediction error (c.f. explain away) upon occurrence of the expected deviation, which is, in turn, reflected in a reduced P300.

Two recent studies using high-density electrocorticography during presentation of the local-global auditory oddball paradigm indicates a different relationship between gamma- and beta-band activity during error processing (Chao et al., 2018; El Karoui et al., 2015). In agreement with previous research, these studies show that global regularity violations elicit an early increase in gamma-band power located to early auditory cortex, consistent with generation of prediction error signals. Interestingly, a slightly later gamma-band power increase was observed in the anterior temporal cortex and frontopolar and orbitofrontal cortices, which may reflect the cascade of ascending prediction error through stages of the auditory hierarchy (Chao et al., 2018). However, these studies also observed a later, sustained beta-band power suppression which was distributed across frontal and temporal cortices – which seems to be in conflict with previous studies linking error-updating to enhanced beta-band power (e.g. Chang et al., 2016; Sedley et al., 2016). Nevertheless, the beta suppression observed by Chao and colleagues correlated with the magnitude of the preceding gamma power within trials, consistent with downstream predictive updating. Moreover, spectral connectivity estimates indicated directed alpha/beta-band connectivity from prefrontal areas to superior temporal areas, which was argued to reflect the same underlying updating process indexed by the beta suppression.

The findings linking predictive violations to suppression of beta power can also be interpreted according to frameworks that construe beta oscillations as reflecting promotion of the current sensorimotor or cognitive set, or maintenance of the “status quo” (Engels & Fries, 2010). In accordance with this view, stimuli that violate the currently maintained prediction should abolish or reduce ongoing beta-band activity during updating.

Research Question and Hypotheses

This thesis aims to explore the neurophysiological responses involved in hierarchical predictive processing of long-term auditory patterns; that is, patterns unfolding according to a global rule. A specific aim is to uncover how this predictive process is modulated by selective attention; in particular whether distinct hierarchical stages are differentially modulated by top-down attentional processes. In line with the increasing focus on the modulation of oscillatory

dynamics as a key mechanism underlying predictive message-passing and top-down attention, an additional aim is to investigate frequency-band-specific modulations by predictability and attention. To these ends, ERPs and time-frequency power estimates from two conditions of global predictability (unpredictable vs. predictable) and attentional engagement (attended vs. unattended) are subjected to analyses.

It is hypothesized that the interplay between prediction and attention will be expressed differently across hierarchical levels of processing. Analyses of the evoked potentials are expected to show that early levels of processing exhibit an attention-independent effect of predictability, consistent with recent results which indicates that global regularities are encoded at lower hierarchical levels (e.g. Kompus et al., 2020; Recasens et al., 2014; Sauer et al., 2017). Specifically, it is expected that an MMN to global regularity violations (i.e. global deviance MMN) will be observed in both the attended and unattended contrasts, with no difference in magnitude between conditions. At later stages of processing, in contrast, the effect of predictability is expected to be attention-dependent, expressed as a global deviance P300 which should be observed only in the attended contrast.

Source localization of the early effect of predictability is expected to reveal evidence for the involvement of a frontotemporal network. This is because (i) the encoding of the global regularity should rely heavily on prefrontal areas with extended temporal tuning curves (e.g. Chao et al., 2018; Durschmid et al., 2016) and (ii) the early effect should reflect the integration of backpropagated predictions from these frontal areas with the incoming acoustic signal at the level of auditory cortical areas along the superior temporal gyrus.

Previous intracranial electrophysiological work has revealed that global pattern violations give rise to a bi-phasic response in the gamma-band characterized by early (~100 ms) and late (~300 ms) power-enhancements, the late effect accompanied by a sustained power-suppression in the beta-band (Chao et al., 2018; El Karoui et al., 2015). It is expected that these predictability effects will be replicated. However, it is unclear how these effects will interact with the attention factor. To the extent that these time-frequency signatures represent prediction error signaling and updating, and the auditory system is capable of encoding the global regularity independently of attention, it is expected that they should be observed regardless of attentional engagement. On the other hand, differences in the magnitude of oscillatory modulation due to attentional engagement is often reported in the literature (e.g. Clayton et al., 2015).

Methods

Participants

The participants were 24 healthy adults (14 females) that reported no history of neurological disorders; normal binaural hearing; and normal or corrected-to-normal vision. None of the participants were professional musicians and the majority was right-handed (right-handed, $n = 19$; left-handed, $n = 3$; ambidextrous, $n = 2$). The study was approved by the regional ethics committee (REK – South East Norway), and all participants were informed about the experimental procedure, signed the consent form, and were paid for their participation. Data from four participants were discarded due to excessive artifacts or technical difficulties with the event triggers. The reported analyses are thus based on data from 20 participants (13 females, mean age 34.5, SD 11.05; right-handed, $n = 15$).

Paradigm and Stimuli

A novel variant of the local-global auditory oddball paradigm (Bekinschtein et al., 2009) was used to examine hierarchical predictive processing of global auditory patterns. To examine how attention modulates neural responses to global deviance, the paradigm was implemented in two attention conditions: (i) attention toward sounds and (ii) distraction by visual task. Attention toward sounds was ensured by instructing participants to count rare sequences while visual task distraction involved performing a rapid serial visual presentation (RSVP) task by counting specific letter/color conjunctions.

The scaled local/global auditory oddball paradigm. The defining feature of a local/global auditory oddball paradigm is the orthogonalization of the local and global status of auditory sequences. Previous studies employing this paradigm have used repetition to establish the regularity at the local level, which confounds release from neuronal adaptation and prediction error signaling when interpreting the mismatch response (e.g. Bekinschtein et al., 2009).

In this variant of the paradigm, auditory sequences of tone quintuples were presented, in which the local status of a sequence was determined by whether the last tone conformed to a regular pitch-scaling rule (i.e. each subsequent tone was up-or down-scaled in pitch relative to the preceding tone). As such, local deviants were defined by unexpected reversal of pitch-scaling direction. Global status was determined by the frequency of a particular sequence within a block. Across separate blocks the global standards and deviants were either locally standard or deviant (i.e. local and global status was factorized to yield orthogonalization

across blocks). Hence, global deviants were defined by being improbable in a given block ($p \sim .15$). The use of pitch-scaling avoids the confound associated with using repetition of tones to establish the local regularity, because pitch-scaling prevents adaptation to repeated sounds, and thus ensures that the mismatch response does not reflect release from SSA.

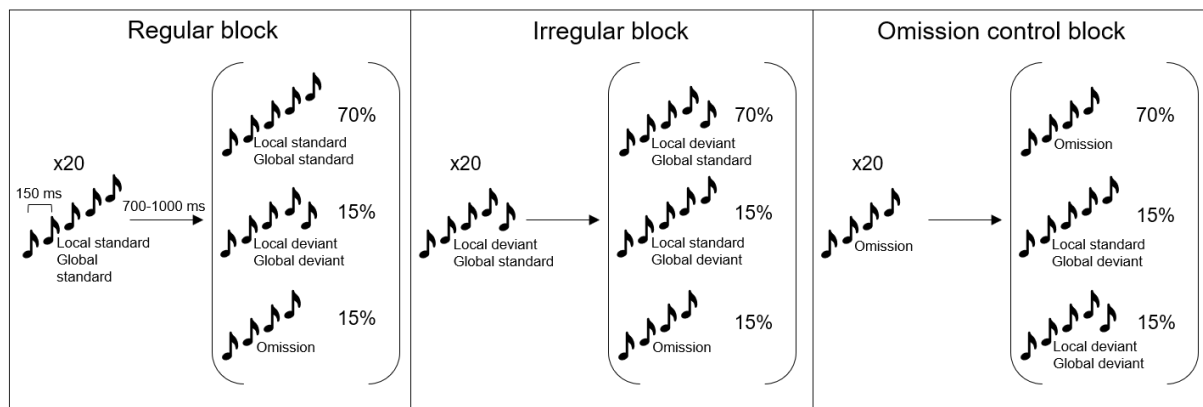


Figure 2. Illustration of the pitch-scaled local-global auditory oddball paradigm. In regular blocks, the local standard sequence was also the global standard, while in irregular blocks, the local deviant was locally standard. Both blocks had two types of deviant sequences: (i) sequences in which the last tone was unexpected given the global regularity and (ii) sequences in which the last tone was omitted. An omission control block was included to provide comparison sequences for the deviant omission sequences, in which the globally standard sequences were composed of four tones. Note that in half of the blocks, the sequences were descending in pitch rather than ascending as depicted in the illustration.

The paradigm had three block types: regular, irregular, and omission control blocks. In regular blocks, the global standard was also a local standard, and accordingly, the global deviant was also a local deviant. In irregular blocks, the global standard was locally deviant, while the global deviant was locally standard. The omission control block was implemented with globally standard omission sequences (i.e. four tones was expected at the global level) to serve as a control for omission sequences presented in regular and irregular blocks. However, as the reported analyses were geared towards examining predictive processing of sounds that violate the long-term statistics of auditory input, results from the omission sequences are not reported here.

Each block type was implemented with two repetitions of both ascending and descending pitch-scaling, resulting in four repetitions of a given block type, and thus 12 blocks in total per attention condition. Within each block type, three different sequence types could occur: (i) global standard, (ii) global deviant, and (iii), omission (i.e. last tone of sequence omitted), with factorization of local and global status (i.e. standard/deviant) across blocks. The reported analyses are focused on the contrast of global deviant and standard

sequences (i.e. [global deviant/local deviant and global deviant/local standard] versus [global standard/local standard and global standard/local deviant]).

A block would start with a habituation phase involving 20 repetitions of the global standard sequence, which served to establish that sequence as a global regularity. After the habituation phase, the global standard sequence kept occurring at a probability of 0.7 while the two infrequent deviant sequences (i.e. global deviants and omissions) both occurred pseudorandomly with a probability around 0.15. Pseudorandom selection of sequences were implemented to ensure a high level of expectation of global standards. Specifically, this involved the constraint that 2-5 global standards were presented between consecutive deviants. The inter-sequence interval was drawn from a uniform distribution over the interval 700-1000 ms with steps of 50 ms. The interval between blocks was at least 20 s, after which participants could opt to start the next block or have an extended break if needed.

The sequences were composed of harmonic tones of 50 ms duration and 7 ms rise/fall time, with 150 ms stimulus onset asynchrony (SOA). The harmonic tones were made up of 3 sinusoids: fundamental frequency, f_0 , along with the two first harmonics. Seven unique tones were used (X₁-X₇), each with f_0 separated by 3 semitones: the respective f_0 of tones X₁-X₇ were 370, 440, 523.3, 622.3, 740, 880, 1047, and 1245 Hz. Each sequence type overlapped at the fourth tone position (i.e. X₄, $f_0 = 622.3$ Hz).

Visual distraction task. The RSVP task involved monitoring a stream of colored letters and counting specific instances of a letter/color conjunction. The letters (A, E, J, P, or T) and their color (red, green, blue, yellow, or magenta) were presented randomly with an on-screen time of 150 ms. The inter-stimulus interval was drawn from a uniform distribution over the interval 750-1050 ms with steps of 50 ms. The variable SOA ensured that visual and auditory stimulation remained asynchronous such that visual activity would be averaged out during EEG analyses.

Experimental Procedure and EEG Recording

Participants were seated approximately 70 cm before a computer monitor and subjected to the two attention conditions during recording of EEG. To prevent order-effects, the attention conditions were counter-balanced across participants. During the attend sequences condition, participants were instructed to count any rare sequence and report this count at the end of the block. In the visual distraction condition, participants were instructed to perform the RSVP task and to ignore the local-global auditory oddball paradigm that was presented

simultaneously. Prior to each block, participants were informed about the target (i.e. letter/color conjunction) and prompted to report the target count at the end of the block. The auditory stimulation was delivered via stereo speakers placed at each side of the computer monitor and participants were instructed to maintain center-screen fixation during all experimental blocks.

EEG data were recorded and digitized at a rate of 1024 Hz using 64 Ag/AgCl active electrodes (BioSemi Active Two System) placed in accordance with the International 10-20 system. For monitoring eye movements, four electrooculography (EOG) were placed above and below the right eye and at the outer canthi of each eye. Additionally, two external electrodes were placed on the right and left earlobe for offline re-referencing.

Preprocessing and Data Analyses

EEG preprocessing and analysis steps were performed with custom MATLAB (R2019a, Mathworks Inc) scripts and functions provided in the FieldTrip Toolbox (Oostenweld, Fries, Maris, & Schoffelen, 2011). EEG data was re-referenced to mathematically linked earlobes and the linear trend was subtracted. The continuous data was high-pass filtered with an infinite impulse-response (IIR) zero-phase Butterworth filter (order: 3), half-amplitude cutoff at 0.1 Hz. Spectral interference by power line noise was ameliorated by applying a discrete Fourier transform (DFT) filter targeting the line noise frequency (50 Hz) and its first four harmonics. Noise-contaminated channels and segments were visually identified and rejected (an average of 3.45 channels were rejected per subject and the average percentage of rejected trials for the conditions were 13.16 % for attended-unpredicted, 15.46% for attended-predicted, 15.85% for unattended-unpredicted, and 16.65% for unattended-predicted), while contributions from eye movements were isolated by independent component analysis (ICA) and projected out of the time-series. Rejected channels were subsequently interpolated with a spherical spline procedure (Perrin, Pernier, Bertrand, & Echallier, 1989). Epochs time-locked to onset of auditory sequences were then extracted from the continuous data (-1800-2400 ms relative to sequence onset).

ERP analyses. ERPs were calculated by time-domain averaging of the stimulus-locked epochs for each condition. Prior to averaging, epochs were down-sampled to 512 Hz and baseline corrected by subtracting the mean voltage over the 0-450 ms range relative to sequence-onset. In addition to removing voltage offset, this window for the baseline correction was chosen to reduce the contribution of the contingent negative variation (CNV), which is known to build up gradually during presentation of the sequence, reflecting a higher-

order expectation of global deviance in the last tone position when several standards have been presented consecutively (Chennu et al., 2013).

Two repeated-measure two-way ANOVAs with within-subject factors attention (attended, unattended) and predictability (predicted, unpredicted) were performed to test for main and interaction effects on the amplitude derived from the MMN and P300 time-ranges. For the MMN time-range, the mean amplitude across frontocentral electrodes (Fz, FCz, Cz) was calculated in the interval between the time-points at which the voltage equaled 50% of the amplitude of the largest negative peak between 50-250 ms relative to the P50 component in the grand average of all conditions (attended-predicted, attended-unpredicted, unattended-predicted, unattended-unpredicted), which was from 73 to 196 ms relative to the sequence-defining fifth tone. The electrodes (Fz, FCz, Cz) for the mean amplitude calculation was chosen because the MMN is typically expressed frontocentrally with maximum amplitude at these electrodes (Duncan et al., 2009). For the P300 time-range, the amplitude was quantified by determining the area under the curve (AUC) in the time-range 300-600 ms at electrode Pz. The AUC calculation is considered as a robust approach to quantify the amplitude of the P300 (e.g. Farwell & Donchin, 1988; Kompus et al., 2020), which is typically expressed with maximum amplitude at Pz and peaks within the chosen interval (Duncan et al., 2009). Normality of the variables were checked by Shapiro-Wilks test, and one variable for the P300 analysis differed significantly from a normal distribution ($p > .05$), but after visual inspection of the Normal Q-Q plot, it was decided to proceed with a parametric test.

To follow up on significant main and interaction effects from the ANOVA, post-hoc dependent-samples cluster-based nonparametric t-tests (Maris & Oostenveld, 2007) were performed on global deviants and standards within attention conditions over the time-range 0-800 ms relative to the sequence-defining fifth. To examine the modulation by attention, a separate cluster-based permutation test (CBPT) was performed over the same time-range on the difference waves calculated by condition-wise subtraction of the global standard from the global deviant ERP. The threshold for clustering over adjacent spatiotemporal points on the basis of the univariate statistical tests (i.e. cluster-formation threshold) was set to .05 and the alpha-level of the cluster-based test was set to .025 to control the Type-I error-rate for both tails of the test distribution (i.e. two-tailed test).

Source Reconstruction of ERPs. To localize the generators of sensor-level ERP effects, an adaptive spatial filtering approach based on linearly constrained minimum variance (LCMV) beamforming was used (e.g. Van Veen et al., 1997). Prior to construction of the

adaptive spatial filters, trials were balanced by randomly selecting trials from the condition with most trials (to ensure similar signal-to-noise characteristics between conditions), epochs were re-sampled to 1000 Hz, and interpolated channels were discarded before re-referencing to the average of the remaining electrodes. Adaptive spatial filters were constructed for a 3D grid of dipole locations with an isotropic resolution of 5 mm with the Montreal Neurological Institute (MNI) template MRI and standard electrode positions according to the 10-20 system. The forward model was computed based on a realistic three-layer boundary-element method (BEM) volume conduction model (Fuchs et al., 2002) to derive the leadfield matrices for each grid point. For each grid point, a common spatial filter with unity-gain and minimum output constraints was constructed by integrating the leadfield matrix and covariance matrix based on the pooled data from the experimental conditions. The covariance estimate was computed between each pair of electrodes within an integration window of 450-1400 ms relative to sequence onset. Finally, the data covariance matrices from the experimental conditions were separately projected through the common filter to yield the time-series of source amplitudes (i.e. dipole moments) for all grid locations.

To localize the neuroanatomical loci of the experimental effects, dipole moments were averaged around the peak of the effects and the relevant contrasts tested with CBPTs. For the MMN, the average dipole moment within an interval of 120-140 ms relative to the last tone was statistically compared between global deviant and standard within attention conditions and the percent signal change from standard to deviant was compared between attention conditions. The same tests were performed for the P300 effect based on an interval of 300-400 ms encompassing the peak of the P300 wave. The threshold for clustering across adjacent grid points was set to .05 and the alpha-level was set to .025.

Time-frequency analysis. Epochs were re-sampled to 1000 Hz prior to time-frequency analysis. The time-resolved spectral decomposition was performed by complex Morlet wavelet convolution to extract frequency-specific power time-series for each condition. Complex Morlet wavelet convolution was performed on single epochs by using a family of wavelets spanning the range from 3 to 120 Hz (in steps of 1 Hz for frequencies 3-29 Hz, and steps of 2 Hz for frequencies 30-120 Hz), with power estimates calculated in steps of 50 ms over the interval -200-1400 ms relative to sequence onset. The width was held constant at 5 cycles across wavelets, which achieves a reasonable compromise between spectral and temporal precision (De Moortel, Munday, & Hood, 2004). The resulting time-frequency power estimate for each epoch was then normalized per frequency by subtracting the mean

from the 0-450 ms interval relative to sequence onset and dividing by the standard deviation, yielding z-transformed power estimates.

To test for power modulations by attention and predictability, dependent-samples t-tests implemented under the nonparametric cluster-based permutation approach were performed, clustering over frequencies, time points, and sensors. To test for effects of predictability, a test was performed on global deviant and standard z-transformed time-frequency power estimates over the interval from last tone onset up to the end of the epoch (0-800 ms relative to last tone) for the attention conditions separately. To test for attention effects, a test was performed over the same interval on the deviant-standard z-transformed time-frequency power difference between attention conditions. Tests were implemented with a cluster-formation threshold of .05 and an alpha-level of .025.

Results

Attention Manipulation

Performance indicators for the tasks used to manipulate attentional engagement showed that subjects complied with task instructions. For the attend auditory task, the mean percent counting error was 5.52 (range 1.34-18.88, SD 5.11), while for the visual distraction task, the mean percent error was 4.15 (range 0.35-35.71, SD 7.75).

ERPs

Repeated-Measures ANOVA of Attention and Predictability Effects on Amplitude Parameters of Early and Late ERP Components. The repeated-measures ANOVA of the mean amplitude across frontocentral electrodes (Fz, FCz, Cz) in the MMN time window revealed a main effect of attention ($F(1,19) = 48.087, p < .001, \eta_p^2 = .671$) and predictability ($F(1,19) = 38.76, p < .001, \eta_p^2 = .671$) but no interaction ($F(1,19) = .013, p = .911, \eta_p^2 = .001$). This indicates that both attention and predictability exert independent influences on the amplitude of the neuronal response at the early hierarchical level indexed by the negative peak in the MMN time-window (see **Figure 3A**). Specifically, while unpredicted input elicits an enhanced neuronal response relative to predicted input, attentional engagement indiscriminately increases the amplitude of the response.

The corresponding test on the area under the curve (AUC) in the P300 time-frame on electrode Pz revealed a main effect of attention ($F(1,19) = 69.571, p < .001, \eta_p^2 = .785$), predictability ($F(1,19) = 77.33, p < .001, \eta_p^2 = .803$), and showed that these factors interact

($F(1,19) = 51,645$, $p < .001$, $\eta_p^2 = .731$). This interaction effect is expressed as an attention-dependent amplitude enhancement (see **Figure 3B**).

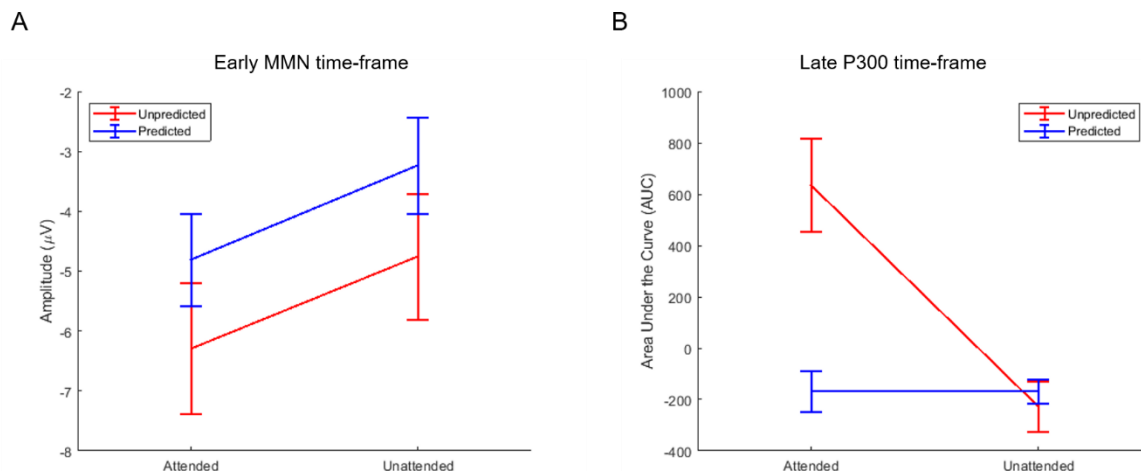


Figure 3. Profile Plots of the Marginal Means of the Amplitude Parameters Derived from the MMN and P300 Time-Frame. (A) Marginal means of the mean amplitude over frontocentral electrodes in the MMN time-frame grouped by attention (horizontal axis) and predictability (separate lines). (B) Corresponding profile plot of the AUC on electrode Pz in the P300 time-frame.

Attended Deviant versus Standard. The dependent-samples cluster-based permutation t-test performed over the time-range 0-800 ms relative to the onset of the fifth tone showed that the response to sequences that violate the global regularity is significantly different from the response to regularity-conforming sequences (see **Figure 4**). A difference between the deviant and standard response is captured by a negative cluster ($t_{\text{sum}}(19) = -11611.15$, $p = .014$) extending from 50 to 230 ms with an anterior distribution and frontocentral maximum, consistent with elicitation of an MMN to global deviance (see **Figure 4A**, top).

A positive cluster ($t_{\text{sum}}(19) = 46114.04$, $p < .001$) captures a later difference in the 230-800 ms time-range expressed at posterior electrodes with a posterocentral maximum. This cluster corresponds to the P300 elicited by global deviance.

Attended sequences

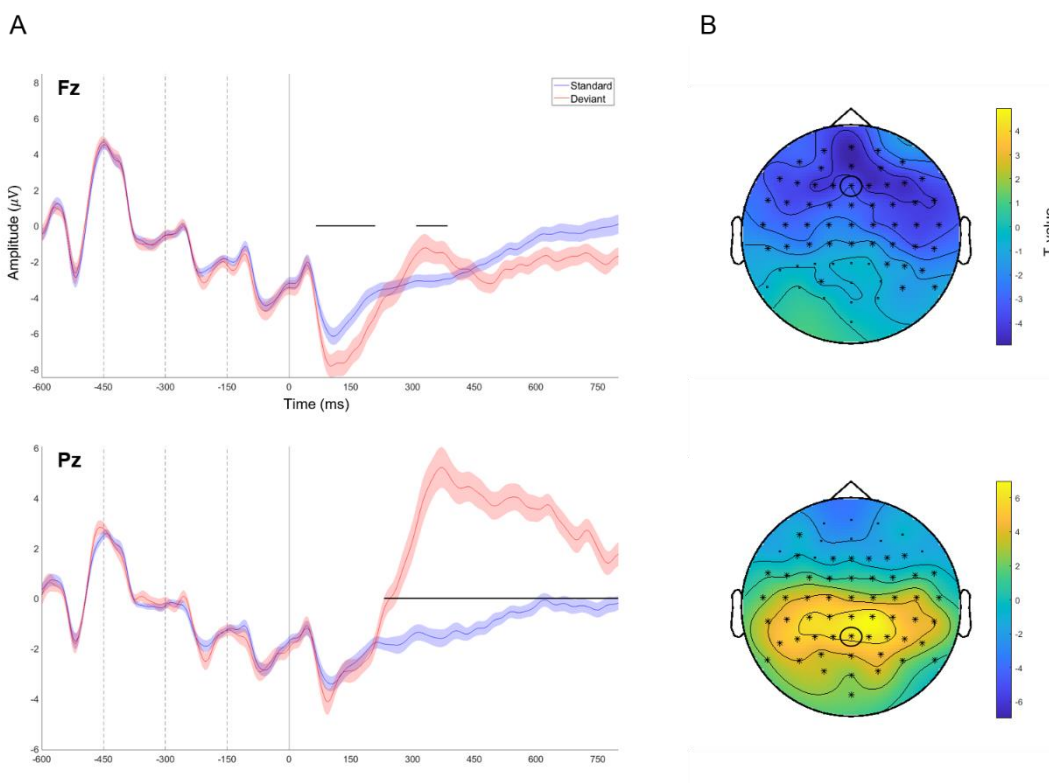


Figure 4. Summary of ERP Results for Attended Sequences. (A) Grand average ERP waveforms from the attended global standard and deviant conditions plotted from electrode Fz (top) and Pz (bottom). Plots extend from the onset of the first tone of the sequence (-600 ms) to 800 ms following the sequence-defining fifth tone. Tone onsets are depicted by dashed lines up until the defining tone which is indicated by a solid line. Significant differences between conditions are indicated by horizontal black lines. (B) Topographical plots of T-values over the time-range encompassing the early negative cluster (top) and the later positive cluster (bottom). Electrodes spanned by clusters are marker by asterisks and the location of plotted electrodes (in A) are indicated by black circles.

Unattended Deviant versus Standard. A corresponding CBPT on ERPs of regularity-violating and conforming sequences in the unattended condition confirms that the differential response by global predictability persists when attention is directed towards a visual task (see **Figure 5**). This differential response is characterized by an early negative cluster ($t_{\text{sum}}(19) = -11\,562.51$, $p = .007$) extending from 60 to 210 ms and encompassing most of the scalp electrodes with a frontocentral maximum, which is consistent with the elicitation of an MMN by unattended global deviants (see **Figure 5A**). Two additional negative clusters passed the significance threshold: the second cluster ($t_{\text{sum}}(19) = -8372.29$, $p = .007$) extended from around 230 to 480 ms while the third cluster ($t_{\text{sum}}(19) = -6051.57$, $p = .015$) extended from around 480 to 685 ms, both encompassing most of the scalp electrodes and with frontocentral maxima. The grand averaged ERPs (**Figure 5A**) shows that both clusters reflect

a sustained negativity in the response to deviant relative to standard following the rebound of the MMN.

Unattended sequences

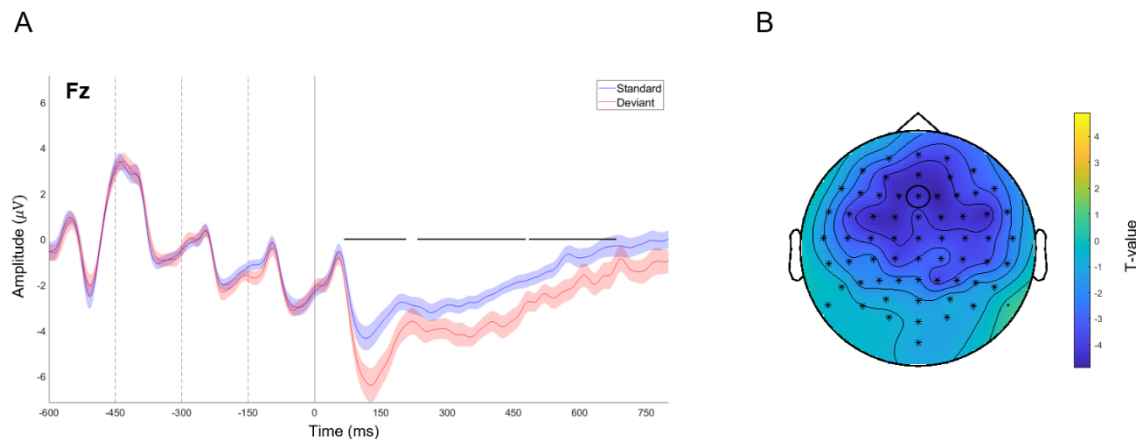


Figure 5. Summary of ERP Results for Unattended Sequences. (A) Grand average ERP waveforms from the global standard and deviant conditions from electrode Fz. Plots extend from the onset of the first tone of the sequence (-600 ms) to 800 ms following the sequence-defining fifth tone. Tone onsets are depicted by dashed lines up until the defining tone which is indicated by a solid line. Significant differences between conditions are indicated by horizontal black lines. (B) Topographical plot of T-values over the time-range encompassing the first negative cluster capturing the MMN. Electrodes spanned by the cluster are marker by asterisks and the location of plotted electrode (in A) is indicated by a black circle.

Attended versus Unattended. The CBPT on the difference waves (i.e. global deviant – standard) from the attended and unattended conditions captures the interaction between attention and predictability at a late stage of processing (see **Figure 6**). A single positive cluster ($t_{\text{sum}}(19) = 49\,087.26$, $p < .001$) corresponding to the P300 passed the significance threshold, which extends from around 225 to 800 ms. From the grand averaged difference waves (**Figure 6A**), it is evident that there is no differential response as a function of attention in the MMN time-frame.

Attention contrast

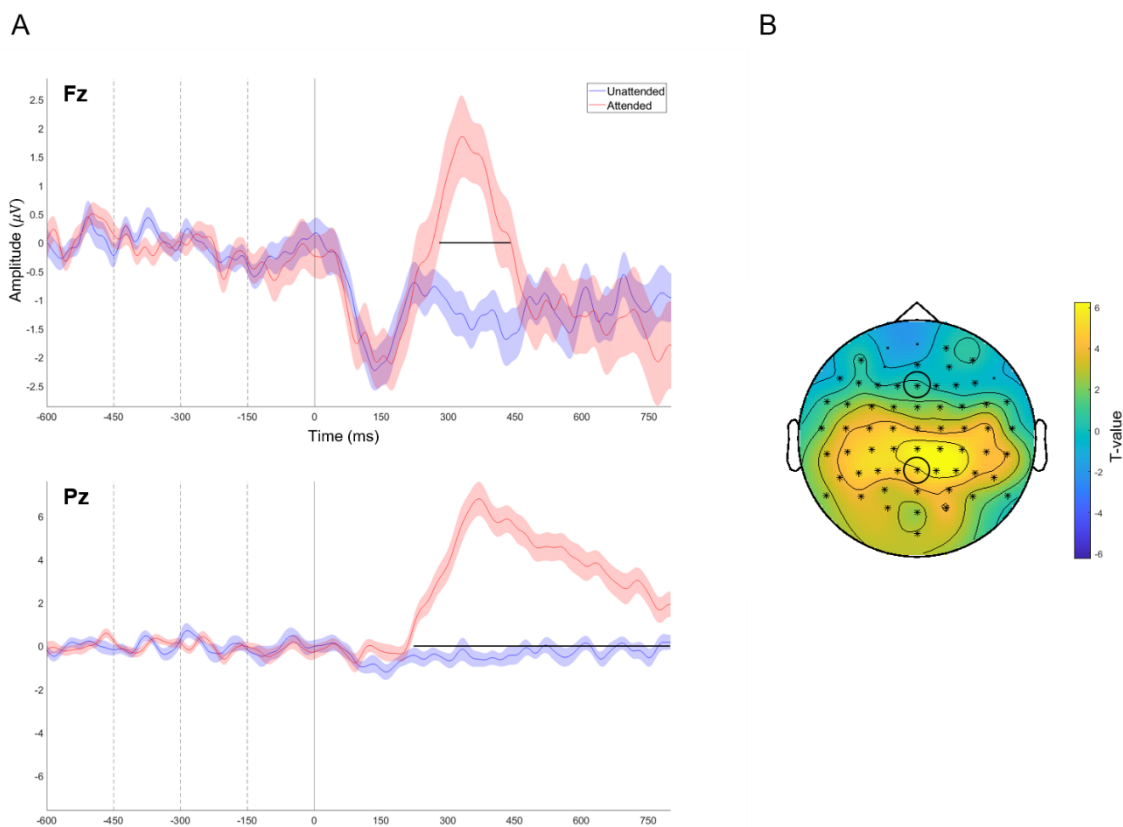


Figure 6. Summary of ERP Results for the Attention Contrast. (A) Grand average difference waves (deviant – standard) from the attended and unattended conditions from electrode Fz (top) and Pz (bottom). Plots extend from the onset of the first tone of sequence (-600 ms) to 800 ms following the sequence-defining fifth tone. Tone onsets are depicted by dashed lines up until the defining tone which is indicated by a solid line. Significant differences are indicated by horizontal black lines. (B) Topographical plot of T-values over the time-range of the significant positive cluster. Electrodes contributing to the cluster are marked by asterisk and the location of the plotted electrodes (in A) are indicated by black circles.

Source Reconstruction

Attended Low-Level Response. The CBPT performed on the contrast of the source solutions for the attended global deviant and standard responses in the MMN time-frame revealed a statistically significant positive cluster of source power difference ($t_{\text{sum}}(19) = 14212.69$, $p < .001$). The neuroanatomical extent of the cluster indicates that the low-level response is generated in a distributed temporofrontoparietal network (see **Figure 7A**). In the right hemisphere, the cluster includes the superior and middle temporal gyri extending towards the temporal pole, the anterior part of the medial temporal cortex, the inferior, middle and superior frontal gyri including motor cortical areas, the dorso- and ventromedial frontal cortex, the superior parietal lobule, posterior cingulate cortex, and insular cortex. The left-

hemispheric contribution largely included the homologous areas, in addition to the temporoparietal junction/inferior parietal cortex, areas in lateral occipital cortex and occipitotemporal inferomedial aspects, and excluding the anteromedial temporal cortex.

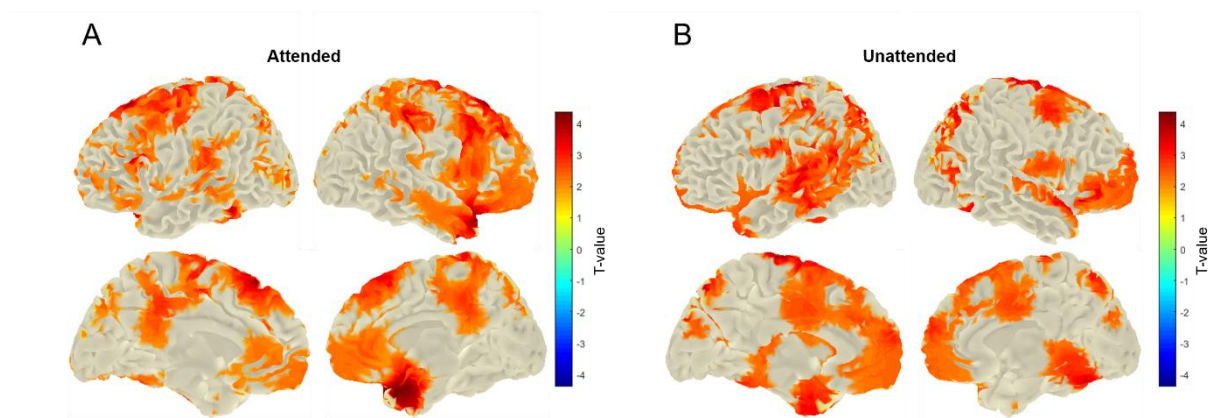


Figure 7. Source Results in the MMN Time-Frame. (A) Lateral (top) and medial (bottom) cortical surface plots of grid points masked by the significant positive cluster found in the attended contrast. (B) Corresponding cortical surface plots for the unattended contrast.

Unattended Low-Level Response. The test on the corresponding unattended contrast also revealed a statistically significant cluster of source power difference ($t_{\text{sum}}(19) = 14\,320.45$, $p < .001$). The cluster-extent indicates that a similar temporofrontoparietal network underlies the early response to unattended global deviations (see **Figure 7B**).

Attended versus Unattended Low-Level Response. In line with the overlap in the condition-specific source results, and in accordance with the expectation of attention-independent prediction error signaling at the early level and the sensor-level results, the test on the percent signal change from standard to deviant across attention conditions in the MMN time-frame did not reveal differences between conditions (largest positive cluster: $t_{\text{sum}}(19) = 16.40$, $p = .886$; largest negative cluster: $t_{\text{sum}}(19) = -137.31$, $p = .235$).

Attended High-Level Response. The CBPT performed on the global deviant and standard source solutions in the P300 time-frame revealed a statistically significant difference in source power ($t_{\text{sum}}(19) = 12\,527.11$, $p < .001$). The difference in source power is captured by a positive cluster spanning distributed areas of the frontal, parietal, and temporal cortices, similar to the early-level response (see **Figure 8A**). The right-hemispheric contributions to the cluster includes large parts of the rostral prefrontal cortex, areas on the inferior and medial frontal gyri, large parts of the medial frontal cortex, the superior parietal lobule, areas of the superior temporal gyrus lateral to Heschl's gyrus, the temporal pole, and anterior parts of the

medial temporal lobe, and the retrosplenial cortex. The left-hemispheric homologous areas are encompassed by the cluster in addition to the temporoparietal junction/inferior parietal cortex.

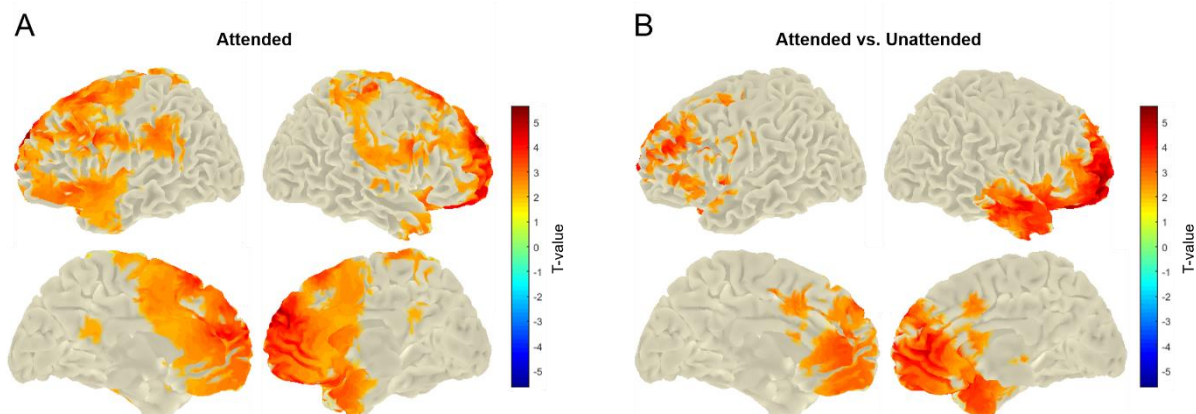


Figure 8. Source Results in the P300 Time-Frame. (A). Lateral (top) and medial (bottom) cortical surface plots of grid points contributing to the significant positive cluster found in the attended contrast. (B) Corresponding plots for the contrast of percent signal change across attention conditions.

Attended versus Unattended High-Level Response. A CBPT on the contrast of the percent signal change from standard to deviant across attention conditions revealed an expected difference in the time-frame of the P300 ($t_{\text{sum}}(19) = 7748.09$, $p < .001$). The observed positive clusters encompassed frontotemporal areas in both hemispheres (see **Figure 8B**). The right-hemispheric cluster-contributions included the superior, middle and inferior temporal gyri extending towards the temporal pole, the anteromedial temporal cortex, large parts of the rostrolateral prefrontal cortex, dorso- and ventromedial aspects of prefrontal cortex, the dorsal anterior cingulate cortex, and the insular cortex. In the left hemisphere, areas in the anterior portion of superior temporal and inferior frontal gyri, middle and superior frontal gyri including rostrolateral prefrontal cortex, dorso- and ventromedial prefrontal cortex, and dorsal anterior cingulate cortex contributed to the cluster.

Time-Frequency Power

Attended Deviant versus Standard. The CBPT on the time-frequency power estimates from the attended global deviant and standard conditions (**Figure 9A**) revealed a condition difference in the spectral power time-series (**Figure 9B**). This difference is characterized by two different-sign spatio-spectrotemporal clusters. The positive cluster ($t_{\text{sum}}(19) = 14\,698.18$, $p = .015$) encompasses the delta and theta range (3-7 Hz), spans the duration from the sequence-defining fifth tone up until the end of the epoch (0-800 ms), and includes all scalp electrodes (**Figure 9C**, left). The negative cluster ($t_{\text{sum}}(19) = -38\,027.85$, $p <$

.001) also includes all scalp electrodes and encompasses a broad frequency-range including the theta, alpha, beta, and gamma bands from 50 to 800 ms (**Figure 9C**, right).

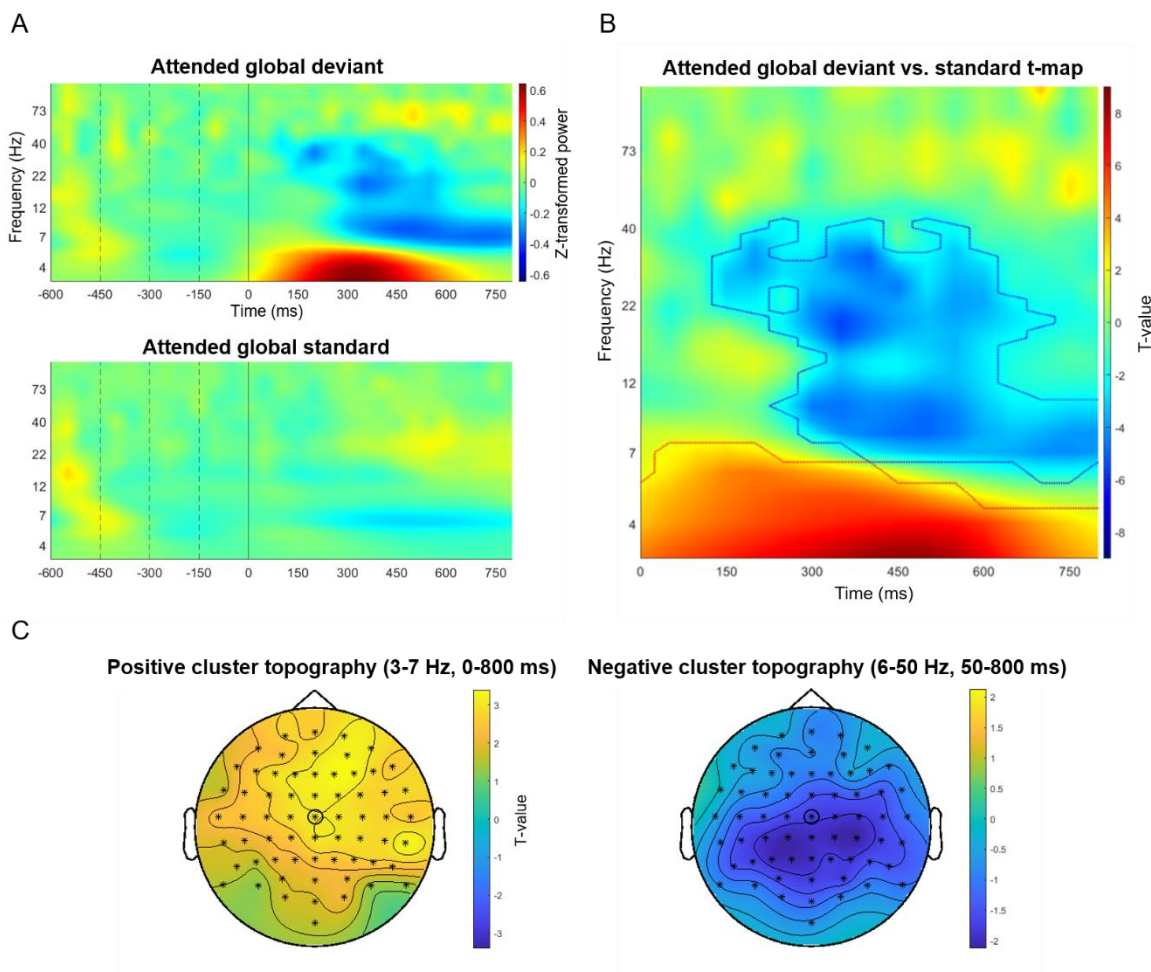


Figure 9. Summary of the Time-Frequency Power Comparison of Attended Global Deviant and Standard Conditions. (A) Z-transformed time-frequency power estimates for attended deviant (top) and standard (bottom) in the time-range from sequence onset (-600 ms) until 800 ms following the sequence-defining fifth tone from electrode Cz. Tone onsets are indicated by dashed lines until the sequence-defining fifth tone which is indicated by a solid line. Frequencies are plotted on a logarithmic scale to emphasize lower frequencies. (B) Time-frequency plot of T-values from the univariate statistical tests on time-frequency power pairs for electrode Cz. The positive and negative cluster that passed the significance threshold of the CBPT are outlined by red and blue dashed lines, respectively. (C) Topographical plots of T-values from the time-frequency range of the significant positive (left) and negative (right) clusters. The electrode (Cz) plotted in A and B are outlined by circle.

Unattended Deviant versus Standard. The corresponding CBPT for the unattended contrast did not reveal a significant difference time-frequency power (largest positive cluster: $t_{\text{sum}}(19) = 2700.304$, $p = .094$; largest negative cluster: $t_{\text{sum}}(19) = -2327.329$, $p = .126$; **Figure 10**).

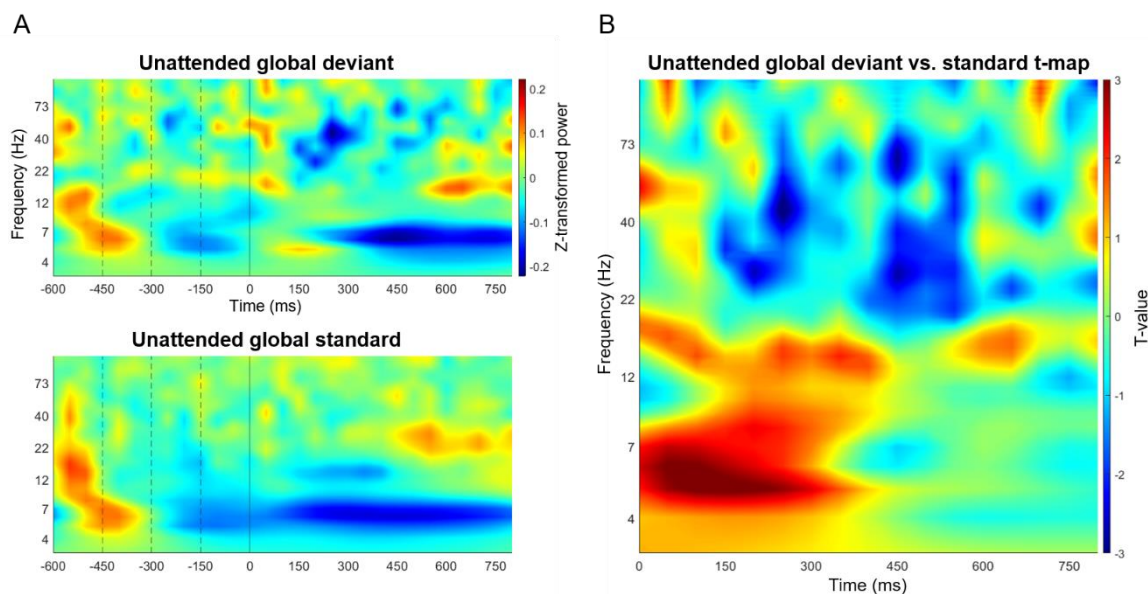


Figure 10. Summary of Time-Frequency Power Comparison of Unattended Global Deviant and Standard Conditions. (A) Z-transformed time-frequency power estimates for attended deviant (top) and standard (bottom) in the time-range from sequence onset (-600 ms) until 800 ms following the sequence-defining fifth tone from electrode Cz. Tone onsets are indicated by dashed lines until the sequence-defining fifth tone which is indicated by a solid line. (B) Time-frequency plot of T-values from the univariate statistical tests on time-frequency power pairs for electrode Cz.

Attended versus Unattended. The CBPT on the time-frequency power difference (deviant – standard) between the attention conditions revealed an attention effect characterized by two different-sign clusters (see **Figure 11**). The positive cluster ($t_{\text{sum}}(19) = 10\,273.85$, $p < .001$), which included all scalp electrodes, encompassed the delta and theta bands (3-7 Hz) from 0 to 800 ms. The similarly scalp-distributed negative cluster ($t_{\text{sum}}(19) = -25\,027.31$, $p < .001$) encompassed a broad frequency range extending from the upper theta band, through the alpha and beta bands, up to lower gamma (6-48 Hz) from around 200 to 800 ms.

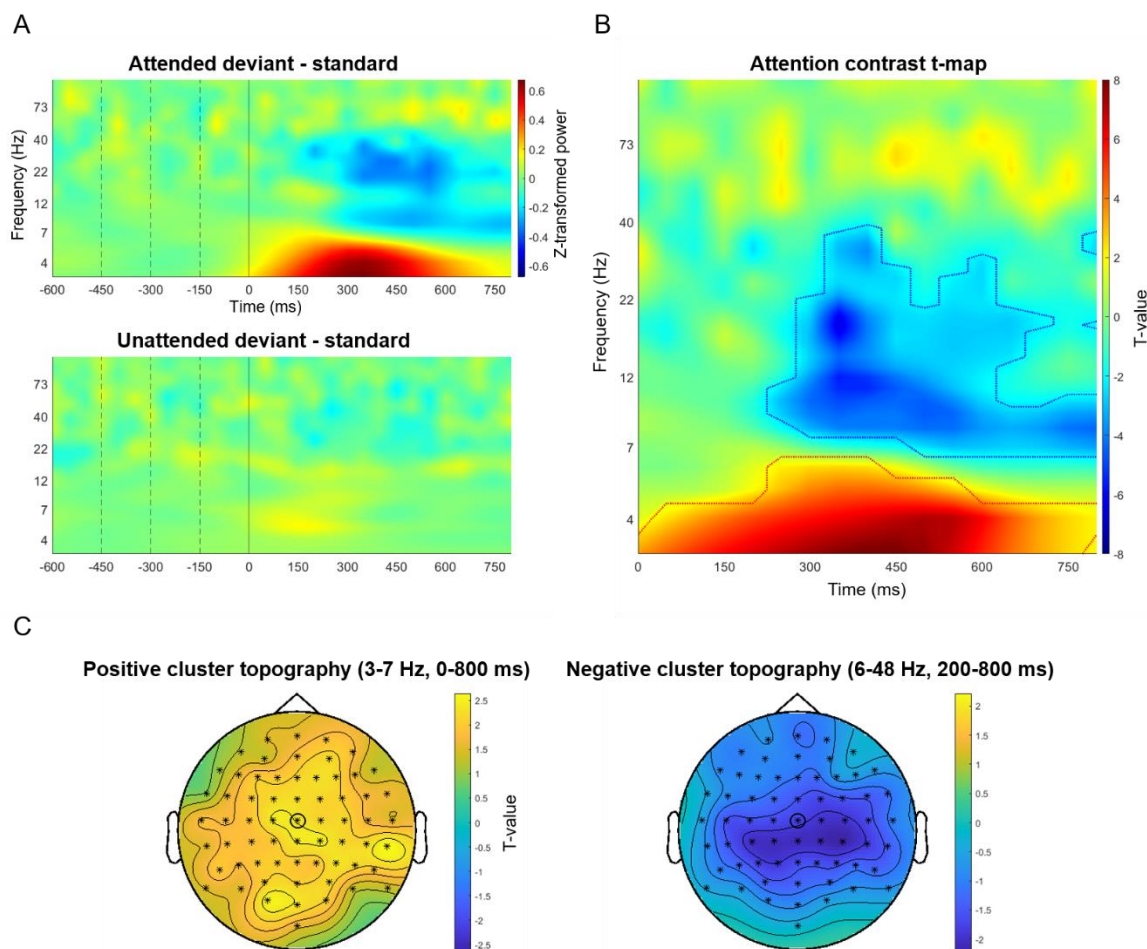


Figure 11. Summary of the Contrast of Time-Frequency Power Difference Between Attention Conditions.

(A) Z-transformed time-frequency power difference (deviant – standard) for the attended (top) and unattended (bottom) conditions in the time-range from sequence onset (-600 ms) until 800 ms following the sequence-defining fifth tone from electrode Cz. Tone onsets are indicated by dashed lines until the sequence-defining fifth tone which is indicated by a solid line. (B) Time-frequency plot of T-values from the univariate statistical tests on the time-frequency power difference pairs for electrode Cz. The dashed red and blue lines indicates the time-frequency extent of the statistically significant positive and negative cluster, respectively. (C) Topographical plots of T-values from the time-frequency range of the significant positive (left) and negative (right) clusters. The electrodes plotted in A and B are outlined by circle.

Discussion

The purpose of this study was to investigate the attentional modulation of predictive processing of auditory global patterns with a particular focus on how this may vary across hierarchical levels of processing. This question was explored by a set of analyses optimized to reveal different parts of the event-related response, i.e. ERP and time-frequency analyses.

In accordance with the hypothesis that attentional modulation would interplay differently with predictive processing across hierarchical levels, the ERP analyses showed

that the response at an early stage (i.e. in the MMN time-frame) is independent of attentional engagement, in contrast to the response at a later stage of processing (i.e. in the P300 time-frame), which is highly attention-dependent. Source localization of the attention-independent early response indicates that it is generated by a distributed network of cortical areas that includes a prominent frontotemporal contribution.

Contrary to the expectation that the time-frequency analyses would reveal a similar pattern of oscillatory modulations, both early and late time-frequency power modulations by predictability were attention-dependent. Moreover, the analyses did not reveal the expected early, transient gamma-band power modulation, but rather showed that the early part of the response was limited to a modulation centered on the theta-band, which was sustained for at least 800 ms post-stimulus. However, the results did reveal the hypothesized late-stage beta-power suppression, which has been speculated to be a signature of predictive updating at higher hierarchical levels (e.g. Chao et al., 2018).

ERP Analyses: Early and Late Responses to Global Deviance Interplay Differently with Attentional Engagement

The ERP analyses provide support for the hypotheses that early and late levels of processing, respectively indexed by the MMN and P300 ERP components, are differently modulated by attentional engagement towards the auditory stream. The ANOVA results show that the early-level response is not modulated by attentional engagement, while the late-level response interacts with attentional engagement. The post-hoc CBPTs provides evidence that global deviance elicits an MMN response irrespective of attentional allocation which is followed by the P300 only when the auditory stream is attended.

Notably, however, the presence of a main effect of attention in the MMN time-frame shows that attention increases the amplitude of the response to both unpredicted and predicted input (hence leaving the amplitude of the MMN unaffected). This observation is consistent with the opponent-process model of the relationship between attention and prediction at the early level of processing (see Figure 1, left), as suggested by previous work (e.g. Foldal et al., 2019; Garrido et al., 2018). The ANOVA and CBPT results for the late P300 time-frame together supports an interaction model, in which unpredicted input is selectively amplified contingent on attentional engagement (Figure 1, middle), in line with previous MEEG work examining responses to global deviance (e.g. Bekinschtein et al., 2009; Chennu et al., 2013; Kompus et al., 2020; Wacongne et al., 2011).

In relation to previous work, the MMN to global deviance is particularly noteworthy, as it provides evidence for an early-level response to global pattern violations that has not been consistently reported in comparable work. The MMN has been widely reported as a signature of local deviance across studies using similar paradigms as the current study (Bekinschtein et al., 2009; Chennu et al., 2013; Marti et al., 2014; Strauss et al., 2015; Wacongne et al., 2011); however, the global deviance MMN has only been reported recently (Kompus et al., 2020; Sauer et al., 2017). Previous work on auditory global/local processing have thus suggested that the process underlying the MMN is only able to resolve predictive violations defined over a short time-frame (e.g. violations of transition probabilities within a narrow temporal window). The current results concur with two recent studies (Kompus et al., 2020; Sauer et al., 2017) to suggest, on the contrary, that the MMN process can represent temporally extended dependencies in the auditory stream regardless of attentional allocation.

The attention-independent global deviance MMN offers an alternative interpretation of previous results when considered alongside the attention-dependent global deviance P300. In previous reports, the MMN and P300 has been interpreted as reflecting a cascade of prediction errors within a recurrently connected hierarchy (e.g. Chennu et al., 2013; Wacongne et al., 2011). Specifically, the MMN system is viewed as feeding local-level prediction errors into the P300 system, which can then extract the global regularity and subsequently emit prediction errors in response to global deviance. However, the current results show that the MMN system responds to global deviance even when the auditory stream is unattended, and, consequently, no P300 is elicited. Thus, the global rule is represented in the auditory system in a context in which the P300 is not elicited by global violations (i.e. when the auditory stream is unattended) – an observation which seems to rule out that the view of the P300 as a unique marker of global rule learning (e.g. Bekinschtein et al., 2009; Chennu et al., 2013; Wacongne et al., 2011).

As to the nature of the P300 effect, the suggestion that it reflects the ignition of a globally distributed neuronal workspace is consistent with the reported results (e.g. Bekinschtein et al., 2009; Marti et al., 2014). Global neuronal workspace theory (GNWT) stipulates that sensory stimuli are first processed at the level of modality-specific networks (e.g. the perisylvian or frontotemporal auditory network) before they can be gated to a global neuronal workspace (e.g. Dehaene & Changeaux, 2011). Gating to the workspace is postulated to be reflected in an all-or-nothing event referred to as ignition which signifies the broadcasting of the gated stimulus to encapsulated subsystems throughout the cortex, which

then allows the stimulus to guide deliberate thought and action. Viewed together, the ERP results in the current study are consistent with a framework in which a lower-level network track and signal deviations from temporally extended regularities regardless of attentional engagement. The P300 response may therefore be interpreted as indexing the gating of task-relevant information to a large-scale network associated with working memory and conscious access, as proposed by GNWT. Crucially, the absence of a late effect when the auditory stream is unattended would therefore reflect a lack of ignition due to the unavailability of the workspace (i.e. there is a higher threshold to ignite the workspace when it is occupied by another task), and not the absence of a surprise response (i.e. prediction error) due to a failure to learn the long-term dependency governing the auditory stimuli. Related to these conjectures, it is notable that recent efforts have attempted to integrate predictive processing and GNWT (see Witon et al., 2020; Whyte, 2019).

In general, the ERP results are consistent with both predictive processing and GNWT and extends earlier results by suggesting that even long-term auditory dependencies are modeled and represented at an early stage of processing independently of attention – as reflected by the global deviance MMN. In this regard, it is notable that neuronal adaptation has been forwarded as an alternative neurophysiological mechanism of the MMN (Jääskeläinen et al., 2004; May & Tiitinen, 2010). In the current paradigm, adaptation at the local level (i.e. within-sequences) was controlled for by the use of scaled pitch sequences (see Millichamp, 2019 for local-level results); however, higher-level neuronal adaptation cannot be principally ruled out as an explanation of the global deviance MMN. This is because it is the unexpected deviation from sequence-repetition (i.e. the block-level regularity) that constitutes a global deviant. However, this adaptation would have to occur at higher-level neuronal population with a long enough integration window to represent the entirety of a sequence (i.e. 600 ms), and not at the level of simple feature-selective neurons in auditory cortex as have been proposed for the traditional MMN. Future work may resolve this question by employing variable sequences that conform to a global structure (i.e. to avoid repetition also at the block-level).

Source Reconstruction of Evoked Components

The statistical comparisons of the LCMV beamformer source solutions for the deviant and standard response in the MMN and P300 time-windows offer clues to the underlying functional neuroanatomy of the observed effects, i.e. the global deviance MMN and P300.

In the MMN time-range, a statistically significant cluster extending over temporal, frontal, and parietal areas was observed for both the attended and unattended contrasts, and the direct comparison of the attention conditions revealed no difference. The observed results are in line with the a priori expectation of a frontotemporal involvement in the global deviance MMN (e.g. Chao et al., 2018; Dürschmid et al., 2016; El Karoui et al., 2015). Previous MEEG source reconstruction and hemodynamic imaging studies have consistently implicated the perisylvian auditory areas in the MMN response, with the most consistently implicated areas being the bilateral superior temporal gyrus and the right inferior frontal gyrus (Alho, 1995; Deouell, 2007; Fitzgerald & Todd, 2020; Opitz et al., 2002; Sauer et al., 2017; Schönwiesner et al., 2007). The current results are consistent with the involvement of these areas but implicates a more distributed temporofrontoparietal network than typically observed, including large parts of the frontal cortex bilaterally as well as parietal areas. This discrepancy may be explained by the nature of the global deviance response, which is expected to reflect the predictive violation of a long-term dependency in the auditory stream, and hence may involve more complex inter-regional interactions among distributed cortical areas as compared to the simple physical-deviant MMN that has been explored in most previous source localization efforts. Although, it should be noted that Sauer et al. (2017) source localized the global deviance MMN elicited in the context of the classical local/global paradigm with a similar algorithmic approach as the current study (i.e. LCMV beamforming), finding activations mostly restricted to auditory cortical areas. The discrepancy with their results may be explained by differences in auditory stimulation (i.e. ascending/descending pitch-sequences in the current work vs. simple repetition).

For the P300 time-range, a statistically significant cluster spanning a similar temporofrontoparietally distributed set of areas was observed in the attended contrast, while a cluster of primarily rostrolateral- and medial frontal areas, along with the right anteromedial temporal cortex, emerged as statistically significant in the contrast between the attention conditions. Previous efforts to localize the sources of the P300 have often linked the response to a network distributed over association cortical areas in the frontal cortex, where the lateral prefrontal and anterior cingulate cortices are often reported; parietal cortex, where the superior and inferior parietal cortices are commonly reported; and the temporal cortex, where the superior temporal cortex and medial temporal areas have been implicated (e.g. Bekinschtein et al., 2009; Linden, 2005; Uhrig et al., 2014; Wang et al., 2015). It has also been shown that the temporoparietal junction appears to be a particularly important substrate,

as lesions to this area has been reported to severely reduce the amplitude of the P300 (e.g. Knight, Scabini, Woods, & Clayworth, 1989; Verleger, Heide, Butt, & Kömpf, 1994). The current source results concur with the previous literature by implicating the lateral prefrontal, medial frontal cortex including anterior cingulate, superior temporal cortex, anteromedial temporal cortex, and superior and inferior parietal cortex extending into the temporoparietal junction in the global deviance P300. These results are broadly consistent with the recruitment of a global neuronal workspace (Dehaene & Changeaux, 2011)

Analyses of Time-Frequency Power

The analyses of time-frequency power were motivated by the idea that neural oscillations represents a means for intra- and inter-areal communication, with distinct frequency-bands thought to subserve prediction error signaling and prediction updating (e.g. Arnal & Giraud, 2012).

The observed results deviates from the hypothesis about an early attention-independent, transient gamma-band power modulation. Instead, the early part of the response included an attention-dependent modulation of the theta-band (3-7 Hz) which was sustained for the duration of the epoch (800 ms post-stimulus). It is likely that this lower-frequency modulation reflects, in part, the evoked components of the event-related response (i.e. the MMN and P300), which are known to be expressed in the delta/theta range (Bastiaansen, Mazaheri, & Jensen, 2012).

However, in that case, an early theta-modulation in the MMN time-frame is expected in the unattended condition, such that the pattern of results would conform to an attention-independent modulation of the early response as observed in the ERP analyses. Examination of the time-frequency t-value plot for the unattended condition does indicate a trend towards such a modulation (Figure 10B). It may be that the unexpected pattern of results arise from the mechanics of the cluster-based nonparametric testing procedure (i.e. cluster-formation and calculation of the test statistic based on cluster-extent). Specifically, in the attended condition, the spatio-spectrotemporal contiguity of the early (MMN-related) and late (P300-related) lower-frequency power modulations subsumes these effects in one spatiotemporally expansive cluster, whereas the transitory low-frequency modulation in the unattended condition may not survive statistical thresholding due to the large spatio-spectrotemporal space over which the cluster-based FWER correction is applied.

Another interpretation of the results is that the time-frequency analyses capture an early-onset interaction between attention and prediction expressed in the lower-frequency bands. Indeed, time-frequency analysis is sensitive to other parts of the event-related response relative to evoked potential analysis and may thus have captured a non-phase-locked (or induced) process not visible in the ERP results. Supporting such an interpretation is the oft-reported association between attention and modulations in lower frequency bands, especially in the theta range (e.g. Clayton et al., 2015; Missonnier et al., 2006), which may interact with predictability as suggested by the time-frequency difference comparison between the attention conditions. This interpretation is also consistent with recent studies that have associated theta oscillations with feedforward signaling during prediction error processing in both vision (e.g. Bastos et al., 2015) and audition (e.g. Recasens et al., 2018).

As to the absence of the gamma-band modulation that has been reported in previous intracranial work (Chao et al., 2018; El Karoui et al., 2015), it can be noted that gamma-band oscillations are not consistently observed in non-invasive recordings (e.g. Hoogenboom, Schoffelen, Oostenveld, Parkes, & Fries, 2006; Muthukumaraswamy, 2013). This is especially the case for EEG, as the interleaved cascade of volume and capacitive conduction underlying the propagation of the extracellular voltage potential to the scalp electrodes is essentially equivalent to a stack of low-pass filters. In comparison, MEG is relatively better suited for noninvasive demonstrations of gamma-band modulations (e.g. Hoogenboom et al., 2006), as magnetic fields pass unimpeded through the skull.

The analyses did support the presence of beta power suppression, which was linked to global deviance processing in two recent intracranial electrocorticographic studies (Chao et al., 2018; El Karoui et al., 2015). This suppression was subsumed in a cluster with a spectral extent that covered the extent of the classical alpha- and beta-bands and extended into the lower-gamma range, and had a temporal extent that ranged from around 50 ms up to 800 ms following the onset of global deviance. Examination of the spectrotemporal evolution of this cluster reveals that the suppression in the beta-range starts relatively early (~150 ms at Cz, Figure 9B) while the alpha suppression has a later onset (~300 ms at Cz, Figure 9B). Hence, it may be that this cluster captures multiple distinct processes related to global deviance processing: a process centered on the beta-band and another centered on the alpha-band.

The beta-band has been considered as a vector of feedback prediction (e.g. Arnal & Giraud, 2012; Bastos et al., 2012) and the maintenance of the cognitive status quo (Engels & Fries, 2010). Consequently, the association between global error processing and suppression

in the beta-band has previously been interpreted as reflecting the updating of predictions (e.g. Chao et al., 2018; El Karoui et al., 2015). Specifically, Chao et al. speculated that oscillatory desynchrony in the beta-band may be necessary to transiently halt feedback to lower levels of the hierarchy during the updating process. It can be speculated that the alpha-band suppression represents a distinct process related to attention. An influential view of the functional role of alpha oscillations is that they are involved in information gating, c.f. gating by inhibition (Jensen & Mazaheri, 2010). Selective alpha suppression in neuronal populations responding to an attended stimulus is a widely replicated finding, which has been linked to an increase in neuronal excitability (Klimesch, Sauseng, & Hanslmayr, 2007). The alpha suppression observed in the current results may therefore be interpreted to reflect an increase in cortical arousal induced by a regularity-deviating stimulus. In relation to the alpha-band, it is also noteworthy that a recent study linked modulations in alpha-band power to expectations about precision in the sensory stream (Sedley et al., 2016). The observed alpha-band power suppression could be interpreted in line with these findings, to the extent that global deviance signifies a decrease in the expected precision of the sensory stream.

The attention-dependence of the alpha/beta suppression is notable. To the extent that (i) the beta-band suppression reflect an updating process and the alpha-band suppression reflect increased vigilance due to prediction error and (ii) the auditory system detects unattended global deviance as indicated by the ERP results, these processes may have been expected to occur also during the unattended condition. Examination of the time-frequency plot of t-values from the unattended condition does indicate the that there may be a suppression in the upper beta range that the analyses was underpowered to detect (Figure 10B). In future work, hypothesis-driven tests may be able to detect these oscillatory dynamics if present.

Limitations and Future Directions

The present work aimed to characterize how attention interplays with and modulates the predictive processing of global auditory patterns. One interpretational limitation arises from the tasks used to manipulate attentional engagement. Specifically, we cannot disentangle ERP and time-frequency effects related to the predictive process from processes related to task performance. Thus, it may be that some of the observed attention-dependent effects (e.g. global deviance P300 and the power modulations in lower-frequencies) were partly driven by the task of counting deviants (e.g. working memory and updating).

Another limitation concerns the interpretation of the global deviance MMN as reflecting lower-level predictive modeling of global patterns. As mentioned above, the MMN has been suggested to reflect a passive process of neurophysiological adaptation due to repeated stimulation. Since the global regularity in the current study were implemented by repeating sequences at the block-level, it is theoretically plausible that adaptation of a higher-level population of neurons may underlie the effect. However, the distributed network indicated by the source analyses speaks against this interpretation. Future work may rule out adaptation underlying the global MMN by showing that it is also sensitive to more abstract global regularities. For example, a paradigm in which sequences vary in tonal composition whilst abiding to the same rule (e.g. pitch-scaling as used in the current study) could resolve this interpretational issue.

Furthermore, although the analyses indicates that the global deviance MMN is attention-independent, it was not ruled out whether this is an experimental order effect. Although the order of attention conditions were counter-balanced between subjects to prevent order effects, it is plausible that the observed attention-independence of the MMN were driven by the subgroup of subjects that were exposed to the attend condition first. Previous work has indeed shown that this effect can occur for the MMN to complex regularities (e.g. Tervaniemi et al., 2001). For example, Tervaniemi and colleagues showed that the MMN to complex melodic contour deviations were only observed in an unattended condition when the subjects were first exposed to the auditory regularity in an attended condition. This indicates that attention may be necessary to encode some complex regularities, but that deviations from these regularities can subsequently be detected independently of attention.

Finally, results from the source analyses must be interpreted with caution. Due to unavailability of anatomical MRIs and electrode positions, the forward model was calculated based on a template MRI and standard electrode positions, which may substantially affect the accuracy of the forward solution. It has been shown that the inverse model is exquisitely sensitive to the accuracy of the volume conductor model (e.g. Steinsträter, Sillekenms, Junghoefer, Burger, & Wolters, 2010). Hence, source localization errors and false positives due to inaccuracies in the forward model cannot be ruled out.

Concluding Remarks

The current work investigated how global regularity processing is affected by attentional engagement by means of ERP and time-frequency power analyses. Results from the ERP

analyses show an early attention-independent response to global regularity violations, putatively associated with the operations of lower levels of the predictive hierarchy, and an attention-dependent response at a later stage of processing. Source analyses indicates that both early and late responses to predictive global deviations arise from a highly distributed network of cortical areas. Results from the time-frequency power analyses suggests attention-dependent oscillatory dynamics in the lower frequency bands, respectively an early-onset theta power enhancement and a later-onset beta power suppression, in response to unexpected auditory pattern deviants.

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