

When predictions about the "what",
"where" and "when" interact with
statistical learning, from a
behavioural and neural perspective.



Barbara Tsogli

Thesis for the degree of Philosophiae Doctor (PhD)
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Thesis for the degree of Philosophiae Doctor (PhD)
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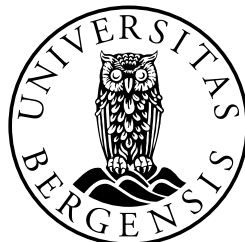
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Scientific environment

The PhD thesis was written at the University of Bergen. As a PhD student, I was affiliated with the research group “Brain and Music” at the Department of Biological and Medical Psychology (IBMP), and the PhD training program was performed through the International Graduate School in Integrated Neuroscience (IGSIN).



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Vera Tsogli

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Abstract

As listeners we tend to detect patterns in what we hear regardless of whether this is music, language or abstract sounds. The fundamental underlying mechanism that supports this process is called statistical learning. Prediction lies at the heart of statistical learning, in the sense that accuracy of predictions influences learning, whether this is implicit or explicit. Numerous studies have investigated the predictive processes during statistical learning from a behavioural or neural perspective. However, it remains unknown how listeners respond to events that violate their predictions which are based on prior implicit learning. In other words, if exposure to a patterned sequence of sounds builds up specific expectations about upcoming sounds, then how does the brain respond to events that violate these expectations? This was the primary research question of the present thesis, and different aspects of the main question were tackled over three experiments.

Experiment 1 examined how listeners respond to events that violate predictions that regard the content or the location of the sounds. We used a variant of an established statistical learning paradigm, and electroencephalography (EEG) as a means of measurement. Participants were exposed to a continuous auditory stream of sound triplets with deviants that were either (a) statistical, in terms of transitional probability, (b) physical, due to a change in sound location (left or right speaker) or (c) double deviants, i.e. a combination of the two. Therefore, statistical deviants violated predictions about the content of the stimuli, that is given the prior two sounds *what* will be the next sound. On the other hand physical deviants violated predictions about the sound location, that is given the location of the prior sounds from *where* will the next sound be played. Sta-

tistical and physical deviants elicited a statistical mismatch negativity (MMN) and a location MMN respectively, reflecting that participants' prediction about the content or the location of the stimuli was violated. Most importantly, when a double deviant occurred, namely an unexpected sound from an unexpected location, participants' sensitivity to unexpected "what" was reduced. Our results show that processing of physical properties (location) of the sounds suppresses processing of the structural properties (content) of the sounds.

Experiment 2 further examined how predictions about different attributes of a stimulus interact with each other, and whether such an interaction affects learning. In that experiment the same experimental paradigm as in Experiment 1 was employed, except that the pause between the sounds was not constant anymore but varied randomly. In that way it became harder for participants to predict accurately the timing of the stimuli. By comparing the results from Experiments 1 and 2 we found that learning was impaired in Experiment 2. Temporal unpredictability due to random pauses reduced the neurophysiological responses to statistical and location deviants, as indexed by the statistical MMN and the location MMN. Our results suggest that when it comes to learning capabilities, the human brain requires isochronous, or perhaps at least regular, stimulation because processing of the "what" is tightly interconnected to the processing of the "when". In other words, if we cannot make predictions on the "when", it impedes the precision of our predictions about the "what".

The last experiment of the present thesis aimed to reveal the neural underpinnings of processing violations of predictions, using functional magnetic resonance imaging (fMRI). The experimental paradigm was simpler than the one used in the other two experiments because it presented only statistical deviants. Participants underwent a learning phase outside the scanner followed by an fMRI session. Processing of statistical deviants activated a network of regions encompassing the superior temporal gyrus bilaterally, the right deep frontal operculum including lateral orbitofrontal cortex, and the right premotor cortex. Our results demonstrate that violation of predictions about

the “what” within a statistical learning paradigm, involved areas over different levels of the cortical hierarchy. Interestingly, processing of the occurring irregularities resembled the processing of local syntactic structures in language.

Within predictive coding framework the human brain may be seen as an inference machine, yet our results show that the way inferences are produced may not be so mechanistic. We humans tend to perceive stimuli in their totality taking into account all their aspects, and perception of one stimulus aspect influences perception of another stimulus aspect. Perceiving, predicting and learning are operating together to help us capture the salient regularities in an uncertain world and survive in a constantly changing reality.

List of Publications

1. Tsogli, V., Jentschke, S., Daikoku, T., & Koelsch, S. (2019). When the statistical MMN meets the physical MMN. *Scientific reports*, 9(1), 1-12.
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3. Tsogli, V., Skouras, S., & Koelsch, S. (submitted). Brain-correlates of processing local dependencies within a statistical learning paradigm. *NeuroImage*.

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Chapter 1

Introduction

Our external world and our life in general, are far from a random continuum of events, and rather contain a certain degree of structure and regularity (Geisler, 2008). To survive in an uncertain but not so irregular world, prediction and learning play a key role. Humans come endowed with the capability to learn, and recent accounts from cognitive and computational neuroscience have established the underlying role of prediction for learning (Friston et al., 2003; Hasson, 2017; Koelsch et al., 2019; Pearce et al., 2010; Pickering & Clark, 2014).

In our everyday life we implicitly detect patterns regarding the order or the frequency of the events, and eventually we tend to form predictions about upcoming events. Statistical learning has been suggested as a core mechanism for the detection of patterns in our environment (for reviews, see Conway, 2020; Daikoku, 2018; Rohrmeier & Rebuschat, 2012). Assuming that prediction is crucial for statistical learning (R. Dale et al., 2012; Hasson, 2017; Karuza et al., 2014), then predictive coding stands as a compelling framework to explain the underlying predictive processes. Within the framework of predictive coding, learning is a continuous optimization of a generative model that reflects the world around us and attempts to explain the causes of the sensory events (Clark, 2013; Friston, 2010). Furthermore, given that we are constantly exposed to a multitude of stimuli, featuring a wide range of properties (such as object identity, timing, location, etc.) it is expected that our generative predictive model

encompasses all these different aspects of the stimuli.

This invites the question, how does the brain respond to violations of predictions based on prior implicit statistical learning? How do predictions over one stimulus dimension (e.g. object identity) affect predictions over other stimulus dimensions (e.g. location, timing or timbre), and how would possible interactions between predictive mechanisms affect learning? The purpose of the thesis was to investigate these questions by using neurophysiological measures, namely event-related brain potentials (ERPs) recorded with the method of electroencephalography (EEG), and Blood-Oxygen-Level-Dependent (BOLD) response recorded with functional Magnetic Resonance Imaging (fMRI).

1.1 Statistical learning

The process by which listeners respond to the statistical structure of the stimuli has been the focus of implicit learning studies originating back in the 60s as conducted by Reber (1967). At that time, two procedures were mainly used to arrange the stimuli in a specific statistical structure: artificial grammar learning or probability learning (Cleermans & Elman, 1993; A. S. Reber, 1989). The former specified the order of the stimuli according to an artificial grammar whereas in the latter there was a careful manipulation of the conditional probabilities between stimuli transitions. A few decades later Saffran et al. (1996) investigated the experience-dependent mechanisms of language acquisition of infants by using an artificial grammar paradigm where transitional probabilities between syllables were manipulated so as to cue for word boundaries. This experiment commenced a new research tradition with the name ‘statistical learning’. Although implicit learning and statistical learning are considered different research traditions it is suggested that they describe the same phenomenon (Perruchet & Pacton, 2006).

Statistical learning has been established as domain-general learning mechanism. Yet, the main focus of the related studies has been within the context of language ac-

quisition (Romberg & Saffran, 2010) and music (Loui, 2012; Rohrmeier et al., 2011; Saffran et al., 1999; Schön et al., 2008; Tillmann & McAdams, 2004). Studies within the domain of language acquisition have demonstrated word segmentation effects, namely that participants became familiarised with the words presented throughout the experiment and could detect the word-boundaries. The rationale behind the employed paradigm is that the transitional probability between the words is lower compared to the transitional probability within words. A high transitional probability from A to B means that the occurrence of A highly predicts the occurrence of B. Under this perspective, prediction appears to be a key process towards the inducement of word boundaries.

Adjacent syllables at word-boundaries have low transitional probability, and thus are less predictable. Previous studies have shown an increased N100 or the equivalent magnetic component N100m (Abla et al., 2008; Francois & Schön, 2011; François & Schön, 2014; Sanders & Neville, 2003) indicating the different processing load during the word onset. Similarly, the N400 ERP component reflecting the recognition of a word has been found sensitive to word-onsets (Abla et al., 2008; Cunillera et al., 2009, 2006; Sanders et al., 2002).

Recently, statistical learning studies have investigated brain responses to violations of learned patterns. For this purpose the traditional paradigm was modified by introducing unexpected events that violated the predictions based on prior implicit learning. The unexpected events elicited stronger responses compared to regular events (Daikoku et al., 2014, 2015; Furl et al., 2011; Paraskevopoulos et al., 2012). Interestingly, Koelsch et al. (2016) varied the probability of the events to high, low and medium, and showed that the magnitude of the effect in the ERP responses was analogous to the probability. The authors referred to the recorded ERP response as statistical MMN. In a similar vein, the primary scope of this thesis was to investigate the brain responses to low-probability events that violate prior implicit statistical learning. Specifically, Experiment 1 investigated the time-course of the predictive processes to unexpected events by using EEG whereas Experiment 3 studied the brain-correlates by using fMRI.

To date, statistical learning studies have presented unexpected events that violated the “structure” of the stimuli, for instance when a “B” occurs instead of the expected “C”. However, everyday we are exposed to a multitude of stimuli featuring structural properties (i.e., transitional probability from A to B) but also physical properties (such as location, frequency, intensity etc.). Previous studies have investigated how the brain responds to changes on the physical or abstract properties of the sound, reporting the physical MMN or the abstract feature MMN (Näätänen, 1987; Paavilainen et al., 1989; Saarinen et al., 1992; Sams et al., 1985; Tervaniemi et al., 1997). However, to our knowledge, there is no study so far exploring the statistical manipulation of transitional probabilities and physical attributes of sounds within the same paradigm. It remains unexplored if learning is affected by violations occurring over several dimensions. Thus, introducing more than one type of irregularity would allow to address the question how statistical learning is affected by irregularities spanning over more than one dimension and to investigate plausible interaction effects. To that end, in Experiment 1 deviations were either (a) statistical, in terms of transitional probability, (b) physical, due to a change in sound location or (left or right speaker) or (c) a double deviants, i.e. a combination of the two. Last, in Experiment 2 a third stimulus aspect was manipulated, the stimuli onset to alter the temporal predictability.

Typically, statistical learning studies and artificial grammar learning studies, use isochronous or predictable stimulus presentation (for implicit learning of rhythm or temporal patterns, see Rohrmeier & Rebuschat, 2012; Selchenkova et al., 2014). In addition, computational models of implicit learning disregard stimuli-onset because it is not part of the regularities underlying the simulated learning process. Presumably, within the context of formal language theory (Fitch & Friederici, 2012; Jäger & Rogers, 2012) the grammar rules remain identical suggesting that learning is independent of iso- or non-isochronous stimulus presentation. Similarly, transitional probabilities may be independent of iso- or non-isochronous stimulus presentation. Yet, Experiment 2 aimed to examine possible interaction of isochronicity with learning by manipulating temporal

predictability of stimulus-onset within a statistical learning paradigm. Experiment 2 differed from Experiment 1 in terms of stimulus-onset asynchronies (SOAs) which was changed from isochronous to random. According to predictive coding this change would increase listeners' uncertainty regarding the "when" of the stimuli and possibly impede learning of the "what" and responses to changes of the "where" (Hasson, 2017).

1.2 Predictive coding

Predictive coding along with other theories furnish a compelling unified brain theory based on the free-energy principle (Friston, 2010). Put simply, free-energy is regarded as "the difference between the way the world is represented as being, and the way it actually is" (Clark, 2013, p. 186). Ideally, an optimal representation of the world "consumes" less energy and therefore the free-energy is minimal. Friston (2005) suggests that cortical responses can be seen as the brain's attempt to minimize the free energy or in other words to minimize the surprise or prediction errors, namely any mismatches between incoming sensory signal and neuronal representations. In that respect, prediction error minimization reflects the perpetual attempt to optimize the predictions about the world and explain away the surprises.

In real life, we form predictions about all the aspects of the stimuli and according to predictive coding our predictive model encompasses all the aspects of the occurring events. However, it remains an open question if predictions about different aspects of the stimuli interact with each other and whether this interaction affects learning. Do listeners form prediction about the "what" independently of the "when" or the "where"? And if there is an interaction between these dimensions, how is the precision of the generative model affected?

In a traditional auditory oddball paradigm with isochronous stimulation, the repeated presentation of standards dispels uncertainty about the stimuli (i.e. an increase of the precision of predictions) in terms of their onset and content. This results in a reduction in ERPs to standards and to the elicitation of an error-signal (the MMN) in re-

sponse to deviants (Garrido, Kilner, Kiebel, & Friston, 2009; Garrido, Kilner, Stephan, & Friston, 2009). On the other hand, when stimuli are presented non-isochronously (e.g., random SOAs), the establishment of first-order predictions about stimulus-onset becomes less precise because the suppression of prediction errors is less efficient (Garrido, Kilner, Kiebel, & Friston, 2009). Thus, the cost of reduced precision is reflected in smaller error-signal responses to deviants.

Within the context of predictive coding, when predictions are violated a prediction error is propagated towards higher cortical levels to adjust predictions and suppress future prediction errors. A neurophysiological marker of prediction error is the MMN (Friston, 2005) which in Experiments 1 and 2 is used to investigate predictions about the different aspects of the stimuli and the interactions among them. Specifically, in Experiment 1 the statistical MMN was used to study predictions about the content of the stimuli or the “what”, and the location MMN to study predictions about the “where” of the stimuli. Their interaction was examined to reveal whether processing of sounds’ physical attributes affects processing of learned statistical properties. In Experiment 2, random SOAs were used which allowed a comparison of the statistical and location MMN between the two experiments and examine whether predictability about the “when” of the stimuli affects processing of statistical regularities (“what”) or physical properties of the sounds (“where”).

Although, a significant number of MMN studies have manipulated stimulus-onset predictability, the results are not consistent. Some studies have reported diminished MMN when random SOAs are used (Bouwer et al., 2016; Costa-Faidella et al., 2011; Takegata & Morotomi, 1999) whereas others found no effect (Roerber et al., 2003; Schwartze et al., 2011). Thus, the question whether temporal predictability affects the underlying processing for the elicitation of the MMN remains open and Experiment 2 aims to fill this gap.

1.3 Auditory sensory memory and beyond

Another principal question of the thesis was to examine the brain-correlates of processing violations of predictions which are established within a statistical learning paradigm. This research question was addressed in Experiment 3 and lies at the intersection of two research traditions, that of implicit statistical learning and of deviance detection. The main findings from both research traditions will be analysed further down along with the specific differences of our research question.

Implicit learning research has used the artificial grammar learning paradigm to examine the neural mechanisms of processing stimuli structures with either local (e.g., “The boy was tall.”; Folia & Petersson, 2014; Forkstam et al., 2006; Friederici et al., 2006; Opitz & Friederici, 2007; Petersson et al., 2012, 2004; Skosnik et al., 2002) or non-local dependencies (e.g., “The boy *that the girl kissed* was tall.”; Bahlmann et al., 2008; Friederici, 2011, 2018; Friederici et al., 2006; Opitz & Friederici, 2007). However, the research question in this thesis went beyond the neural underpinnings of local dependencies in the stimuli structure. Instead, the aim was to examine brain responses to deviant local dependencies that violate predictions about the “what” and that are based on prior implicit learning. Previous neuroimaging studies have shown that processing or violation of local dependencies activates the deep frontal and superior temporal areas (Friederici et al., 2006; Opitz & Friederici, 2007) whereas others report also activation of Broca’s area (Folia & Petersson, 2014; Forkstam et al., 2006; Petersson et al., 2012, 2004). Nevertheless, in these studies, violation of local dependencies was tested after the learning blocks. Thus, Experiment 3 aimed to fill this gap, by investigating brain responses to violations of predictions about local dependencies that occurred during the learning blocks, or while learning is ongoing.

To date, fMRI studies on statistical learning have mainly focused on segmentation effects within the context of language acquisition and therefore, to the best of our knowledge, these studies have not either investigated brain responses to breaches

of predictions that are based on learned statistical regularities. Yet, the main findings from these studies are relevant for the current research question, and show that word learning and recognition are supported by the superior temporal gyrus for both auditory (Barascud et al., 2016; Cunillera et al., 2009; Karuza et al., 2013; McNealy et al., 2006; Plante et al., 2015) and visual (Ordin et al., 2020) stimuli, the inferior frontal gyrus (Barascud et al., 2016; Cunillera et al., 2009; Fletcher et al., 1999; Karuza et al., 2013; McNealy et al., 2006; Ordin et al., 2020) and the basal ganglia (Karuza et al., 2013; McNealy et al., 2006). To answer our research question, the classical statistical learning paradigm was extended by manipulating transitional probabilities also within the word (ex: “pretty baby” vs “pretty babies”) and thus present events that violate induced expectations based on prior learning.

How the brain responds to unexpected events has been traditionally the main focus of oddball studies using the classical MMN response (Näätänen, 1987). Previous neuroimaging oddball studies have shown that unpredicted events activate a cortical network involving the superior temporal gyrus and occasionally the inferior frontal gyrus, notably similar to the one observed during statistical learning (Cacciaglia et al., 2019; Celsis et al., 1999; Doeller et al., 2003; Molholm et al., 2005; Opitz et al., 2002, 2005; Sabri et al., 2004, 2006). However, in these studies predictive processes entail regularities that are established on a moment-to-moment basis and represent information accumulated in a timescale of seconds, and in that respect they are different from regularities established during a statistical learning paradigm. It is important to note that perception of a statistical irregularity requires first the establishment of a memory representation of the statistical regularity which does not occur instantly, but requires an extended period of statistical (implicit) learning. As initially suggested by Koelsch et al. (2016), the establishment of such representations goes beyond auditory sensory memory capabilities. Thus, in Experiment 3 the aim was to investigate predictive processes representing information that is accumulated over longer learning periods and most likely involve higher-order areas, namely beyond the auditory sensory memory

(Hasson et al., 2015).

1.4 Experimental Paradigms

In principle the experimental paradigm in all the experiments was the same with some variations and was developed from a previous study by Koelsch et al. (2016). During the experiments listeners were exposed to a continuous stream of sounds, organised in triplets with deviants that were up to three different types, namely (a) statistical, in terms of transitional probability, (b) physical, due to location change (“standards” were presented from one direction, whilst “deviants” were presented from the other direction) or (c) double deviants, i.e. a combination of the two. Statistical and physical deviants tapped different stimulus aspects. Specifically, statistical deviants regarded the stimuli content, or the “what”, whilst the physical deviants regarded the stimuli location, or the “where”. Finally, by replacing the constant SOAs with random ones a third stimulus aspect was manipulated which was the time, or the “when”. In Experiment 1 three deviant types were presented (i.e., statistical, physical and double) with constant SOAs (see Fig. 1.1). Experiment 2 was identical to Experiment 1 except from the SOAs which were changed from constant to random (see Fig. 1.2). In Experiment 3 only statistical deviants were presented and the SOA was constant similar to Experiment 1 (see Fig. 1.3).

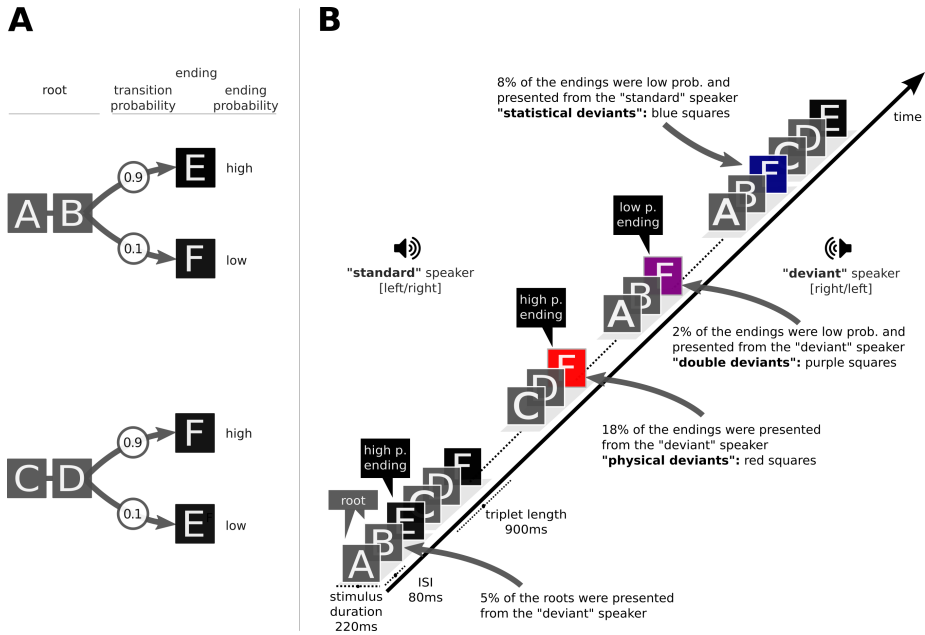


Figure 1.1: The Experimental paradigm for Experiment 1. (A) The four triplets generated from 6 sounds. The letters A to F are used to refer to the sounds. The first two items of the triplet are named root (AB and CD) and the last item is name ending (E and F). Statistical deviants were created by varying the transitional probability from root to ending within two levels, high ($p = 0.9$) and low ($p = 0.1$). Triplet roots (AB or CD) are occurring with a constant transitional probability ($p = 0.5$) from any of the triplet endings (E or F). Interstimulus interval is constant at 80 ms. (B) The auditory stream of pseudorandomly concatenated triplets with standard ending triplets (letter in black box), statistical deviant ending triplets (letter in blue box), physical deviants (letter in red box) and double deviants (letters in purple box). Physical deviants were generated by switching speaker.

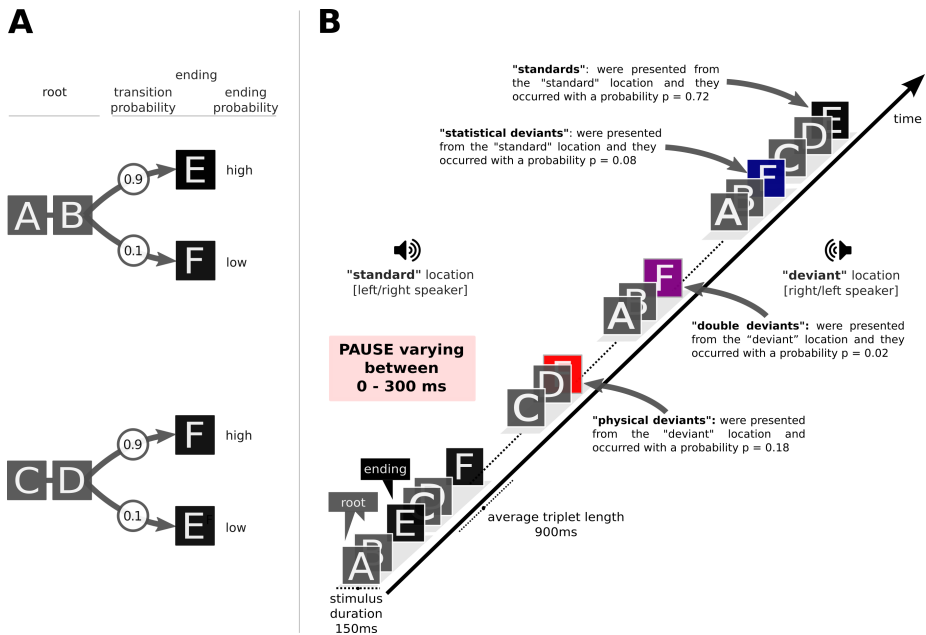


Figure 1.2: Experimental paradigm for Experiment 2. (A) The four triplets generated from 6 sounds. The letters A to F are used to refer to the sounds. The first two items of the triplet are named root (AB and CD) and the last item is name ending (E and F). Statistical deviants were created by varying the transitional probability from root to ending within two levels, high ($p = 0.9$) and low ($p = 0.1$). Triplet roots (AB or CD) are occurring with a constant transitional probability ($p = 0.5$) from any of the triplet endings (E or F). Interstimulus interval varies randomly from 0 to 300 ms. (B) The auditory stream of pseudorandomly concatenated triplets with standard ending triplets (letter in black box), statistical deviant ending triplets (letter in blue box), physical deviants (letter in red box) and double deviants (letters in purple box). Physical deviants were generated by switching speaker.

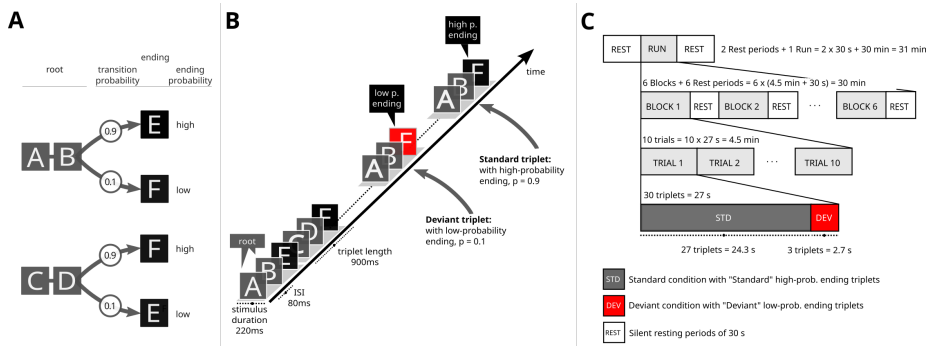


Figure 1.3: The experimental paradigm for Experiment 3. (A) The four triplets generated from the 6 sounds. The letters A to F are used to refer to the sounds. The first two items of the triplet form the root (AB and CD) and the last item the triplet ending (E or F). Statistical deviants were created by varying the transitional probability from root to ending within two levels, high ($p = 0.9$) and low ($p = 0.1$). Triplet roots (AB or CD) were occurring with a constant transitional probability ($p = 0.5$) from any of the triplet endings (E or F). (B) The auditory stream throughout the learning phase outside the scanner. The triplets were pseudorandomly concatenated and were either standard with high-probability endings ($p = 0.9$) or deviant with low-probability endings ($p = 0.1$). (C) The auditory stream inside the scanner. Scanning comprised of a single run of approximately 31 min in duration during which 6 blocks of 4.5 min duration each, interleaved with resting periods of 30 sec were presented. Within each block, 10 trials of 27 sec duration each were concatenated. In each trial, 27 consecutive standard triplets were presented followed by 3 deviant triplets.

Chapter 2

Research questions and hypotheses

The thesis investigated how the brain responds to violation of predictions based on prior implicit statistical learning. Electrophysiological and fMRI measurements were used to reveal the time-course and the activation pattern of the underlying processes.

2.1 Experiment 1

Experiment 1 investigated the neural responses to deviant events within a statistical learning paradigm using EEG. Deviants were either (a) statistical, in terms of transitional probability, (b) physical, due to a change in sound location (left or right speaker) or (c) a double deviants, i.e. a combination of the two. The statistical MMN was used as a neurophysiological marker of statistical learning and the location MMN as a marker of auditory deviance detection. It was hypothesised that (a) statistical deviants (i.e., triplet endings with low vs. high transitional probability) would elicit a statistical MMN, (b) that physical deviants would elicit a location MMN, and (c) that the physical deviants would diminish the effect of the statistical deviants. Thus we expected events that violated predictions about the “what” to elicit a statistical MMN whereas events that violated predictions about the “where” to elicit a location MMN. Additionally, we expected that statistical learning as reflected in the statistical MMN to be influenced by the presence of physical deviants. In other words, we expected an interaction of pre-

diction errors elicitation due to physical and statistical deviants. The existence of an interaction effect would indicate that statistical learning, as reflected in the predictions errors about the “what”, is influenced by prediction errors about the “where”.

2.2 Experiment 2

Experiment 2 was identical to Experiment 1 except from the SOAs which were changed from constant to random. It was hypothesised that low-probability events would still elicit a statistical and a location MMN even with random SOAs. Additionally, by comparing the results of Experiment 1 and 2, it was expected to find an interaction between the ERPs to deviant events and the isochronicity. With random SOAs, it was expected that participants would feel uncertainty with regard to the timing and the type of upcoming stimuli. Within the predictive coding framework, the level of uncertainty for the upcoming events can be expressed based on Shannon entropy (Shannon, 1948) and low entropy is indicative of highly probable upcoming events (Friston, 2010). In Experiment 2, the entropy in terms of the “what” (what tones are presented) and “where” (sound direction) remained the same as in Experiment 1, but the entropy in terms of the “when” changed from minimal (isochronous events with low uncertainty) to maximal (random SOAs with high uncertainty; Cohen, 1962; Ravnani & Madison, 2017). Therefore, we expected that manipulating the entropy of the “when” (by switching from isochrony with zero entropy in the temporal structure, to randomly varied SOAs with maximal entropy) would impact the predictive processes of “what” and “where”. In predictive coding terms, this manipulation (switching to random SOAs) would reduce precision of the predictive model, which we expected to be reflected in a reduction of the amplitudes of error signals (the statistical MMN and the location MMN).

2.3 Experiment 3

Experiment 3 investigated the brain-anatomical location of violations of predictions, established through statistical learning. We defined three hypotheses. First, beyond the auditory cortex, mismatch responses reflecting the detection of auditory deviance would activate areas associated with violation of local dependencies (Folia & Petersson, 2014; Forkstam et al., 2006; Friederici et al., 2006; Opitz & Friederici, 2007; Petersson et al., 2012, 2004; Skosnik et al., 2002), specifically the temporal and the inferior frontal cortex mediated by parts in the premotor cortex. Second, the activation pattern would evolve over the duration of a session, revealing the time-course of statistical learning effects. Third, the engaged cortical network would differ between “good” and “bad” learners as ranked by their performance on the behavioural task.

Chapter 3

Neurophysiological measures of cognitive processing

Cognitive psychology aims to identify the underlying brain processes and mechanisms that are involved in cognitive functions, namely perception, learning, memory, emotion, language and thought. Besides, the traditional behavioural approaches, other neurophysiological measures may provide insights to these functions in terms of their temporal or spatial properties (Rugg & Coles, 1995). In the experiments described in this thesis, two neurophysiological measures were employed, the EEG and the fMRI. The following sections aim to present both methods along with a justification for choosing them.

3.1 EEG and ERPs

EEG is a method of recording voltage changes at the scalp level. These voltage changes reflect the excitatory postsynaptic potentials as generated from a population of neurons and are detectable only if the neurons are synchronized and parallel to each other (da Silva, 2013; Rugg & Coles, 1995).

The EEG signal is recorded in digital form, therefore is not continuous, but it can be sampled at high rates and thus reveal the time course of a cognitive process at the level

of milliseconds. The comparative advantage of EEG over fMRI lies at the very high temporal resolution of EEG (Luck, 2014) which is suitable to study the time-course of effects of interest. An additional advantage of EEG is that the voltage changes, as captured at the scalp level, reflect the underlying synaptic activity in real-time (Luck & Kappenman, 2011).

When the voltage fluctuations are time-locked to an event (i.e., presentation of a stimuli) then this is called an ERP. The ERPs are of smaller magnitude compared to the background “noise” but when averaged over several stimuli repetitions, the signal to noise ratio improves. In other words, the average ERP will emerge from the background noise which tends to average to zero.

The 10-10 system

The positioning of EEG electrodes follows international references as a way to promote the use of a standardised and reproducible method of electrodes placement. The 10-20 system (Jasper, 1958), which has been used for over half a century, defined the positions for a relatively small number of electrodes (typically 21) placed at relative distances (10% or 20%) between specific scalp areas. Over the last two decades the development of multi-channel EEG hardware equipment and advanced topographic source localization methods led to reference systems with higher number of electrodes. The 10-10 system extended the 10-20 system by incorporating supplementary electrodes midway between the 10-20 leads which allows measuring ERPs with 64 channels (Chatrian et al., 1985).

The electrode position nomenclature refers to particular scalp areas but this does not imply that the recorded activity from any of the electrodes is generated solely at the brain region located under that electrode. Because, the measured voltage at a single electrode represents the sum of many underlying dipoles and this is known as the superposition principle (Logothetis, 2003; Luck, 2014; Näätänen, 1987; Rugg & Coles, 1995). Thus, EEG is not an appropriate method to determine the location of the gener-

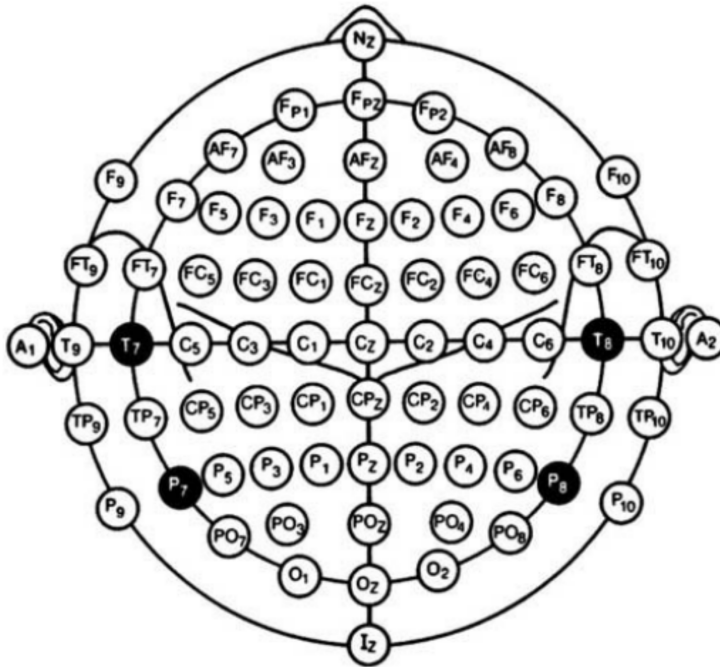


Figure 3.1: Nomenclature for the 10-10 system .

ated activity. The low spatial resolution of EEG can be counterbalanced by using fMRI which features a high spatial resolution and will be described in the following section.

3.2 Functional Magnetic Resonance Imaging (fMRI)

fMRI has become a dominant non-invasive neuroimaging method since its introduction in early 90's. Ogawa et al., (1990), was the first to observe that changes in the BOLD response can indicate, with relatively high spatial resolution, functional brain mapping. fMRI is based on the coupled mechanisms of (a) neural activation, (b) cerebral blood flow and (c) energy consumption (Logothetis, 2003). During fMRI, there is no direct observation of the neural activity. Instead, the induced effects of neural activity are observed as reflected in the hemodynamic response (changes in blood flow and volume) and in the metabolic response (oxygen levels; Buxton, 2012). Therefore, during fMRI, it is expected that any experimental manipulation of the stimuli can be reflected in the

BOLD signal during neural activation (Faro & Mohamed, 2010).

Although the BOLD signal does not represent neural activity, several studies suggest a linear relationship between neural activity and the subsequent hemodynamic response (Logothetis, 2003). Logothetis (2003) claims that “BOLD response indisputably directly reflects a local increase in neural activity assessed by the mean extracellular field potentials signal”(p. 3966), thus justifying the use of the BOLD contrast mechanism as an neurophysiological indicator of neural responses elicited by a stimulus. Nonetheless, fMRI measures hemodynamic rather than neuronal responses and this comes with the cost of low temporal resolution because “hemodynamic signal changes are observed with a delay of one to two seconds after the onset of neural stimulation and reaches the maximum at four to eight seconds” (Faro & Mohamed, 2010, p. 17).

For the fMRI experiment (Experiment 3) the paradigm from the EEG experiments (Experiments 1 and 2) had to be adapted to counterbalance the hemodynamic delay of the cerebral flow during the fMRI measurement. The adaptation was mainly in the duration of the deviant condition. That is, in the fMRI experiment the deviant condition entailed the presentation of three consecutive deviant triplets resulting in deviant mini-block with a duration of 2.7 sec whereas in the EEG experiment the deviant condition entailed the presentation of a deviant triplet-ending with a duration of 300 ms.

A block design was used in the fMRI experiment. The idea behind the block design approach is that each block corresponds to a certain cognitive task and when subtracting the activity of one block from the other it is expected that the observed difference is indicative of the difference in the cognitive task. The limitation of a block design approach is that most brain processes are highly nonlinear and thus a detailed analysis of the individual cognitive components is advisable prior to the experiment (Logothetis, 2008).

To sum up, the employed methods aimed at bringing a better understanding regarding the neural mechanisms underlying statistical learning as well as the processing of deviants. EEG provides a suitable time-resolution and therefore it was used to study

the time-course of the effects of interest whilst fMRI provides a high spatial resolution and was used to identify the brain structures of the underlying neural processes.

Chapter 4

Methods

4.1 Experiment 1: Methods and procedure

4.1.1 Participants

Datasets from 21 adults (12 females; mean age = 22.43 years, $SD = 2.39$) were included in the analysis. All participants were recruited at the University of Bergen and reported no use of hearing impairments, no history of neurological disease, and no musical training more than 2 years besides regular school lessons (according to self-report). All participants were compensated (200 NOK, approx. 20 EUR) at the end of the experiment.

4.1.2 Stimuli

Sound triplets

To form the triplets, six sounds were created. Each sound was a combination of a Shepard tone and a percussion sound. Shepard tones (Shepard, 1964) were employed to reduce any percept of pitch along with any auditory grouping based on pitch. Six Shepard tones for six frequencies were generated (F3: 174.61 Hz, G3: 196.00 Hz, A3: 220.00 Hz, B3: 246.94 Hz, C#4: 277.18 Hz and D#4: 311.13 Hz) where each tone re-

sulted from the superposition of nine sinusoidal components spaced one octave apart. The use of pure tones was rejected during pilot testing because emergent Gestalt formations (i.e., ascending or descending triads) were confounding learning of the triplet structure (Bregman, 1994; Koelsch & Siebel, 2005). The particular feature of Shepard tones is that although they differ in frequency, yet they are ambiguous when it comes to judging the relative pitch. Therefore, the six Shepard tones would sound differently, but still participants would be unable to judge the direction of the tones (i.e., whether the tones were going “up” or “down”). These six Shepard tones were combined with six percussive sounds (surdo, tambourine, agogo bells, hi-hat, castanet and woodblock, which were downloaded from The Philharmonia Orchestra website). All sounds were sampled at 44100 Hz and normalised based on the RMS amplitude so that they were matched in overall loudness. Each sound had a duration of 220 ms, including a fade in of 10 ms and fade out of 20 ms. The interstimulus interval was 80 ms (thus, the inter-onset interval was 300 ms). The six sounds, corresponding to the letters A to F (see Fig 1.1A), were combined into triplets. Specifically, sounds A, B, C and D were combined in two pairs (AB and CD) to form the “root” of the triplet (i.e., the first two items of the triplet). Sounds E and F were used for the last position or item of the triplet. Thus, four unique triplets were obtained (Fig 1.1).

For the practice trials before the experiment, a second set of six sounds was created. These sounds were created similar to the sounds of the main experiment, but differed in frequency of the Shepard tones (E3: 164.81 Hz, F#3: 184.99 Hz, G#3: 207.65 Hz, A#3: 233.08 Hz, C4: 261.62 Hz and D4: 293.66 Hz) and in which percussive sounds were used (woodblock, tambourine, agogo bells, castanet, hi-hat and bass drum). Finally, an additional sound was created (C#5: 554.37 Hz, not combined with a percussive sound) to serve as target sound for the cover task that participants had during practice trials and the experiment.

Importantly, the arrangement of sounds (A to F) was permuted across participants as a way to guarantee that possible acoustical differences between sounds would not bias

the brain responses of interest.

The stimuli arrangement of the current paradigm represents a 1st-order Markov model or bigram model with strictly 2-local distribution (Jäger & Rogers, 2012) and can be placed in the subregular hierarchy within the extended Chomsky hierarchy (Rohrmeier et al., 2015) or in the regular hierarchy within the classical Chomsky hierarchy. Subregular structures are less complex compared to regular ones and the extended Chomsky hierarchy accounts for this difference by placing the two types of structures in different classes.

Stimuli location

To generate physical deviants, the location of the sounds stimulus was manipulated, featuring a spatial location change of 60° angle in the azimuthal plane: If the standard stimuli were presented from the direction of one speaker, the physical deviants were presented from the other one. The stimulus location was arranged as follows: The sound of the triplet root (A to D) was presented in 95% of the times from the “standard” and 5% of the times from the “deviant” location. The last sound of the triplet was presented in 80% of the times from the “standard” side, and 20% of the times from the “deviant” side. Only sounds at the last position were evaluated when assessing physical deviance. “Standard” and “deviant” location was balanced across blocks and counter-balanced between participants whether they would have left or right as preferential (standard) direction for the first block.

Triplet endings

Triplets endings differed in respect to (1) the frequency of occurrence of their ending within the experiment block and (2) the sound location of their ending. Therefore, four categories of triplet endings occurred:

1. Standards: featured a high transition probability ($p = 0.90$) and were presented from the “standard” location ($p = 0.80$). Thus, they occurred with a probability p

= 0.72.

2. Statistical Deviants: featured a low transition probability ($p = 0.10$) and were presented from the “standard” location ($p = 0.80$). Thus, they occurred with a probability of $p = 0.08$.
3. Physical deviants: featured a high transition probability ($p = 0.90$) and were presented from the “deviant” location ($p = 0.20$). Thus, they occurred with a probability of $p = 0.18$.
4. Double deviants: featured a low transition probability ($p = 0.10$) and were presented from the “deviant” location ($p = 0.20$). Thus, they occurred with a probability of $p = 0.02$.

Triplet streams

The triplets were arranged into six pause-free streams or blocks. Each block consisted of 400 triplets and was 7 min long. Triplets were presented in a pseudorandom order so that triplets from the low probability set were separated by at least three triplets from another set. Triplet roots (AB or CD) followed any of the two triplet endings (E or F) with a constant transitional probability (TP = 0.5). So, for example ABE could be followed by either ABE, CDF, ABF or CDE.

4.1.3 Procedure

The experiment took place inside an electro-magnetically shielded chamber. Participants were asked to seat in a chair in front of a desk with a monitor. Their seating position was chosen so that it formed an equal side triangle with the speakers and that their eyes were at the level of the centre of the screen. The experiment consisted of 6 blocks each one comprising an exposition phase of about 7 min followed by a behavioural task of about 2 min, resulting in a total duration of the experiment (including pauses) of about 1 hour. During the exposition phase, auditory stimuli were presented

via the speakers while participants could watch a silent movie on the monitor in front of them. The EEG was recorded during the whole experiment. The experimenter was present in an adjacent room throughout the experiment. He could monitor the participants state at all times with a camera directed at the participants head. Participants were instructed to give a sign to the camera should they need to interrupt the experiment.

The experiment started with a set of instructions. Participants were not informed about the regularities in the arrangement of the stimuli, to ensure that any kind of learning throughout the experiment was implicit. At the same time, to ensure that participants were attentive to the stimuli, a cover task was used: The participants were asked to press the space bar every time they heard the (higher-pitched) target sound. There were examples of the target sound in the instructions, followed by practice trials (lasting about 1 min) containing a relatively high number of target sounds. The practice trials were repeated if participants did not detect at least 80% target sounds (or had a too large number of false alarms). Participants were asked to avoid movement, especially jaws and eyes, to minimize artifacts in the EEG recording.

Familiarity test and confidence rating

At the end of each block, a behavioral test assessed whether participants were able to distinguish two triplet sequences ending on a sound with either high or low transitional probability. Each test had 12 trials where participants were presented with three repetitions of all four possible triplet combinations (ABE vs. ABF, ABF vs. ABE, CDF vs. CDE, or CDE vs. CDF). All sequences were presented binaurally, none contained a location change, and there was a pause of 335 ms between the triplets. Participants were asked to choose which sequence sounded more familiar (pressing either “1” for the first or “2” for the second sequence). Afterwards, they rated their level of confidence about their choice of sequence (pressing from “1” absolute unsure, could have thrown a coin; to “5” absolutely certain). Consecutive trials did not use the same triplet root and the

order of presentation of the endings was counterbalanced.

4.1.4 Data recording and analysis

EEG recording

The EEG signal was recorded from 59 scalp electrodes placed in an electrode cap in compliance with the 1010system (see Fig 4.1) at 500 Hz sampling rate using BrainAmps DC (Brain Products GmbH, Munich, Germany). Additional electrodes were placed on the left and right mastoids (the left mastoid serving as reference during recording), on the back of the neck (serving as ground), as well as at the outer canthi of the eyes (bipolarly recording the horizontal electrooculogram [EOG]) and above and below the right eye (for the vertical EOG). All electrode impedances were kept below 5 k Ω .

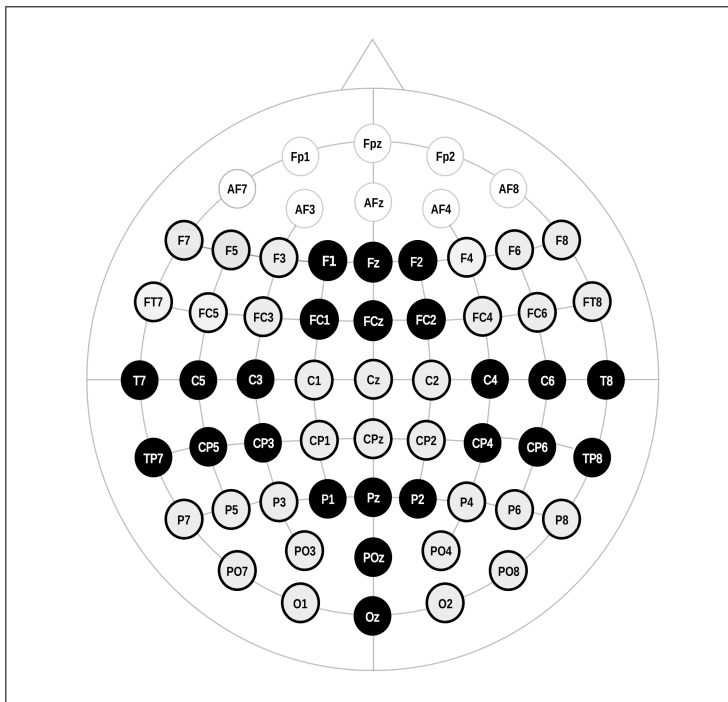


Figure 4.1: Electrodes Clusters. The electrodes were clustered in 9 regions of interest which are shown in grey and black

Processing of EEG data

EEG data were analysed using EEGLAB 13 (Delorme & Makeig, 2004) within MATLAB® R2016b (The MathWorks Inc., Natick, MA). EEG data during the behavioural part of the experiment (at the end of every block) were not evaluated. EEG data were manually inspected and excluded from analysis if they contained faulty channels or periods with excessive artifacts. An Independent Component Analysis was used to remove eye and muscle artifacts. Afterwards, EEG data were re-referenced to the algebraic mean of the left and right mastoid electrodes and filtered using a 30 Hz low-pass filter (2750 points, finite impulse response, Blackman).

Samples were rejected whenever the standard deviation within a 200 or 800 ms gliding window exceeded $25 \mu\text{V}$ at any electrode channel (including the EOG channels). Afterwards, data were epoched, excluding epochs following acoustical deviants or button presses (within 3 secs; i.e., rejecting activity related to the cover task of the participant). ERPs were calculated for low and high probability triplet endings with or without location change of the sound, from -100 to 400 ms relative to stimulus onset and using a 100 ms pre-stimulus baseline correction. In addition, to determine whether participants' brain responses reflected the triplet structure of the stimulus stream, ERPs for the triplet root were calculated from 100 to 1000 ms (relative to the onset of the preceding triplet end). These ERPs were restricted to roots following standard triplets to avoid contamination of the N1 with brain responses to low transitional probability triplet ends. These ERPs did not use baseline correction but were instead 0.5 Hz high-pass filtered (550 point, finite impulse response, Blackman) to remove slow drifts and other low frequency trends (Widmann et al., 2015). Baseline correction was chosen for triplet endings to avoid any bias of previous activity (location change for root) whereas for roots high-pass filtering was chosen as a more appropriate method in relation to root length.

For statistical evaluation, electrodes were clustered into nine regions of interest as shown in Fig 4.1, namely frontal left (F7, F5, F3, FT7, FC5, FC3), frontal middle (F1,

FZ, F2, FC1, FCZ, FC2), frontal right (F8, F6, F4, FT8, FC6, FC4), central left (T7, C5, C3, TP7, CP5, CP3), central middle (C1, CZ, C2, CPZ), central right (T8, C6, C4, TP8, CP6, CP4), parietal left (P7, P5, P3, PO7, PO3, O1), parietal middle (P1, PZ, P2, POZ, OZ) and parietal right (P8, P6, P4, PO8, PO4, O2). The time windows for statistical analysis were selected in accordance with the previous study (Koelsch et al., 2016) and based upon visual inspection.

4.1.5 Statistical analyses

Statistical analyses were conducted using SPSS 25 (IBM Corp., Armonk, NY, USA). Behavioural data comprised participants' responses to the familiarity test and the cover task. For the familiarity test, responses were classified as correct when participants chose the sequence that contained the high probability transition (and was played more frequently during exposition phase). Mean percentage of correct responses was calculated for each participant and subsequently compared against chance level (0.5; one sample t-test, $\alpha = 0.05$). Similarly, for the cover task the mean percentage of correct responses was calculated.

For the ERPs to triplet endings three analysis of variance (ANOVAs) were conducted to examine: (1) the ERPs of statistical deviants (low vs high probability endings), (2) the EPRs to physical deviants (with or without location change), and (3) the interaction effects of statistical and physical deviants. For the ERPs to triplet roots an additional fourth ANOVA was conducted where the ERPs to the 1st, 2nd and 3rd triplet item were compared. ANOVAs were conducted by including the following factors: (a) scalp area (frontal, central, posterior), (b) lateralisation (left, midline, right) and (c) experiment block (1 to 3; the first, middle and last two blocks of the 6 blocks of the experiment were grouped to obtain a better signal-to-noise-ratio).

4.1.6 Ethical considerations

The study was carried out in accordance with the guidelines of the Declaration of Helsinki, and approved by the Regional Committee for Medical and Health Research Ethics for Western Norway (Reference Number: 2014/313). Participants provided written informed consent before the experiment.

4.2 Experiment 2: Methods and procedure

4.2.1 Participants

Datasets from 21 adults (11 females; mean age = 24.10 years, $SD = 6.21$) were included in the analysis. Exclusion criteria were hearing impairments, history of neurological disease, and musical training for more than 2 years beyond regular school lessons (according to self-report). The 21 datasets from Experiment 2 were compared with 21 datasets (12 females; mean age = 22.43 years, $SD = 2.39$) from Experiment 1 (Tsogli et al., 2019). See Table 4.1 for a comparative view of demographic information between Experiment 1 and 2.

	Non-isochronous stimulation Experiment 2	Isochronous stimulation Experiment 1
Sample size	21 (11 women)	21 (12 women)
Mean age	24.10 ($SD = 6.21$)	22.43 ($SD = 2.39$)

Table 4.1: Comparative view of demographic information between Experiment 1 and 2.

4.2.2 Stimuli

In Experiment 2 the experimental stimuli were essentially the same as the ones used in Experiment 1 except that the sound duration was reduced to 150 ms (compared to 220 ms in Experiment 1), including a fade in of 10 ms and a fade out of 20 ms. Additionally, in Experiment 2, stimuli were delivered in a non-isochronous fashion, which was implemented by inserting a randomly varying pause (between 0 and 300 ms) after each sound (see Fig 1.2). Therefore, the stimulus-onset asynchrony (SOA) varied randomly between 150 and 450 ms, with an average SOA of 300 ms (identical to the SOA in Experiment 1). See Table 4.2 for a comparative view for the details of the experiment design for Experiments 1 and 2.

	Non-isochronous stimulation Experiment 2	Isochronous stimulation Experiment 1
Sounds (Shepard tone & percussive sound)	F3: 174.61 Hz & surdo G3: 196.00 Hz & tambourine A3: 220.00 Hz & agogo bells B3: 246.94 Hz & hi-hat C#4: 277.18 Hz & castanet D#4: 311.13 Hz & woodblock	
Stimuli duration	150 ms	220 ms
Target sound	C#5: 554.37 Hz	
Interstimulus interval	randomly varying between 0 and 300 ms	80 ms
SOAs	300 ms (on average)	300 ms
Probabilities of triplet endings	Standards: $p = 0.72$ Statistical deviants: $p = 0.08$ Physical deviants: $p = 0.18$ Double deviants: $p = 0.02$	
Triplet stream	6 blocks of 7 min	

Table 4.2: Comparative view of experiment design details for Experiments 1 and 2.

4.2.3 Information Content and Conditional Entropy values

In the paradigm of Experiment 2 the values of information content and conditional entropy are indicative of the level of predictability or uncertainty (see Table 4.3). Specifically, the information content of triplet endings decreases in analogous manner to the probability of occurrence. For instance, standard endings are characterised by the lowest information content or surprisal ($IC = 0.15$) whereas the information content of statistical deviants is higher ($IC = 3.32$) because they are less frequent and therefore are expected to induce greater surprise. Within the larger setting of information theory and predictive coding, “surprisal” is suggested to express the surprise due to a mismatch between the sensory signals and predictions made based upon previous learning ex-

periences (Clark, 2013). Information content and conditional entropy were calculated based on the equations (4.1) and (4.2) (MacKay, 2003). In the current paradigm the conditional entropy at the triplet ending is relatively low ($H(\text{ending}|\text{root}) = 0.46$). Thus, an interesting aspect of this paradigm is the presentation of an unpredictable event in a position with low expected surprisal. While the predictability in regard to the “what” and “where” remained identical compared to Experiment 1 the predictability in regard to the “when” has changed. An isochronous temporal structure, from an information theory perspective, does not represent any surprise and therefore is characterised by zero entropy and thus low uncertainty (Ravignani & Madison, 2017) contrary to a non-isochronous structure which features increased entropy and uncertainty. In the current paradigm the entropy of the irregular temporal structure was calculated on the basis that the pause between the stimuli varied randomly from 0 and 300 ms, therefore, the set of pauses comprised of 301 equiprobable elements with $p = 1/301$, which results in an entropy of 8.23 bits during non-isochronous stimulation, according to the equation (4.3).

$$h(\text{ending}) = \log\left(\frac{1}{P(\text{ending})}\right) \quad (4.1)$$

The conditional entropy at the triplet ending, for all possible triplet endings, was calculated based on equation (4.2):

$$H(\text{ending}|\text{root}) := \sum P(\text{ending}|\text{root}) \log\left(\frac{1}{P(\text{ending}|\text{root})}\right) \quad (4.2)$$

The entropy of the irregular temporal structure was calculated based on equation (4.3):

$$H(\text{ISIs}) := \sum P(\text{ISI}) \log\left(\frac{1}{P(\text{ISI})}\right) \quad (4.3)$$

	Predicting the “what”	
	Standard ending (p = 0.9)	Statistical deviant (p = 0.1)
IC	0.15	3.32
H(endingroot)	0.46	
	Predicting the “where”	
	Standard location (p = 0.8)	Deviant location (p = 0.2)
IC	0.32	2.32
H(endingroot)	0.72	
	Predicting the “when”	
	Isochronous mode	Non-isochronous mode
H	0	8.23

Table 4.3: Predictability values for triplet endings. Information content (IC); Entropy (H).

4.2.4 Procedure

The procedure of Experiment 2 was similar to the one used in Experiment 1 except that participants were asked to respond to a discrimination test prior to the main experiment.

Discrimination test for acoustical perception of sounds prior to the main experiment

The purpose of the test was to ensure that the stimuli that would be presented during the main experiment were acoustically distinguishable in terms of pitch despite the shorter duration of the sounds compared to the one used in Experiment 1. The test consisted of twelve trials. In each trial, participants heard two sound sequences with 1 sec silence gap between the sequences. Each sequence comprised of three sounds. The sequences were either the same or different in terms of the tones that were presented. Participants were asked to press “1” if they felt that the sequences sounded the same or “2” if they were different. The discrimination test started with practice trials. The participant could proceed to the main test only if he had answered correctly three trials. The order of the trials was randomized between subjects.

For the discrimination test the same sounds as for the main experiment were used. The sounds were combined into triplets (such as AEF, BAF, FEB, EDC etc.) which

were different from those presented in the main experiment (see Fig.1.2). The inter-stimulus interval was 50 ms. The arrangement of the sounds (A to F) was permuted across participants.

4.2.5 Data Recording and Analysis

EEG recording

The EEG signal was recorded in a similar way as for Experiment 1.

Processing of EEG data

EEG data were processed in a similar way as for Experiment 1. To ensure cleaner EEG data over the MMN window, only epochs with at least 200 ms from the adjacent trigger were included in the analysis.

4.2.6 Statistical analyses

Behavioural data from the discrimination test, the cover task and the familiarity test were analysed using JASP (JASP Team, 2019, version 0.11). For each test or task a mean percent correct was calculated. Only for the familiarity test, the mean score was subsequently compared against chance level (0.5; one sample t-test, $\alpha = 0.05$).

Statistical analyses for brain responses were conducted using JASP (JASP Team, 2019) for both frequentist statistics and Bayesian statistics (van den Bergh et al., 2020). Repeated measures analyses of variance (ANOVAs) were carried out to assess: (1) the ERPs of statistical deviants (statistical MMN) under non-isochronous stimulation (2) the EPRs to physical deviants (location MMN) under non-isochronous stimulation, (3) the interaction of the isochronicity with the statistical MMN which would entail a comparison between the results of Experiment 2 (random SOAs) and Experiment 1 (constant SOA) and (4) the interaction of the isochronicity with the location MMN which would entail a comparison between the results of Experiment 2 (random SOAs) and

Experiment 1 (constant SOA). ANOVAs were conducted by including the following factors: (a) scalp area (frontal, central, posterior), (b) lateralisation (left, midline, right) and (c) experiment block (first, second, third; the first, middle and last two blocks of the 6 blocks of the experiment were grouped to obtain a better signal-to-noise-ratio). ERPs for the statistical MMN were assessed over two time windows, the established statistical MMN time window 180 - 260 ms from Experiment 1 and an earlier time window 150 - 200 ms. ERPs for the location MMN were assessed over the time window 150 - 220 ms. See Table 4.4 for a comparative view of the methodological details for Experiments 1 and 2.

	Non-isochronous stimulation Experiment 2	Isochronous stimulation Experiment 1
Data processing	EEGLAB 13, MATLAB® 2016B	
Statistical analyses	JASP 0.11	SPSS 25
Procedure	Discrimination test Practice Main experiment	— Practice Main experiment
Behavioural data	Discrimination test Cover task during exp. phase Familiarity test	— Cover task during exp. phase Familiarity test
Statistical analyses	Bayesian ANOVA Frequentist ANOVA	Frequentist ANOVA
Statistical MMN		
Time window	180 to 260 ms 150 to 200 ms	180 to 260 ms
Within subject factors		transition probability scalp area lateralisation block
Location MMN		
Time window	150 to 220 ms	150 to 220 ms
Within subject factors		physical deviance scalp area lateralisation block

Table 4.4: Comparative view of methodological details for Experiments 1 and 2.

4.2.7 Ethical considerations

All participants were compensated financially (200 NOK, equivalent to 20 EUR). Participants provided written informed consent before the experiment. The study was carried out in accordance with the guidelines of the Declaration of Helsinki, and approved by the Regional Committee for Medical and Health Research Ethics for Western Norway (Reference Number: 2018/2409).

4.3 Experiment 3: Methods and procedure

4.3.1 Participants

Thirty-three participants (16 females and 17 males; mean age = 24.97 years, $SD = 5.60$) were included in the analyses. All participants reported no hearing or language impairments, no history of neurological disease, or musical training of more than 2 years besides regular school lessons (according to self-report).

4.3.2 Stimuli

Sound triplets

The experimental stimuli were the same as the ones used in Experiment 1.

Triplet types

Triplets differed in respect to their frequency of occurrence in the experimental blocks. The “Standard” triplets comprised 90% of all presented triplets and featured endings with high transition probability ($p = 0.9$), whereas the “Deviant” triplets comprised 10% of all presented triplets and featured endings with low transition probability ($p = 0.1$). In Experiment 3 contrary to Experiment 1 and 2 there was no location change and thus there were no physical deviants.

Triplet stream outside the scanner

Auditory streams of about 7 min duration were created and consisted of 400 triplets (see Fig 1.3B). Triplets were pseudorandomly concatenated, namely deviant triplets were occurring only after three standard triplets. Additionally, no more than two consecutive and identical standard triplets were presented. Triplet roots (AB or CD) followed any of the two triplet endings (E or F) with a constant transitional probability ($TP = 0.5$). So, for example ABE could be followed by either ABE, CDF, ABF or CDE.

Triplet stream inside the scanner

The auditory stream inside the scanner was adjusted so as to compensate for the delay in the BOLD response. So, mini-blocks were created consisting of 27 standard triplets followed by three deviant triplets (see Fig 1.3C). Therefore, three consecutive deviant triplets were presented at a time, instead of one as it was the case for the auditory stream outside the scanner.

4.3.3 Procedure

Learning phase outside the scanner

Prior to the image acquisition participants underwent a learning phase in a room adjacent to the MRI scanner. The learning phase was almost identical to that used in Experiment 1 (see Procedure of Experiment 1). The difference was that the learning phase consisted of 3 blocks instead of 6 and there were no physical deviants.

Familiarity test and confidence rating outside the scanner

At the end of each block of the learning phase a behavioural test of about 2 min assessed participants' familiarisation with the stimuli. The test was almost identical with the one used in Experiments 1 and 2. The difference was that participants were not only asked to distinguish standard triplets from deviant triplets (i.e., *ABE* vs *ABF*) but also standard triplets from "non-triplets", namely triplets that did not occur during the exposition phase (i.e., *ABE* vs *EFD*).

Acquisition phase inside the scanner

The scanning phase comprised of a single run of about 31 min (see Fig 1.3C). In total, 6 blocks of 4.5 min duration each, interleaved with resting periods of 30 sec were presented. Within each block, 10 periods of 27 sec duration each were concatenated. Within each period, there were 30 triplets, encompassing 27 consecutive stan-

dard triplets followed by 3 deviant triplets. Participants were asked to watch a silent movie while listening to the sounds. The movie was projected on a screen located at the back of the scanner and participants could watch through a mirror display. A cover task identical to the one used in Experiment 1 was employed. Participants were asked to lie still throughout the duration of the experiment in order to minimize noise. Auditory stimuli were presented via the MRI-compatible headphones and participants were provided with earplugs to alleviate any disturbances from the scanner noise.

4.3.4 Data Analysis

Behavioural data analysis

Behavioural performance during the familiarity test and the cover task was analysed using SPSS (IBM Corp., Armonk, NY, USA). Participants' responses were marked as correct if they corresponded to the standard triplet that was presented more frequently. Mean percent correct was calculated for each participant and subsequently compared against chance level (0.5; one sample t-test, $\alpha = 0.05$). Similarly, for the cover task the mean percentage of hits was calculated.

1st level data modeling

A general linear model (GLM) was defined within SPM (Wellcome Trust Centre for Neuroimaging, London, UK) for the 1st-level of statistical inference. To remove low-frequency noise a high-pass filter with a cutoff frequency of 1/128 Hz was used. An explicit binary mask, based on all subjects normalized gray matter images, was used. The 1st-level GLM included 26 regressors comprising of (a) two regressors for cerebrospinal fluid (CSF) and white-matter (WM) and (b) 24 regressors comprising the Volterra expansion of the realignment parameters that modeled signal fluctuations related to movement (Friston et al., 1996). Three analytical investigations were performed which corresponded to the three hypotheses of the experiment. For each subject, we defined a contrast between deviant and standard triplets, using an event-related

design. In relation to the second hypothesis, to model the evolution of deviance detection across the course of the experiment, an additional regressor was used, expressing the ‘Time x Condition’ interaction, that was constructed based on the onsets of the standard and deviant mini-blocks. This regressor corresponded to each functional volume a label denoting the condition.

2nd level data modeling

To control for Type I error the activation map of the second level contrast ‘Deviant > Standard’ as generated by SPM was applied to a probabilistic Threshold-free Cluster Enhancement (pTFCE; Spisák et al., 2019) which yielded an effect at $p = 0.05$ corrected. In accordance with the three hypotheses, three analyses were conducted.

The first analysis aimed to investigate the brain responses in regard to the detection of a statistical deviance (‘deviance detection’). To assess whether the activations differed between the two conditions (Deviant and Standard) a group-level analysis (one-sample t-test) was conducted. The analysis was performed using the Local Indicators of Spatial Association (LISA) tool (Lohmann et al., 2018) to ensure that even small activations are detected. LISA is a non-parametric and threshold-free framework that incorporates spatial context and thus preserves spatial precision without loss of statistical power. Within LISA, multiple comparison correction is implemented by controlling the false discovery rate (FDR) which gives the advantage of a more sensitive analysis. LISA takes into account topological features of the activation by applying a spatial filter to the z-map before the voxel-wise control of FDR. Control of FDR uses a Bayesian two-component mixture model, and subsequent FDR scores for every voxel are estimated after 5000 random permutations. The individual contrast maps (as generated by SPM for the contrast ‘Deviant > Standard’) were subjected to a one-sample t-test using LISA.

An additional aim of the first analysis was to examine for a possible activation of the the pars opercularis of the IFG (BA 44i). For this purpose, we used FSLeys (*Mc-*

Carthy, 2021; <http://doi.org/10.5281/zenodo.4704476>) and the Harvard-Oxford Cortical Structural Atlas to create a thresholded region of interest mask for the pars opercularis. Subsequently, the region of interest analysis was conducted using the SPM toolbox MARSeille Boîte À Région d'Intérêt (MarsBaR; <http://marsbar.sourceforge.net/>)

The second analysis examined how deviance detection evolved over the course of the experiment. Finally, the third analysis examined whether there was any quantitative difference between “good” and “bad” learners within the regions of interest for the deviance detection.

For the third analysis, we removed three subjects; two were missing data on the familiarity test and one other was confused and performed too many false alarms (132 false alarms). The 30 subjects were divided into two groups of “good” (14 subjects) and “bad” (16 subjects) learners based on the median value of their scores in the pre-fMRI learning task. We restricted the comparison within nine anatomical regions of interest corresponding to the nine clusters that showed significant activation during the processing of the deviant vs standard triplets (see Table 5.1). We used the SPM toolbox MarsBaR to estimate a mean value for each participant in each of the nine clusters, from the contrast ‘Deviant > Standard’. Subsequently, these mean values were entered in nine two-sample t-tests using MATLAB® to investigate possible differences between the two groups, during deviance detection in any of the nine regions of interest. The results were visualized using xjView toolbox (<https://www.alivelearn.net/xjview>) and the figures were created using MRIcroGL (<http://www.mricro.com>, version v1.0.20180623).

4.3.5 Ethical considerations

Informed consent was obtained from all participants prior to the experiment. The study was carried out in accordance with the guidelines of the Declaration of Helsinki, and approved by the Regional Committee for Medical and Health Research Ethics for Western Norway (Reference Number: 2018/590). At the end of the experiment all participants received a compensation for their participation (200 NOK, approximately 20 EUR).

Chapter 5

Scientific results

5.1 Experiment 1

In Experiment 1 participants listened to a continuous auditory stream of sound triplets and we examined their responses to deviants that were either violating the “what” (statistical deviants) or the “where”(physical deviants) or both (double deviants).

5.1.1 Behavioural data

Cover Task during the exposition phase

As mentioned earlier, participants were not informed about the statistical regularities underlying the stimuli presented during the exposition phase, but instead were provided with a cover task, namely to detect a (higher-pitched) target sound. Participants detected 99.5% ($SEM = 0.18\%$) of the (higher-pitched) target sounds successfully.

Familiarity test

At the end of each exposition block, a familiarity test was presented to test whether participants had learned the underlying regularities of the stimuli. It was expected that participants would classify the sequences ending with high probability sounds as more familiar compared with those ending with low probability sounds (see Methods).

Participants achieved an overall score of 52.5% correct responses ($SEM = 2.5\%$) and their performance did not differ significantly from chance level ($p = 0.38$, Cohen's $d = 0.196$). Only one participant (out of 21) reported during debriefing that she became aware of the statistical regularities underlying the arrangement of the stimuli; She also performed above chance level (64% correct responses).

5.1.2 Electroencephalographic data

ERPs of statistical deviants (statistical MMN) under isochronous stimulation

Figure 5.1 shows the ERPs elicited by standards (high probability endings) and statistical deviants (low probability endings) under isochronous stimulation with high temporal predictability. Statistical deviants, compared to standards, elicited a statistical MMN with a maximum amplitude of $1.50 \mu V$ at around 210 ms. An ANOVA for repeated measurements with the factors transition probability (high vs. low), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) for the time window of 180 to 260 ms after the onset of the triplet ending revealed a significant effect of transition probability ($F_{(1,20)} = 35.54, p < 0.0001, \eta^2 = 0.106$), but no significant effect of block ($p = 0.30, \eta^2 = 0.009$), and no interaction between probability and block ($p = 0.59, \eta^2 = 0.004$). This confirmed our hypothesis that statistical deviants (low probability endings) would elicit a greater negativity. This increased negativity was already present during the first block and did not vary significantly throughout the experiment. Furthermore, the following significant interactions were found: (a) transition probability and scalp area (reflecting that the statistical MMN effect was largest at anterior and diminishes towards posterior sites; $F_{(2,40)} = 12.45, p < 0.001, \eta^2 = 0.010$), and (b) transition probability and lateralisation (reflecting that the statistical MMN was largest at midline sites; $F_{(2,40)} = 10.96, p < 0.001, \eta^2 = 0.005$).

Both low and high probability endings elicited a P1-like positivity maximal at around 140 ms, which did not differ between high and low probability endings ($p = 0.16$).

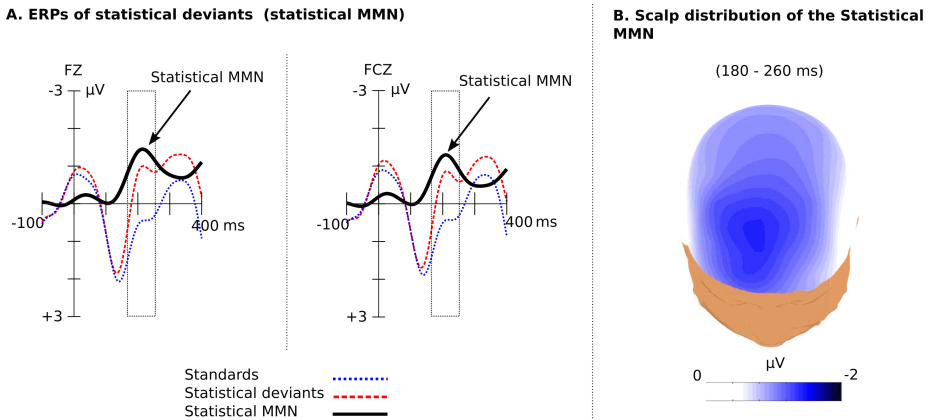


Figure 5.1: The statistical MMN under isochronous stimulation. (A) The statistical MMN generated due to the violation of the high transitional probability as captured at electrodes Fz and FCz. Last tone (triplet ending) onset is at 0 ms and has a duration of 300 ms. ERPs are baseline corrected 100 ms prior to the onset of the trigger. (B) The scalp distribution of the statistical MMN over the time window (180 to 260 ms) was maximal over the frontal-midline region.

ERPs of physical deviants (location MMN) under isochronous stimulation

Figure 5.2 shows the location MMN elicited under isochronous stimulation (high temporal predictability). The location MMN reached a maximum amplitude of $4.20 \mu\text{V}$ at around 180 ms over central-midline electrodes. An ANOVA for repeated measurements with factors physical deviance (standards with vs. without location change), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) over the time window of 150 to 220 ms after the onset of the triplet ending showed a significant effect of physical deviance ($F_{(1,20)} = 83.15, p < 0.001, \eta^2 = 0.415$). Significant effects were also found for block ($F_{(1.9,39.8)} = 8.05, p < 0.01, \eta^2 = 0.018$), lateralisation ($F_{(1.8,36.8)} = 10.04, p < 0.001, \eta^2 = 0.007$) and significant interactions for: (1) block and scalp area (reflecting that the activity varied over the blocks mainly for the anterior and central scalp sites; $F_{(1.9,38.2)} = 17.84, p < 0.001, \eta^2 = 0.006$), (2) block and lateralisation (reflecting that the activity diminished over the blocks mainly over the midline; $F_{(3.2,64.5)} = 3.62, p < 0.05, \eta^2 = 0.001$), (3) physical deviance and scalp area (reflecting that the effect was greater over the anterior and central scalp sites; $F_{(1.0,21.9)} = 66.06, p < 0.001, \eta^2 = 0.064$), (4) physical deviance and lateralisation (re-

flecting that the effect was greater over the midline; $F_{(1.6,33.4)} = 19.30, p < 0.001, \eta^2 = 0.011$), (e) physical deviance, scalp area and lateralisation (reflecting that the effect was mainly over the anterior-central sites and the midline; $F_{(2.9,58.2)} = 4.85, p < 0.01, \eta^2 = 0.001$).

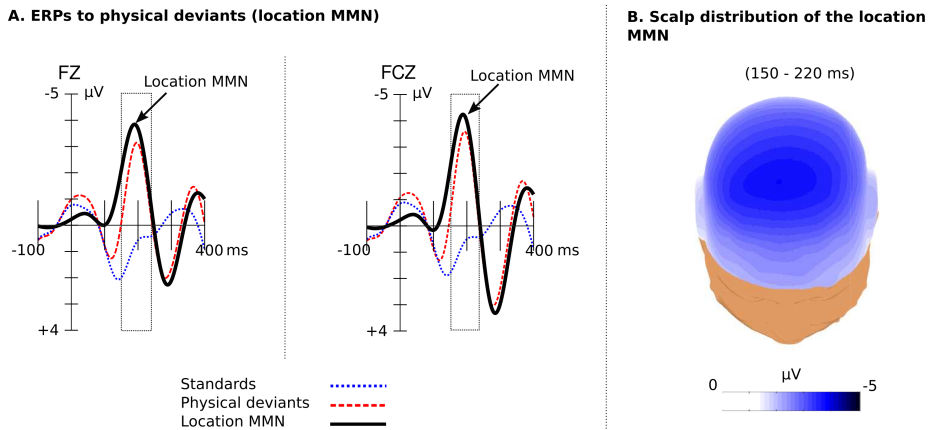


Figure 5.2: The location MMN under isochronous stimulation. (A) The location MMN (black line) generated due to the violation of sound location of triplet ending from the “standard” to the “deviant” side, as captured at electrodes Fz and FCz. Last tone (triplet ending) onset is at 0 ms and has a duration of 300 ms. ERPs are baseline corrected 100 ms prior to the onset of the trigger. (B) The scalp distribution of the location MMN over the time window (150 to 220 ms) was maximal over the frontal and central midline regions.

Triplet endings with location changes elicited consistently larger negativities throughout the course of the experiment even though the amplitude size diminished over blocks. Regardless of that reduction in amplitude size, the two ending types differed significantly within the first ($p < 0.001$, Cohen’s $d = 1.96$), the second ($p < 0.001$, Cohen’s $d = 1.85$) and the third block ($p < 0.001$, Cohen’s $d = 1.59$) of the experiment.

The P1 time window (80 to 180 ms) was assessed using an ANOVA with the factors physical deviance (standards with vs. without location change), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3). It revealed a significant effect of physical deviance ($F_{(1,20)} = 27.28, p < 0.001, \eta^2 = 0.157$). Significant effects were also found for block ($F_{(2,40)} = 8.17, p = 0.001, \eta^2 = 0.036$) and significant interactions for physical deviance and lateralisation (indicating that the effect was greater over the midline; $F_{(2,40)} = 7.80, p = 0.001, \eta^2 = 0.006$).

Interaction of statistical and physical deviance

To investigate the interaction between the two types of deviances, (i.e., violating the “what” along with the “where”), we conducted an ANOVA with statistical deviance (standard vs. deviant), physical deviance (with vs. without location change), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) in the time window from 160 to 260 ms after the onset of the triplet ending.

The analysis revealed a significant effect of statistical deviance ($F_{(1,20)} = 14.14, p = 0.001, \eta^2 = 0.024$), of physical deviance ($F_{(1,20)} = 35.02, p < 0.0001, \eta^2 = 0.114$), and interaction of these two ($F_{(1,20)} = 4.95, p = 0.038, \eta^2 = 0.005$). Pairwise comparisons showed that at the presence of physical deviance the effect of statistical deviance almost disappears ($p = 0.205$; see Fig 5.3B). Statistical deviance produced a significant effect ($p < 0.0001$) only under the condition that there was no physical deviance.

ERPs of Triplet Roots

To examine whether the continuous auditory stream was segmented into discrete triplets, we examined the ERP responses to the triplet roots (i.e., the first two triplet items). We hypothesized that any difference in the ERP responses within a late N1 window (170 to 250 ms) between the first two triplet items should reflect such segmentation effect. This analysis assessed the first and the second sound (both coming from within triplets that were preceded by standard triplets; i.e., those having high probability endings and no physical deviance).

An ANOVA with factors position (first and second sound), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) for the N1 time window (from 170 to 250 ms) revealed no significant effect of position ($p = 0.496$), no significant effect of block ($p = 0.225$) but a significant interaction between these two ($F_{(2,40)} = 3.79, p = 0.031$). Therefore, segmentation effect on the first item could not be observed in the current study. Figure 5.4 depicts ERP responses, separately for each of the triplet tones. Each item elicited a P1-like positivity at around 140 ms,

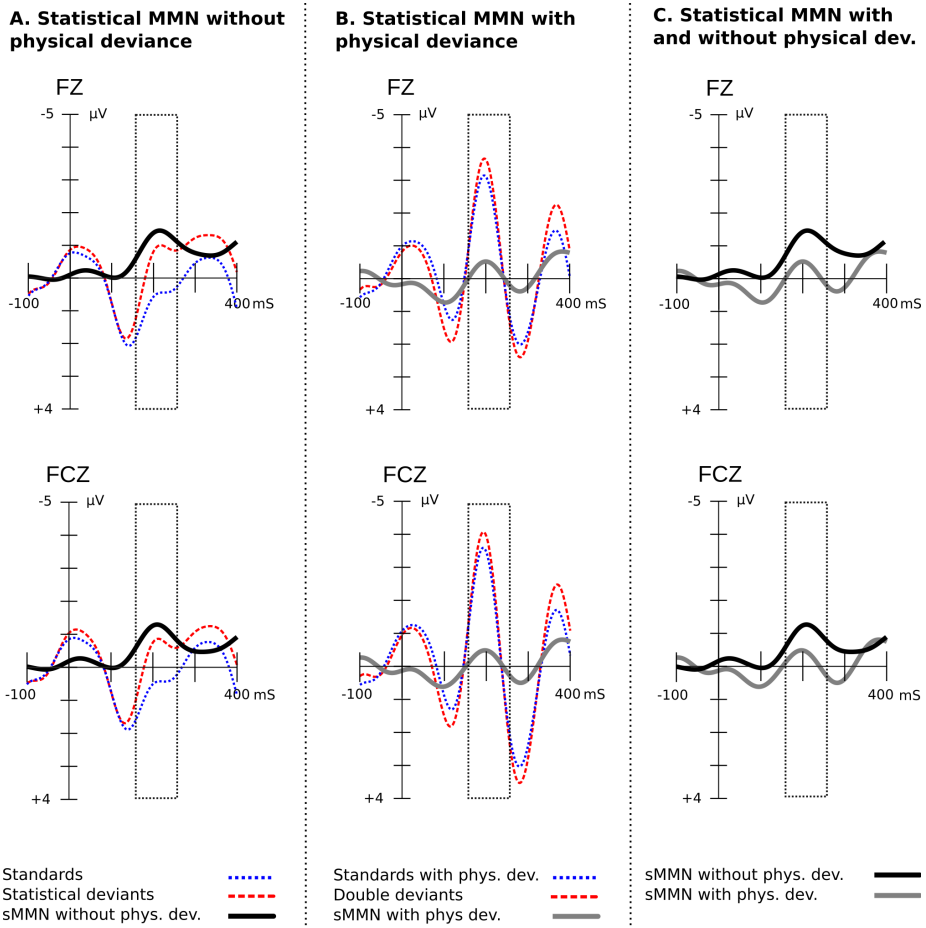
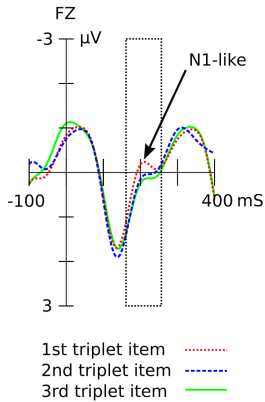


Figure 5.3: Interaction of statistical and physical deviance. Triplet ending onset is at 0 ms and has a duration of 300 ms. ERPs are baseline corrected 100 ms prior to the onset of the trigger. (A) The statistical MMN (black line) without physical deviance, as captured at electrode Fz and FCz. The trace depicted for electrodes Fz and FCz is identical to the one in Fig 5.1A. (B) The statistical MMN (grey line) with physical deviance. (C) Separate traces for the statistical MMN with or without physical deviance. At the presence of location MMN the statistical MMN diminishes.

and N1-like negativity at about 200 ms. This N1-like negativity differed between the three triplet items. The ANOVA for the P1 time window from (100 to 200 ms after the onset of the triplet item) revealed no significant effect of position ($p = 0.390$), a no significant effect of block ($p = 0.670$) neither a significant interaction between these two ($p = 0.160$).

A. Mean Amplitude of triplet items



B. Mean amplitude of triplet items over the three blocks

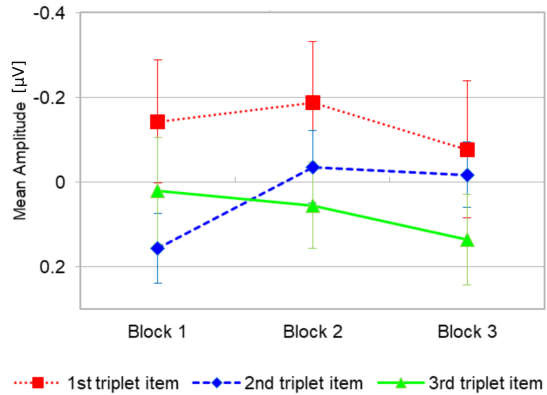


Figure 5.4: N1-like wave for the three items of the triplet. (A) Triplet item onset is at 0 ms with a duration of 300 ms. ERPs are filtered 100 ms prior to the onset of the trigger. There is no segmentation effect of the auditory stream into triplets, over the window 170 to 250 ms. (B) The mean amplitudes of the triplet items over the blocks. There is no significant difference between them.

5.2 Experiment 2

In Experiment 2, contrary to Experiment 1, the SOAs varied randomly and thus we examined how decreased predictability about the “when” affected responses to statistical deviants (“what”) and physical deviants (“where”).

5.2.1 Behavioural data

Prior to the main experiment, a discrimination test was conducted to guarantee that the stimuli were acoustically distinguishable in terms of pitch (see Methods). Participants correctly differentiated sound sequences that were of the same or different pitches with an average score of 95.6% ($SEM = 1.24\%$). Thus, all participants could discriminate the stimuli well (despite the relatively short duration of the sounds).

Cover task during the exposition phase

As mentioned earlier, participants were not informed about the statistical regularities underlying the stimuli presented during the exposition phase, but instead were provided with a cover task, namely to detect a (higher-pitched) target sound. Participants detected on average 97.9% of the target sounds ($SEM = 0.85\%$), indicating that, participants attended the sounds although they were watching a silent movie.

Familiarity Test

At the end of each exposition block, a familiarity test was presented to test whether participants had learned the underlying regularities of the stimuli. It was expected that participants would classify the sequences ending with high probability sounds (“standards”) as more familiar compared with those ending with low probability sounds (“statistical deviants”). Participants achieved an overall score of 50.6% ($SEM = 2.00\%$) in classifying the sequences ending with high probability sounds correctly as more familiar. The performance was not different from chance level ($p = 0.77$, Cohen’s $d = 0.065$)

indicating that participants remained unaware of the regularities governing the arrangement of the stimuli. During the debriefing session no participant showed awareness of the underlying stimuli structure.

5.2.2 Electroencephalographic data

ERPs of statistical deviants (statistical MMN) under non-isochronous stimulation

Figure 5.5A shows ERPs elicited by standards and statistical deviants (high and low probability triplet endings) under non-isochronous stimulation with low temporal predictability. Although it seems that statistical deviants, compared to standards, elicited a tiny statistical MMN at around 190 ms, this difference was statistically not significant. A GLM ANOVA with factors transition probability (high vs. low), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) for the time window from 180 to 260 ms after the onset of the triplet ending showed no significant effect of transition probability ($p = 0.80$, $\eta^2 < 0.0001$), no significant effect of block ($p = 0.61$, $\eta^2 = 0.004$) and no interaction between transition probability and block ($p = 0.63$, $\eta^2 = 0.004$).

To assess whether or not the current data support the hypothesis that statistical deviants elicit a statistical MMN, a Bayesian ANOVA was conducted with identical factors as for the GLM ANOVA and an identical time window. The normality of the residuals was assessed. For transition probability, a Bayes factor of $BF_{01} = 1.254e^{10}$ (error = 3.81%) provided substantial stronger evidence in favour of the null hypothesis, i.e., the assumption that standards and statistical deviants did not elicit different brain responses (i.e., no amplitude difference in the assessed time window from 180 to 260 ms).

Therefore, the current data are more likely not to represent a statistical MMN elicitation. To ensure that the present finding, of no effect of triplet ending, is not simply due to the choice of the time window from 180 to 260 ms (which was based Experiment 1; Tsogli et al., 2019), the analysis was repeated over the time window from 150

to 200 ms, during which the difference between the waveforms appeared to be largest. The normality of the residuals was assessed prior to the analysis. Again, the Bayesian ANOVA showed no evidence for any effect of transition probability, $BF_{01} = 1.254e^8 / 1.254 \cdot 10^8$ indicating that the current data by a factor of $1.254e^8$ are more likely with the null hypothesis, indicating no elicitation of a statistical MMN.

Triplet endings also elicited an early negativity with a latency of 50 ms which was followed by a positivity with a latency of 130 ms. A GLM ANOVA with factors transition probability (high vs. low), scalp area (anterior, central and posterior), lateralisation (left, midline and right) for the time window from 0 to 100 ms after the onset of the triplet ending showed no effect of probability for the early negativity ($p = 0.43$, $\eta^2 = 0.003$). The lack of difference was in agreement with the Bayesian ANOVA, indicating that the current data by a factor of $9.225e^{24}$ do not most likely show an effect of probability. Likewise, the analysis for the positivity with identical factors for the time window from 100 to 200 ms showed not effect of probability ($p = 0.71$, $\eta^2 = 0.001$) and in a similar vein the Bayesian ANOVA indicated that the current data by a factor of $1.965e^4$ more likely do not show an effect of probability. The normality of the residuals was assessed prior to the analysis.

ERPs of physical deviants (location MMN) under non-isochronous stimulation

Figure 5.5B shows that physical deviants, compared to standards (high probability endings with and without physical deviance), elicited a location MMN which was maximal at around 170 ms. A GLM ANOVA with factors physical deviance (with vs without location change), scalp area (anterior, central and posterior), lateralisation (left, mid-line and right) and block (1 to 3) for the time window from 150 to 220 ms after the onset of the triplet ending showed a significant effect of physical deviance ($F_{(1,20)} = 69.30$, $p < 0.001$, $\eta^2 = 0.265$) and block ($F_{(2,40)} = 3.67$, $p < 0.05$, $\eta^2 = 0.012$). Significant effects were also found for scalp area ($F_{(2,40)} = 18.97$, $p < 0.001$, $\eta^2 = 0.043$), lateralisation ($F_{(2,40)} = 8.13$, $p = 0.001$, $\eta^2 = 0.009$) and significant interactions for: (1) physical deviance and scalp area (reflecting that the effect was largest

over the frontal scalp areas; $F_{(2,40)} = 38.33, p < 0.001, \eta^2 = 0.042$), (2) physical deviance and lateralisation (reflecting that the effect was greater over midline electrodes with slight left lateralisation, see Fig 5.5C; $F_{(2,40)} = 11.93, p < 0.001, \eta^2 = 0.005$) and (3) physical deviance, scalp area and lateralisation (showing the effect was largest over the middle frontal scalp sites and slightly left-lateralised; $F_{(4,80)} = 3.07, p < 0.05, \eta^2 = 0.001$). The analysis was performed within the identical time-window as in Experiment 1.

Triplet endings also elicited an early negativity with a latency of 50 ms (N50). The early negativity was assessed with a GLM ANOVA for repeated measurements with the within-subject factors physical deviance (with vs. without location change), scalp area (anterior, central and posterior), lateralisation (left, mid-line and right) over the time window from 0 to 100 ms which showed no effect of physical deviance ($p = 0.888, \eta^2 < 0.001$). Likewise, the results of the Bayesian ANOVA showed that by a factor of $1.295e^{44}$ the data did not represent an effect of physical deviance within this time window. The normality of the residuals was assessed prior to the analysis.

Interaction of statistical deviance and isochronicity

To investigate whether the mode of stimulation (i.e., isochronous or non-isochronous) interacted with the elicitation of the statistical MMN, a comparison between the results of Experiment 1 with a constant SOA at 300 ms (see Fig 5.5D) and the results of Experiment 2 with random SOAs was carried out. Specifically a repeated measures ANOVA was conducted with the within-subjects factors: (1) transition probability (high vs low probability triplet ending), (2) scalp area (anterior, central and posterior), (3) lateralisation (left, midline and right) and (4) block (1 to 3) and with the between-subjects factor isochronicity (isochronous vs non-isochronous), for the time window from 180 to 260 ms after the onset of the triplet ending. The analysis showed a significant effect of probability ($F_{(1,40)} = 15.32, p < 0.001, \eta^2 = 0.032$) and a significant interaction of transition probability and isochronicity ($F_{(1,40)} = 12.41, p = 0.001, \eta^2 = 0.026$) reflecting that the effect of statistical deviance was significant under isochronous, but not

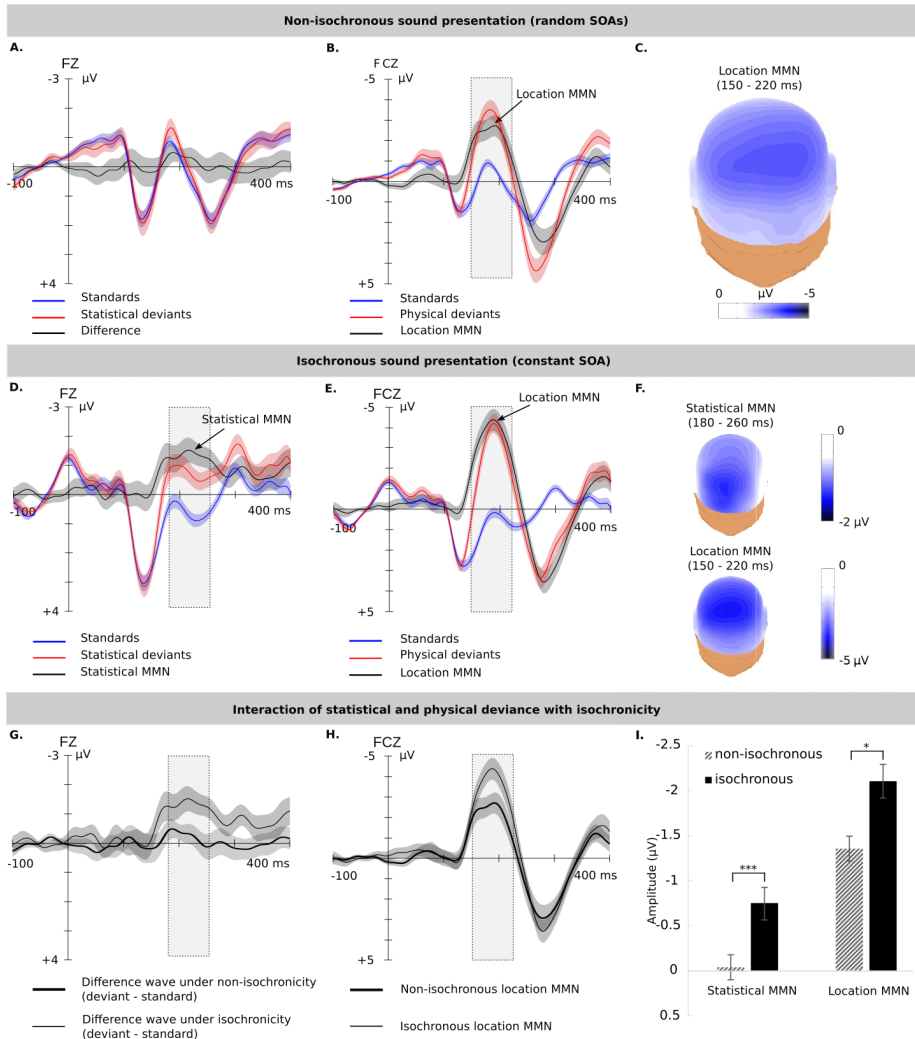


Figure 5.5: ERPs of statistical and physical deviants and their interaction with isochronicity. (A) Mean ERP waves for standards and statistical deviants and the difference (no statistical MMN) under non-isochronous as recorded at electrode Fz. The dotted rectangle indicates the time-window for statistical analysis (180-260 ms). (B) The location MMN, as recorded from the electrode FCz. The dotted rectangle indicates the time-window for statistical analysis (150-220 ms). (C) Isopotential map showing the scalp distribution of the location MMN over the time-window (150-220 ms). (D) The statistical MMN under isochronous (high temporal predictability) stimulation as captured at electrode Fz. (E) The location MMN under isochronous stimulation as captured at electrode FCz. (F) Isopotential maps showing the scalp distribution of the statistical MMN over the window (180-260 ms) and the location MMN over the window (150-220 ms). (G) Separate traces for the differences to statistical deviants under isochronous and non-isochronous stimulation as captured at electrode Fz. (H) Separate traces for the location MMN under isochronous and non-isochronous stimulation as captured at electrode FCz. (I) Both statistical MMN and location MMN amplitudes decline significantly under non-isochronous stimulation.

under non-isochronous stimulation (see Fig 5.5 A,D and G). The observed interaction between transition probability and isochronicity, further demonstrates the effect of the entropy in regard to the timing of the events; switching from an auditory input of zero entropy to an input with high entropy ($H = 8.23$; see Table 4.3) diminished significantly the effect transition probability (see Fig 5.5I).

To ensure that the finding of an interaction between the transition probability and the isochronicity is not due to the choice of the time window from 180 to 260 ms (which was based on Experiment 1), the same analysis was repeated over the time window from 150 to 200 ms. Again, the analysis showed significant effects of probability ($F_{(1,40)} = 8.40, p < 0.01, \eta^2 = 0.017$), of block ($F_{(2,80)} = 4.89, p < 0.05, \eta^2 = 0.013$) and a significant interaction of probability and isochronicity ($F_{(1,40)} = 8.22, p < 0.05, \eta^2 = 0.016$).

Interaction of physical deviance and isochronicity

In the same way the effect of isochronicity to the physical deviance was examined by comparing the results of Experiment 2 with random SOAs and Experiment 1 with a constant SOA of 300 ms (see Fig 5.5 E and F). A mixed-model ANOVA was conducted with within-subjects factors: (1) physical deviance (with vs without location change), (2) scalp area (anterior, central and posterior), (3) lateralisation (left, mid-line and right) and (4) block (1 to 3) and with one between-subjects factor the mode (isochronous vs non-isochronous), for the time window from 150 to 220 ms after the onset of the triplet ending. The analysis revealed a significant effect of physical deviance ($F_{(1,40)} = 150.11, p < 0.001, \eta^2 = 0.338$), a significant effect of block ($F_{(2,80)} = 10.25, p < 0.001, \eta^2 = 0.013$) and a significant interaction between physical deviance and isochronicity ($F_{(1,40)} = 6.96, p < 0.05, \eta^2 = 0.016$) reflecting that the effect of physical deviance diminishes significantly under non-isochronous stimulation (see Fig 5.5 B,E and H). Similarly to the statistical deviance, switching from an auditory input with low uncertainty ($H = 0$) to an input with high uncertainty ($H = 8.23$; see Table 4.3) diminished significantly the effect physical deviance (see Fig 5.5I).

5.3 Experiment 3

In Experiment 3 the brain correlates of violations of predictions about the “what”, as established through statistical learning, were examined.

5.3.1 Behavioural data outside and inside the scanner

Familiarity test (outside the scanner)

At the end of each block of the learning phase before the fMRI session, a familiarity test was presented to test whether participants had learned the underlying regularities of the stimuli. Similarly to Experiments 1 and 2, it was expected that participants would classify the triplets with high probability endings (“Standard” triplets) as more familiar compared with those with low probability endings (“Deviant” triplets; see Methods). Participants achieved an overall score of 66.5% (SEM = 2.5%) in classifying the standard triplets as more familiar (performance differed significantly from chance level, $p < .0001$). Participants scored higher compared to Experiments 1 and 2. The improvement, most likely is due to the fact that participants familiarity was not assessed only in respect to standard vs deviant triplets but also in respect to standard vs non-triplets (see Methods) which in turn rendered the task easier. During the debriefing after the fMRI session, participants were asked whether they detected any patterns in the stimuli. Several participants answered affirmatively, however only one (out of 33) was able to describe the triplet structure of the presented stimuli and she performed well above chance level (80.5% correct responses).

Cover task (outside and inside the scanner)

Similarly to Experiments 1 and 2, participants were not informed about the statistical regularities underlying the stimuli (see Methods), but instead were provided with a cover task, namely to detect a (higher-pitched) target sound. During the learning phase (outside the scanner) participants detected on average 99.4% of the (higher-pitched) tar-

get sounds whereas inside the scanner they detected 100%. Thus, participants attended the sounds while they were watching the silent movie.

5.3.2 Neuroimaging data

The contrast Deviant > Standard, i.e. the contrast of triplets with low-probability endings (“Deviant”) and with high-probability endings (“Standard”), showed activations in the auditory cortex (superior temporal gyrus) bilaterally, the orbitofrontal cortex of the deep frontal operculum / the right anterior superior apex of the insula, the anterior portion of the middle cingulate gyrus including area a24b, the rostral cingulate zone, the pre-supplementary motor area, the left precuneus, and the left putamen (see Fig 5.6 and Table 5.1; results were corrected for multiple comparisons with voxel-wise control of the FDR at a threshold of $p < 0.05$). In the left hemisphere, activation was observed along the superior temporal gyrus, the precuneus, and the putamen. The region of interest analysis performed with the pars opercularis mask did not reveal any significant activation within this region ($p = 0.43$).

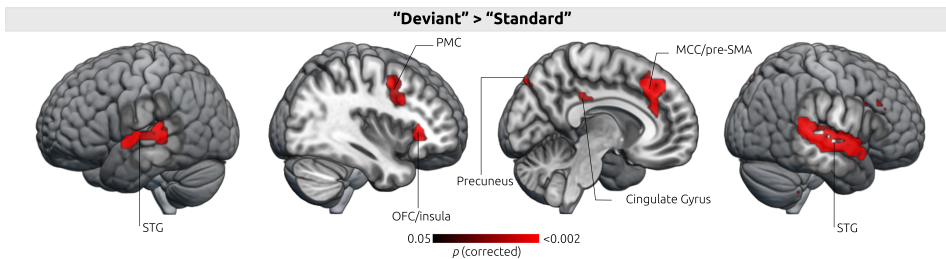


Figure 5.6: Brain activation pattern during violation of prediction (deviance detection). Activations during presentation of “Deviant” triplets contrasted with activations during presentation of “Standard” triplets (Deviant > Standard). Activation map thresholded at $p < 0.05$ (FDR). Superior Temporal Gyrus (STG); Orbitofrontal cortex (OFC); Premotor Cortex (PMC); Middle Cingulate gyrus (MCC); pre-supplementary motor area (pre-SMA).

A second analysis was conducted to reveal changes in the activity pattern for deviance detection throughout the experiment which did not yield any significant results, indicating that there was no different hemodynamic response to deviants (compared to standards) throughout the experiment.

Anatomical region	Hemisphere	MNI-coordinates			t-value	Cluster size
		x	y	z		
Deviant > Standard						
Superior and middle temporal gyrus and insula (BA 22, BA 42, BA 21, BA 38)	L	-56.50	0.81	-4.51	0.99	147
Superior and middle temporal gyrus and insula (BA 22, BA 21, BA 42, BA 38)	R	56.81	7.48	-8.40	1	367
Putamen	L	-16.50	10.81	-8.40	0.97	10
Anterior superior apex of the insula and orbitofrontal cortex of the deep frontal operculum	R	33	31	3.27	0.98	31
Anterior portion of the middle cingulate gyrus including area a24b, anterior rostral cingulate zone and pre-supplementary motor area	R	6.82	37.48	42.21	0.98	119
Premotor cortex	R	40.15	10.81	30.53	0.98	95
Cingulate gyrus (BA 23)	R	3.49	-32.51	30.53	0.98	12
Precuneus	L	-3.17	-79.17	46.10	0.98	35
Frontal lobe (BA 8)	L	-3.17	27.48	50.00	0.97	7

Table 5.1: Significant clusters activated more strongly during deviance detection. Low-probability ending triplets contrasted to high-probability ending triplets, i.e., Deviant > Standard. The table shows the results that survived the correction for multiple comparisons ($p < 0.05$).

Furthermore, a third analysis was conducted to investigate differences in activation patterns for the deviance detection between “good” and “bad” learners. This analysis did not reveal any significant differences neither when conducted within SPM nor when done as a 2-sample t-test in LISA (see Methods).

Chapter 6

Discussion

The present experiments aimed at investigating particular aspects of predictive processes during statistical learning from a behavioural and neural perspective. The aim was to explore how predictive processes regarding different attributes of the stimuli interact with each other and affect the learning outcomes. The employed experimental paradigm was a novel variation of the established statistical learning paradigm.

The stimulus material was a continuous auditory stream of sound triplets with deviants that tapped different stimuli dimensions such as the content, the location and the timing. Statistical deviants (low vs high triplet ending probability) referred to the content of the stimuli, or the “what”. Physical deviants, due to a change in sound location referred to the location of the stimuli, or the “where”. Last, the manipulation of temporal predictability by using random SOAs instead of constant, referred to the timing of the stimuli, or the “when”. EEG was used to study the time-course of the effects whilst fMRI revealed the engaged brain structures. The two EEG experiments differed with respect to the predictability of the stimulus-onset, namely with or without randomly varied SOAs. In the fMRI experiment stimulus-onset was predictable (constant SOAs) and the deviants were only of statistical nature.

6.1 Experiment 1

In Experiment 1 we examined how the brain processes events that violate predictions about the “what” and the “where”. Additionally, we examined how statistical learning, as reflected in the predictions errors about the “what”, is influenced by predictions errors about the “where”.

Violating predictions about the “what” or processing a statistical deviant

Experiment 1 showed that sound triplets with high or low probability endings were processed differently reflecting processing load due to violation of prediction about the content of the upcoming stimuli. Low-probability endings compared to high-probability endings elicited a statistical MMN, a fronto-central negativity within a time window between 180 to 260 ms. This finding is in accordance with previous studies showing similar ERP effects when manipulating transitional probabilities within a triplet (Furl et al., 2011; Koelsch et al., 2016; Paraskevopoulos et al., 2012). Thus, the statistical MMN can be used as an ERP component to investigate neurophysiological effects reflecting the tracking of statistical regularities acquired through implicit statistical learning. It is important to note that knowledge about the statistical regularities is not acquired instantly but requires an extended period of listening. Therefore, the statistical MMN compared to the MMN observed in traditional oddball paradigms involves memory representations beyond the capabilities of sensory memory. Experiment 3 provided additional evidence for this claim and this will be described in a following section.

Contrary to the neurophysiological responses, the behavioural responses did not provide any evidence that participants formed an intuition about the upcoming regularities, which is the expected outcome of incidental learning (Rohrmeier & Rebuschat, 2012). Participants scored only marginally above chance level during the familiarity test indicating that their intuition about the occurring regularities was not accurate. The discrepancy between behavioral and neurophysiological evidence is not unusual

in implicit learning studies (Koelsch et al., 2016; Paraskevopoulos et al., 2017, 2012). Possibly, the performance was low because of the repetitive root (AB or CD) in both standard and deviant triplets. The repetitive root rendered both standard and deviant triplets familiar and shadowed the changing ending of the triplet (Perruchet & Pacteau, 1990; Perruchet & Pacton, 2006; Servan-Schreiber & Anderson, 1990). The strength of recurring chunks has been evidenced also in studies with unsupervised online-learning of artificial grammars (Rohrmeier & Cross, 2014).

Violating predictions about the “where” or processing a physical deviant

Triplet-endings with physical deviants violated predictions about the “where” and elicited effects within the P1-time window, followed by a clear physical MMN (which appeared to have a shorter peak latency than the statistical MMN; Sonnadara et al., 2006). The location change was rather salient compared to the statistical deviant and most likely this perceptual difference is reflected in the larger amplitude of the physical MMN. In line with previous studies, the scalp distribution of physical deviants processing was maximal over midline electrodes within the fronto-central region (Kujala et al., 1992; Paavilainen et al., 1989).

Interaction of statistical and physical deviant processing

Statistical deviants with location change (double deviants) elicited a reduced statistical MMN due to the interaction between the two deviances. The effect of statistical deviants diminishes when co-occurring with a location change. Our results show, for the first time, that processing of prediction errors due to statistical learning is affected by prediction errors due to physical deviance. The observed interaction implies that prediction error processing due to physical sound attributes suppresses processing of learned statistical properties of sounds.

Additionally, the interaction effect suggests that the neural substrates underlying the processing of statistical and physical deviants overlap at least partly. According to Schröger (2007) and Koelsch (2009a) four processes are required to elicit an MMN

(see Fig. 6.1). The auditory signal is analysed in four steps; At first the acoustical features are extracted so as to establish representations of the auditory input. Subsequently, regularities embedded in the auditory input are detected so as to establish a model. Upon establishment of the model, predictions about upcoming auditory events are possible. The last process regards the comparison between the incoming stimuli and model predictions. In case of a mismatch between the two, an MMN is triggered. In Experiment 1 the establishment of stimuli representations (first process) most likely relies on different neural populations. Similarly, a different model (second process) is established to represent structural and the acoustical regularities. On the other hand, the observed interaction suggests an overlap of neural resources which occurs during the formation of predictions (third process) and the comparison (fourth process). Thus, in Experiment 1 the elicitation of the MMN (whether it is due to statistical, physical or double deviance), most probably relies in part on the same mechanisms, but is elicited by different input representations.

Segmentation Effect

Besides the ERP responses to deviances, Experiment 1 was designed to examine also whether participants segmented the auditory stream into discrete triplets. The comparison of the N1-like amplitude for the first two triplet items showed that they did not differ significantly. This finding suggests that no segmentation effect was observed in Experiment 1, presumably because the transitional probability between the words was relatively high ($TP = 0.5$) and thus prevented participants from perceiving a clear statistical word boundary. Interestingly, in the study by Koelsch et al. (2016) where the transitional probability between words was lower ($TP = 0.33$) there was a significant word segmentation effect.

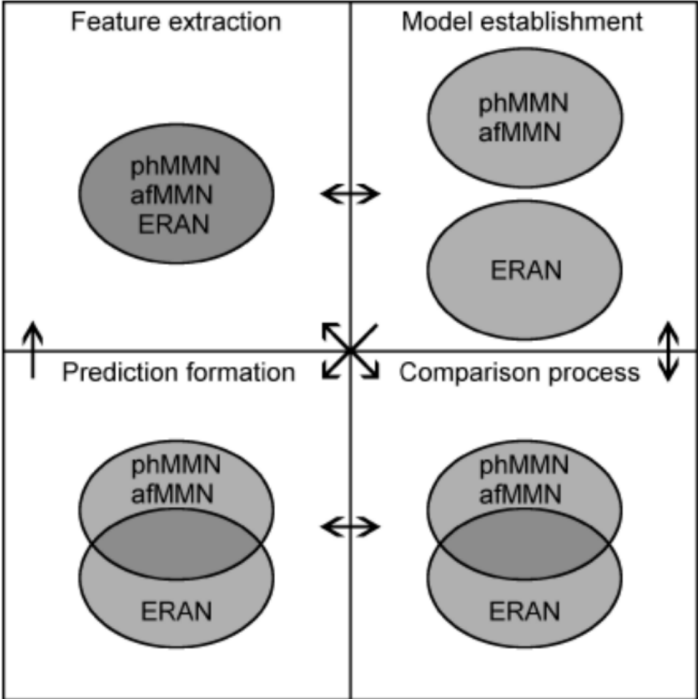


Figure 6.1: Systematic overview of processes required to elicit MMN and ERAN. Figure from Koelsch 2009a

6.2 Experiment 2

Experiment 1 showed that predictions about different attributes of the stimuli interact with each other and affect learning. Precisely, predictions about the content of the stimuli (“what”) interacted with predictions regarding the location of the stimuli (“where”). What about if a stimulus attribute that is not directly relevant to the content of the stimuli is modulated, would this have any impact on learning? Experiment 2 examined this question by using random stimulus onset that affected the temporal predictability, or the “when” of the stimuli.

Violating predictions about the “what” under non-isochronous stimulation

In Experiment 2, under non-isochronous stimulation, no statistical MMN was observed contrary to what was observed in Experiment 1. In other words, high- and low- probability endings did not elicit significantly different brain responses indicating that the reduced predictability due to random SOAs affected predictions about the statistical properties of the sounds. This finding is important because it reflects the different nature of functional operations taking place during the elicitation of the statistical MMN compared to the MMN observed in traditional oddball paradigms (Costa-Faidella et al., 2011; Lumaca et al., 2019; Schwartz et al., 2011; Takegata & Morotomi, 1999; Tavano et al., 2014). As suggested previously (Koelsch et al., 2016; Tsogli et al., 2019), the statistical MMN is a neurophysiological marker for deviance detection in regard to the learned structural properties of sequential stimuli, namely the probability of a stimulus item given (two) preceding stimulus items. The detection of such local dependencies is not occurring instantaneously, as is the case for the detection of acoustical features in traditional oddball studies, but necessitates longer exposition (i.e. learning) so that individuals can form neural representations of these dependencies.

Violating predictions about the “where” under non-isochronous stimulation

The impact of non-isochronous stimulation to physical deviants was not as pronounced as for statistical deviants because a location MMN was elicited. Thus, in both Experiments 1 and 2 a significant location MMN was obtained. Previous studies assessing change detection over irregular temporal structure have reported similar results (Costa-Faidella et al., 2011; Lumaca et al., 2019; Schwartze et al., 2011; Takegata & Morotomi, 1999; Tavano et al., 2014). While auditory information ascends the cortical hierarchy, physical features are processed at a lower level (e.g. primary auditory cortex) in contrast to the structural features that are processed at a higher level and are likely more prone to temporal manipulations. In addition, the saliency of the physical deviance, namely sound direction, presumably contributes to the elicitation of the location MMN, even though there was a high level of uncertainty about the onset of the stimuli.

Processing of the “what” is tightly interconnected to the processing of the “when”

The comparison of the elicited error-signals to statistical deviants as recorded in Experiment 1 and Experiment 2 revealed an interaction between isochronicity and processing violation of predictions about the “what”. Specifically, no statistical MMN was observed in Experiment 2. This presents a finding of great interest from predictive coding perspective. In Experiments 1 and 2, participants attempted to construct a predictive model of the auditory input. The statistical or the location MMN signify a failed guess of the predictive model. During non-isochronous stimulation, predictions about the timing of the stimuli became very imprecise due to the higher entropy (see Table 4.3). The induced uncertainty (high entropy) regarding the “when” of the upcoming events subsequently affected the establishment of predictions about the “what”. The elicitation of an MMN requires an a-priori establishment of an accurate prediction about the standards (Rao & Ballard, 1999). Under non-isochronous stimulation predictions for standard triplets became imprecise and thus deviant detection mechanisms were im-

ped. Thus, the significant reduction of the statistical MMN amplitude is to a large extent driven by the difference in ERPs to standards between the Experiments 1 and 2 and this indicates that isochronous, or perhaps at least regular, stimulation is likely a prerequisite to form a stimuli memory trace of the statistical regularities. This finding corroborates previous studies showing attenuated prediction error responses when precision diminishes (Dzafic et al., 2020; Garrido, Kilner, Kiebel, & Friston, 2009; Garrido, Kilner, Stephan, & Friston, 2009; Lumaca et al., 2019; Quiroga-Martinez et al., 2019).

The transitional probabilities between the tones were identical in Experiment 1 and 2 and according to the ‘Bayesian coding hypothesis’ sensory information is represented probabilistically in the brain (Knill & Pouget, 2004). In light of this, participants were expected to form almost identical probabilistic models regarding the content (“what”) of the two experiments, given that the content remained identical. The finding that participants could not construct a probabilistic model for the statistical deviants under non-isochronous stimulation suggests that the processing of the “what” is tightly interconnected to the processing of the “when”. In other words, if we cannot make predictions on the “when” most likely we cannot make predictions on the “what” either. The findings are in line with a previous study showing an interaction of “what” and “when” predictability, giving rise to reduced amplitudes of auditory evoked responses when using random SOAs (Auksztulewicz et al., 2018). We argue that stimulation timing, a seemingly irrelevant dimension for learning performance, influences the learning outcomes, and thus may be regarded as an important factor within fundamental models of perception and learning, such as predictive coding or computational simulations of implicit learning. Music is a domain where temporal and structural expectations are tightly intertwined (Huron, 2006; Koelsch et al., 2019; Rohrmeier & Koelsch, 2012) and the IDyOM model of musical melody processing has integrated the inter-onset-interval as one of the models parameters (Pearce & Wiggins, 2012).

Findings of Experiment 2 shed light on the interaction of sensory systems with syn-

chronisation and learning. They motivate further research especially considering the fact that the primary auditory difficulties for children with reading or language problems appear to involve rhythmic processing (Goswami, 2011). Human brain capacities in regard to temporal processing are limited and it seems that regularity facilitates encoding and therefore predictions about upcoming events (Drake & Bertrand, 2001; Large & Jones, 1999). Temporal regularity is a predominant feature of communication systems, and as suggested by Lumaca et al. (2018) it is rooted in the neural constraints for information processing. Additionally, according to dynamic attending theory (Jones & Boltz, 1989), attention tends to oscillate in synchrony (entrainment) with the periodicities of external events. In light of the predictive coding framework, a steady beat can be considered as a factor that increases the precision of predictions and thus the attentional gain. In the current study, the non-isochronous stimulation probably prevented participants from attending selectively to information which could possibly resolve uncertainty (Koelsch et al., 2019).

6.3 Experiment 3

Experiment 3 revealed that the neural substrates involved during violation of predictions comprised mainly of the superior and middle temporal gyrus, the insula, the left putamen, the right frontal operculum, the posterior and middle cingulate gyrus, the premotor cortex and the precuneus. The extended activation in the left and right superior temporal gyrus, is in line with previous MMN studies (Cacciaglia et al., 2019; Celsis et al., 1999; Doeller et al., 2003; Molholm et al., 2005; Opitz et al., 2002, 2005; Sabri et al., 2004, 2006) and statistical learning studies (Barascud et al., 2016; Cunillera et al., 2009; Karuza et al., 2013) where a similar activation pattern was observed along the planum temporale. These results indicate the important role of the superior temporal gyrus during the processing of structured stimuli, regardless of whether these are presented within an oddball MMN or a statistical learning paradigm. It is likely that the computation of stimulus statistics, namely the frequency of deviants' occurrence, is a

common process in both paradigms. However, in the case of statistical learning, the statistical cues are more sophisticated and thus more demanding in terms of processing effort and acquisition time, which presumably also explains the lack of activation in the primary auditory cortex (BA 41) in Experiment 3.

Across the three experiments, deviance detection required listeners to implicitly learn the underlying structural properties of the stimuli, and not merely their acoustic properties. We suggest that the activations observed beyond the superior temporal gyrus, namely in the right hemisphere cluster in the orbitofrontal cortex, supported the establishment of the underlying structural relations (i.e., local dependencies) in the stimuli. This finding is reminiscent of findings from artificial grammar learning studies, showing that the processing of local dependencies does not necessitate Broca's area but rather more posterior-medial areas of the frontal operculum, also referred to as the deep frontal operculum (Friederici et al., 2006, 2003; Opitz & Friederici, 2007). Furthermore, the deep frontal operculum and the premotor cortex may be regarded as being involved in the extraction and prediction of sequential auditory information. Previous studies examining violation of more abstract stimuli structures occurring in music and language have underlined the involvement of the inferior frontolateral cortex (BA 44), along with the premotor cortex, during both the recognition of regular structure and the detection of syntactical irregularities (Friederici, 2012; Koelsch, 2009b; Koelsch et al., 2005). Thus, in Experiment 3, it is likely that the orbitofrontal cortex served an analogous role to that of the inferior frontolateral cortex (BA 44) but for sequential structures.

In accordance with the predictive coding theory (Friston, 2005), our findings indicate that predictive processes engaged during statistical learning and deviance detection, involve different levels of the cortical hierarchy, including subcortical areas, sensory cortices and the prefrontal cortex. Prediction errors (i.e., statistical deviants) are propagated bottom-up in the cortical hierarchy, whereas predictions are considered to be passed top-down, influencing the processing of new prediction errors at lower

levels (Friston, 2008). Thus, the activity over the orbitofrontal cortex is suggested to reflect the updating of predictions regarding sequential regularities due to the processing of prediction errors. This finding is in line with previous research where the orbitofrontal cortex has been shown to be sensitive to statistical parameters of the stimuli or breaches of expectations (Nobre et al., 1999; O'Neill & Schultz, 2018; Schultz & Dickinson, 2000).

Another structure that has been suggested to encode error signals during predictive processes is the anterior cingulate cortex, of which the rostral parts show enhanced sensitivity to more abstract errors (Kim et al., 2011; Zarr & Brown, 2016). Several neuroimaging studies have illustrated the critical role of the anterior cingulate cortex during conflict monitoring and error processing (Iannaccone et al., 2015, Alexander & Brown, 2019; for a review see, Botvinick et al., 2004). Moreover, statistical learning studies have also reported activation of the anterior cingulate cortex or anterior parts of the medium cingulate gyrus, consistent with the notion that activation in this brain region reflects the cognitive demands of a task (Cacciaglia et al., 2019; Ordin et al., 2020; Petersson et al., 2012; Plante et al., 2015). In light of this, deviance detection within our statistical learning paradigm is likely to reflect a state of error processing or conflict resolution which engaged the cingulate cortex, namely in the rostral cingulate zone, the anterior portion of the middle cingulate gyrus, and the pre-supplementary motor area. Nonetheless, the observed activation may also reflect a state of conflict associated with the cover task. During the scanning, participants were asked to respond to the higher-pitched sound by pressing a button in the MRI-compatible handheld device. Thus, whenever a statistical deviant occurred, participants had to decide whether the deviant sound was a target sound or not, and to guide their behaviour accordingly (by not pressing the response button).

An additional finding of our study was the sub-cortical activation in the putamen (basal ganglia) during deviance detection. Although the basal ganglia are commonly connected to movement control, previous work has underlined their additional role in

non-motor and language perception functions (for a review, see Kotz et al., 2009). Furthermore, activation of the basal ganglia has been reported during learning tasks; e.g. word segmentation in statistical learning (Cunillera et al., 2009; Karuza et al., 2013), processing of artificial grammar violations (Opitz & Friederici, 2007), implicit category learning (for a review see, P. J. Reber, 2013), action-sequence learning (Graybiel, 2005), etc. However, in Experiment 3, the putamen activation can be attributed to deviance detection, rather than learning, due to auditory attentive processing as has previously been suggested (Opitz et al., 2005). Similar results were observed by den Ouden et al. (2010) in a study where the BOLD signal in the putamen increased alongside the level of surprise generated by visual stimuli, thus reflecting the prediction error. This issue needs to be specified in future studies.

6.4 Limitations and future directions

6.4.1 Attention and statistical MMN

In Experiment 1 we found an interaction between statistical and physical deviance as reflected in the substantial reduction of the statistical MMN at the presence of the physical MMN. The interaction indicated neural overlap for the processing of the “what” and “where” as mentioned earlier, but an alternative explanation for this effect is that both deviances were competing for attention and due to limited attentional resources an interaction effect was observed. The contingency that processing of physical deviances interferes, via attention or not, with processing of learning statistical regularities cannot be excluded. Although, MMN is widely regarded as preattentive, still it can be modulated by attention (for a review, see Sussman, 2007). According to Sussman (2007), “deviance detection is highly context-dependent” (p. 171), meaning that perception of deviants depends on the context in which the deviants appear and also on the instructions participants are given. In Experiment 1, participants were instructed to respond to pitch deviants (i.e., physical deviants with a higher pitch). Thus, they had to atten-

tively process the “non-target” location deviants and to decide to not press the button in response to the location deviants. This attentive effort is reflected in the elicitation of the P3b which occurred only after the physical MMN (see Fig 7.1). In that respect, location deviants had already an attention advantage, which likely contributed to the interaction effect.

Future experiments can clarify the role of attention on the interaction of statistical and physical MMN. For instance, participants’ attention can be directed away from physical deviants if sporadically these are synchronised with a visual task. Alternatively, attention can be controlled between blocks by instructing participants to either read a book while listening to the sounds or to discriminate deviants from standards (Schröger, 1995). So far, statistical learning is affected by manipulation of attentional resources (Daikoku & Yumoto, 2017; Gao & Theeuwes, 2020; Toro et al., 2005). It remains to be investigated if the statistical MMN remains impervious to this kind of manipulations.

6.4.2 Oscillatory characteristics of the statistical MMN

Currently, there is increasing interest to study statistical learning effects through a neural entrainment measure. Several studies provide evidence that cognitive processes are linked to specific patterns of neural oscillations (for a review see Ward, 2003). Within the domain of statistical learning, neural entrainment at the frequency of words, reflects speech segmentation process (Batterink & Paller, 2017). Recently, beta-band activity has been reported as a signature of visual statistical learning (Bogaerts et al., 2020). The authors found increased beta band (20 Hz) activity at triplet boundaries that correlated with behavioural learning outcomes (Bogaerts et al., 2020). In a similar vein, future investigations can address the study of oscillatory characteristics of the statistical MMN. Moreover neural oscillations to the standards (high-probability endings) during isochronous and non-isochronous stimulation can potentially reveal substantial difference in the neural entrainment indicating that the difference in the MMN is

largely driven by the standards. Although, the elicitation of the MMN is most commonly thought as a deviance detection process, the formation of neural representation of standards is equally important (Sussman, 2007).

6.4.3 Source localization of the statistical MMN

In the current thesis, we used two complementary neuroimaging methods; the EEG and the fMRI to investigate spatiotemporal aspects of specific predictive processes. The evidence described in the thesis can be strengthened by using the method of source localization to identify the MMN generators directly from the EEG data. Source localization has been criticized because it requires assumptions regarding the current dipoles and the scalp distribution (Luck & Kappenman, 2011). The major problem of source localisation is that there is not a unique solution to explain the obtained data. However, this problem can be circumvented if *a priori*-assumptions restrain the number of solutions (Hämäläinen et al., 1993; Ramírez, 2008; Sarvas, 1987). To identify the statistical MMN generators, the *a priori* assumptions (i.e., number of sources and their anatomical characteristics) can be set based on the findings of Experiment 3. Although, source localisation is an ill-posed inverse problem, the EEG data from Experiments 1 and 2 when used synergistically with the findings of Experiment 3 offer the opportunity to obtain a better understanding of the underlying neural sources.

6.4.4 Capturing a subtle effect

In Experiment 3 the periods for the standard triplets had a duration of 24.3 sec whereas the deviant triplets had a duration of 2.7 sec. Given that the magnitude of the BOLD signal is optimal during the first 5 sec of the transition between conditions (Purves et al., 2008) a limitation of Experiment 3 was that the “Standard” periods were relatively long whilst the “Deviant” periods were short. This partly explains the low magnitude of the reported activations (see Table 5.1). Nevertheless, as indicated by Experiment 1 deviance detection exhibited a small effect and thus we expected to find also a small

effect in Experiment 3. A way to address this design limitation is by using a scanner of higher field strength (i.e., > 3T).

6.4.5 Dynamic causal modelling

Over the last two decades more and more neuroimaging analyses go beyond the classical identification of the brain correlates of a cognitive process (Stephan et al., 2010). New approaches allow to construct neural models to better explain how the data were generated. For instance, Dynamic Causal Modelling (DCM) aims to specify a model of effective connectivity. In other words, DCM estimates how the activity of one brain region affects the activity of another region (Zeidman et al., 2019) and it is used to test specific hypotheses (Friston et al., 2003). In Experiment 3 the main hypothesis was that mismatch responses reflecting the detection of auditory deviance would activate areas beyond the auditory cortex. Our findings offered compelling evidence in favour of our hypothesis and subsequently DCM was used to elucidate how prediction errors are forwarded up in the hierarchy whilst predictions are passed down the hierarchy (Friston, 2008). Contrary to our expectations, the DCM was not completed because the magnitude of the effect was not sufficiently high.

Chapter 7

Conclusion

The present thesis examined how listeners respond to violations of predictions that are based on prior implicit statistical learning. Exposure to a patterned sequence of sounds allowed participants to build up expectations about the content, the location and the timing of the upcoming sounds. Participants' predictions were violated by occasional deviant events. Statistical deviants, violated participants' prediction as to *what* will be the next sound given the prior two, and elicited a statistical MMN. Location deviants, violated participants' prediction about the sound location (i.e., the *where*) given the location of the prior two sounds, and elicited a location MMN. Interestingly, double deviants (i.e., a combination of the two) generated an interaction effect, indicating a neural overlap for the processing of the two types of deviances. Presumably, processing of sound location consumed a great amount of the neural resources and suppressed processing of the structural properties of the sounds. To further violate participants' predictions, random pauses were introduced, which significantly diminished the statistical MMN but not the location MMN (see Fig 5.5I). We suggest that the ensued temporal unpredictability, due to random pauses, impaired the accuracy of the predictions, leading to reduced amplitudes of the elicited statistical MMN and location MMN. The fMRI experiment revealed the neural underpinnings of processing violations of predictions about the "what". Specifically, it showed that violation of regularities, acquired within a short period of time, generated a frontotemporal activation pattern suggesting

that within the current paradigm predictive processes went beyond the capabilities of the auditory cortex.

Overall, our results provide insights into particular aspects of predictive processes during implicit statistical learning and highlight the role of prediction during learning. Predictions about the “what”, the “where” and the “when” of upcoming events are not formed independently, and aspects seemingly irrelevant to the content of learning can affect learning outcomes.

Appendix

Experiment 1

The P3b scalp topographies for physical deviants.

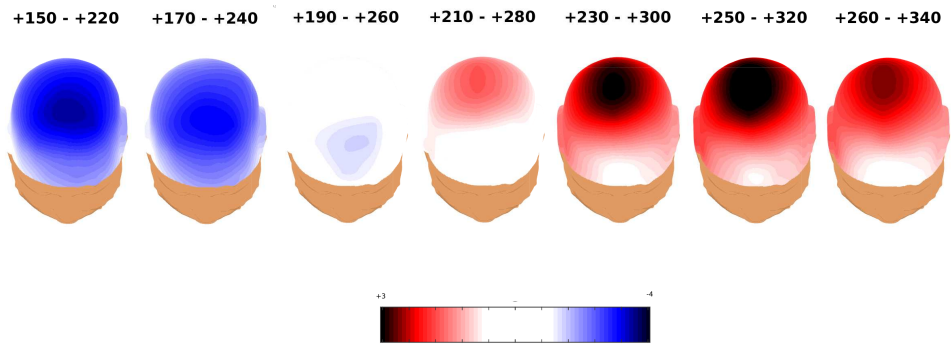


Figure 7.1: The P3b effect. Scalp topographies for the distinct P3b which followed the physical MMN and reached a peak over the time window from 150 to 320 ms.

Experiment 3: Methods

Image Acquisition

The experiment was carried out using a 3T scanner (Siemens Prisma, Erlangen) and a 20-channel head coil. An anatomical reference T1-weighted ($T1_w$) image was acquired prior to the functional session, with voxel resolution = $1 \times 1 \times 1 \text{ mm}^3$, FOV = [220 220 144.08]. At the end of the anatomical scanning participants were reminded the instructions of the task. Functional T2-weighted images were acquired using a gradient-echo EPI sequence with voxel resolution = $3.3 \times 3.3 \times 3.3 \text{ mm}^3$, interslice gap = 0.594 mm

and repetition time (TR) set at 2000 ms. In total 1074 volumes were acquired. The acquisition plane was tilted 30° from the AC-PC plane to decrease signal dropout in the orbitofrontal cortex (Weiskopf et al., 2007).

Preprocessing

All preprocessing steps were performed using the fMRIPrep preprocessing pipeline (Esteban et al., 2019) apart from smoothing which was implemented in SPM12 (www.fil.ion.ucl.ac.uk/spm).

Anatomical data preprocessing

The T1-weighted (T1w) image was corrected for non-uniformity intensity using `N4BiasFieldCorrection` (Tustison et al., 2010), distributed with ANTs 2.2.0 (Avants et al. 2008, RRID:SCR_004757), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with a *Nipype* implementation of the `antsBrainExtraction.sh` workflow (from ANTs), using OASIS30ANTs as the target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using `fast` (FSL 5.0.9, RRID:SCR_002823, Zhang et al. 2001). Brain surfaces were reconstructed using `recon-all` (FreeSurfer 6.0.1, RRID:SCR_001847, A. M. Dale et al. 1999), and the brain mask estimated previously was refined with a custom variation of the method to reconcile the ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (RRID:SCR_002438, Klein et al. 2017). Volume-based spatial normalization to one the MNI standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with `antsRegistration` (ANTs 2.2.0), using brain-extracted versions of both the T1w reference and the T1w template. The following template was selected for spatial normalization: *ICBM 152 Nonlinear Asymmetrical template version 2009c* (Fonov et al. 2009, RRID:SCR_008796; TemplateFlow ID:MNI152NLin2009cAsym).

Functional data preprocessing

For each BOLD run (1 per subject), the following preprocessing was performed. First, a reference volume and its skull-stripped version were generated using a custom methodology of *fMRIPrep*. The BOLD reference was then co-registered to the T1w reference using `bbregister` (FreeSurfer) which implements boundary-based registration Greve & Fischl (2009). Co-registration was configured with nine degrees of freedom to account for distortions remaining in the BOLD reference. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using `mcflirt` (FSL 5.0.9, Jenkinson et al. 2002). BOLD runs were slice-time corrected using `3dTshift` from AFNI 20160207 (Cox & Hyde 1997, RRID:SCR_005927). The BOLD time-series, were resampled to surfaces on the *fsaverage5* spaces. The BOLD time-series (including slice-timing correction when applied) were resampled onto their original, native space by applying a single, composite transform to correct for head-motion and susceptibility distortions. These resampled BOLD time-series will be referred to as preprocessed BOLD in original space, or just preprocessed BOLD. The BOLD time-series were resampled into standard space, generating a *preprocessed BOLD run in [MNI152NLin2009cAsym] space*. Several confounding time-series were calculated based on the *preprocessed BOLD*: framewise displacement (FD), DVARS and three region-wise global signals. FD and DVARS are calculated for each functional run, both using their implementations in *Nipype* (following the definitions by Power et al. 2014). Three signals are extracted within CSF, WM, and whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (*CompCor*, Behzadi et al. 2007). Principal components were estimated after high-pass filtering the *preprocessed BOLD* time-series (using a discrete cosine filter with 128s cut-off) for the two *CompCor* variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components were then calculated from the top 5% variable voxels within a mask covering the subcortical regions. This subcortical mask

was obtained by heavily eroding the brain mask, which ensures it does not include cortical GM regions. For aCompCor, components were calculated within the intersection of the aforementioned mask and the union of CSF and WM masks calculated in T1w space, after their projection to the native space of each functional run (using the inverse BOLD-to-T1w transformation). Components were also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values were retained (so that the retained components time series are sufficient to explain 50 percent of variance across the nuisance mask - CSF, WM, combined, or temporal). The remaining components were dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al., 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardised DVARS were annotated as motion outliers. All resamplings were performed with a *single interpolation step* comprised of all the pertinent transformations (i.e., head-motion transform matrices, susceptibility distortion correction when available, and co-registrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using `antsApplyTransforms` (ANTs), configured with Lanczos interpolation to minimize the smoothing effects of other kernels (Lanczos, 1964). Non-gridded (surface) resamplings were performed using `mri_vol2surf` (FreeSurfer).

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7

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OPEN When the statistical MMN meets the physical MMN

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How do listeners respond to prediction errors within patterned sequence of sounds? To answer this question we carried out a statistical learning study using electroencephalography (EEG). In a continuous auditory stream of sound triplets the deviations were either (a) statistical, in terms of transitional probability, (b) physical, due to a change in sound location (left or right speaker) or (c) a double deviant, i.e. a combination of the two. Statistical and physical deviants elicited a statistical mismatch negativity and a physical MMN respectively. Most importantly, we found that effects of statistical and physical deviants interacted (the statistical MMN was smaller when co-occurring with a physical deviant). Results show, for the first time, that processing of prediction errors due to statistical learning is affected by prediction errors due to physical deviance. Our findings thus show that the statistical MMN interacts with the physical MMN, implying that prediction error processing due to physical sound attributes suppresses processing of learned statistical properties of sounds.

Statistical learning lies at the heart of our everyday lives. It is a mechanism that enables individuals to detect statistical patterns in the environment without explicit intent to learn. Statistical learning comes under the umbrella term of implicit learning¹. It has been investigated using a range of stimulus types (for reviews, see refs^{2,3}) such as syllables⁴, tones⁵, sung language⁶, and visual stimuli⁷, reflecting the domain-general aspect of this mechanism⁸. However, most statistical learning studies have focussed on the domain of language acquisition and specifically on word segmentation, which is based on the principle that adjacent syllables within a word have greater transitional probabilities compared with adjacent syllables between words. A number of studies explored the neural correlates of statistical learning assessing event-related potential (ERP) or event-related magnetic field (ERF) components such as the N400^{9–13} or the N100/N100m^{9,13–15}. Earlier components have also been reported such as auditory brainstem responses (ABR)¹⁶ or the P50m^{17,18}.

Only recently, some studies using statistical learning paradigms began to explore neural correlates beyond those related to word segmentation (for a review, see ref.³), using the “Mismatch Negativity (MMN)” as a neurophysiological marker of processing “statistical deviance” (by comparing low and high transition probabilities). The main question in those studies was how the human brain responds to surprising events that violate learned regularities, and especially when these irregularities occurred within a word or a sound pattern (ex: “beautiful cactus” vs “beautiful cacti” or “pretty baby” vs “pretty babies”). Koelsch *et al.*¹⁹, generated such irregularities by manipulating the transitional probability between the second and the third tone within tone triplets. They found that more unexpected events (i.e., with low transitional probability) elicited a larger mismatch response. The authors referred to this ERP effect as statistical MMN (sMMN). Another study by Moldwin *et al.*²⁰, observed that the MMN elicited by equiprobable deviant tones was stronger when the violation occurred within rather than between melodic patterns. Thus, the MMN was larger for violations occurring in positions with high transition probability, within a melodic pattern, compared with positions with low transition probability such as between melodic patterns. The reported MMN could also be regarded as sMMN since it reflects learning of probabilistic properties of sounds. François *et al.*²¹, found that violations to word structure (regular: ABC vs irregular: CBA) disrupted the transitional probabilities of the syllables within the word, evoking negativities within the time windows of the MMN/N200 that had a dominance over fronto-central scalp regions. It appears that very few statistical learning studies with EEG have investigated effects beyond perception of word boundaries. Therefore, the primary scope of our study was to investigate neural correlates of statistical learning by varying transitional probabilities not only between the words but also within the word.

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Another question that remains unexplored in statistical learning studies is if and how the statistical manipulation of physical attributes of the audio stimuli, such as loudness, spatial location or frequency, interacts with learning. Several studies have investigated how the brain responds to changes on the physical or abstract features of the sound, reporting the physical MMN (phMMN) or the abstract feature MMN^{22–26}. However, to our knowledge, there is no study so far exploring the statistical manipulation of transitional probabilities and physical attributes of sounds within the same paradigm. Thus, a secondary scope of our study was to provide insights into a possible interaction between the sMMN (elicited by transition probabilities) and the phMMN (elicited by a sound location change). If an interaction can be observed between statistical and physical MMN, this would imply that processing of the transitional probabilities and of the location change of the sound overlap. In other words, the mechanism engaged for change detection would be the same for both types of MMN. In a study by Koelsch *et al.*²⁷, it was found that the amplitude of LAN, a component elicited by morphosyntactic violations in speech, was not affected by the presence of physical violations. This indicates that the underlying cognitive processes are independent. However, compared to the LAN with its higher latency (about 100 to 300 ms), the statistical and the physical MMN (explored in our study) occur within a similar time window. This, in turn suggests that an interaction between these two components is more probable.

The current study will allow us to examine processing related to “sensory” features, such as sound location, and more “structural” features of the stimuli, such as transitional probability. Assuming that MMN neural traces reflect how stimuli are represented in auditory memory²⁸, then the different stimuli features should be encoded differently. Of greater interest is the co-occurrence of sound location change and transitional probability deviation and the way these will be encoded in a unitary representation as reflected in the MMN. It is important to note that the critical difference between the phMMN²² and the sMMN is that the former relies on operations of the auditory sensory memory and sensory-memory-representations that are updated instantly^{29,30}. The latter, in contrast, relies on memory representations that are formed due to a learning process that leads to memory representations going beyond the capabilities of the sensory memory. To illustrate this, a deviance in terms of sound location would elicit instantly a phMMN caused by a mismatch of the recent auditory input compared with the deviant sound, as processed in the auditory sensory memory. In contrast, deviations in terms of learned transitional probabilities elicit a sMMN under the condition that (implicit) knowledge of the statistical regularities was acquired. We expected the physical deviance (elicited by a change in sound location) compared with the statistical deviance (elicited by low in comparison to high transitional probability) would be more prominent and easier to process (i.e., be cognitively less demanding). Additionally, from the perspective of predictive coding³¹ both deviant events (i.e., statistical and physical) would generate prediction errors that the brain would try to minimise. Most probably, the physical prediction errors would be easier to resolve due to the higher saliency of the exteroceptive stimuli. As a consequence, we expected that the phMMN would have a larger amplitude compared to the sMMN and that the phMMN would attenuate the sMMN.

A third aspect of our study was to develop an experimental paradigm suitable for investigations with children. So far, most of the studies employing statistical learning paradigms focused on the segmentation of the auditory stream into words or word-like units. The age of the participants in those studies ranged from infants to adults. For example, several statistical learning studies with children have investigated effects of musical training^{10,11}, or reading ability³² in children with typical development, or differences between children with typical development and atypical language development^{33,34}. It appears that children with language disorders have impaired performance in statistical learning tasks³⁵. However, given that these studies focused on word segmentation processes, it remains to be explored whether and how the sMMN, reflecting the cognitive processing of different transition probabilities within a word, is able to differentiate between children with typical and with impaired language development.

To this end, the experimental paradigm of the current study was developed from a previous study by Koelsch *et al.*¹⁹. In this experiment, a continuous stream of sounds, organised in triplets, was presented (see Fig. 1A). The first two sounds of the triplet, denoted as root, can be considered as one unit (the transition probability between the first and the second sound was always 1). The transition probability (TP) between the root and the last sound of the triplet was manipulated to be either low (TP = 0.1), intermediate (TP = 0.3), or high (TP = 0.6). The current experiment follows the same rationale but simplified the paradigm: The transition probability of the last sound of the triplet had only two steps, either high (TP = 0.9) or low (TP = 0.1). Given that the two sounds within the root always appeared together, our paradigm represents a 1st-order Markov model or bigram model with strictly 2-local distribution³⁶. Also, the transition probability between the words was constant (TP = 0.5). The current paradigm furthermore introduces a physical deviance, elicited by location change of the sound. Standard sounds would be presented from a default direction (either right or left speaker) whereas deviant sounds would be presented from the opposite direction (either left or right speaker).

We hypothesised that low probability events (i.e., triplet endings with low vs. high transitional probability) would elicit a sMMN. The second hypothesis was that physical deviants would elicit a phMMN. Third, we tested for an interaction of transition probability and physical deviance (i.e., an interaction between statistical and physical MMN), and hypothesised that the physical deviants would diminish the effect of the statistical deviants.

Results

Behavioral data. *Familiarity Test.* Participants achieved an overall score of 52.5% correct responses (SEM = 2.5%) and their performance did not differ significantly from chance level ($p = 0.38$). Only one participant (out of 21) reported during debriefing that she became aware of the statistical regularities underlying the arrangement of the stimuli; she also performed above chance level (64% correct responses).

Cover Task. Participants detected 99.5% of the (higher-pitched) target sounds successfully.

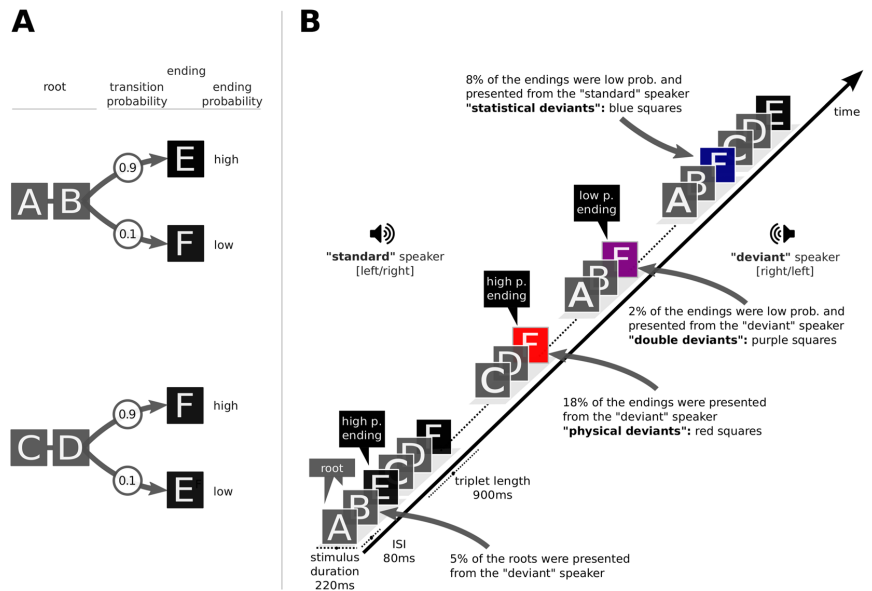


Figure 1. Experimental Paradigm. (A) The four triplets generated from 6 pairs of sounds. The first two items of the triplet are named root and the last item is name ending. Statistical deviants were created by varying the transition probability from root to ending within two levels, high ($p = 0.9$) and low ($p = 0.1$). Triplet roots (AB or CD) are occurring with a constant transitional probability ($p = 0.5$) from any of the triplet endings (E or F). (B) The auditory stream of pseudorandomly concatenated triplets with standard ending triplets (letter in black box), statistical deviant ending triplets (letter in blue box), physical deviants (letter in red box) and double deviants (letters in purple box). Physical deviants were generated by switching speaker.

Electroencephalographic data. The results for the ERPs will be presented first for the triplet endings and subsequently for the triplet roots.

ERPs of Triplet Endings. **Statistical Deviants.** Both low and high probability endings elicited a P1-like positivity maximal at around 140 ms, which did not differ between high and low probability endings ($p = 0.16$), followed by a negative deflection at around 200 ms that was larger for low probability endings compared with the high probability endings (see Fig. 2A). The amplitude difference (between high and low probability endings) is denoted as statistical MMN (sMMN). It had a size of $-1.50 \mu\text{V}$ at the peak maximum (latency: 210 ms). This effect was analysed statistically with an ANOVA for the time window of 180 to 260 ms relative to the onset of the triplet ending with factors transition probability (high vs. low), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3). It revealed a significant effect of transition probability ($F_{(1,20)} = 35.54$, $p < 0.0001$, Cohen's $d = 5.10$), no significant effect of block ($p = 0.30$), no interaction between probability and block ($p = 0.59$), thereby confirming our hypothesis that low probability endings would elicit a greater negativity. Furthermore, the following significant interactions were found: (a) transition probability and scalp area (reflecting that the sMMN effect was largest at anterior and diminishes towards posterior sites; $F_{(2,19)} = 6.9$, $p < 0.006$), (b) transition probability and lateralisation (reflecting that the sMMN was largest at midline sites; $F_{(2,19)} = 23.13$, $p < 0.0001$) and (c) block, scalp area and lateralisation ($F_{(4,17)} = 4.19$, $p = 0.015$). A linear trend was found for the interaction between transition probability and scalp area ($p = 0.001$). This reflects that the amplitude difference between low and high transition probability diminished from anterior towards posterior scalp sites. Pairwise comparisons for effect of triplet ending across all ROIs showed that the effect was significant ($p < 0.05$) in all of them (see Table 1). However, the effect was maximum in the frontal-midline region (with the maximum observed at electrode Fz, see Fig. 2B).

Pairwise comparisons examined how the effect of transition probability evolved across the experiment (see Fig. 2C). The analysis showed that low probability ending elicited a significant sMMN already in the first block ($p = 0.002$), increased in size for the second ($p = 0.001$), and then decreased for third block of the experiment ($p = 0.028$).

Physical Deviants. To investigate the effect of the physical deviance, we compared the ERP responses to triplet endings either containing physical deviance or not. The analysis compared the brain response to triplet endings where low transition probability co-occurred with the sound being presented either from the standard

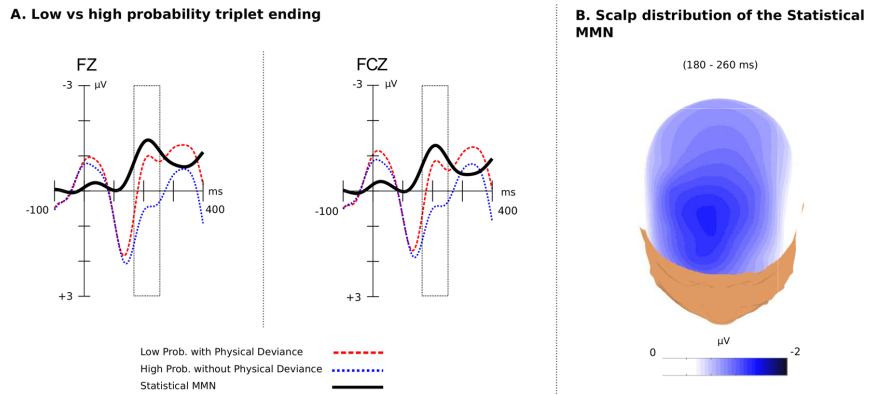


Figure 2. The statistical MMN (sMMN) over the three blocks. (A) The sMMN (black line) generated due to the violation of the standard transitional probability of the triplet ending from high TP = 0.9 to low TP = 0.1 and as captured at electrodes Fz and FCz. Last tone (triplet ending) onset is at 0 ms and has a duration of 300 ms. ERPs are baseline corrected 100 ms prior to the onset of the trigger. (B) The scalp distribution of the sMMN over the time window (180 to 260 ms) was maximal over the frontal-midline region.

	Left hemisphere		Middle hemisphere		Right hemisphere		ROI means	
	Mean difference (low-high)	<i>p</i>	Mean difference (low-high)	<i>p</i>	Mean difference (low-high)	<i>p</i>	Mean difference (low-high)	<i>p</i>
Anterior	-0.87	<0.001	-1.28	<0.001	-0.97	<0.001	-1.04	<0.001
Central	-0.59	<0.001	-1.01	<0.001	-0.58	<0.05	-0.73	<0.001
Posterior	-0.46	<0.05	-0.65	<0.05	-0.30	<0.05	-0.47	<0.05

Table 1. Mean amplitudes of the statistical MMN (comparing the difference in the neurophysiological brain response to low minus high transition probability endings; in μV) averaged over the participants.

or the opposite direction. For the effect of physical deviance on the high-probability triplet ending see the Supplementary Fig. 5. As shown in Fig. 3A, triplet endings with physical deviance elicited a positive-going wave with a latency of about 100 ms (P1) and a phMMN reaching the maximum amplitude of $-3.65 \mu\text{V}$ at around 180 ms over central-midline electrodes. The phMMN was followed by a distinct P3b (see Supplementary Fig. 6). The effect of physical deviance appeared to be larger and earlier (amplitude: $-3.65 \mu\text{V}$, latency: 180 ms) compared with the effect of statistical deviance (amplitude: $-1.50 \mu\text{V}$, latency: 210 ms).

An ANOVA with the factors physical deviance (with vs. without location change), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) over the time window of 150 to 220 ms after the onset of the triplet ending showed significant effect of physical deviance ($F_{(1,20)} = 38.90$, $p < 0.0001$, Cohen's $d = 7.26$). No significant effect of block was found or any interaction between block and triplet ending.

Triplet endings with location changes elicited consistently larger negativities throughout the course of the experiment even though the amplitude size diminished over blocks (see Fig. 3C). However, the two ending types differed significantly within the first ($p = 0.001$), the second ($p < 0.0001$) and the third block ($p = 0.014$) of the experiment.

With respect to the scalp distribution, the physical deviance led to an amplitude difference ($p < 0.05$) across all ROIs except from the posterior right one. Furthermore, it reached maxima in the frontal and central midline electrodes (and a maximum amplitude difference at FCz, see Fig. 3A).

The P1 time window (80 to 180 ms) was assessed using an ANOVA with the factors physical deviance (with vs. without location change), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3). It revealed a significant effect of physical deviance ($F_{(1,20)} = 38.90$, $p < 0.00016$, Cohen's $d = 3.42$), no significant effect of block or any interaction involving block and physical deviance. Yet, the physical deviance affected the ERP responses in a decreasing rate; it was significant only during the first block ($p = 0.028$). The distribution of the effect was not symmetrical but rather left-lateralised and diminished towards right scalp sites ($F_{(2,40)} = 3.54$, $p = 0.038$).

Interaction of probability and change location. To investigate the interaction between the two types of deviances, (i.e., the varying transition probability of the triplet ending and² the presence or absence of location change), we conducted an ANOVA with transition probability (high vs. low), physical deviance (with vs. without location

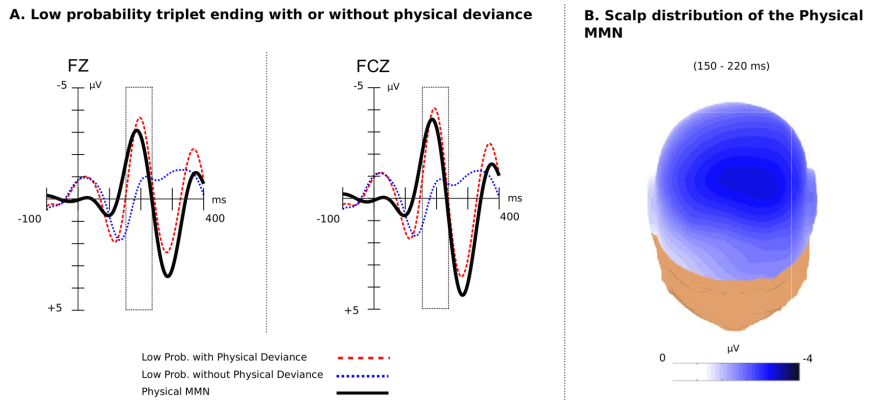


Figure 3. The physical MMN (phMMN). (A) The phMMN (black line) generated due to the violation of sound location of triplet ending from the “standard” to the “deviant” side, as captured at electrodes Fz and FCz. Last tone (triplet ending) onset is at 0 ms and has a duration of 300 ms. ERPs are baseline corrected 100 ms prior to the onset of the trigger. (B) The scalp distribution of the phMMN over the time window (150 to 220 ms) was maximal over the frontal and central midline regions.

change), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) in a the time window from 160 to 260 ms after the onset of the triplet ending.

The analysis revealed a significant effect of probability ($F_{(1,20)} = 14.14$, $p = 0.001$, Cohen’s $d = 3.14$), of physical deviance ($F_{(1,20)} = 35.02$, $p < 0.0001$, Cohen’s $d = 6.40$), and interaction of these two ($F_{(1,20)} = 4.95$, $p = 0.038$). Pairwise comparisons showed that at the presence of physical deviance the effect of statistical deviance almost disappears ($p = 0.205$; see Fig. 4B). Statistical deviance produced a significant effect ($p < 0.0001$) only under the condition that there was no physical deviance.

ERPs of Triplet Roots. To examine whether the continuous auditory stream was segmented into discrete triplets, we examined the ERP responses to the triplet roots (i.e., the first two triplet items). We hypothesized that any difference in the ERP responses within a late N1 window (170 to 250 ms) between the first two triplet items should reflect such segmentation effect. This analysis assessed the first and the second sound (both coming from within triplets that were preceded by standard triplets; i.e., those having high probability endings and no physical deviance).

An ANOVA with factors position (first and second sound), scalp area (anterior, central and posterior), lateralisation (left, midline and right) and block (1 to 3) for the N1 time window (from 170 to 250 ms) revealed no significant effect of position ($p = 0.496$), no significant effect of block ($p = 0.225$) but a significant interaction between these two ($F_{(2,40)} = 3.79$, $p = 0.031$). Therefore, typical word segmentation effect on the first item could not be observed in the current study.

Figure 5 depicts ERP responses, separately for each of the triplet tones. Each item elicited a P1-like positivity at around 140 ms, and N1-like negativity at about 200 ms. This N1-like negativity differed between the three triplet items.

The ANOVA for the P1 time window from (100 to 200 ms after the onset of the triplet item) revealed no significant effect of position ($p = 0.390$), a no significant effect of block ($p = 0.670$) neither a significant interaction between these two ($p = 0.160$).

Discussion

Low-probability triplet endings elicited a sMMN, i.e. a larger fronto-central negativity within a time window between 180 to 260 ms (compared with high probability triplet endings). The observation of this sMMN is in accordance with previous studies that manipulated the transitional probability of deviants and reported similar ERP effects^{15,17,19}. Thus, the present study confirms that the sMMN can be used to investigate neurophysiological effects due to the acquisition of knowledge about transition probabilities based upon statistical (implicit) learning. Importantly, the sMMN (elicited by the low-probability triplet endings) was due to the transitional probability with which the triplet endings occurred, and not due to any acoustical or perceptual differences. Thus, we can exclude that the sMMN received any contributions from a physical or abstract feature MMN. Moreover, due to the fact that knowledge about the underlying statistical regularities is not acquired instantly (as is the case with physical features of the sound), this statistical mismatch involves memory representations beyond the capabilities of sensory memory.

Although the ERP results indicate that participants acquired implicit knowledge about the regularities underlying the arrangement of tones within the triplets, they did not exhibit explicit knowledge: The performance in the behavioural part (assessing familiarity with the more frequently played sequence containing the high transition

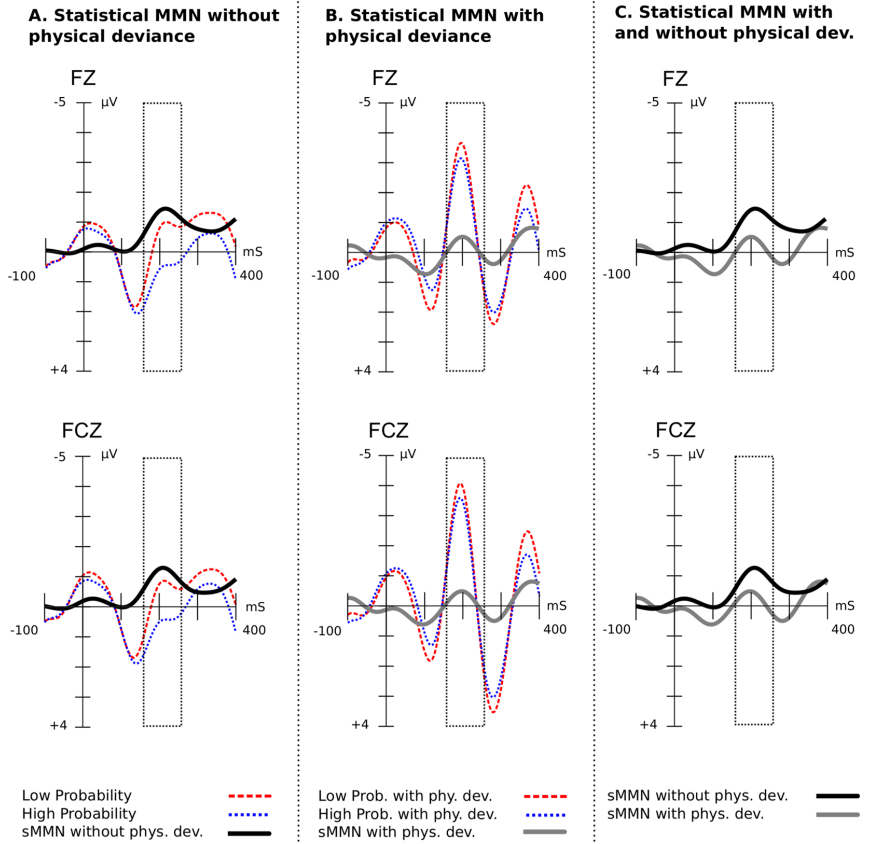


Figure 4. Interaction of transition probability and physical deviance. Triplet ending onset is at 0 ms and has a duration of 300 ms. ERPs are baseline corrected 100 ms prior to the onset of the trigger. (A) The statistical MMN (black line) without physical deviance, as captured at electrode Fz and FCz. The trace depicted for electrodes Fz and FCz is identical to the one in Fig. 3A. (B) The statistical MMN (gray line) with physical deviance. (C) Separate traces for the statistical MMN with or without physical deviance. At the presence of physical MMN the statistical MMN diminishes.

probability continuation) was only marginally above chance level and did not reach significance. Participants were also not able to express verbally what they learned when explicitly asked to do so. Therefore, it appears that the statistical learning during the experiment, as indicated by the sMMN, was implicit. The discrepancy between behavioral and neurophysiological evidence is not unusual in implicit learning studies^{17,19,37}. However, perhaps an easier behavioral task could have revealed learning effects (as evidenced in the neurophysiological data). Future studies might consider using also “non-words”, i.e., triplets that did not occur during the exposition phase (such as FEA, FEB, EFC and EFD), in addition to triplets that were presented during the exposition phase (ABE, ABE, CDF and CDE).

When triplet endings were presented in a different spatial location (with low probability of the physical location change), these location deviants elicited effects within the P1-time window, followed by a clear phMMN (which appeared to have a shorter peak latency than the sMMN)³⁸. These observations suggest that sound location change identification is an earlier process compared to statistical deviance detection (at least during the early phases of learning, i.e. within the first hour of learning, as investigated in the present study). In contrast to the statistical deviants, the location changes were rather salient (with a rather large angle of 60° location change)³⁹. This difference in saliency is also reflected in the observation that the amplitude of the phMMN was larger than the amplitude of the sMMN. The scalp distribution of the present MMN was maximal over midline electrodes within fronto-central regions, which is in agreement with previous studies^{25,40}.

Interestingly, the co-occurrence of statistical and physical deviance did not produce an additive effect, but an interaction. As shown in Fig. 4, the sMMN elicited by deviants with low transition probability diminished in

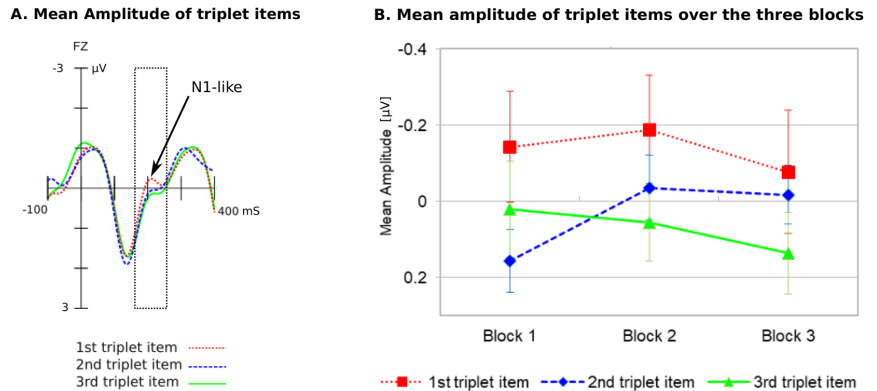


Figure 5. N1-like wave for the three items of the triplet. (A) Triplet item onset is at 0 ms with a duration of 300 ms. ERPs are filtered 100 ms prior to the onset of the trigger. There is no typical segmentation effect over the window 170 to 250 ms. (B) The mean amplitudes of the triplet items over the blocks. There is no significant difference between them.

the presence of physical deviance. In other words, the effect of statistical deviance is smaller when co-occurring simultaneously with a location change. This interaction suggests that neural substrates underlying the processing of transition probability and physical deviance overlap at least partly.

To explain this interaction we refer to the four necessary processes for MMN elicitation as presented in Schröger⁴¹ and Koelsch⁴². Assuming that the elicitation of an MMN requires a pre-established representation of the stimuli in the auditory sensory memory (ASM)²⁸, the formation of these representations is regarded as the first phase. In principle, at this early phase, mainly sensory processes such as feature extraction or detection of source location are carried out. The outcome is a unitary stimulus representation of the auditory event where different features of the stimuli are integrated²⁸. Therefore, in our study, we may assume that three different types of representations were formed for sMMN, phMMN and double deviance MMN. In the second phase, a model is established that embeds all acoustical or structural regularities of the input. In our experiment participants established a model with certain physical features that are perceived in real time (i.e., standard vs. deviant sound location). In contrast, transition probabilities between triplet items require some time to be learned. This knowledge is reflected by the physical and statistical MMN when tested solely. In a third phase, upon establishment of a model, predictions are made about specific future auditory events. In the fourth phase, the model is tested; if the newly incoming stimuli mismatch with the model predictions, an MMN is triggered. Based on our findings we propose that the elicitation of the MMN (whether it is due to statistical, physical or double deviance), relies on partly the same mechanism, but is elicited by different input representations. The interaction suggests an overlap of neural resources during prediction formation (third phase) and comparison (fourth phase). By contrast, stimuli representation formation (first phase) relies on different neural populations. We propose that statistical deviance encoding engages more top-down operations, compared with physical or double deviance encoding, since it requires some time for learning the underlying regularities. Particularly in the case of double deviance, the prominent physical deviance dominates the formation of the stimulus representation along with the predictions, and accordingly affects the comparison process more significantly. Along the same line, our results also support the notion that neural traces in MMN generation reflect the perceived stimuli rather than the actual properties of the stimuli²⁸.

An important question that remains to be answered is whether attention affects the interaction of statistical and physical deviance. To our knowledge, there is no study investigating the role of attention for the elicitation of the sMMN or the interaction of statistical and physical MMN. Therefore, we cannot exclude the contingency that processing of physical deviances interferes, via attention or not, with processing of learning statistical regularities. However, the finding that the sMMN is influenced by a physical deviance remains; but we are not able to tell if the learning is actually disturbed by the physical deviance. Hence, the interference effect of attention to the sMMN remains to be specified.

Within the predictive coding framework the deviances are viewed as prediction errors which are ascending the auditory cortical hierarchies to evince better predictions⁴³. Presumably, prediction errors due to statistical deviances have to ascend higher the hierarchy to be resolved compared with prediction errors due to physical deviances. On the basis that physical deviants are more precise and predictable, they also gain greater attention. Thus, attending to the physical deviants suppresses processing of statistical cues by ignoring evidence for statistical prediction errors. Although physical prediction errors are probably resolved lower in the auditory hierarchy than the statistical prediction errors, our results indicate that there is some overlap in the levels of prediction error processing in the auditory hierarchy.

This study was primarily about responses related to processing of high vs low probability, and less to the perception of word boundaries. Thus, along with the ERP responses to deviances, we also examined whether

the participants segmented the auditory stream into discrete triplets. For this purpose, we compared the N1-like wave as generated by the first two triplet items. We found that the amplitude between the first and the second item did not differ significantly. Thus, we did not obtain a typical word segmentation effect in our study. This may be due to the fact that the transitional probability between words was relatively high ($TP = 0.5$), thus, not creating a clear statistical boundary. Interestingly, in the study by Koelsch *et al.*¹⁹ where the transitional probability between words was lower ($TP = 0.33$) there was a significant word segmentation effect (see Supplementary Fig. 1) Thus, we may draw the conclusion that a transitional probability between words of 0.5 is not sufficiently low to produce a clear word segmentation effect. Nonetheless, as it was noted in the introduction, the primary aim of this study was not on word segmentation per se, but to give a deeper understanding on the mechanisms employed during statistical learning using a novel paradigm.

The presented paradigm seems to be appropriate to conduct studies with children, both with typical and impaired language development. First, the stimuli are of musical rather than syllabic nature. This ensures that statistical learning would not be biased by interindividual differences in phoneme perception skills. Second, the experimental paradigm features a child-appropriate duration of an experimental session. Third, in addition to word segmentation learning it incorporates processing of high- and low-probability events which is suited to investigate the so-called sMMN. Fourth, it allows comparison of responses due to statistical learning (sMMN) with responses due to sensory learning, i.e. acoustical mismatch detection of the auditory sensory memory as reflected in the “physical mismatch negativity” (phMMN, we used a location MMN to achieve this). Fifth, it meets the requirement to investigate possible interactions between statistical and sensory learning (i.e., between the sMMN and the phMMN).

Conclusion

Our study replicates the sMMN, an ERP component triggered by events that deviate from regularities acquired within a statistical (implicit) learning paradigm. The novelty of our paradigm lies on the fact that we combined within one experimental paradigm the violation of statistical expectancies (i.e., implicit knowledge about the different transition probabilities at the last tone of a sound triplet acquired over the course of the experiment) with a violation of expectancies regarding physical features (i.e., a change in sound location). As expected, both types of deviance elicited clear ERP effects (i.e., either a sMMN or a phMMN). The current paradigm seems promising for future studies involving children with typical and non-typical language development. This might elucidate neural substrates involved in specific language impairment, and could potentially lead to the design of a diagnostic tool for language impairments⁴⁴.

A new finding of our study was that the sMMN interacts with the phMMN: The sMMN was diminished in the presence of a location change. This finding suggests that the elicitation of statistical and physical MMN share neural resources, mostly with regard to processing resources, rather than resources for representations. Additionally, it indicates that the brain responds selectively to deviations that are easy to detect and consequently do not require learning.

Methods

Participants. 21 adults (12 females; mean age = 22.43 years, $SD = 2.39$) were recruited at the University of Bergen. None of the participants had hearing impairments, history of neurological disease, or musical training more than 2 years besides regular school lessons (according to self-report). All participants were compensated (200 NOK, approx. 20 EUR) at the end of the experiment. The study was carried out in accordance with the guidelines of the Declaration of Helsinki, and approved by the Regional Committee for Medical and Health Research Ethics for Western Norway (Reference Number: 2014/313). Participants provided written informed consent before the experiment.

Stimuli. *Sound triplets.* In order to form the triplets we created six sounds. Each sound was a combination of a Shepard tone and a percussion sound. Shepard tones⁴⁵ were employed in order to reduce any percept of pitch along with any auditory grouping based on pitch. We generated six Shepard tones for six frequencies (F3: 174.61 Hz, G3: 196.00 Hz, A3: 220.00 Hz, B3: 246.94 Hz, C#4: 277.18 Hz and D#4: 311.13 Hz) where each tone resulted from the superposition of nine sinusoidal components spaced one octave apart. These six Shepard tones were combined with six percussive sounds (surdo, tambourine, agogo bells, hi-hat, castanet and woodblock, which were downloaded from http://www.philharmonia.co.uk/explore/sound_samples. The Philharmonia Orchestra website). All sounds were sampled at 44100 Hz and normalised based on the RMS amplitude so that they were matched in overall loudness. Each sound had a duration of 220 ms, including a fade in of 10 ms and fade out of 20 ms. The interstimulus interval was 80 ms (thus, the inter-onset interval was 300 ms). The six sounds, corresponding to the letters A to F (see Fig. 1), were combined into triplets. Specifically, sounds A, B, C and D were combined in two (AB and CD) in order to form the “root” of the triplet. The word “root” was used to refer to the first two items of the triplet. Sounds E and F were used for the last position or item of the triplet. Thus, we obtained four unique triplets (Fig. 1).

For the practice trials before the experiment, a second set of six sounds was created. These sounds were created similar to the sounds of the main experiment, but differed in frequency of the Shepard tones (E3: 164.81 Hz, F#3: 184.99 Hz, G#3: 207.65 Hz, A#3: 233.08 Hz, C4: 261.62 Hz and D4: 293.66 Hz) and in which percussive sounds were used (woodblock, tambourine, agogo bells, castanet, hi-hat and bass drum).

Finally, an additional sound was created (C#5: 554.37 Hz, not combined with a percussive sound) to serve as target sound for the cover task that participants had during practice trials and the experiment.

Importantly, the arrangement of sounds (A to F) was permuted across participants as a way to guarantee that possible acoustical differences between sounds would not bias the brain responses of interest.

	Triplet Ending	
Location	High Probability ($p=0.90$)	Low Probability ($p=0.10$)
Standard ($p=0.80$)	Standards ($p=0.72$)	Statistical Deviant ($p=0.08$)
Deviant ($p=0.20$)	Physical Deviant ($p=0.18$)	Double Deviant ($p=0.02$)

Table 2. Distribution of transition probabilities and location change in triplet endings.

Stimulus Location. In order to generate physical deviants, the location of the sounds stimulus was manipulated, featuring a spatial location change of 60° angle in the azimuthal plane: If the standard stimuli were presented from the direction of one speaker, the physical deviants were presented from the other one. The stimulus location was arranged as follows: The sound of the triplet root (A to D) was presented in 95% of the times from the “standard” and 5% of the times from the “deviant” location. The last sound of the triplet was presented in 80% of the times from the “standard” side, and 20% of the times from the “deviant” side. Only sounds at the last position were evaluated when assessing physical deviance. “Standard” and “deviant” location was balanced across blocks and counterbalanced between participants whether they would have left or right as preferential (standard) direction for the first block.

Triplet Endings. Triplets endings differed in respect to (1) the frequency of occurrence of their ending within the experiment block and (2) the location of their ending (Table 2). Therefore, four categories of triplet ending occurred:

1. **Standards:** represented the 90% of the triplets, featured a high transition probability ending ($p=0.9$) and were presented from the “standard” location.
2. **Transitional Probability Deviants:** 10%, featured a low transition probability ending ($p=0.1$) and were presented from the “standard” location.
3. **Physical Deviants:** 20%, featured an ending presented from the “deviant” location.
4. **Double Deviants:** transition probability and physical deviants represented 2% of the triplets. They featured a low transition probability ending and were presented from the “deviant” location.

Triplet Streams. 400 triplets were pseudorandomly concatenated into pause-free streams or blocks of about 7 min duration each. Triplets were presented in a pseudorandom order so that triplets from the low probability set were separated by at least three triplets from another set. Triplet roots (AB or CD) followed any of the two triplet endings (E or F) with a constant transitional probability (TP = 0.5). So, for example ABE could be followed by either ABE, CDF, ABF or CDE.

Procedure. The experiment took place inside an electro-magnetically shielded chamber. Participants were asked to seat in a chair in front of a desk with a monitor. Their seating position was chosen so that it formed an equal side triangle with the speakers and that their eyes were at the level of the center of the screen. The experiment consisted of 6 blocks each one comprising an exposition phase of about 7 min followed by a behavioural task of about 2 min, resulting in a total duration of the experiment (including pauses) of about 1 hour. During the exposition phase, auditory stimuli were presented via the speakers while participants could watch a silent movie on the monitor in front of them. The electroencephalogram (EEG) was recorded during the whole experiment. The experimenter was present in an adjacent room throughout the experiment. He could monitor the participant's state at all times with camera directed at the participant's head. Participants were instructed to give a sign to the camera should they need to interrupt the experiment.

The experiment started with a set of instructions. Participants were not informed about the regularities in the arrangement of the stimuli, to ensure that any kind of learning throughout the experiment was implicit. At the same time, to ensure that participants were attentive to the stimuli, a cover task was used: The participants were asked to press the spacebar every time they heard the (higher-pitched) target sound. There were examples of the target sound in the instructions, followed by practice trials (lasting about 1 min) containing a relatively high number of target sounds. The practice trials were repeated if participants did not detect at least 80% target sounds (or had a too large number of false alarms). Participants were asked to avoid movement, especially jaws and eyes, in order to minimize artifacts in the EEG recording.

Familiarity test and Confidence Rating. At the end of each block, a behavioral test assessed whether participants were able to distinguish two triplet sequences ending on a sound with either high or low transitional probability. Each test had 12 trials where participants were presented with three repetitions of all four possible triplet combinations (ABE vs. ABF, ABF vs. ABE, CDF vs. CDE, or CDE vs. CDF). All sequences were presented binaurally, none contained a location change, and there was a pause of 335 ms between the triplets. Participants were asked to choose which sequence sounded more familiar (pressing either “1” for the first or “2” for the second sequence). Afterwards, they rated their level of confidence about their choice of sequence (pressing from “1” – absolute unsure, could have thrown a coin – to “5” – absolutely certain). Consecutive trials did not use the same triplet root and the order of presentation of the endings was counterbalanced.

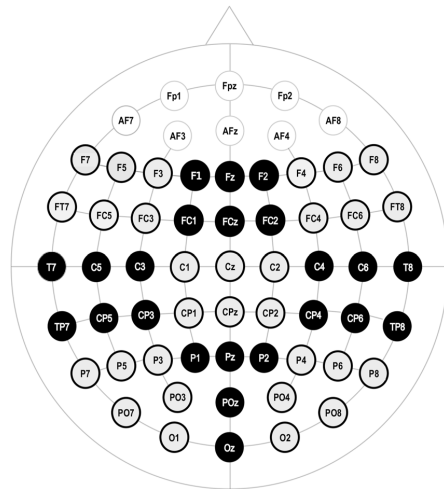


Figure 6. Electrodes Clusters. The electrodes were clustered in 9 ROIs which are shown in grey and black.

Data Recording and Analysis. *EEG recording.* The EEG signal was recorded from 59 scalp electrodes placed in an electrode cap in compliance with the 10–10 system (see Fig. 2) at 500 Hz sampling rate using BrainAmps DC (Brain Products GmbH, Munich, Germany). Additional electrodes were placed on the left and right mastoids (the left mastoid serving as reference), on the back of the neck (serving as ground), as well as at the outer canthi of the eyes (bipolarly recording the horizontal electrooculogram [EOG]) and above and below the right eye (for the vertical EOG). All electrode impedances were kept below 5 k Ω .

Processing of EEG data. EEG data were analysed using EEGLAB 13⁴⁶ within MATLAB[®] R2016b (The MathWorks Inc., Natick, MA). EEG data during the behavioral part of the experiment (at the end of every block) were not evaluated. EEG data were manually inspected and excluded from analysis if they contained faulty channels or periods with excessive artifacts. An Independent Component Analysis was used to remove eye and muscle artifacts. Afterwards, EEG data were re-referenced to the algebraic mean of the left and right mastoid electrodes and filtered using a 30 Hz low-pass filter (2750 points, finite impulse response, Blackman).

Samples were rejected whenever the standard deviation within a 200 or 800 ms gliding window exceeded 25 μ V at any electrode channel (including the EOG channels). Afterwards, data were epoched, excluding epochs following acoustical deviants or button presses (within 3 secs; i.e., rejecting activity related to the cover task of the participant). ERPs were calculated for low and high probability triplet endings with or without location change of the sound, from -100 to 400 ms relative to stimulus onset and using a 100 ms pre-stimulus baseline correction. In addition, to determine whether participants' brain responses reflected the triplet structure of the stimulus stream, ERPs for the triplet root were calculated from -100 to 1000 ms (relative to the onset of the preceding triplet end). These ERPs were restricted to roots following high transitional probability sounds at the end of the previous triplet in order to avoid contamination of the N1 with brain responses to low transitional probability triplet ends. These ERPs did not use baseline correction but were instead 0.5 Hz high-pass filtered (550 point, finite impulse response, Blackman) in order to remove slow drifts and other low frequency trends⁴⁷. Baseline correction was chosen for triplet endings to avoid any bias of previous activity (location change for root) whereas for roots we chose high-pass filtering as a more appropriate method in relation to root length.

For statistical evaluation, electrodes were clustered into nine regions of interest (ROIs) as shown in Fig. 6, namely frontal left (F7, F5, F3, FT7, FC5, FC3), frontal middle (F1, Fz, F2, FC1, FCz, FC2), frontal right (F8, F6, F4, FT8, FC6, FC4), central left (T7, C5, C3, TP7, CP5, CP3), central middle (C1, Cz, C2, CPz), central right (T8, C6, C4, TP8, CP6, CP4), parietal left (P7, P5, P3, PO7, PO3, O1), parietal middle (P1, Pz, P2, POz, Oz) and parietal right (P8, P6, P4, PO8, PO4, O2). The time windows for statistical analysis were selected in accordance with previous studies (see Introduction) and based upon visual inspection.

Statistical analyses. Statistical analyses were conducted using SPSS 25 (IBM Corp., Armonk, NY, USA). Behavioural data were participants' responses to the familiarity test. Responses were classified as correct when participants chose the sequence that contained the high probability transition (and was played more frequently during exposition phase). Mean percent correct was calculated for each participant and subsequently compared against chance level (0.5; independent sample t-test, $\alpha = 0.05$).

Three analysis of variance (ANOVAs) were conducted assessing the brain responses to the end of the triplet for either (1) statistical deviance (low and high transitional probability between triplet root and end), (2) physical deviance (standard location vs. deviant location), or (3) the combination of statistical and physical deviance.

A fourth ANOVA explored the segmentation of the sound stream into the triplet structure comparing sound position within the triplet (1st, 2nd, 3rd triplet item). Each of these four ANOVAs furthermore contained two factors assessing scalp distribution: (a) scalp area (frontal, central, posterior) and (b) lateralisation (left, midline, right) as well as one factor assessing development over the course of the experiment: (c) experiment block (1 to 3; the first, middle and last two blocks of the 6 blocks of the experiment were grouped in order to obtain a better signal-to-noise-ratio).

Data Availability

The datasets generated during and/or analysed during the current study are available from the corresponding author (Barbara.Tsogli@uib.no) on reasonable request.

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Author Contributions

S.K., S.J. and V.T. conceived the experiment, V.T. and T.D. conducted the experiment. All authors analysed the results and reviewed the manuscript.

Additional Information

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	Skjerve, Arvid	Assessing mild dementia – a study of brief cognitive tests.

	Kjønniksen, Lise	The association between adolescent experiences in physical activity and leisure time physical activity in adulthood: a ten year longitudinal study
	Gundersen, Hilde	The effects of alcohol and expectancy on brain function
	Omvik, Siri	Insomnia – a night and day problem
2009 V	Molde, Helge	Pathological gambling: prevalence, mechanisms and treatment outcome.
	Foss, Else	Den omsorgsfulle væremåte. En studie av voksnes væremåte i forhold til barn i barnehagen.
	Westrheim, Kariane	Education in a Political Context: A study of Knowledge Processes and Learning Sites in the PKK.
	Wehling, Eike	Cognitive and olfactory changes in aging
	Wangberg, Silje C.	Internet based interventions to support health behaviours: The role of self-efficacy.
	Nielsen, Morten B.	Methodological issues in research on workplace bullying. Operationalisations, measurements and samples.
	Sandu, Anca Larisa	MRI measures of brain volume and cortical complexity in clinical groups and during development.
	Guribye, Eugene	Refugees and mental health interventions
	Sørensen, Lin	Emotional problems in inattentive children – effects on cognitive control functions.
	Tjomsland, Hege E.	Health promotion with teachers. Evaluation of the Norwegian Network of Health Promoting Schools: Quantitative and qualitative analyses of predisposing, reinforcing and enabling conditions related to teacher participation and program sustainability.
	Helleve, Ingrid	Productive interactions in ICT supported communities of learners
2009 H	Skorpen, Aina Øye, Christine	Dagliglivet i en psykiatrisk institusjon: En analyse av miljøterapeutiske praksiser
	Andreassen, Cecilie Schou	WORKAHOLISM – Antecedents and Outcomes
	Stang, Ingun	Being in the same boat: An empowerment intervention in breast cancer self-help groups
	Sequeira, Sarah Dorothee Dos Santos	The effects of background noise on asymmetrical speech perception
	Kleiven, Jo, dr.philos.	The Lillehammer scales: Measuring common motives for vacation and leisure behavior
	Jónsdóttir, Guðrún	Dubito ergo sum? Ni jenter møter naturfaglig kunnskap.
	Hove, Oddbjørn	Mental health disorders in adults with intellectual disabilities - Methods of assessment and prevalence of mental health disorders and problem behaviour
	Wageningen, Heidi Karin van	The role of glutamate on brain function

	Bjørkvik, Jofrid	God nok? Selvaktelse og interpersonlig fungering hos pasienter innen psykisk helsevern: Forholdet til diagnoser, symptomer og behandlingsutbytte
	Andersson, Martin	A study of attention control in children and elderly using a forced-attention dichotic listening paradigm
	Almås, Aslaug Grov	Teachers in the Digital Network Society: Visions and Realities. A study of teachers' experiences with the use of ICT in teaching and learning.
	Ulvik, Marit	Lærerutdanning som danning? Tre stemmer i diskusjonen
2010	Skår, Randi	Læringsprosesser i sykepleieres profesjonsutøvelse. En studie av sykepleieres læringserfaringer.
V	Roald, Knut	Kvalitetsvurdering som organisasjonslæring mellom skole og skoleeigar
	Lunde, Linn-Heidi	Chronic pain in older adults. Consequences, assessment and treatment.
	Danielsen, Anne Grete	Perceived psychosocial support, students' self-reported academic initiative and perceived life satisfaction
	Hysing, Mari	Mental health in children with chronic illness
	Olsen, Olav Kjellevod	Are good leaders moral leaders? The relationship between effective military operational leadership and morals
	Riese, Hanne	Friendship and learning. Entrepreneurship education through mini-enterprises.
	Holthe, Asle	Evaluating the implementation of the Norwegian guidelines for healthy school meals: A case study involving three secondary schools
H	Hauge, Lars Johan	Environmental antecedents of workplace bullying: A multi-design approach
	Bjørkelo, Brita	Whistleblowing at work: Antecedents and consequences
	Reme, Silje Endresen	Common Complaints – Common Cure? Psychiatric comorbidity and predictors of treatment outcome in low back pain and irritable bowel syndrome
	Helland, Wenche Andersen	Communication difficulties in children identified with psychiatric problems
	Beneventi, Harald	Neuronal correlates of working memory in dyslexia
	Thygesen, Elin	Subjective health and coping in care-dependent old persons living at home
	Aanes, Mette Marthinussen	Poor social relationships as a threat to belongingness needs. Interpersonal stress and subjective health complaints: Mediating and moderating factors.
	Anker, Morten Gustav	Client directed outcome informed couple therapy

	Bull, Torill	Combining employment and child care: The subjective well-being of single women in Scandinavia and in Southern Europe
	Viig, Nina Grieg	Tilrettelegging for læreres deltakelse i helsefremmende arbeid. En kvalitativ og kvantitativ analyse av sammenhengen mellom organisatoriske forhold og læreres deltakelse i utvikling og implementering av Europeisk Nettverk av Helsefremmende Skoler i Norge
	Wolff, Katharina	To know or not to know? Attitudes towards receiving genetic information among patients and the general public.
	Ogden, Terje, dr.philos.	Familiebasert behandling av alvorlige atferdsproblemer blant barn og ungdom. Evaluering og implementering av evidensbaserte behandlingsprogrammer i Norge.
	Solberg, Mona Elin	Self-reported bullying and victimisation at school: Prevalence, overlap and psychosocial adjustment.
2011	Bye, Hege Høivik	Self-presentation in job interviews. Individual and cultural differences in applicant self-presentation during job interviews and hiring managers' evaluation
V	Notelaers, Guy	Workplace bullying. A risk control perspective.
	Moltu, Christian	Being a therapist in difficult therapeutic impasses. A hermeneutic phenomenological analysis of skilled psychotherapists' experiences, needs, and strategies in difficult therapies ending well.
	Myrseth, Helga	Pathological Gambling - Treatment and Personality Factors
	Schanche, Elisabeth	From self-criticism to self-compassion. An empirical investigation of hypothesized change processes in the Affect Phobia Treatment Model of short-term dynamic psychotherapy for patients with Cluster C personality disorders.
	Våpenstad, Eystein Victor, dr.philos.	Det tempererte nærvær. En teoretisk undersøkelse av psykoterapeutens subjektivitet i psykoanalyse og psykoanalytisk psykoterapi.
	Haukebø, Kristin	Cognitive, behavioral and neural correlates of dental and intra-oral injection phobia. Results from one treatment and one fMRI study of randomized, controlled design.
	Harris, Anette	Adaptation and health in extreme and isolated environments. From 78°N to 75°S.
	Bjørknes, Ragnhild	Parent Management Training-Oregon Model: intervention effects on maternal practice and child behavior in ethnic minority families
	Mamen, Asgeir	Aspects of using physical training in patients with substance dependence and additional mental distress
	Espevik, Roar	Expert teams: Do shared mental models of team members make a difference
	Haara, Frode Olav	Unveiling teachers' reasons for choosing practical activities in mathematics teaching

2011 H	Hauge, Hans Abraham	How can employee empowerment be made conducive to both employee health and organisation performance? An empirical investigation of a tailor-made approach to organisation learning in a municipal public service organisation.
	Melkevik, Ole Rogstad	Screen-based sedentary behaviours: pastimes for the poor, inactive and overweight? A cross-national survey of children and adolescents in 39 countries.
	Vøllestad, Jon	Mindfulness-based treatment for anxiety disorders. A quantitative review of the evidence, results from a randomized controlled trial, and a qualitative exploration of patient experiences.
	Tolo, Astrid	Hvordan blir lærerkompetanse konstruert? En kvalitativ studie av PPU-studenters kunnskapsutvikling.
	Saus, Evelyn-Rose	Training effectiveness: Situation awareness training in simulators
	Nordgreen, Tine	Internet-based self-help for social anxiety disorder and panic disorder. Factors associated with effect and use of self-help.
	Munkvold, Linda Helen	Oppositional Defiant Disorder: Informant discrepancies, gender differences, co-occurring mental health problems and neurocognitive function.
	Christiansen, Øivin	Når barn plasseres utenfor hjemmet: beslutninger, forløp og relasjoner. Under barnevernets (ved)tak.
	Brunborg, Geir Scott	Conditionability and Reinforcement Sensitivity in Gambling Behaviour
2012 V	Hystad, Sigurd William	Measuring Psychological Resiliency: Validation of an Adapted Norwegian Hardiness Scale
	Roness, Dag	Hvorfor bli lærer? Motivasjon for utdanning og utøving.
	Fjermestad, Krister Westlye	The therapeutic alliance in cognitive behavioural therapy for youth anxiety disorders
	Jenssen, Eirik Sørnes	Tilpasset opplæring i norsk skole: politikeres, skolelederes og læreres handlingsvalg
	Saksvik-Lehouillier, Ingvild	Shift work tolerance and adaptation to shift work among offshore workers and nurses
	Johansen, Venke Frederike	Når det intime blir offentlig. Om kvinners åpenhet om brystkreft og om markedsføring av brystkreftsaken.
	Herheim, Rune	Pupils collaborating in pairs at a computer in mathematics learning: investigating verbal communication patterns and qualities
Vie, Tina Løkke	Cognitive appraisal, emotions and subjective health complaints among victims of workplace bullying: A stress-theoretical approach	

	Jones, Lise Øen	Effects of reading skills, spelling skills and accompanying efficacy beliefs on participation in education. A study in Norwegian prisons.
2012	Danielsen, Yngvild Sørebo	Childhood obesity – characteristics and treatment. Psychological perspectives.
H	Horverak, Jøri Gytte	Sense or sensibility in hiring processes. Interviewee and interviewer characteristics as antecedents of immigrant applicants' employment probabilities. An experimental approach.
	Jøsendal, Ola	Development and evaluation of BE smokeFREE, a school-based smoking prevention program
	Osnes, Berge	Temporal and Posterior Frontal Involvement in Auditory Speech Perception
	Drageset, Sigrunn	Psychological distress, coping and social support in the diagnostic and preoperative phase of breast cancer
	Aasland, Merethe Schanke	Destructive leadership: Conceptualization, measurement, prevalence and outcomes
	Bakibinga, Pauline	The experience of job engagement and self-care among Ugandan nurses and midwives
	Skogen, Jens Christoffer	Foetal and early origins of old age health. Linkage between birth records and the old age cohort of the Hordaland Health Study (HUSK)
	Leversen, Ingrid	Adolescents' leisure activity participation and their life satisfaction: The role of demographic characteristics and psychological processes
	Hanss, Daniel	Explaining sustainable consumption: Findings from cross-sectional and intervention approaches
	Rød, Per Arne	Barn i klem mellom foreldrekonflikter og samfunnsmessig beskyttelse
2013	Mentzoni, Rune Aune	Structural Characteristics in Gambling
V	Knudsen, Ann Kristin	Long-term sickness absence and disability pension award as consequences of common mental disorders. Epidemiological studies using a population-based health survey and official ill health benefit registries.
	Strand, Mari	Emotional information processing in recurrent MDD
	Veseth, Marius	Recovery in bipolar disorder. A reflexive-collaborative exploration of the lived experiences of healing and growth when battling a severe mental illness
	Mæland, Silje	Sick leave for patients with severe subjective health complaints. Challenges in general practice.
	Mjaaland, Thera	At the frontiers of change? Women and girls' pursuit of education in north-western Tigray, Ethiopia
	Odéen, Magnus	Coping at work. The role of knowledge and coping expectancies in health and sick leave.

	Hynninen, Kia Minna Johanna	Anxiety, depression and sleep disturbance in chronic obstructive pulmonary disease (COPD). Associations, prevalence and effect of psychological treatment.
	Flo, Elisabeth	Sleep and health in shift working nurses
	Aasen, Elin Margrethe	From paternalism to patient participation? The older patients undergoing hemodialysis, their next of kin and the nurses: a discursive perspective on perception of patient participation in dialysis units
	Ekornås, Belinda	Emotional and Behavioural Problems in Children: Self-perception, peer relationships, and motor abilities
	Corbin, J. Hope	North-South Partnerships for Health: Key Factors for Partnership Success from the Perspective of the KIWAKKUKI
	Birkeland, Marianne Skogbrott	Development of global self-esteem: The transition from adolescence to adulthood
2013	Gianella-Malca, Camila	Challenges in Implementing the Colombian Constitutional Court's Health-Care System Ruling of 2008
H	Hovland, Anders	Panic disorder – Treatment outcomes and psychophysiological concomitants
	Mortensen, Øystein	The transition to parenthood – Couple relationships put to the test
	Årdal, Guro	Major Depressive Disorder – a Ten Year Follow-up Study. Inhibition, Information Processing and Health Related Quality of Life
	Johansen, Rino Bandlitz	The impact of military identity on performance in the Norwegian armed forces
	Bøe, Tormod	Socioeconomic Status and Mental Health in Children and Adolescents
2014	Nordmo, Ivar	Gjennom nåløyet – studenters læringserfaringer i psykologutdanningen
V	Dovran, Anders	Childhood Trauma and Mental Health Problems in Adult Life
	Hegelstad, Wenche ten Velden	Early Detection and Intervention in Psychosis: A Long-Term Perspective
	Urheim, Ragnar	Forståelse av pasientaggresjon og forklaringer på nedgang i voldsrate ved Regional sikkerhetsavdeling, Sandviken sykehus
	Kinn, Liv Grethe	Round-Trips to Work. Qualitative studies of how persons with severe mental illness experience work integration.
	Rød, Anne Marie Kinn	Consequences of social defeat stress for behaviour and sleep. Short-term and long-term assessments in rats.
	Nygård, Merethe	Schizophrenia – Cognitive Function, Brain Abnormalities, and Cannabis Use

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Tjora, Tore	Smoking from adolescence through adulthood: the role of family, friends, depression and socioeconomic status. Predictors of smoking from age 13 to 30 in the "The Norwegian Longitudinal Health Behaviour Study" (NLHB)
Vangsnes, Vigdis	The Dramaturgy and Didactics of Computer Gaming. A Study of a Medium in the Educational Context of Kindergartens.
Nordahl, Kristin Berg	Early Father-Child Interaction in a Father-Friendly Context: Gender Differences, Child Outcomes, and Protective Factors related to Fathers' Parenting Behaviors with One-year-olds
Sandvik, Asle Makoto	Psychopathy – the heterogeneity of the construct
Skotheim, Siv	Maternal emotional distress and early mother-infant interaction: Psychological, social and nutritional contributions
Halleland, Helene Barone	Executive Functioning in adult Attention Deficit Hyperactivity Disorder (ADHD). From basic mechanisms to functional outcome.
Halvorsen, Kirsti Vindal	Partnerskap i lærerutdanning, sett fra et økologisk perspektiv
Solbue, Vibeke	Dialogen som visker ut kategorier. En studie av hvilke erfaringer innvandrerdømmen og norsksfødte med innvandrereforeldre har med videregående skole. Hva forteller ungdommenes erfaringer om videregående skoles håndtering av etniske ulikheter?
Kvalevaag, Anne Lise	Fathers' mental health and child development. The predictive value of fathers' psychological distress during pregnancy for the social, emotional and behavioural development of their children
Sandal, Ann Karin	Ungdom og utdanningsval. Om elevar sine opplevingar av val og overgangsprosessar.
Haug, Thomas	Predictors and moderators of treatment outcome from high- and low-intensity cognitive behavioral therapy for anxiety disorders. Association between patient and process factors, and the outcome from guided self-help, stepped care, and face-to-face cognitive behavioral therapy.
Sjølie, Hege	Experiences of Members of a Crisis Resolution Home Treatment Team. Personal history, professional role and emotional support in a CRHT team.
Falkenberg, Liv Eggset	Neuronal underpinnings of healthy and dysfunctional cognitive control
Mrdalj, Jelena	The early life condition. Importance for sleep, circadian rhythmicity, behaviour and response to later life challenges
Hesjedal, Elisabeth	Tverrprofesjonelt samarbeid mellom skule og barnevern: Kva kan støtte utsette barn og unge?

2015 V	Hauken, May Aasebø	« <i>The cancer treatment was only half the work!</i> » A Mixed-Method Study of Rehabilitation among Young Adult Cancer Survivors
	Ryland, Hilde Katrin	Social functioning and mental health in children: the influence of chronic illness and intellectual function
	Rønsen, Anne Kristin	Vurdering som profesjonskompetanse. Refleksjonsbasert utvikling av læreres kompetanse i formativ vurdering
	Hoff, Helge Andreas	Thinking about Symptoms of Psychopathy in Norway: Content Validation of the Comprehensive Assessment of Psychopathic Personality (CAPP) Model in a Norwegian Setting
	Schmid, Marit Therese	Executive Functioning in recurrent- and first episode Major Depressive Disorder. Longitudinal studies
	Sand, Liv	Body Image Distortion and Eating Disturbances in Children and Adolescents
	Matanda, Dennis Juma	Child physical growth and care practices in Kenya: Evidence from Demographic and Health Surveys
	Amugsi, Dickson Abanimi	Child care practices, resources for care, and nutritional outcomes in Ghana: Findings from Demographic and Health Surveys
	Jakobsen, Hilde	The good beating: Social norms supporting men's partner violence in Tanzania
	Sagoë, Dominic	Nonmedical anabolic-androgenic steroid use: Prevalence, attitudes, and social perception
	Eide, Helene Marie Kjærgård	Narrating the relationship between leadership and learning outcomes. A study of public narratives in the Norwegian educational sector.
2015 H	Wubs, Annegreet Gera	Intimate partner violence among adolescents in South Africa and Tanzania
	Hjelmervik, Helene Susanne	Sex and sex-hormonal effects on brain organization of fronto-parietal networks
	Dahl, Berit Misund	The meaning of professional identity in public health nursing
	Røykenes, Kari	Testangst hos sykepleierstudenter: «Alternativ behandling»
	Bless, Josef Johann	The smartphone as a research tool in psychology. Assessment of language lateralization and training of auditory attention.
	Løvvik, Camilla Margrethe Sigvaldsen	Common mental disorders and work participation – the role of return-to-work expectations
	Lehmann, Stine	Mental Disorders in Foster Children: A Study of Prevalence, Comorbidity, and Risk Factors
	Knapstad, Marit	Psychological factors in long-term sickness absence: the role of shame and social support. Epidemiological studies based on the Health Assets Project.

2016 V	Kvestad, Ingrid	Biological risks and neurodevelopment in young North Indian children
	Sælør, Knut Tore	Hinderløyper, halmstrå og hengende snører. En kvalitativ studie av håp innenfor psykisk helse- og rusfeltet.
	Mellingen, Sonja	Alkoholbruk, partilfredshet og samlivsstatus. Før, inn i, og etter svangerskapet – korrelerer eller konsekvenser?
	Thun, Eirunn	Shift work: negative consequences and protective factors
	Hilt, Line Torbjørnsen	The borderlands of educational inclusion. Analyses of inclusion and exclusion processes for minority language students
	Havnen, Audun	Treatment of obsessive-compulsive disorder and the importance of assessing clinical effectiveness
	Slåtten, Hilde	Gay-related name-calling among young adolescents. Exploring the importance of the context.
	Ree, Eline	Staying at work. The role of expectancies and beliefs in health and workplace interventions.
	Morken, Frøydis	Reading and writing processing in dyslexia
2016 H	Løvoll, Helga Synnevåg	Inside the outdoor experience. On the distinction between pleasant and interesting feelings and their implication in the motivational process.
	Hjeltnes, Aslak	Facing social fears: An investigation of mindfulness-based stress reduction for young adults with social anxiety disorder
	Øyeflaten, Irene Larsen	Long-term sick leave and work rehabilitation. Prognostic factors for return to work.
	Henriksen, Roger Ekeberg	Social relationships, stress and infection risk in mother and child
	Johnsen, Iren	«Only a friend» - The bereavement process of young adults who have lost a friend to a traumatic death. A mixed methods study.
	Helle, Siri	Cannabis use in non-affective psychoses: Relationship to age at onset, cognitive functioning and social cognition
	Glabek, Mats	Workplace bullying and expulsion in working life. A representative study addressing prospective associations and explanatory conditions.
	Oanes, Camilla Jensen	Tilbakemelding i terapi. På hvilke måter opplever terapeuter at tilbakemeldingsprosedyrer kan virke inn på terapeutiske praksiser?
	Reknes, Iselin	Exposure to workplace bullying among nurses: Health outcomes and individual coping
	Chimhutu, Victor	Results-Based Financing (RBF) in the health sector of a low-income country. From agenda setting to implementation: The case of Tanzania

	Ness, Ingunn Johanne	The Room of Opportunity. Understanding how knowledge and ideas are constructed in multidisciplinary groups working with developing innovative ideas.
	Hollekim, Ragnhild	Contemporary discourses on children and parenting in Norway. An empirical study based on two cases.
	Doran, Rouven	Eco-friendly travelling: The relevance of perceived norms and social comparison
2017	Katisi, Masego	The power of context in health partnerships: Exploring synergy and antagonism between external and internal ideologies in implementing Safe Male Circumcision (SMC) for HIV prevention in Botswana
V	Jamaludin, Nor Lelawati Binti	The “why” and “how” of International Students’ Ambassadorship Roles in International Education
	Berthelsen, Mona	Effects of shift work and psychological and social work factors on mental distress. Studies of onshore/offshore workers and nurses in Norway.
	Krane, Vibeke	Lærer-elev-relasjoner, elevers psykiske helse og frafall i videregående skole – en eksplorerende studie om samarbeid og den store betydningen av de små ting
	Søvik, Margaret Ljosnes	Evaluating the implementation of the Empowering Coaching™ program in Norway
	Tonheim, Milfrid	A troublesome transition: Social reintegration of girl soldiers returning ‘home’
	Senneseth, Mette	Improving social network support for partners facing spousal cancer while caring for minors. A randomized controlled trial.
	Urke, Helga Bjørnøy	Child health and child care of very young children in Bolivia, Colombia and Peru.
	Bakhturidze, George	Public Participation in Tobacco Control Policy-making in Georgia
	Fismen, Anne-Siri	Adolescent eating habits. Trends and socio-economic status.
2017	Hagatun, Susanne	Internet-based cognitive-behavioural therapy for insomnia. A randomised controlled trial in Norway.
H	Eichele, Heike	Electrophysiological Correlates of Performance Monitoring in Children with Tourette Syndrome. A developmental perspective.
	Risan, Ulf Patrick	Accommodating trauma in police interviews. An exploration of rapport in investigative interviews of traumatized victims.
	Sandhåland, Hilde	Safety on board offshore vessels: A study of shipboard factors and situation awareness
	Blågestad, Tone Fidje	Less pain – better sleep and mood? Interrelatedness of pain, sleep and mood in total hip arthroplasty patients
	Kronstad, Morten	Frå skulebenk til deadlines. Korleis nettjournalistar og journaliststudentar lærer, og korleis dei utviklar journalistfagleg kunnskap

	Vedaa, Øystein	Shift work: The importance of sufficient time for rest between shifts.
	Steine, Iris Mulders	Predictors of symptoms outcomes among adult survivors of sexual abuse: The role of abuse characteristics, cumulative childhood maltreatment, genetic variants, and perceived social support.
	Høgheim, Sigve	Making math interesting: An experimental study of interventions to encourage interest in mathematics
2018	Brevik, Erlend Joramo	Adult Attention Deficit Hyperactivity Disorder. Beyond the Core Symptoms of the Diagnostic and Statistical Manual of Mental Disorders.
V	Erevik, Eilin Kristine	User-generated alcohol-related content on social media: Determinants and relation to offline alcohol use
	Hagen, Egon	Cognitive and psychological functioning in patients with substance use disorder; from initial assessment to one-year recovery
	Adólfssdóttir, Steinunn	Subcomponents of executive functions: Effects of age and brain maturations
	Brattabø, Ingfrid Vaksdal	Detection of child maltreatment, the role of dental health personnel – A national cross-sectional study among public dental health personnel in Norway
	Fylkesnes, Marte Knag	Frykt, forhandlinger og deltakelse. Ungdommer og foreldre med etnisk minoritetsbakgrunn i møte med den norske barnevernstjenesten.
	Stiegler, Jan Reidar	Processing emotions in emotion-focused therapy. Exploring the impact of the two-chair dialogue intervention.
	Egelandsdal, Kjetil	Clickers and Formative Feedback at University Lectures. Exploring students and teachers' reception and use of feedback from clicker interventions.
	Torjussen, Lars Petter Storm	Foreningen av visdom og veltalenhet – utkast til en universitetsdidaktikk gjennom en kritikk og videreføring av Skjervheims pedagogiske filosofi på bakgrunn av Arendt og Foucault. <i>Eller hvorfor menneskelivet er mer som å spille fløyte enn å bygge et hus.</i>
	Selvik, Sabreen	A childhood at refuges. Children with multiple relocations at refuges for abused women.
2018	Leino, Tony Mathias	Structural game characteristics, game features, financial outcomes and gambling behaviour
H	Raknes, Solfrid	Anxious Adolescents: Prevalence, Correlates, and Preventive Cognitive Behavioural Interventions
	Morken, Katharina Teresa Enehaug	Mentalization-based treatment of female patients with severe personality disorder and substance use disorder

	Braatveit, Kirsten Johanne	Intellectual disability among in-patients with substance use disorders
	Barua, Padmaja	Unequal Interdependencies: Exploring Power and Agency in Domestic Work Relations in Contemporary India
	Darkwah, Ernest	Caring for “parentless” children. An exploration of work-related experiences of caregivers in children’s homes in Ghana.
	Valdersnes, Kjersti Bergheim	Safety Climate perceptions in High Reliability Organizations – the role of Psychological Capital
2019 V	Kongsgården, Petter	Vurderingspraksiser i teknologirike læringsmiljøer. En undersøkelse av læreres vurderingspraksiser i teknologirike læringsmiljøer og implikasjoner på elevenes medvirkning i egen læringsprosess.
	Vikene, Kjetil	Complexity in Rhythm and Parkinson’s disease: Cognitive and Neuronal Correlates
	Heradstveit, Ove	Alcohol- and drug use among adolescents. School-related problems, childhood mental health problems, and psychiatric diagnoses.
	Riise, Eili Nygard	Concentrated exposure and response prevention for obsessive-compulsive disorder in adolescents: the Bergen 4-day treatment
	Vik, Alexandra	Imaging the Aging Brain: From Morphometry to Functional Connectivity
	Krossbakken, Elfrid	Personal and Contextual Factors Influencing Gaming Behaviour. Risk Factors and Prevention of Video Game Addiction.
	Solholm, Roar	Foreldrenes status og rolle i familie- og nærmiljøbaserte intervensjoner for barn med atferdsvansker
	Baldomir, Andrea Margarita	Children at Risk and Mothering Networks in Buenos Aires, Argentina: Analyses of Socialization and Law-Abiding Practices in Public Early Childhood Intervention.
	Samuelsson, Martin Per	Education for Deliberative Democracy. Theoretical assumptions and classroom practices.
	Visted, Endre	Emotion regulation difficulties. The role in onset, maintenance and recurrence of major depressive disorder.
2019 H	Nordmo, Morten	Sleep and naval performance. The impact of personality and leadership.
	Sveinsdottir, Vigdis	Supported Employment and preventing Early Disability (SEED)
	Dwyer, Gerard Eric	New approaches to the use of magnetic resonance spectroscopy for investigating the pathophysiology of auditory-verbal hallucinations
	Synnevåg, Ellen Strøm	Planning for Public Health. Balancing top-down and bottom-up approaches in Norwegian municipalities.

	Kvinge, Øystein Røsseland	Presentation in teacher education. A study of student teachers' transformation and representation of subject content using semiotic technology.
	Thorsen, Anders Lillevik	The emotional brain in obsessive-compulsive disorder
	Eldal, Kari	Sikkerhetsnettet som tek imot om eg fell – men som også kan fange meg. Korleis erfarer menneske med psykiske lidingar ei innlegging i psykisk helsevern? Eit samarbeidsbasert forskingsprosjekt mellom forskarar og brukarar.
	Svendsen, Julie Lillebostad	Self-compassion - Relationship with mindfulness, emotional stress symptoms and psychophysiological flexibility
2020 V	Albæk, Ane Ugland	Walking children through a minefield. Qualitative studies of professionals' experiences addressing abuse in child interviews.
	Ludvigsen, Kristine	Creating Spaces for Formative Feedback in Lectures. Understanding how use of educational technology can support formative assessment in lectures in higher education.
	Hansen, Hege	Tidlig intervensjon og recoveryprosesser ved førsteepisode psykose. En kvalitativ utforsking av ulike perspektiver.
	Nilsen, Sondre Aasen	After the Divorce: Academic Achievement, Mental Health, and Health Complaints in Adolescence. Heterogeneous associations by parental education, family structure, and siblings.
	Hovland, Runar Tengel	Kliniske tilbakemeldingssystemer i psykisk helsevern – implementering og praktisering
	Sæverot, Ane Malene	Bilde og pedagogikk. En empirisk undersøkelse av ungdoms fortellinger om bilder.
	Carlsen, Siv-Elin Leirvåg	Opioid maintenance treatment and social aspects of quality of life for first-time enrolled patients. A quantitative study.
	Haugen, Lill Susann Ynnesdal	Meeting places in Norwegian community mental health care: A participatory and community psychological inquiry
2020 H	Markova, Valeria	How do immigrants in Norway interpret, view, and prefer to cope with symptoms of depression? A mixed method study
	Anda-Ågotnes, Liss Gøril	Cognitive change in psychosis
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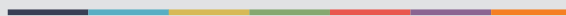
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