BEHAVIORAL AND CORTICAL EVIDENCE OF IMPLICIT STATISTICAL LEARNING OF TEMPORAL VISUAL REGULARITIES

Szabolcs Sáringer MD

PhD Thesis

Szeged,

2024

University of Szeged
Albert Szent-Györgyi Medical School
Doctoral School of Theoretical Medicine

Behavioral and cortical evidence of implicit statistical learning of temporal visual regularities

PhD Thesis

Szabolcs Sáringer MD
Department of Physiology, Albert Szent-Györgyi Medical School, University of Szeged

Supervisor:
Péter Kaposvári MSc, PhD
Department of Physiology, Albert Szent-Györgyi Medical School, University of Szeged

Szeged,
2024

Table of Contents

List of publications related to the thesis

Sáringer, Szabolcs, Ágnes Fehér, Gyula Sáry, and Péter Kaposvári
"Online measurement of learning temporal statistical structure in categorization tasks"
Memory & Cognition 50, no. 7 (2022): 1530-1545.
IF: 2.4, SJR indicator (Experimental and Cognitive Psychology): Q1

Sáringer, Szabolcs, Ágnes Fehér, Gyula Sáry, and Péter Kaposvári.
"Gamma oscillations in visual statistical learning correlate with individual behavioral differences"
Frontiers in Behavioral Neuroscience 17 (2023)
IF: 3.0, SJR indicator (Neuropsychology and Physiological Psychology): Q1

Cumulative IF: 5.4

Other publications

Sáringer, Szabolcs, Péter Kaposvári, and András Benyhe
"Visual linguistic statistical learning is traceable through neural entrainment."
Psychophysiology (2024): e14575.
IF: 3.7, SJR indicator (Cognitive Neuroscience): Q1

Sáringer, Szabolcs, Ágnes Fehér, Gyula Sáry, and Péter Kaposvári
"Perceptual Expectations Are Reflected by Early Alpha Power Reduction."
Journal of Cognitive Neuroscience (2024): 1-15.
IF: 3.2, SJR indicator (Cognitive Neuroscience): Q1

Cumulative IF: 12.3

Other abstract

A process running in the background: EEG correlates of implicit, visual statistical learning - **Szabolcs Sáringer**, András Benyhe, Ágnes Fehér, Péter Kaposvári (CuttingEEG 2021)

Beta activity during implicit, visual statistical learning - **Szabolcs Sáringer**, Ágnes Fehér, Péter Kaposvári (IBRO 2022)

Alpha activity change during implicit visual statistical learning - **Szabolcs Sáringer**, András Benyhe, Ágnes Fehér, Péter Kaposvári (FENS 2022)

The role of gamma activity in affinity to statistical learning - **Szabolcs Sáringer**, Ágnes Fehér, Péter Kaposvári (TEX 2022)

Late gamma activity influencing the information recollection in visual statistical learning - **Szabolcs Sáringer**, Ágnes Fehér, Péter Kaposvári (MIT-ANA 2023)

Tracing statistical learning with frequency tagging in a visual linguistic paradigm - András Benyhe, **Szabolcs Sáringer**, Ágnes Fehér, Péter Kaposvári (MIT-ANA 2023)

Time-frequency correlates of personal face familiarization - **Szabolcs Sáringer**, Ágnes Fehér, Péter Kaposvári, Géza Ambrus, Gyula Kovács (MIT-ANA 2023)

Recollection of acquired probabilities correlates with late gamma activity - **Szabolcs Sáringer**, Ágnes Fehér, Péter Kaposvári (IBRO 2023)

Expected stimuli modulate early, low-frequency cortical activity - **Szabolcs Sáringer**, Ágnes Fehér, Péter Kaposvári (INC 2024)

List of abbreviations

2AFC, two-alternative forced choice
DF, degree of freedom
EEG, electroencephalography
EMM, estimated marginal mean
EOG, electrooculogram
ERP, event-related potential
fMRI, functional magnetic resonance imaging
IQR, interquartile range
ITPC, intertrial phase coherence
MEG, magnetoencephalography
PFC, prefrontal cortex
RT, reaction time
SD, standard deviation
SEM, standard error of mean
SL, statistical learning
SRT, serial reaction time
TF, time-frequency
VSL, visual statistical learning

Introduction

Our nervous system collects a plethora of information from the environment surrounding us. The processing of this information amount directly would overload the system and the formation of meaningful perception would be impossible. The sensory system employs several methods to reduce the load on itself, e.g. sensory filtering, during which the brain extracts relevant signals, while simultaneously suppressing noise (Nakajima et al., 2019). It can also segment the continuous information flow into meaningful chunks (F. Zhou et al., 2007). One foundation of the segmentation process can be based on the statistical relationship between stimuli since this information flow is not random. Spatial and/or temporal co-occurrences of certain stimuli can create environmental regularities, which can be discovered, acquired, and later used by the sensory system. This course can also create an internal representation of the environment which has many beneficial traits for information processing (Frost et al., 2019; Pelucchi et al., 2009). It can reduce the sensory load by not processing redundant information again and again (Rao & Ballard, 1999) and it can also facilitate the sensory process since stimuli can become predictable and the cortical areas can anticipate the appearance of a stimulus (Denham & Winkler, 2020). The consolidation of these above-mentioned neural mechanisms, the discovery, acquisition, and usage of environmental statistical information is called statistical learning.

Statistcal learning (SL) has been a widely examined phenomenon for decades and there is a general agreement that it is a fundamental part of sensory processing and perception. Many studies have found behavioral and neural evidence which resulted in hypotheses regarding the background of SL, yet there is still a considerable gap in the SL literature to build a unifying theory.

The generality of statistical learning

Before the term was coined, the phenomenon we now know as SL was originally called ‘Artificial Grammar Learning’ and later ‘Implicit learning’ (A. S. Reber, 1967, 1993). The term ‘statistical learning’ was first used to describe the language acquisition of infants (Saffran et al., 1996). Since then, its definition has expanded to linguistic (Batterink & Paller, 2017; Pinto et al., 2022) and non-linguistic (Henin et al., 2021) paradigms and has been observed in several modalities. It has extensive literature in auditory (Saffran et al., 1999) and visual paradigms (Fiser & Aslin, 2002; Kaposvari et al., 2018), but it was also examined in tactile (Conway & Christiansen, 2005) and multimodal studies (Seitz et al., 2007). The statistical relationship between stimuli has two main domains: spatial or temporal. Spatial connection refers to the case, when stimuli appear simultaneously and the location of different stimuli provides the statistical information (Fiser & Aslin, 2001), while temporal relationship defines the order of the stimuli that appear in a sequence (Fiser & Aslin, 2002). In the case of temporal regularities, we can describe this relationship with the transitional probabilities between the stimuli. The transitional probability describes the chance that a certain stimulus is followed by another. For example, if a visual sequence contains associated stimulus pairs that always follow each other in a fixed order, the transitional probability between the two will be 1.

Since its initial description, SL has been at the focus of cognitive research and an increasing number of features have been reported. SL is incidental, meaning the nervous system extracts these regularities without any external instruction or without being aware of their presence (Arciuli et al., 2014; Aslin, 2017). It is also a form of implicit learning; thus, the learning and the learned regularities do not necessarily become conscious knowledge and this information cannot be recalled voluntarily (Christiansen, 2019; Perruchet & Pacton, 2006). A growing number of papers also suggest that SL is a fundamental cognitive process, influencing several other cortical mechanisms. This fundamentality is supported by the facts that SL has been observed across stimulus and task complexity (Perfors & Kidd, 2022), across different age groups (Bertels et al., 2015; Nemeth et al., 2013; Zwart et al., 2019) and even across different species, like primates (Hauser et al., 2001; Kaposvari et al., 2018), dogs (Boros et al., 2021) or rats (Toro & Trobalón, 2005). It also shows a close, intertwined relationship with other cognitive functions. Although it is not crucial (Duncan & Theeuwes, 2020), attention impacts the progress of SL (Turk-Browne et al., 2005). It has been reported that environmental regularities in the focus of attention are acquired more efficiently (Musz et al., 2015). Besides, SL can also shift attention creating a ‘pop-out’ effect. SL can reallocate the cortical resources of attention, distributing neural assets towards the processing of new, unrecognized stimuli that violate the previously learned regularities (Kristjánsson et al., 2007). Apart from attention, the connection between SL and working memory has been reported too. It has been suggested that working memory capacity plays a role in implicit SL (Cashdollar et al., 2017). Despite this suggestion, reports on the topic provide mixed results (Janacsek & Nemeth, 2013), since many has reported null findings (Kaufman et al., 2010).

The elemtariness and its connection to several cognitive function gives SL a broad definition, but not all forms of SL can be combined directly. An ongoing discussion regarding SL is whether it is domain-general or modality specific (Frost et al., 2015). Domain-generality implies that all statistical information is computed in one center regardless of stimulus modality.

This hypothesis is supported by both behavioral and neural evidence. Behavioral evidence includes observation of a link between SL scores and other cognitive functions in different modalities (Bogaerts et al., 2022). This would suggest a general SL ability that would bring together other cognitive functions and unite them under one umbrella term. One possible candidate for the domain-general center is the hippocampus (Turk-Browne et al., 2010). Considering its role in mnemonic functions (Burgess et al., 2002) and its rich connections the cortex (Lavenex & Amaral, 2000), it is a very plausible option, that it computes statistical properties of stimuli relationships across the modalities. Other structures that could function as a domain-general SL center could be the basal ganglia (Karuza et al., 2013) or the inferior frontal lobe (Fedorenko et al., 2012; McNealy et al., 2006). These regions have been associated with SL, and their involvement in different studies are not necessarily contradictive since as mentioned before, SL involves several cognitive functions, thus all could play a part in the complex processing what we call SL (Sherman et al., 2020). The other possibility is that every modality-specific cortical area is sensitive to statistical information and is able to compute these interstimulus relationships. The evidence for that is that we can observe different affinities towards co-occurrences in different modalities. One notable phenomenon regarding modality-specificity is the different developmental trajectories in different modalities. SL in the visual domain appeared to improve with age, while auditory SL abilities did not show change with age (Raviv & Arnon, 2018). Besides, auditory and visual SL scores do not show correlations indicating distinct backgrounds (Siegelman & Frost, 2015). Changes in the modality specific cortices have been observed regarding stimulus expectancy, as well. An fMRI study found that an expected stimulus elicits neural responses with lower amplitude in the primary visual cortex while simultaneously increasing stimulus representation in the same area (Kok et al., 2012). It has also been reported that sensory expectations can result in smaller wave amplitudes in both ERPs and frequency bands, like the gamma, or the alpha band (Todorovic et al., 2011; Y. J. Zhou et al., 2020). However, these observations do not invalidate the domain-general theory as we currently have limited information about the source of these modulatory effects on the sensory areas.

Regardless of the domain-general vs. modality specific debate, the mentioned behavioral and neural evidence implies that results in different SL modalities are not interchangeable. Separate investigation of these phenomena is necessary to fully explore this cognitive function. Not only the modality, but the supervision of the paradigm affects the learning outcome. As mentioned before, SL can emerge in unsupervised paradigms that is without any explicit instructions about the statistical information. In these case participants of the experiment are usually instructed, for example, to attend a stimulus sequence and unbeknownst to them, certain stimuli have higher than chance statistical relationship with each other. This way the acquired information remains implicit knowledge and many times participants are not able to recall the regularity despite other behavior or neural evidence of regularity acquisition. Yet many studies implement a quasi-supervised manner, where participants are told about a hidden regularity, but the exact parameters remain untold. This leads to the participants actively searching for statistical relationships which can result in explicit knowledge. The underlying mechanisms also show differences when participants are explicitly instructed to look for regularities rather than being exposed passively to stimulus sequences. This phenomenon is evidenced by RT difference between an explicit and implicit group in a SL paradigm along with the electrophysiological changes in the amplitude of the P300 component of the participants' ERP (Batterink, Reber, Neville, et al., 2015; Batterink, Reber, & Paller, 2015). Taking these reports into consideration we can conclude that not all SL findings can be grouped together without restraints and in many cases, we must treat these results as individual entities based on their modalities, supervision, and other parameters of the paradigm.

Neural background of SL

The neural background of SL is a widely studied topic in neuroimaging. Many cortical and subcortical structures have been identified regarding SL. Several hypotheses have emerged about the background networks, but we have yet to find a definitive answer to the question.

Talking about the cortical structures calls for their categorization. SL paradigms have demonstrated the involvement of both modality-specific and non-specific areas. For example, statistical regularities in a speech stream resulted in the activation of higher-level auditory cortices, like the left superior temporal gyrus and the left inferior frontal gyrus (Cunillera et al., 2009; Karuza et al., 2013). Visual stimuli elicited similar results with the activation of the lateral occipital cortex (Turk-Browne et al., 2009) and the V1 region (Kok et al., 2012). These observations led to the conclusion that statistical information is computed in their respective, modality-specific sensory areas (Frost et al., 2015). This idea was also supported by the observation that while low-level sensory areas can retain information for milliseconds, higher levels can do the same for seconds, or even minutes (Farbood et al., 2015; Kiebel et al., 2008). The fact that sensory areas can store information for prolonged times makes the integration of temporal regularities within the cortex possible.

On the other hand, statistical patterns seem to activate other cortical structures, not only their respective sensory areas. The left inferior frontal gyrus was activated by not only speech patterns (Karuza et al., 2013), but by non-linguistic tone sequences (Abla et al., 2008) and visual stimuli, as well (Turk-Browne et al., 2009). Other domain-general areas showed affinity toward statistical information, like the prefrontal cortex or the parietal cortex (Forkstam et al., 2006). The engagement of the PFC is hardly surprising, considering its role in the working memory system or selective attention which are closely connected to SL (Funahashi, 2017; Knight et al., 1995). The observed activation of both modality-specific and domain-general cortical areas proposed the frontoparietal or rostro caudal network hypothesis (Conway, 2020). It describes the functional connectivity between the frontal areas, like the PFC and the sensory areas. The PFC is responsible for the executive functions with its contribution to the working memory, behavior, and planning while the posterior areas are responsible for the perceptual computing. Neuroimaging has shown the simultaneous activation of the PFC and sensory areas, like the inferotemporal area in case of visual memories, the superior temporal gyrus with auditory or the posterior parietal cortex with spatial relationship (Fuster & Bressler, 2012). Another theory integrates the role of domain-general areas and modality-specific cortices. Domain-general parts are responsible for global processing on a larger scale or in case of non-adjacent regularities, while the importance of sensory regions lies in local computation on a smaller scale (Uhrig et al., 2014).

Despite these theories the relationship between the PFC and sensory areas is still ambiguous. Many studies reported a rather antagonistic relationship between the explicit attention network, involving the PFC and the automatic, implicit learning networks. The functional connectivity in the anterior areas showed a negative correlation with the outcomes of an implicit learning paradigm (Tóth et al., 2017). Additionally, the inhibition of the dorsolateral PFC improved the learning outcome in SL (Ambrus et al., 2020). This study led to the hypothesis that model-free and model-based learning, which means generating new representation based on environmental information or making predictions based on the already existing internal representation are competitive in nature.

As we can see, SL utilizes an extensive cortical network which is expected considering the scales that SL works along, like modality and timeframes. But subcortical structures seem to be involved in SL alongside the cortex, e.g. the hippocampus, the cerebellum, or the basal ganglia. Cerebellum has been associated with motor learning (Steinmetz et al., 2000) besides other learning types, like associative learning (Timmann et al., 2010). The role of subcortical sites in the different memory networks is well-known. The hippocampus and the medial temporal lobe have a function in declarative memory (Squire 2004), while the basal ganglia seem to play a role in the nondeclarative, procedural memory system (Ullman, 2004). SL was found to use both networks (Batterink et al., 2019). Yet, the hippocampus might not be as crucial for SL as previously thought. Patients with extensive hippocampus and medial temporal damage were reported to underperform in SL task, but this result was argued by the fact, that many healthy participants do not perform above chance in these tasks. The authors argue that the hippocampus has major contribution to SL performance, but it is not crucial to it (Siegelman & Frost, 2015). The background structure of SL seemingly activates both cortical and subcortical areas. The co-operation of these systems is bound together by the following hypothesis based on three main structures: the hippocampus, posterior neocortex, and the PFC (Atallah et al., 2004). In the model, the hippocampus was assigned to be responsible for the quick learning of details, while the role of the neocortex is the acquisition of general statistical information. The PFC with its connections to the basal ganglia (Poldrack & Rodriguez, 2004) maintains the information in the nervous system and together they are responsible for the acquisition and utilization of this information.

The wide network described here play potential roles in the course of SL. Studies show that different sites are activated based on the modality of stimuli, the task connected to paradigm, the relationship between the associated stimuli and the timescale between obtaining and using the statistical information. Since both cortical and subcortical sites are concerned, their simultaneous examination is a great challenge.

EEG findings in VSL

EEG is a suitable tool for the examination of SL considering its high temporal resolution which is able to detect short lived cortical changes regarding learning effects. Both amplitude changes in ERPs and power changes in the time-frequency domain have shown modulation by SL. EEG components, especially ERP waves show SL related modulations, like the expectation suppression and prediction error (Summerfield & de Lange, 2014; Summerfield & Koechlin, 2008). Expectation suppression is represented as smaller components in case of a pattern or high stimulus expectancy. Expectancy related ERP modulations were reported between 100-700 ms diffusely (Feuerriegel et al., 2018), while more limited components were reported to be sensitive to predictability, as well. The P50 wave exhibited smaller amplitudes while presenting predictable auditory stimuli, which was previously considered a preattentional component (White & Yee, 2006). Subsequent components also showed suppression, like the N100 and

N400 components in linguistic, speech segmentation paradigms (Hodapp & Rabovsky, 2021; Sanders et al., 2002).

Many ERP signs have been reported to reflect pattern and regularity violations. A widely studied phenomenon, the mismatch negativity in the N200 component showed sensitivity towards statistical information and emerged when violating predictability (Fitzgerald & Todd, 2018). And the amplitude of many late positive components also shows prediction error elevation in their amplitude. These components diffusely emerged between 500 and 1200 ms after stimulus presentation in linguistic paradigms. It is worth mentioning separately the P600 component showing strong prediction error patterns in language paradigms (Van Petten & Luka, 2012).

Despite the numerous reports, the literature consists abundant null ERP results, as well (Bogaerts et al., 2020; Rungratsameetaweemana et al., 2018; Y. J. Zhou et al., 2020). The difficult reproducibility of these findings raised doubt about the validity of these reports. The review of previous papers proposes the argument that in many cases the results are not effects of prediction suppression, but rather co-founds of attentional shifts, repetition suppression and surprise effects (Feuerriegel et al., 2021). It has also been suggested that the ERPs elicited in current paradigms are not suitable indicators of statistical information processing (den Ouden et al., 2023).

Cortical oscillations could also potentially reflect probabilistic computations. Many oscillatory bands have been associated with statistical learning. The low frequency theta band (4-7 Hz) was found to be modulated by expectancy and learning which is not surprising since it its close tie the working memory (Gevins et al., 1997; Hsieh & Ranganath, 2014). Studies have observed that stimulus consistency was coupled with lower frontal theta amplitudes (Crivelli-Decker et al., 2018) and vice versa, expectancy violation and unexpectedness resulted in greater frontal theta power (Cavanagh et al., 2012; Rungratsameetaweemana et al., 2018). Participants with weaker theta oscillations showed better probabilistic learning outcomes, as well (Tóth et al., 2017).

Alpha oscillations (8-12 Hz) also showed a role in expectancy processing (Y. J. Zhou et al., 2020). Alpha power showed a negative relationship with transitional probability, since unexpected stimuli elicited greater alpha powers. Two possible roles of this alpha waves were hypothesized: either it represents the attentional changes that emerge between unexpected and expected stimuli or it can act as so-called travelling waves These travelling waves carry forward and backward computations and they can connect large scale cortical networks to integrate spatial and temporal information (Alamia & VanRullen, 2019; Bastos et al., 2015; Strube et al., 2021).

Beta band differences also appeared in both visual and auditory paradigms. Comparing low-expectancy and high expectancy stimuli, low expectancy auditory tones elicited higher beta (14-30 Hz) power over the parietal lobe (Pearce et al., 2010). Beta waves (~20 Hz) also showed a difference in visual sequence with associated triplets, where greater powers were observed between triplet transitions than within triplet transitions. The power difference also showed a positive correlation with learning test scores (Bogaerts et al., 2020).

Pursuit of statistical learning

SL is supposed to reduce computational load and time, which can result in behavioral changes. Tracking these changes can provide us with evidence about regularity acquisition or inform us about learning trajectories. Two main behavioral tracing methods are available: the offline and online method. Both have their place in SL studies with their own advantages and disadvantages.

The offline method usually utilizes the so-called familiarity test (Fiser & Aslin, 2001, 2002; Saffran et al., 1999). Participants are exposed to a stimulus sequence where certain stimuli are predictable or form regularities. After the exposure, participants are reintroduced to the previously experienced regularities while simultaneously inserting foils. These foils are created by combining stimuli with otherwise no above-chance statistical relationships. Then participants must decide whether the originally presented or the new foil patterns are more familiar to them. The benefit of this offline test is that it can show behavioral evidence of SL while the participants' stimulus exposure is passive, thus reducing noise and artefacts. This method is ideal for electrophysiological measurements, since we generate less noise without constant button presses or not inserting additional decision-making strategies into the SL process. The disadvantages include that it only supplies information about the learning outcome, but not about the trajectory and progression of the learning. Also, the familiarity test requires explicit knowledge about the patterns and only measures the recollection of the regularities without any information about the unsupervised, implicit pattern acquisition (Batterink, Reber, Neville, et al., 2015; Batterink, Reber, & Paller, 2015; R. Kim et al., 2009).

The other possibility for tracing behavioral changes of SL is the online, SRT method. This method involves inserting an unrelated cover task to the stimulus stream, for example a categorization task. Participants must decide about every stimulus presented to them with a button press. This way we can collect response and RT data and we expect changes in these data based on whether the stimulus is expected/predictable or not. The data can lead to the description of the learning trajectory and a behavioral level, while also RT changes are more implicit and do not require the explicit recollection of the regularity. The cover task also helps to keep up the attention level during the sequence (Conway, 2020) but studies also have shown that motor task and motor learning can interfere with perceptual learning (Ambrus et al., 2020; Hallgató et al., 2013). Furthermore, we don't have information about the participants' decision-making strategies and how it affects SL. Motor activity can also create noise during electrophysiological recordings.

Interpersonal differences in SL

The methods described above measure average SL scores on the population level. This would not raise skepticism if we could follow the characteristics of SL as first described. Original SL studies characterized the SL as an effect which shows little variance between individuals (A. S. Reber, 1993). However, an increasing number of recent studies suggest that SL does not appear to be a consistent ability. A substantial number of participants in SL paradigms show miniscule or no learning effect at all. On the population level, the variance between participants is great and the population mean is just above the control mean (Arciuli et al., 2014; Conway et al., 2010; Evans et al., 2009; Karuza et al., 2013; Kaufman et al., 2010; Misyak & Christiansen, 2012). These contradictory observations indicate significant individual differences including not just the overall performance variances, but differences in both the extent and the speed or trajectory of learning and the individual variation in the sensitivity to certain stimulus types. How could such an elemental processing mechanism show this considerable difference in individual affinity towards statistical relationships? Many studies have aimed to find a link between SL and other factors such as age, intelligence, and certain cognitive functions.

Studies aiming to find a correlation between SL and age are inconclusive. It has been reported that there's no relationship between age and SL (Bertels et al., 2015; Saffran et al., 1997), unlike explicit learning, where a negative correlation can be observed (Verneau et al., 2014). Contrarily to the null findings in SL paradigms, it has been shown that before early adolescence people have a higher affinity toward statistical relationships (Janacsek et al., 2012; Juhasz et al., 2019; Zwart et al., 2019). One theory suggested that this higher affinity was due to a not fully developed frontal cortex, which reduces the suppression of the frontal lobe on this unconscious form of learning. In a study, the left dorsolateral prefrontal cortex was inhibited via TMS, which supported regularity consolidation resulting in better behavioral results in an alternating serial reaction time task (Ambrus et al., 2020). On the other hand, greater behavioral performance in adults has been reported in the case of non-linguistic paradigms compared to children between the age of 5 to 12 (Shufaniya & Arnon, 2018). These results are somewhat contradictory and do not fully explain the relationship between age and SL.

Another option for an influential factor could be intelligence. Most studies focused on correlating SL score with the g factor of intelligence defined by Spearmen (Spearman, 1904). The g factor characterizes a general intelligence that affects other, specific cognitive abilities. Most studies have concluded that SL (mostly artificial grammar learning paradigms) and g factor have no correlation or only a weak correlation (Gebauer & Mackintosh, 2007). The reason behind this can be the fact that the implicit nature of SL is evolutionarily older than the explicit intelligence measured with psychometric methods (Kaufman et al., 2010). Although it seems like general intelligence has no effect on SL, specific higher cognitive functions have been reported to show a relationship with it. A positive correlation has been found between literacy and both visual and auditory triplet learning (Frost et al., 2013; Qi et al., 2019), while null findings have been reported as well (van Witteloostuijn et al., 2021). The music skills of children and adults and the social competency of young adults alike showed a positive relationship with triplet learning (Mandikal Vasuki et al., 2017a, 2017b; Parks et al., 2020). Age and intelligence differences, however, still cannot explain the interpersonal differences in many cases, since they can be found within relatively homogenous groups as well, like young university students.

The relationship between SL and lower-level, more basic cognitive functions is not so straightforward. Based on the work of Turk-Browne and his colleagues it was theorized that attention was necessary for SL to occur since in a paradigm with visual regularities only attended sequences were learned, but unattended regularities were not acquired (Turk-Browne et al., 2005). Subsequent studies revealed that attention is not indispensable in sequence learning since learning in an unattended stream was observed, but to a smaller extent (Batterink et al., 2019; Musz et al., 2015). Further studies demonstrated that SL and attention have a reciprocal relationship since attended regularities have a higher chance to be acquired and SL can have a “pop-out” effect guiding top-down attention toward previously learned regularities (Conway, 2020; Moorselaar & Slagter, 2019).

Examining the relationship between SL and memory is contradictory, as well. It seems logical that having a greater working memory capacity allows the integration of more regularities. This correlation has not been proven, but it is theorized that various aspects of working memory are linked to SL within their modality, meaning SL and working memory processes within the modality-specific sensory cortices are linked. For example, a greater correlation was found between learning visuospatial sequences and visuospatial working memory than with the acquisition of other types of modalities (Janacsek & Nemeth, 2013). Although the effect of working memory capacity on SL is not fully determined, the existence of some kind of link has evidence, since paired stimuli represented as one can increase the capacity of memory (Brady et al., 2009; Lengyel et al., 2019, 2021). Furthermore, predictions coming from SL can shape memories (Sherman et al., 2020). Violating the previously learned regularities with new sensory information weakens memory representation (G. Kim et al., 2017). Besides, memory units tied to a regularity or even violating said regularity can alter memory encoding (Greve et al., 2017). Through SL, we integrate previous experiences and observations into a model of our environment, which later helps us make optimal decisions (Perkovic & Orquin, 2018). The advantage of this model is that it is flexible, so we can update it with new information, thus adjusting our decision-making strategies (Richards et al., 2014). The shift between relying on the model or applying new, incoming information was investigated in different psychiatric conditions. One paper claimed they found that methamphetamine-dependent individuals are more likely to choose learning-independent strategies in a reward-seeking paradigm. They also found that the dependent group is less likely to update their model and decision-making criteria based on new information compared to the control group (Harlé et al., 2015). The positive symptoms of schizophrenic people such as delusions and hallucinations can be the products of the aberrant function of the inferencing mechanism. The malfunction of this mechanism can be caused by improper integration of new sensory information into the model (Fletcher & Frith, 2009) or the low precision of their prior knowledge (Sterzer et al., 2018). In the case of autistic people, attenuated prior knowledge is theorized to be responsible for more accurate perception (Pellicano & Burr, 2012). This could result in an altered perception since, without prior knowledge or predictions, the speed of the process of environmental information decreases.

Many behavioral and psychometric factors have been investigated, but only a few studies have been done to find neurological traces of this interpersonal affinity difference in SL. In a study, tritone words made of pure tones were presented to participants in three sessions and they had to perform a familiarity test afterward. Based on their behavioral results, subjects were grouped into three categories: high-learners, middle-learners, and low-learners. Differences in the N100 and N400 components were observed between the initial and subsequent tones, and the temporal distribution differed in the three groups. In the case of high-learners, the difference was elicited in early sessions; middle-learners showed a similar difference in later sessions while low-learners showed no difference (Abla et al., 2008).

Another powerful tool to investigate SL and its neural correlates is frequency tagging or neural entrainment. In an EEG study, participants were shown tone triplets along a random tone sequence. A positive correlation was found between behavioral results and the normalized power of the region of interest, which was a left anterior and a right occipital cluster in their case (Buiatti et al., 2009). In a following study, participants were exposed to a random and structured tone sequence during MEG recording. It was observed that the behavioral results showed a positive correlation with intertrial phase coherence of the left pre-central gyrus and the right temporo-frontal area. These results were interpreted as attention changes during the presentation of regularities. The personal differences in the behavioral results were explained as the learned sequences emerged as explicit knowledge on different levels (Moser et al., 2021). Beta activity has been correlated with the behavioral results of SL, as well. In a recent paper, a 19-21 Hz oscillatory activity difference was found comparing within-pattern and between-pattern transitions. This difference emerged before stimulus presentation and this prestimulus beta-power was increased before the first stimulus of a visual triplet (Bogaerts et al., 2020).

Besides EEG and MEG results a positive correlation has been observed between the performance in an offline familiarity test and hemodynamic changes. In the paradigm, participants were presented with stimulus pairs (scenes and faces) during fMRI recording. In the subsequent analysis, results of the offline test positively correlated with neural anticipation in the right intraparietal sulcus and the left middle occipital gyrus. In the study, anticipation was defined as neural changes elicited by the stimulus preceding the predictable stimuli (Turk-Browne et al., 2010).

Implicit, visual statistical learning

The two most commonly studied SL modalities are the auditory and visual. As mentioned before, the results of different modalities and SL paradigms cannot be conflated. A more rarely studied phenomenon is the visual SL that is completely unsupervised and implicit. Several studies use visual stimuli, but in many cases, participants are hinted at a hidden pattern. Thus, the behavioral and neural background and its description is currently incomplete in the literature. We can derive several parameters about implicit VSL from earlier studies.

The learning trajectory of VSL has been described before (Siegelman et al., 2018). In this self-paced paradigm, they successfully described the learning curve of VSL using 2AFC task with online, RT tracking. The exposure was not completely unsupervised, since participants were informed about the hidden pattern in the image sequence, yet it still provides useful information about the behavioral changes during the emergence of VSL.

A completely implicit VSL paradigm has been used before, which contributed both behavioral and neural data to the literature (Turk-Browne et al., 2010). This fMRI study used a picture sequence with faces and scenes. Participants were only instructed to categorize the appearing image with a button-press. Not revealed to the participants, the images formed associated stimulus pairs, that always followed each other in a fixed order. Thus, the second member of the image pairs became predictable. They found RT reduction for predictable images and an anticipatory effect. This anticipatory effect was a prolonged RT for the first member of the associated stimulus pairs. The examination of these effects was possible due to the introduction of so-called single images, which had no above-chance statistical relationship with preceding images, and they had no function in VSL. They also confirmed the pair acquisition with an offline familiarity test after the stream exposure.

The image sequence, however, contained additional information above the associated pairs. Their image pairs were always formed using pictures for different categories (face-scene, scene-face). Thus, from the participants' point of view there was a greater chance that the next image will be of a different category. Besides, category repetition could only occur between a single condition and the first member of the pair. Since there was a smaller probability of category repetition, it could introduce a motor artefact that prolonged the RT of the first members.

Aims

Our goal was to examine unsupervised statistical learning with a visual sequence where an undisclosed, temporal regularity was placed into the stream. Reports were found to be either quasi-supervised (Siegelman et al., 2018) or altered by higher level information (Turk-Browne et al., 2010). To do this we adapted and tested a previously reported unsupervised, visual SL paradigm (Turk-Browne et al., 2010). We examined the possible co-factors impacting the behavioral results and modified the paradigm to investigate the behavioral evidence for SL with an online RT test. The online paradigm also helps us not only to report the evidence for an SL effect, but also to describe the learning curve. The description of the SL trajectory further helps us to understand the complex network behind the cognitive process.

After establishing the behavioral parameters, we further adapted the paradigm to EEG. By recording cortical activity, we wanted to find possible differences, that are not only characteristics of SL but can also help us understand factors affecting the learning processes and possibly provide information about individual traits that influence SL.

Materials and methods

Behavioral study

Experiment 1a

In the first experiment we recreated the paradigm of Turk-Browne (2010) with different images. We increased the number of participants to boost the statistical power. Our goal was to observe the priming and anticipatory effect in the RT and accuracy data. Namely, we wanted to observe the RT reduction to expected stimuli, which are the second members of associated stimulus pairs and RT increase to the first member of the pairs.

Participants

Thirty-eight volunteers (20 females, mean age: 25.34 y, range: 21-41 y) participated in Experiment 1a, who were all right-handed with correct or corrected to normal vision. All of them gave written informed consent; the study protocol was approved by the Human Investigation Review Board of University of Szeged (266/2017-SZTE).

Stimuli

For the stimuli of the experiment, we used gray-scale pictures of everyday objects which were selected from the Bank of Standardized Stimuli (BOSS, Brodeur et al., 2010, 2014). Selection of the stimuli was based on a pilot study, where 5 participants, who were not part of any of the experiments discussed here, performed a 2AFC discrimination test. In this test they had sorted presented objects based on whether they fit inside an imaginary shoebox or not. Stimuli with concordant answers among all participants were included and assigned ‘Large’ or ‘Small’ category. In Experiment 1a we used 96 stimuli in total, 48 from each category. The measurements were divided into 8 runs and in each run, we used 12 of the 96 images previously selected. These stimuli were presented at a 7.5° × 7.5° visual angle.

Design

A stream created from these images was presented to the volunteers. RT and accuracy were measured through 8 runs. In one run, the 12 images formed 4 associated image pairs, that always followed each other in the sequence. The rest of the images served as control, so-called single images. Then these pairs and singles were presented in a pseudorandom manner. One stimulus was never presented in two different runs for one participant. In one run, 72 trials were presented to the subject, which was divided into 6 cycles. In one cycle all 12 images were presented, meaning that the subject had to see every stimulus before presenting the images again. The presentation of the pairs and singles had one constraint, that at least three other stimuli must be presented before the reappearance of an image, which can only happen at the junction of the cycles.

Task and procedure

Participants were seated in a sound-attenuated room with dimmed lighting. They were asked to indicate the category of the presented object with a button press (1 on the numeric keyboard – 'Small', 2 on the numeric keyboard – 'Large'). Participants received no feedback during the task. Every stimulus was presented for 300 ms and the next stimulus was presented 500 ms after the subject's response (Fig. 1.). Subject paced stimulus presentation was carried out using Psychtoolbox (Brainard, 1997; Kleiner et al., 2007) on an HP 650 ProBook G4 (15.6 inches, 1920 × 1080 pixels, 60 fps). Participants were completely naïve to the sequence and the associated pairs. After 8 runs, participants were interviewed to see whether they recognized the pairs, using the following questions: (1) What is your impression of the experiment? (2) Do you have any observations about the experiment (3) Did you recognize any pattern regarding pressing the response keys (4) Did you find any pattern regarding the images (5) Did you find any systematic regularities about the order of the images?

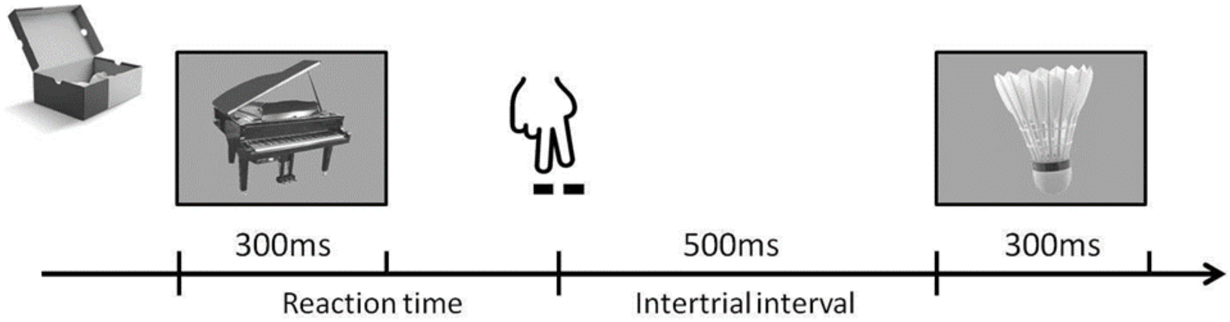

Figure 1: The design of Experiment 1a and 1b. Participants had to categorize the appearing image based on its size and respond with a button press. Images were shown for 300 ms, and a fixed 500 ms ITI was applied after the answer.

Pattern

To create a balanced sequence, 6 stimuli from both categories were randomly selected for each participant. Eight of the 12 images were assigned to be associated stimulus pairs with their order fixed. The image transition could fall under two definitions: category-repeating or category-alternating. These definitions mean that the leading and following images during transition belong to the same, repeating (Small-Small, Large-Large) or different, alternating categories (Large-Small, Small-Large). Experiment 1a only included category-alternating pairs. The remaining images, two Small and two Large were part of the control condition, the single images (Fig. 2.).

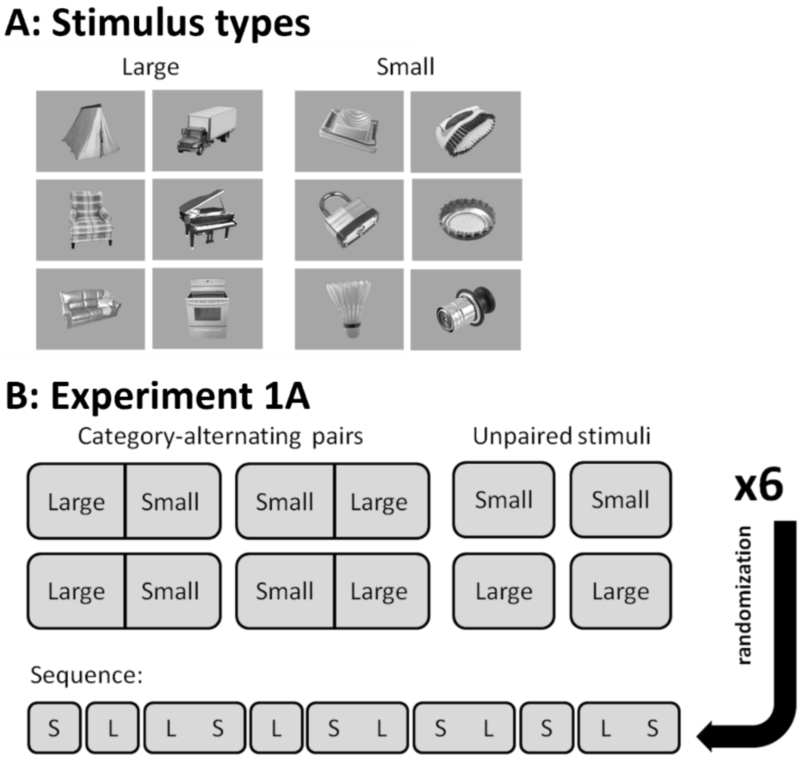

Figure 2: The stimuli and the regularity used in Experiment 1a. ***A****: A few examples of the presented images in both categories (Large and Small).* ***B****: In Experiment 1a all asssociated stimulus pairs were category-alternating. The information chunks were repeated 6 times resulting in the sequence of one run.*

Data processing

During data acquisition we recorded participants' answers and measured their RTs and accuracies. Correct answers for the categorization tasks were determined based on the concordant answers of the previously mentioned pilot. For the RT data, trials with incorrect answers were excluded. The following trials were excluded from the analysis: where RT is shorter than 200 ms, where RT is longer than mean + 3 SD. We further excluded those runs, where accuracy was lower than 80%. Additionally, five subjects were completely omitted from the analysis, due to their mean accuracies being under 60%. To increase signal-to-noise ratio, the first three trials of every run were excluded from the visualization and the first cycle of every trial was further omitted from the statistical analysis, since we do not expect any modulation in those trials. Based on these criteria, we excluded 9.5% of all trials: 0.3% due to long RTs, 0.1% due to short RTs and 9.1% due to accuracy under 80%.

Statistics

Every image was assigned a condition based on their location in the stream: P1, P2 and S. The first images of the stimulus pairs were labelled P1, second images P2 and the single images were labelled S. According to the hypothesis, P1 images induce anticipatory effect, while we should observe priming effects for P2 images. S images serve as control, so we can examine both anticipation and priming.

Mean RTs in all three conditions were compared using one-way repeated measure ANOVA and later Tukey-Kramer test as pairwise *post hoc* analysis. For the accuracy data, Friedman test later Wilcoxon signed-rank test was used to compare the medians.

Experiment 1b

To check the assumed motor pattern in Experiment 1a, the pattern was modified in Experiment 1b to balance the category-alternating and category-repeating transitions in the sequence. Other parameters of the experiment were left unchanged.

Participants

Thirty-eight volunteers (18 females, mean age: 27.6 y, range: 21-42 y) participated in Experiment 1b, who were all right-handed with correct or corrected to normal vision. All of them gave written informed consent; the study protocol was approved by the Human Investigation Review Board of University of Szeged (266/2017-SZTE). We excluded three subjects due to poor performance (mean accuracies were under 60%). We excluded 2.61% of all trials from Experiment 1b using the same criteria as in Experiment 1a: 0.8% for long RTs, 0.02% for short RTs, and 1.8% for low accuracy.

Pattern

In Experiment 1b, we used 12 images for every participant, as well. Out of the 12, 4 pairs were created, but only two were category-alternating, while the remaining were category-repeating. S images still included two Large and two Small images (Fig. 3.). By introducing category-repeating the transition were balanced: 47.6% were category-repeating out of all the transitions. This modification reduced the motor pattern in the stream that could bias the SL effects.

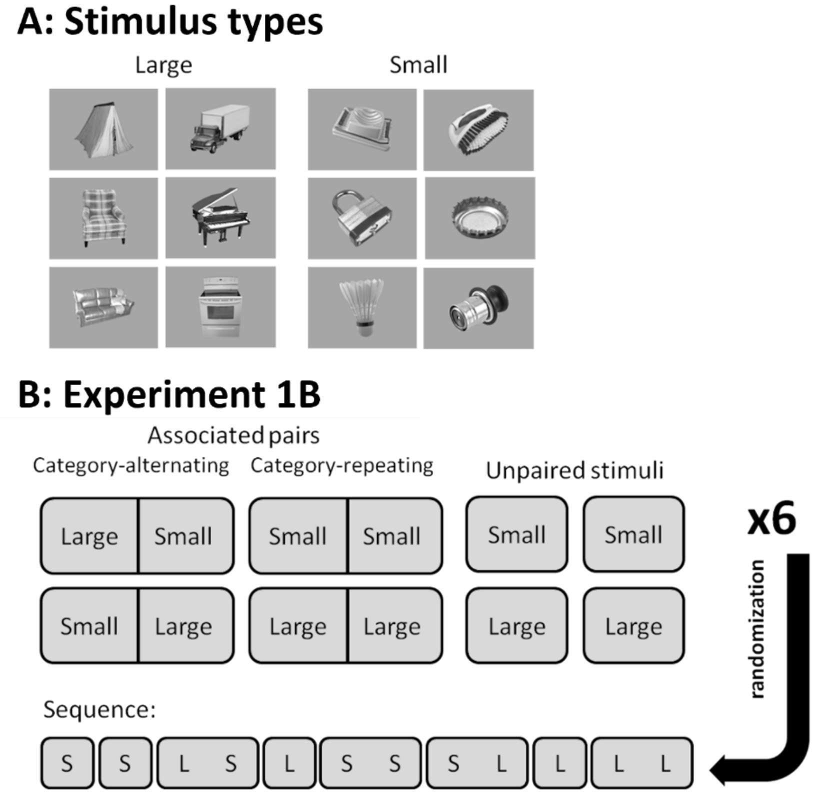

Figure 3: The stimuli and the regularity used in Experiment 1b. ***A****: A few examples of the presented images in both categories (Large and Small).* ***B****: In Experiment 1b two of the pairs were category-alternating and two were category-repeating. Other parametrs of the experiment were kept the same as in Experiment 1a.*

Experiment 2

Based on the observation from Experiment 1a and 1b we made the following modifications on the paradigm to achieve our goal and examine the behavioral effects of VSL. First, we changed the categorization task based on the feedback of the participants. We also increased the number of single stimuli in the stream. This modification reduced the transitional probabilities between non-associated stimulus pairs thus further increasing the contrast between predictable and non-predictable conditions. The number of subjects was increased compared to the first two experiments based on the smaller effect sizes experienced in Experiment 1b. We increased the number of stimulus presentations as well to raise the effect size. To not lose the first trials and to avoid introducing noise into the pseudorandom stream an initial random sequence with the same stimuli was inserted at the beginning of the stream. This way participants got familiarized with the task and we minimized the procedural learning effect (Manahova et al., 2018) skewing the RT data. Finally, to reduce the monotony of the task, a jittered ITI was introduced.

Participants

In Experiment 2, we had 87 healthy participants with correct or corrected-to-normal vision (48 females, mean age: 21.26 y, range: 18-28 y). All of them gave written informed consent; the study protocol was approved by the Human Investigation Review Board of University of Szeged (266/2017-SZTE). Due to low average accuracy, 4 participants were omitted from the analysis.

The exclusion criteria of the trials were changed. Due to the introduction of the random warm-up period, variance in RT dropped and cut off was determined at mean + 2SD. Other criteria were implemented from the previous experiments. This way, 4.15% of all trials were excluded from the analysis (2.1% because of long RT, 0.2% for short RT and 1.8% for accuracies under 80%).

Stimuli

Sixteen images from Bank of Standardized Stimuli were selected for Experiment 2 (Brodeur et al., 2010, 2014). Eight of these images were everyday objects, while the rest were images of animals.

Design

A sequence of images was presented to the participants in two runs, during which we recorded their answers and RTs. For each participant and run 16 images were randomly selected (8-8 from each category, Fig. 4.). The same images were never presented to the same participant in different runs. Each image was presented 25 times, so each run contained 400 trials. The first 10 presentations were the random stream, while the last 15 contained temporally associated stimulus pairs formed from the familiarized stimuli. These were connected without any cue, seamlessly to the participants. The stimuli association and thus the temporal regularity was unique for each run.

Task and procedure

The task was changed from categorization based on size to categorization based on whether it is an object or an animal. Participants had to answer with a button press on the numeric keyboard. The next trial was presented after a jittered ITI (500-1200 ms). Participants sat 60 cm from a desktop computer and screen (1920 × 1080 resolution, 60 fps). All participants were naïve to the regularity and task. To determine the explicitness of the learning, volunteers were interviewed afterwards with the same questions as in Experiment 1a.

Pattern

We used a similar pattern as in Experiment 1b, but the number of single images was increased from 4 to 8. The sequence also contained 4 associated pairs, where two of them were category-alternating and two were category-repeating (Fig. 4.).

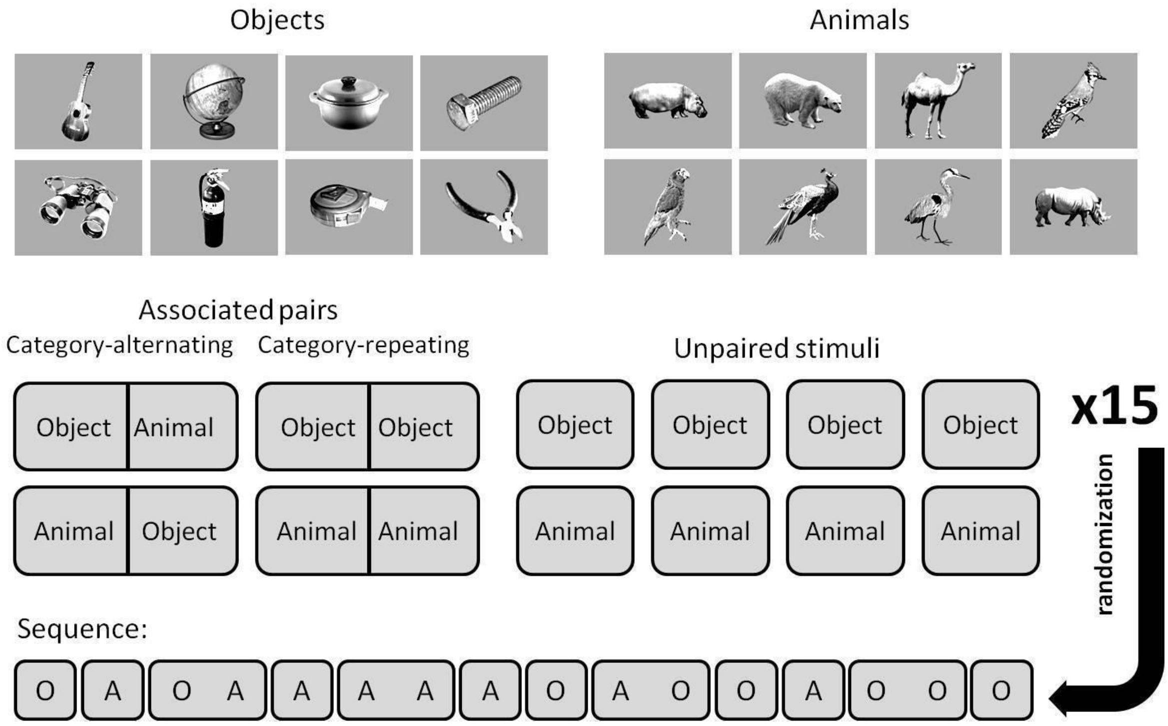

Figure 4: Examples of stimuli and the design of the regularity in Experiment 2. The categorization task, the number of presentation and the number of single stimuli were changed compared to Experiment 1a and 1b.

Statistics

For the evaluation of the RT data, a linear mixed-effect model with restricted maximum likelihood criterion was implemented in the lme4 package in R (Bates et al., 2014). The linear model was chosen instead of a generalized linear model based on the robustness of the model and the residual diagnostics. The following fixed effects were included: the natural logarithm of the repetition number (1 to 15), the conditions (P1, P2, S) their interaction and the ITI. Random effects consisted of the random slope and intercept for the subject, the presented image, and the new variable, called 'NVAR'. NVAR describes the answers of the current image with the previous one: 1 - current and previous answers are correct, 2 – current answer is correct, the previous is wrong, 3 – current answer is wrong, but the previous is correct, 4 - both of the answers are wrong. Likelihood ratio test was used to evaluate random effects in the lmetest package (Zeileis & Hothorn, 2002). Fixed effect was evaluated using type III ANOVA from the lmerTest package (Kuznetsova et al., 2017). Satterthwaite's method was used to obtain degrees of freedom and p values. *Post hoc* analysis included the estimated marginal means with Tukey correction. The interaction was evaluated using the estimated marginal means of linear trend with Tukey correction.

A generalized linear mixed-effect model with binomial distribution was fit to evaluate the accuracy data. To test the fixed effects, we used type III Wald χ^2 test in the lmerTest package. Fixed effect included the natural logarithm of the repetition number, the condition, and the ITI. The random effects were the subject number and image. We performed a *post hoc* power analysis as well using the simr package.

EEG study

After examining the behavioral evidence of implicit VSL, we adapted our paradigm to EEG. This included abandoning the categorization task and online monitoring of SL and changing it to the offline familiarity test. To maintain participants' focus we inserted a detection task in the stream, as well. To confirm the adapted paradigm, we conducted a pilot behavior study.

Participants

In the pilot study we had 17 participants (9 females, mean age: 25.7 y, range: 20–26 y), while we recorded the EEG data of 30 participants (16 females, mean age: 26.4 y, range: 21–37 y) afterwards for course credits. The results of the pilot study were used to determine the effects size and *a priori* sample size calculation. The calculation showed the need for a sample size of 33. All participants provided written, informed consent; all stated having a correct or corrected-to-normal vision and no history of epilepsy or other neurological diseases. One participant showed extremely high noise during the recording; thus, this one participant was excluded from the latter analysis. The study protocol was approved by the Human Investigation Review Board of the University of Szeged (266/2017-SZTE).

Sequence design

The previously used paradigm was adapted to EEG. All participants were exposed to 3 runs of image sequences. In each run, participants were presented with 412 trials. One run was made up of 25 presentations of 16 images of everyday objects. Twelve images of animals were inserted into the stream randomly (Fig. 5.). Similarly, to Experiment 2, the first 10 presentations of the images were random in their presentation order, while the last 15 contained temporal regularity, the image pairs. Eight images formed associated pairs (P1 and P2 images), the rest served as control, single images (S images).

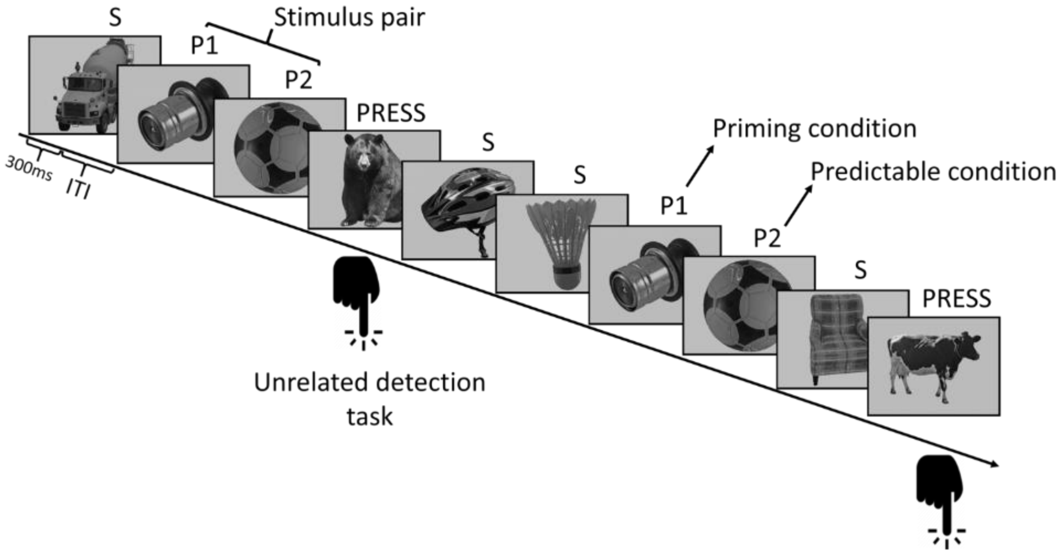

Figure 5: The sequence structure in the EEG study. The associated stimulus pairs and single stimuli were kept intact. The behavioral task was changed to a detection task, where participants had to indicate the appearance of animals with a button press. These trials were omitted from the later analyis.

Task

Participants were instructed that they were going to see an image stream of everyday objects and they had to indicate the appearance of an animal in the sequence as fast as possible with a button press (Fig. 6.). Our goal with the detection task was to maintain the attention level of the participants during the stream.

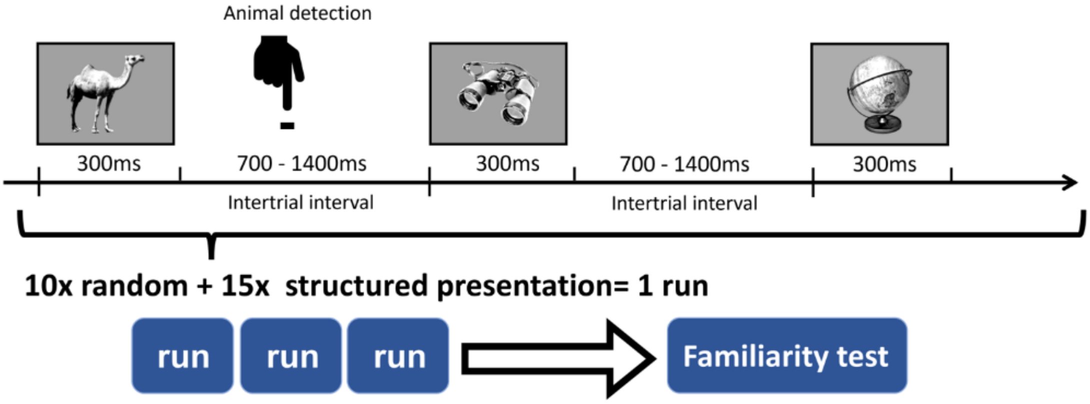

Figure 6: The design of the stimulus presentation. Stimulus presentation was machine-paced. Images were shown for 300 ms and then an ITI of 700-1400 ms was applied. Three runs of sequences were shown to the subjects.

Familiarity test

To evaluate the regularity acquisition participants performed an offline, familiarity test after the presentation of the sequences. The test was a subject-paced 2AFC design with a total of 32 presentations of stimulus pairs. Eight pairs were presented 4 times; 4 out of the 8 were the true pairs presented during the sequence while the rest were foils. Foil pairs were created by swapping the members of the original pairs while keeping the position intact. The presentation of the pairs was identical to the presentation during the sequence. Participants had to answer with a button press whether they find the stimulus pair familiar or not ('S' – familiar, 'K' – not familiar). Subjects' response was followed by the next pair.

Stimulus presentation

All images presented to the participants were gray-scale images selected from the Bank of Standardized Stimuli (Brodeur et al., 2010, 2014). The images were displayed at a visual angle of 7.5°× 7.5° sitting approx. 50 cm from the screen. Stimulus presentation was carried out on an ASUS ROG Swift PG248Q Monitor (1920 × 1080), using Psychtoolbox, MATLAB

(Brainard, 1997; Kleiner et al., 2007). The images were presented for 300 ms and between images a jittered ITI was used (700 – 1400 ms).

Procedure

First, we ran the pilot study to test whether the adaptation of the paradigm still results in pair acquisition. Here, participants were instructed that they are going to see an image sequence and they must indicate the appearance of animals with a button press. After only one run, they performed the familiarity test where they were informed about the hidden pairs.

After establishing the phenomenon in the pilot study, the stimulus presentation was coupled with EEG recording. To increase signal-to-noise ratio, each participant performed three runs of sequences, which took about 25 min. In each run, new images and new regularities were used, so every image was presented 25 times, and every pair was presented 15 times. Between runs, participants had the chance to take a few minutes before continuing. After completing all three streams, participants had to perform the familiarity test based on only the images and pairs of the last sequence.

EEG data acquisition

For the recordings, a 64-channel Biosemi Active II system was used with a sampling rate 2048 Hz. EOG was acquired with four channels: 1 cm above and below the left eye and the outer canthi of both eyes.

Preprocessing was carried out in EEGLAB, MATLAB (Delorme & Makeig, 2004). Channels with significant noise were interpolated based on visual inspection. Then, a Notch filter and a bandpass filter were applied between 48-50 Hz and 1-80 Hz. Rereferencing was based on grand-average, and we resampled the data to 200 Hz. To remove eye-movements and other noise we used EyeCatch (Bigdely-Shamlo et al., 2013) and Multiple Artifact Rejection Algorithm (Winkler et al., 2011, 2014). After removing the EOG channels, we defined the epochs: 700 ms before and 1700 ms after stimulus presentation.

After acquiring segmented data, further analysis was carried out in Fieldtrip, MATLAB (Oostenveld et al., 2010). ERP, TF and ITPC analysis was performed. For the ERPs, the epoched data were baselined to -200 to 0 ms before stimulus presentation. The ERP was calculated for each condition, subject, and channel by averaging the trials.

TF analysis was performed by Morlet wavelet convolution with zero padding between -700 to 1700 ms and between 2 to 80 Hz. To inspect the different frequency bands alternate cycle numbers were applied (4 and 10). After convolution the data was baselined to -400 to -200 ms before presentation and it is given in dB. As a last step, TF data was averaged together across trials. ITPC was computed in the same window as TF according to Tallon-Baudry et al. (1996, Eqs. 1), where F stands for phase, f for frequency, t for time and n for number of trials.

$$ITPC(f,t) = \frac{1}{n}\sum_{k=1}^{n} \frac{F_k\,(f,t)}{|F_k\,(f,t)|} \quad (1)$$

Statistical analysis

The data of the familiarity test was first converted into sensitivity according to the modified Grier's formula (Aaronson & Watts, 1987; Grier, 1971). The formula describes a participant's sensitivity in a 2AFC design (Eqs. 2,3), where hit probability (HIT) and false alarm probability (FA) is converted into A'. This value ranges between 0 and 1. 0.5 marks chance accuracy, while 1 mark 100% accuracy. The modified formula takes into consideration the ratio of hit and false alarm rate and different equation is used, when hit probability is higher than false alarm (Eqs. 2) or vice versa (Eqs. 3).

$$A' = \frac{1}{2} + \frac{(HIT - FA)\times(1+HIT-FA)}{4HIT\times(1-FA)} \quad (2)$$

$$A' = \frac{1}{2} + \frac{(FA - HIT)\times(1+FA-HIT)}{4FA\times(1-HIT)} \quad (3)$$

After collecting subjects' sensitivity values, it was tested against 0.5 with one sided t-test. Additionally, we used these values to divide participants into two groups: chance performers (C), i.e., those whose accuracy was 0.5 or under, and above-chance (AC) performers, who performed above 0.5.

ERPs between conditions were compared using permutation statistics with cluster-based correction. Due to the multiple comparison between conditions, additional Bonferroni correction was applied and channels with *p value* under 0.0167 were accepted. Emerging clusters were tested against a permutated population of 1000 iterations and clusters with were accepted as significant which had a summed t value in 95th percentile of the permutated population.

After acquiring TF data, we determined a window of interest. We followed the methodology of Bogaerts et al. (2020). First, we averaged all trials together across subjects, conditions, and channels. Based on the visual inspection of this data, we determined a window of interest along the time and frequency axes and the average power within the window was used for later analyses. The mean power of this window was correlated with subjects' A' value using Pearson's correlation. Afterwards, the power in the TF window was compared between the AC and C groups and determined the scalp distribution of the difference. Additionally, the power was compared between conditions, as well. In both cases permutation statistics with cluster-based correction was used, similarly to the ERP comparison.

Lastly, the ITPC values in the TF window of interest were compared against a same size window in the prestimulus baseline period using Wilcoxon sign rank test due to the non-normal distribution of the data.

Results

Behavioral study

Experiment 1a

The answers of the post-sequence interview revealed that only one participant suspected some kind of pattern in the stream but was unable to specify the pattern or recall any of the pairs. Based on these answers we did not exclude any subject from Experiment 1a.

Analyzing the RT data of the different conditions showed a great effect in the learning paradigm ($F(2,64) = 10.002$, $p<0.001$, Fig. 7.). Pairwise comparison of the three conditions revealed a priming effect on condition P2 (mean = 0.592 s, SD = 0.123s) as its mean RT was lower than both Condition P1 (mean = 0.614 s, SD = 0.133 s, $q = 3.94$, $p = 0.001$) and Condition S (mean = 0.611 s, SD = 0.133 s, $q = 3.484$, $p = 0.004$). *Post hoc* power analysis showed a statistical power of 98.7% (1000 iterations, Monte Carlo simulation). We could not detect a significant difference between the RT of Condition P1 and S.

Accuracy data also showed the priming effect ($n = 33$, $\chi^2 = 20.33$, $p < 0.001$, Fig. 7.). *Post hoc* analysis showed that Condition P2 (median = 0.95, IQR = 0.063) has a higher accuracy than P1 (median = 0.931, IQR = 0.086, $z = -3.45$, $p < 0.001$) and S (median = 0.919, IQR = 0.070, $z = -3.806$, $p < 0.001$). The power analysis showed a statistical power of 99% in this case.

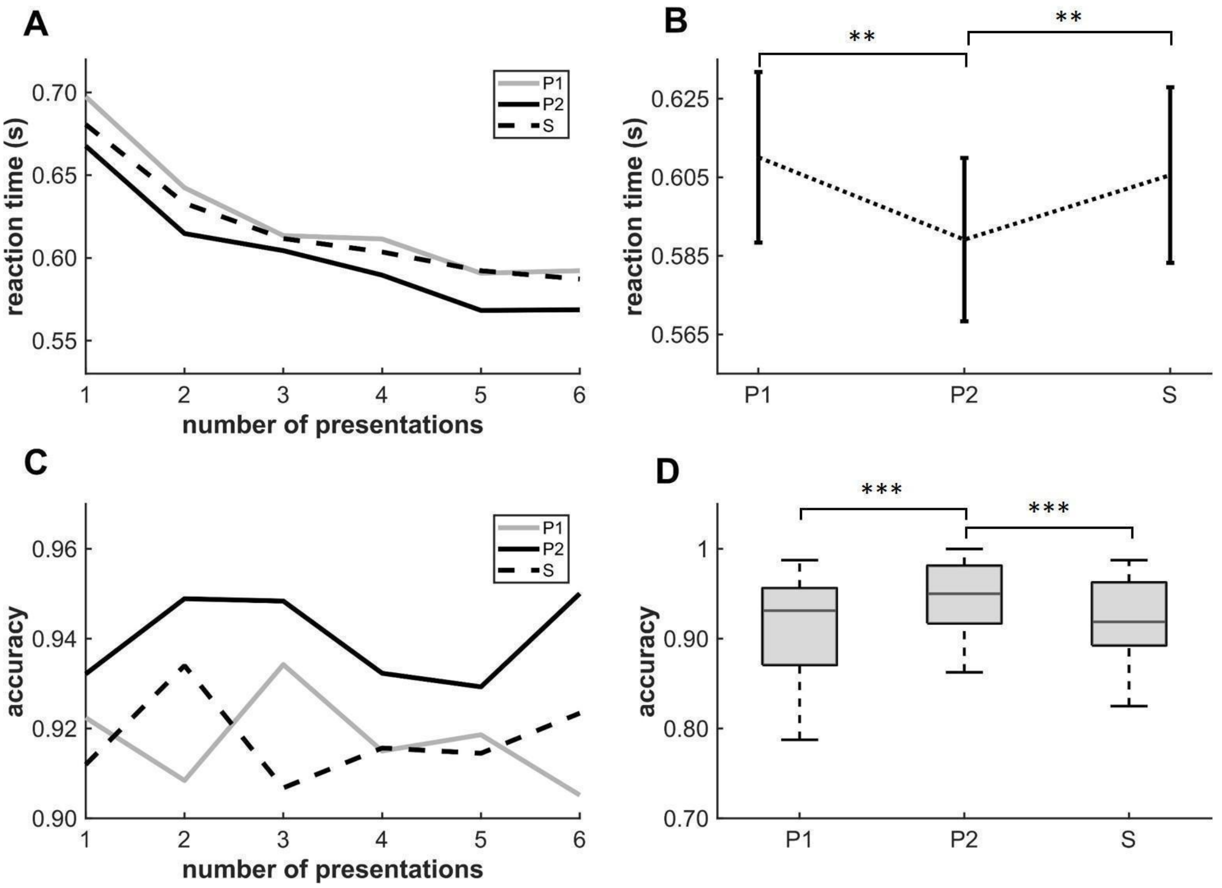

*Figure 7. Performance in Experiment 1a. **A**: RT changes in the three conditions by presentation number. **B**: Mean RT in the three conditions with SD error bars (** p < 0.01). **C**: Accuracy changes in the three conditions by presentation number. **D**: Boxplots of the median accuracy with IQR in the three conditions (*** p<0.001).*

An additional analysis was conducted to confirm the presence of the hypothesized skewing effect of the motor pattern in the sequence. Since the number of category-repeating transitions was substantially lower we removed the trials where the previous image belonged to the same category. This way we lost 38% of all trials and these all belonged to either Condition P1 or Condition S. Due to this removal the effect size observed in the RT and accuracy data decreased. The RT of Condition P2 (mean = 0.592 s, SD = 0.119 s) did not differ significantly from either Condition P1 (mean = 0.595 s, SD = 0.112 s) or Condition S (mean = 0.594 s, SD = 0.132 s) using repeated measure ANOVA (F(2,64) = 0.145, p = 0.866). The effect size of the accuracy showed the same tendency, where the significant difference disappeared (n = 33, $\chi^2 = 0.14$, p = 0.934) between the three conditions (P1: median = 0.942, IQR = 0.084; P2: median = 0.95, IQR = 0.064; S: median = 0.94, IQR = 0.057).

Experiment 1b

During Experiment 1b, one participant reported some suspicion about a hidden regularity, yet again no explicit knowledge could be recalled. For this reason, we kept the data of this participant, similarly, to Experiment 1a.

ANOVA revealed a tendency in the RT data (F(2,68) = 2.458, p = 0.093, Fig. 8.) between the three conditions (P1: mean = 0.618 s, SD = 0.097 s; P2: mean = 0.611 s, SD = 0.097 s; S: mean = 0.617 s, SD = 0.097 s). The accuracy data did not show a significant effect either (n = 35, $\chi^2 = 0.41$, $p = 0.814$; P1: median = 0.944, IQR = 0.064; P2: median = 0.95, IQR = 0.052; S: median = 0.944, IQR = 0.064, Fig. 8.).

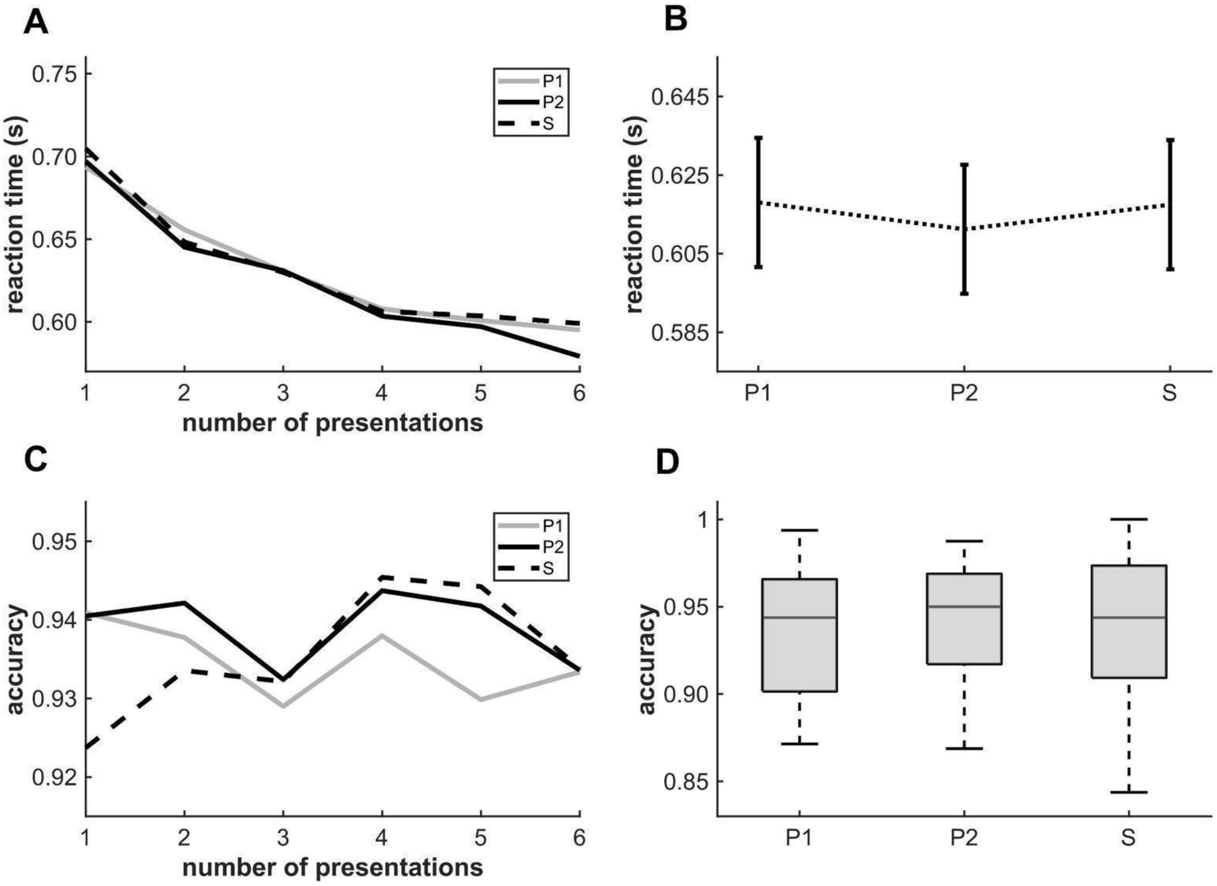

Figure 8. Performance in Experiment 1b. ***A****: RT changes in the three conditions by presentation number.* ***B****: Mean RT in the three conditions with SD error bars.* ***C****: Accuracy changes in the three conditions by presentation number.* ***D****: Boxplots of the median accuracy with IQR in the three conditions.*

Comparing the results of Experiment 1a and 1b

The only modification between Experiment 1a and 1b was the introduction of category-repeating pairs, which greatly reduced the effect experienced in Experiment 1a. Due to the phenomenon, we directly compared the results of the two experiments (Fig. 9.).

Holm-Bonferroni corrected t-test showed tendency (t(66) = 2.083, p = 0.082) in the RT difference between Condition P2 and S in Experiment 1a (mean = 0.019 s, SD = 0.031 s) and Experiment 1b (mean = 0.006 s, SD = 0.019 s), while Holm-Bonferroni corrected Mann-Whitney U test revealed a significant difference (z = -2.56, p = 0.0315) in the accuracy data between Experiment 1a (median = -0.025, IQR = 0.028) and Experiment 1b (median = 0.0, IQR = 0.044).

The difference between Condition P1 and P2 also showed a tendentious change (t(66) = 2.421, p = 0.054) in the RTs of Experiment 1a (mean = 0.022 s, SD = 0.032 s) and Experiment 1b (mean = 0.006 s, SD = 0.021 s). The accuracy difference appeared to be significant between the two experiments (z = -2.33, p = 0.039; Experiment 1a: median = -0.025, IQR = 0.052; Experiment 1b: median = 0.0, IQR = 0.061). Condition P1 and S difference did not show a change in either RT or accuracy data.

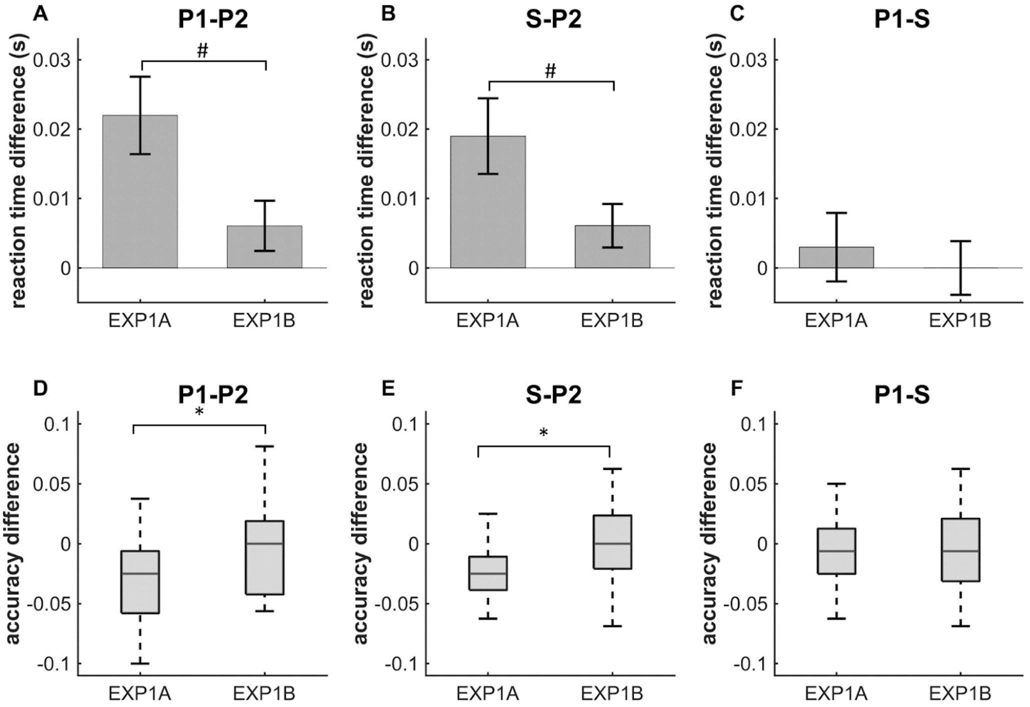

Figure 9. The differences between conditions in Experiment 1a and 1b. ***A****: RT difference between Conditions P1 and P2 (# p<0.1).* ***B****: RT difference between Conditions S and P2 (# p<0.1).* ***C****: RT difference between Conditions P1 and S.* ***D****: Accuracy difference between*

Conditions P1 and P2 ($p<0.05$). E: Accuracy difference between Conditions S and P2 (* $p<0.05$). F: Accuracy difference between Conditions P1 and S.*

Experiment 2

No participant reported explicit knowledge or suspicion about the regularity in the image stream. The mixed model did not detect a significant effect on the accuracy by any of the investigated variables (repetition: $\chi^2 = 1.949$, df = 1, p = 0.163; condition: $\chi^2 = 2.308$, df = 2, p = 0.315; interaction: $\chi^2 = 1.237$, df = 1, p = 0.539) except for the effect of the ITI ($\chi^2 = 14.936$, df = 1, p < 0.001).

The model fitted to the RT data revealed significant effects such as the condition, the interaction of the log(repetition number)×condition and the ITI (Table 1.). Power analysis showed a statistical power of 76% for the interaction.

Table 1. Results of the linear mixed effect model fitted to the RT data

	Degrees of freedom	F value	p value
Repetition	1, 85	0.178	0.674
Condition	2, 38030	3.344	0.035
ITI	1, 38048	407.456	<0.001
Interaction	2, 38018	4.303	0.014

We performed a *post hoc* pairwise comparisons for the categorical significant effects. Examining the estimated marginal means of the condition variable (Table 2A.) led to inconclusion since none of the pairwise contrast reached significance (Table 2B.). However, comparing the linear trends (Table 2C.) of the repetition and condition interaction revealed that P2 and S slopes are significantly different while, P1 and P2 showed tendency (Table 2D.)

Table 2. Results of the pairwise comparison in the RT data. ***A***: *EMMs by conditions.* ***B***: *Z and p values of the comparison of the EMMs.* ***C***: *EMM of linear trends of the interaction in the different conditions.* ***D***: *Z and p values of the pairwise comparisons of the linear trends.*

A	EMM (s)	SEM
S	0.463	0.0281
P1	0.465	0.0282
P2	0.462	0.0282

B	z value	p value
S-P1	-1.804	0.168
S-P2	0.158	0.986
P1-P2	1.701	0.205

C	EMM trend	SEM
S	0.00117	0.0002
P1	0.00058	0.0023
P2	-0.00408	0.0023

D	z value	p value
S-P1	0.32	0.945
S-P2	2.856	0.012
P1-P2	2.195	0.072

In the next step of the analysis, we examined the RT difference slope of Conditions S and P2. This data was fitted to linear regression model as a function of the repetition number (Fig. 10.). To test the hypothesis that the emergence of the behavioral evidence shows a logarithmic trajectory we fitted two models: Model A, with a linear predictor variable and Model B with a logarithmic predictor variable. Both Model A (R^2 = 0.005, F(1,1243) = 6.926, p = 0.012) and Model B (R^2 = 0.008, F(1,1243) = 9.767, p = 0.002) achieved significance. To compare the models, we used encompassing test (lmtest package, R). The test compares the two models to a combined, encompassed model. The test reaches significance when the originals models provide more information compared to the encompassed model, meaning they contribute less to the combined model, thus it is a worse fit. Model A reached significance in the encompassing test (F(-1,1242) = 4.984, p = 0.026), while model B did not (F(-1,1242) = 1.528, p = 0.217).

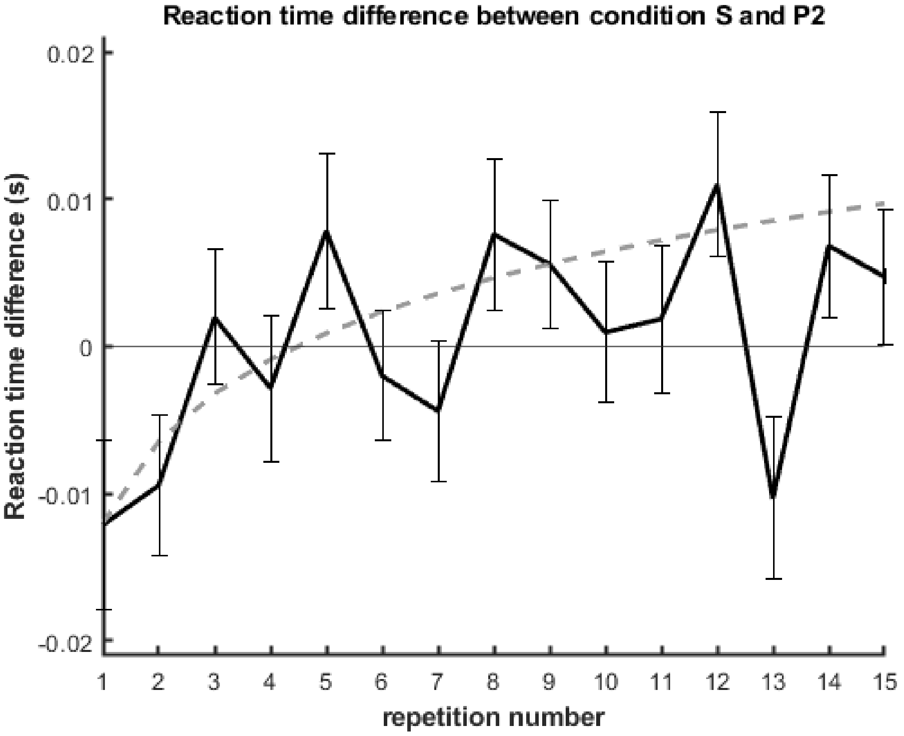

Figure 10. The learning trajectory was determined by the RT difference between Condition S and P2 in Experiment 2.

EEG study

Behavioral results of the pilot study

Testing participants A’ values (mean = 0.6, SD = 0.17) confirmed that the sample mean is significantly above 0.5 (t(16) = 2.44, p = 0.0132). Based on this result, we utilized the adapted paradigm and recorded EEG (Fig 11.).

Behavioral results of the EEG study

One participant reported not comprehending the task in the familiarity test, while we suspect that three additional participants misunderstood the task as they only answered “not familiar” during the test. The first participant was excluded from the familiarity test, but later nobody was excluded after all, as the familiarity test did not influence the stream and the EEG recording. During the EEG study, mean A’ was above 0.5 (mean = 0.53, SD = 0.18), however it did not reach significance (t(28) = 1.002, p = 0.162, Fig. 11.).

The performance of the familiarity test in latter analysis was used to divide participants into two groups: group AC (above chance, those who have A’ above 0.5) and group C (chance, those who have A’ equal or below 0.5).

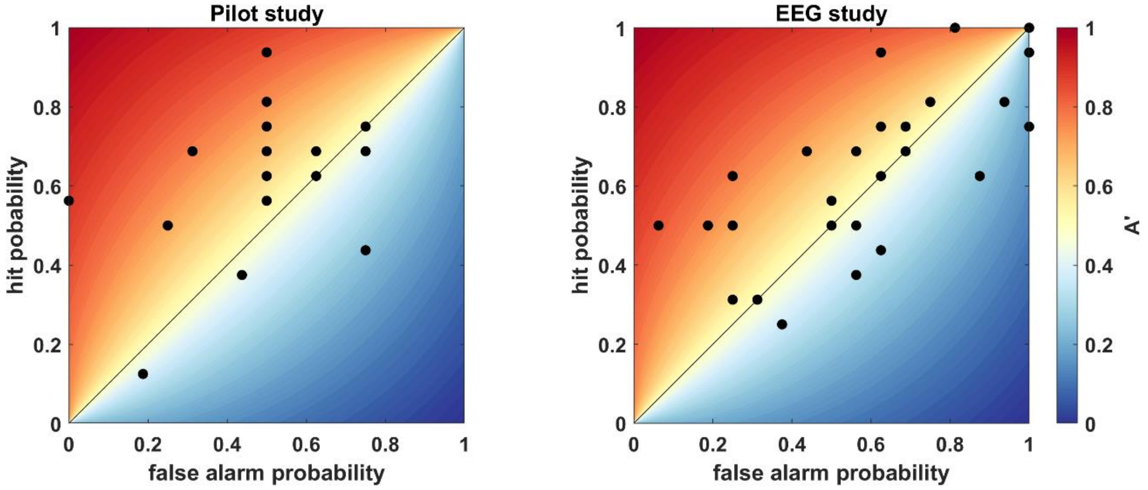

Figure 11. Performance of individual participants in the familiarity test plotted by the hit and false alarm probabilities in the pilot study (left) and the EEG study (right).

ERP results

Analyzing the ERPs in the three conditions did not reveal a significant cluster either including all participants or only including the AC group.

Spectral results

First, we determined a window of interest, by averaging the trials together over subjects, conditions, and channels. Based on the visual inspection of the averaged data, we defined a time-frequency window of interest between 40-70 Hz and 0.5-0.75 s after the start of the stimulus presentation (Fig. 12.)

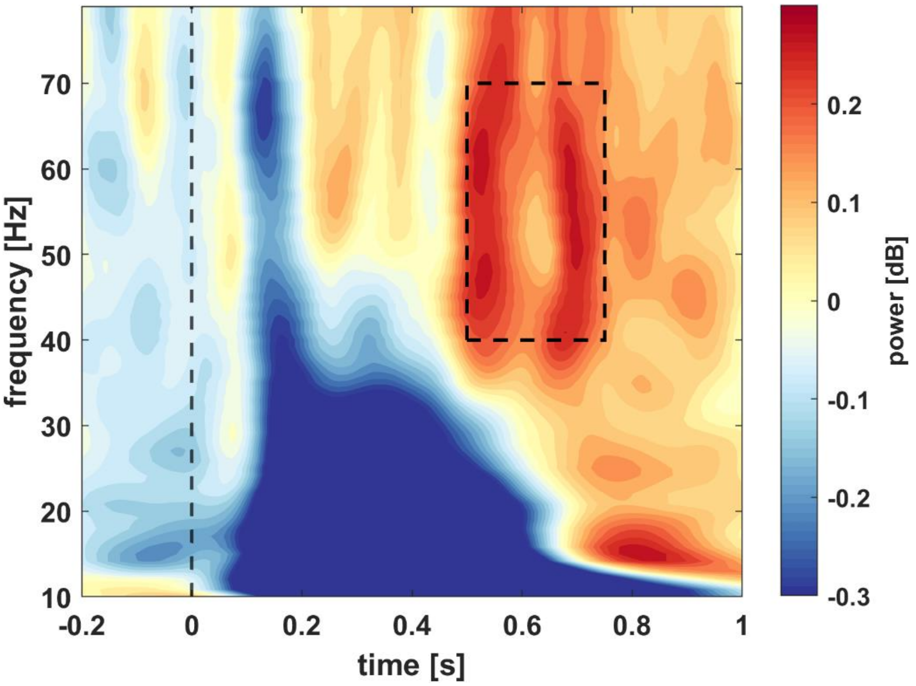

Figure 12. Average power in the post stimulus interval. The dashed window borders the selected window of interest between 40-70 Hz, and 0.5-0.75 s.

After establishing the window, we investigated the relationship between the neural data and the behavioral performance. The average power within the time window showed a positive correlation with the participants' A' values (n = 29, r = 0.371, p = 0.048, Fig. 13.). To confirm this relationship, we reanalyzed the data excluding the previously mentioned four participants, who misunderstood the task. The correlation still emerged with only 25 subjects (n = 25, r = 0.449, p = 0.024).

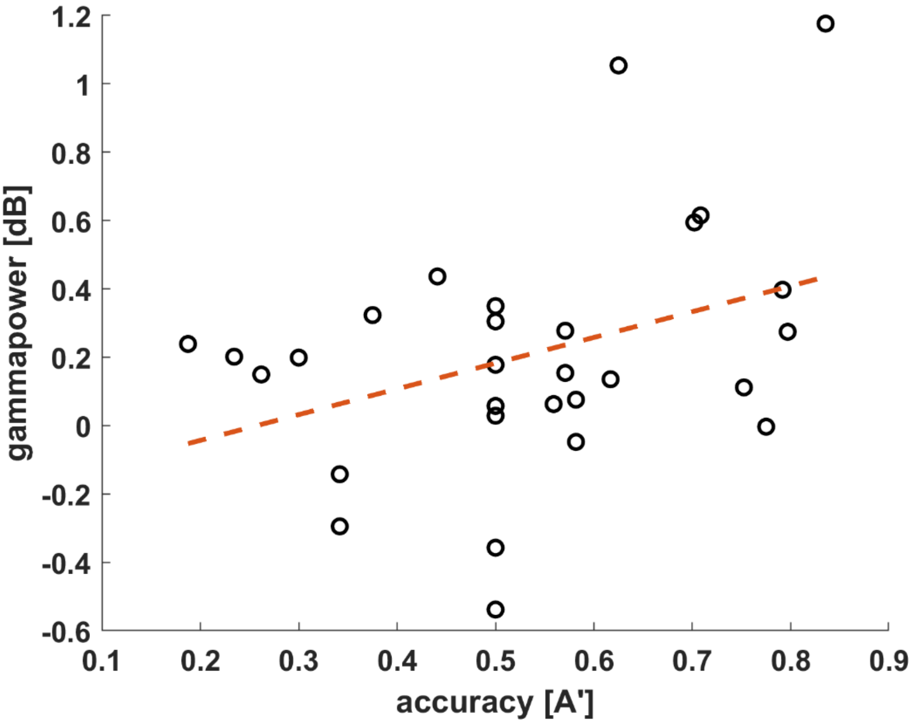

Figure 13. Correlation of the average gamma power (0.5-0.75 s,40-70 Hz) and individual A' values.

Based on this result we pursued the analysis of the gamma window regarding the behavioral results. We compared the AC and C groups to see whether they show a difference and what scalp distribution they exhibit. Permutation statistics revealed an emerging cluster in the average power of the TF window appearing in the left frontoparietal region ($t_{sum} = 860.57$, $p = 0.041$, Fig. 14.). The AC group exhibited higher gamma power (mean = 0.35 dB, SEM = 0.07 dB), than the C group (mean = 0.08 dB, SEM = 0.05 dB).

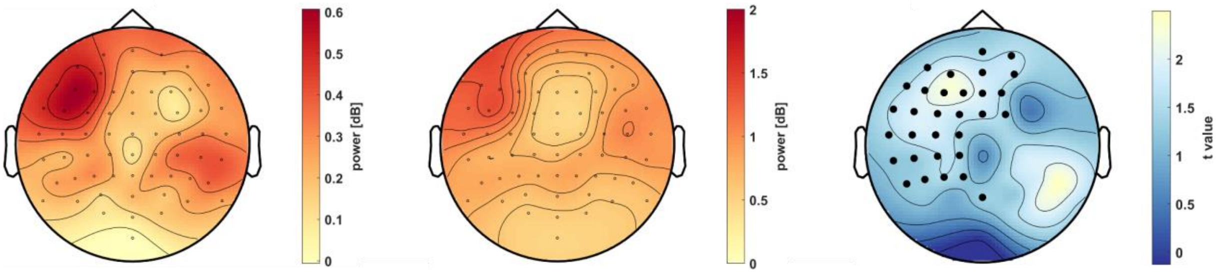

Figure 14. Scalp distribution of the average gamma power (0.5-0.75 s,40-70 Hz). ***Left****: Power difference between AC and C group.* ***Middle****: Standard deviation of the difference between the AC and C group.* ***Right****: Scalp distribution of the statistical difference (t value) between the AC and C group. Channels of the significant cluster (p<0.05) are marked by black dots.*

After determining the scalp distribution of the post stimulus gamma difference, we examined if this activity is whether condition specific. We compared the different conditions (P1, P2 and S) including all subjects first. This analysis did not yield any results as no significant cluster emerged on the scalp. In the next step we compared the condition within the AC and C group separately. The C group again, did not show the appearance of any channel cluster. The examination of the AC group led to the observation of a cluster emerging in the left frontoparietal area ($t_{sum} = 681.3$, $p = 0.021$, Fig.15) when comparing Condition P1 and S.

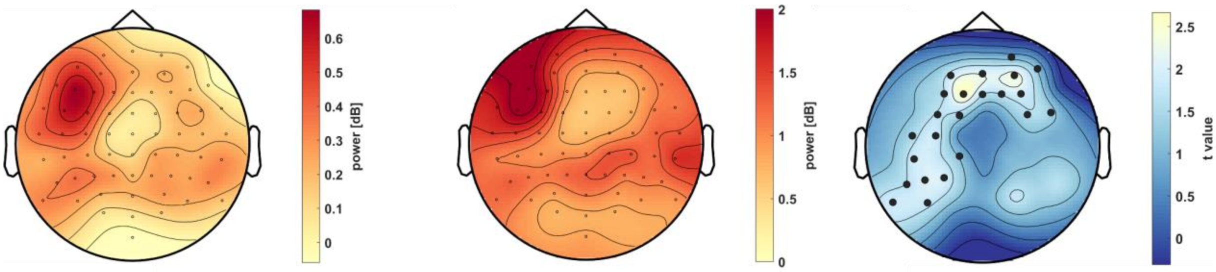

Figure 15. Scalp distribution of the average gamma power (0.5-0.75 s,40-70 Hz). ***Left****: Power difference between Condition P1 and S.* ***Middle****: Standard deviation of the difference between Condition P1 and S.* ***Right****: Scalp distribution of the statistical difference (t value) between the Condition P1 and S. Channels of the significant cluster ($p<0.05$) are marked by black dots.*

Our hypothesis was, that either Condition P2 differs from the other, or Condition P1 shows anticipatory effect thus it shows difference with Condition P2 and S. The isolated difference between Condition P1 and S was not in line with our expectations. To understand the phenomenon, we examined the average power in the TF window (0.5-0.75 s, 40-70 Hz) separately for each condition (Fig. 16.). This observation showed that P1 trials have the highest gamma power on average (mean = 0.469 dB, SEM = 0.118 dB), while the control images have the lowest (mean = 0.219 dB, SEM = 0.049 dB). The means power for Condition P2 was between the other two conditions (mean = 0.322 dB, SEM = 0.102 dB) which can explain why we were not able to detect any difference regarding the predictable images.

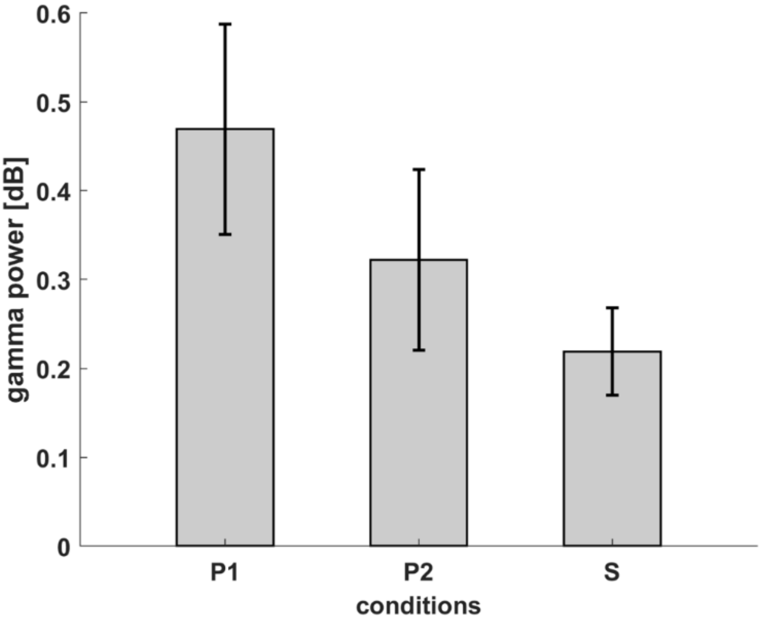

Figure 16. The average gamma power in the window of interest (0.5-0.75 s, 40-70 Hz) by conditions. The error bars indicate SEM.

As the last step, we examined if the gamma activity is phase-locked to the stimulus presentation and performed ITPC analysis in Condition P1 of the AC group and it was compared to a prestimulus baseline window (-0.4 - -0.15 s, 40-70 Hz) in the same group and condition. The ITPC of the AC group (median = 0.07, IQR = 0.005) did not show significant difference (n = 14, z = -0.282, p = 0.78) comparing it against the prestimulus window (median = 0.068, IQR = 0.005).

After demonstrating changes in the gamma range, we examined the theta (4-7 Hz), alpha (8-12 Hz) and beta band (13-30 Hz) but these frequencies did not show any group or condition specific changes or tendencies in the same time window.

Discussion

The apparent fundamentality of SL calls for its meticulous investigation, however this fundamentality also impedes the process. As discussed previously, SL can be observed in numerous paradigms and modalities all with their own distinct cortical and subcortical network. It affects several other cognitive functions and vice versa, while also shows great individual differences. These remarks call for the investigation of SL separately in different modalities and paradigm so we can identify distinct properties that aid us to understand the full picture.

A less frequently studied aspect of SL is the unsupervised paradigm with temporally associated visual stimuli. Our goal was to identify behavioral and cortical properties of unsupervised VSL. To do this we adapted a previously used paradigm (Turk-Browne et al., 2010). First, we established the presence of a skewing motor pattern in the original stream and subsequently modified the temporal regularity to remove this noise. With the new paradigm we managed to observe behavioral features of VSL, like the reduced RT experienced in case of predictable images. Additionally, we examined the learning trajectory which showed a logarithmic trail.

To identify further cortical activities related to VSL we further modified our paradigm, so it is suitable for EEG recording. This way, we observed a high frequency oscillatory activity that showed a positive relationship with the behavioral results of the paradigm. Furthermore, this activity in the left frontoparietal area appeared to be condition specific and emerged between the member of stimulus pairs.

Behavioral study

The aim of the present study was to observe the previously published effects in an unsupervised VSL paradigm: priming and anticipatory effects. We used a modified version of a formerly utilized paradigm in Experiment 1a (Turk-Browne et al., 2010) and replicated their results of reduced RT and greater accuracy for the predictable member of temporally associated image pairs which led to the conclusion of a priming effect, however we could not find any evidence for an anticipatory effect. Notwithstanding this observation, the pattern of the image categories raised doubt whether the results are truly effects of VSL.

Motor learning vs perceptual learning

Experiment 1a only contained category-alternating associated pairs. This resulted in the fact that 65% of the image transitions became category-alternating while category-alternating transition is 100% in the case of a stimulus pair. Furthermore, the smaller chance of category-repeating transitions and thus the violation of the statistical motor information can only occur in Condition P1 and S. The appearance of unexpected stimuli can lead to greater RT (Sebastian et al., 2021) and this further increases the RT difference between category-repeating and category-alternating transitions. This is a form of implicit learning as well, however it cannot be specified as VSL since the acquired information is not visual but rather motor response.

The parallel categorization task and motor responses biased the outcome of the experiment which was proved by a reanalysis of the data of Experiment 1a and the follow-up measurement in Experiment 1b. We reduced the motor pattern by the introduction of category-repeating stimulus pairs, and we experienced a drastic drop in the priming effect size, nevertheless the statistical regularity remained unchanged in the image sequence.

Many have argued before that RT effects in implicit learning paradigms are due to underlying motor learning components rather than perceptual learning (Lungu et al., 2004; Willingham et al., 1989; Zießler, 1994) and in the absence of motor pattern RT changes are not detectable. Since then, the RT effects of sequence learning has been presented (Heyes & Foster, 2002; Mayr, 1996; Robertson & Pascual-Leone, 2001), yet some still question the validity of these results (Dennis et al., 2006) and claim the presence of motor patterns.

The learning trajectory of VSL

After the assessment of Experiment 1a and 1b, we set out to modify this paradigm in a way that shows the behavioral remarks of VSL without underlying motor components. First, we raised the number of subjects and the number stimulus presentation to boost the effect size. We also changed the categorization task to be more straightforward, since participants reported confusion regarding the task. The variance in the RT data and its curve called for the need of insertion a warm-up period at the beginning of the stream so our volunteers can get familiar with task, and we can lower the noise in the data, as well. To reduce the monotone pace of the task random ITI was introduced in the sequence. The modified paradigm appeared as an effective tool to observe behavioral aspects of VSL, since we detected condition specific RT changes and managed to characterize the learning curve.

The analysis of RT data of Experiment 2 revealed the emergence of the priming effect through the changes in the linear trends. Besides, the learning trajectory showed a rather logarithmic curve. This implies the relatively rapid development of SL effect additionally to the evidence, that the number of regularity presentation in the experiments were low compared to other studies (Henin et al., 2021; Moser et al., 2021; Saffran et al., 1997; Siegelman et al., 2018).

This is not the first observation regarding the learning curve of VSL. A previous study had described the phenomenon with similar results (Siegelman et al., 2018). They also experienced an RT drop for expected stimuli compared to unexpected ones after a somewhat low presentation number. They also managed to describe the learning curve which shows a great similarity to our curve, where it exhibits a logarithmic trajectory. A key difference between their and the presented study here is the supervision of the paradigms. Their participants were informed about a regularity thus it cannot be specified as an unsupervised learning similarly the previous designs (Amato & MacDonald, 2010; Gómez et al., 2011; Misyak & Christiansen, 2012). The explicit and implicit learning processes are different and are evidenced by RT difference (Batterink, Reber, Neville, et al., 2015; Batterink, Reber, & Paller, 2015). The explicit instruction also leads to the participants actively searching for regularities, thus changing their attention level (Turk-Browne et al., 2005). Due to this the presented results offer a contribution towards the complete description of different SL phenomena.

A great limitation of the current study is the small effect size experienced in Experiment 2, which is the result of the short learning phase. Many changes have been applied to the original paradigm in one step. Changing the categorization task reduced the effect size in the accuracy data, however more and more studies point towards the direction the accuracy is not a reliable measurement of SL (Y. J. Zhou et al., 2020). Due to this we focused on the effect size in the RT data, which also showed a small effect size. Sacrificing accuracy for the effect size of RT was reasoned, as many viewpoints face towards RT being a reliable implicit measurement of SL (R. Kim et al., 2009). Further action towards boosting the effect size could be increasing the number of presentations. This would lead to longer runs where we must take into consideration the effects of fatigue and lower attention levels.

EEG study

Behavioral results reflect explicit knowledge

Behavioral data of the EEG study showed high variance, which is consistent with previous research (Batterink & Paller, 2017; Bogaerts et al., 2022; Franco et al., 2015; Turk-Browne et al., 2010). This variance can be observed between studies, where some studies report great SL effect (Bogaerts et al., 2020), meanwhile many reports nil behavioral findings (Y. J. Zhou et al., 2020). It is also observable within studies where participants show diverse results, even within a relatively homogeneous population, like young university students (Batterink & Paller, 2017; Pinto et al., 2022).

Though the familiarity test of the EEG study did not yield significant results, the results of the pilot study provided us evidence that the paradigm is adequate to prompt learning effects. Many factors could have played a role in these contradicting results. One factor that cannot be overlooked in this case is fatigue. Participants of the EEG study were exposed to three sequences additional to the time of preparation for the EEG recording, while the volunteers of the pilot study spent considerably shorter time with the measurement. Another likely factor could be the fact that EEG subjects were exposed to three times more pairs during their stimulus presentation. The pictures and the stimulus association were changed in every run, yet it is a possibility that the higher number of regularities took a load on the mnemonic networks. We have evidence that overwriting of previously acquired information is possible and subjects can learn different stimulus associations (Siegelman et al., 2018), but we currently do not have enough information whether the extent of this paradigm is sufficient for this. Despite the nonsignificant results of the familiarity test during the EEG recording, the electrophysiological data cannot be diminished because as discussed before, unsupervised SL utilizes implicit systems while the familiarity test requires explicit knowledge.

High frequency oscillation appeared in correlation with the behavior

The EEG results consist of high frequency oscillation 0.5-0.75 s after post stimulus, which does not appear to be phase-locked to the image presentation. This activity also showed a positive correlation with the behaviors findings and emerged in the frontoparietal region of the scalp. Many cortical oscillations have been associated with SL. Low frequency oscillations, like the theta and alpha band have been observed in regard to stimulus expectancy, where unexpected stimuli were coupled with greater oscillatory power (Cavanagh et al., 2012;

Rungratsameetaweemana et al., 2018; Y. J. Zhou et al., 2020). The beta band also exhibited modulation in previous SL studies. These beta waves appeared diffusely on the scalp and generally had lower power within regularity transition, than between. The power of the beta waves also showed a strong positive correlation with offline measurements of SL (Bogaerts et al., 2020). Currently not many studies have investigated the gamma band in relation to SL, but it's a widely studied frequency band in cognitive and perceptive processes.

Gamma oscillations after stimulus presentation have been divided into early and late activities. Early gamma activity can be identified by its latency, since it usually ends 0.15 s after the presentation of the stimulus, and it is also phase-locked to the stimulus presentation. It is associated with basic perceptual processes in sensory networks (Pulvermüller et al., 1999). These early activities are mostly modulated by exogenous effects. Stimulus properties heavily affect gamma oscillations, both in visual and auditory modalities. Visual stimulus properties, like the size of the stimulus its position from the center, its contrast and details can modulate the gamma activity (Busch et al., 2004; Schadow, Lenz, Thaerig, Busch, Fründ, Rieger, et al., 2007). These modulatory effect caused by the lower level stimulus properties were attributed to the early visual areas (Zaehle et al., 2009). Similar findings were observed in the auditory domain, where basic auditory properties modulate the gamma band in the early auditory areas (Schadow et al., 2009; Schadow, Lenz, Thaerig, Busch, Fründ, & Herrmann, 2007).

Late gamma waves are more diffuse in time and do not appear as phase-locked activity. It can usually be observed anywhere between 0.2-1s from stimulus presentation in the 30-80 Hz range. It was debated whether endogenous effect can alter the gamma response, but since then several cognitive functions have been associated with it. The first to be observed is the relationship of gamma waves and attention (Tiitinen et al., 1993). After this many more factors have been investigated, like stimulus representation (Bertrand & Tallon-Baudry, 2000), mnemonic functions (Busch et al., 2008), language processing (Bastiaansen & Hagoort, 2006) and awareness (Ohla et al., 2007).

The roles and functions of these gamma waves were described in the *match and utilization* model. Early gamma activity represents the matching of the incoming sensory input to previously experienced and acquired environmental information while late gamma is the representation of the utilization process. Utilization involves the control and modification of behavior and other cognitive functions through top-down processes (Herrmann et al., 2004). One cognitive function change could be the control of attention which has been linked to gamma activities before (Fell et al., 2003) and also gamma activity has been observed in the phenomenon that predictable stimuli shift the focus of attention (Gonzalez Andino et al., 2004).

Considering the frequency and temporal properties of the observed gamma activity we can conclude that it can be a late gamma activity representing utilization. The scalp distribution of cortical activities further corroborates their function. Early, posterior oscillations have been tied to lower-level sensory processes, while posterior activities more distant from the stimulus presentation tend to represent executive functions (P. J. Reber et al., 2003; Smittenaar et al., 2013).

Similar observations to the *match and utilization* model have been made, and it was defined as model-free and model-based learning as mentioned previously (Daw et al., 2005; Dayan & Niv, 2008). The two models have a great overlap in their definitions on how to divide cortical processes, however the *match and utilization* model defines its function based on the latencies if the cortical representations, the model-free and model-based learning division rely on the spatial distribution. Stimulus-driven model-free learning is responsible for the extraction and acquisition of environmental stimulus-patterns and regularities. It is hypothesized as a function utilizing bottom-up processes and it is tied to the posterior areas of the brain. Parallelly, model-based learning is a rather top-down process, that makes use of the already collected information and construct a model, an internal representation of the environment. Model-based learning applies the model to adjust cortical function and achieve higher performance, overall leading to a goal-oriented behavior. These processes have been tied to frontal regions. Model-based learning has been linked to the dorsolateral prefrontal cortex (Smittenaar et al., 2013) and SL has its ties with model-free/model-based learning (Tóth et al., 2017; Virag et al., 2015). The model-free/model-based learning theory was tested by disrupting the function of the dorsolateral prefrontal cortex using transcranial magnetic stimulation (Ambrus et al., 2020). Impairing the function of the prefrontal cortex led to the conclusion that model-free and model-based learning are competitive in nature since they found higher SL scores in an SRT task, after manipulating the frontal area.

The frequency, spatial and temporal properties of the observed gamma activity led us to the deduction that this condition specific oscillatory change represents model-based learning, which is analogous to the utilization process. This observation related to explicit processes is valuable, but it does not paint a full picture. Associating frontal gamma activity with explicit knowledge and model-based learning, it does not fully explain the neurological background of the SL variance due to the definition of model-based learning. It involves several cognitive functions (e.g. attention, mnemonic processes, decision-making), thus it does not give a definitive answer. Attention could be a great candidate that would explain the differences experienced here and previously. The performance for attended and unattended stimuli has been observed, where attended stimuli resulted in greater behavioral performance (Richter & de Lange, 2019). Attention is also essential for the formation of explicit memory (Keane et al., 2015), which the familiarity test requires. Future goals involve the systematic investigation of the gamma-band and identification of its source and exact role it plays in the process of SL. Identifying this component helps us understand the neural background and better investigate its function in perception and cognition.

Implicit and explicit aspects of regularity acquisition

We have evidence that both explicit and implicit knowledge emerges during SL (Bertels et al., 2015). However, up until now, there is no accordance about the relationship of these different information. The model-free/model-based frameworks offers a competitive nature between the two, where the inhibition of model-based learning leads to improvements of implicit knowledge (Ambrus et al., 2020). This is also supported by the observation the that inhibition of explicit memory formation aided implicit learning (Frank et al., 2006). We also have evidence that implicit knowledge is unrelated to the recall tests (R. Kim et al., 2009), but these results were questioned claiming the authors conscious knowledge (Bertels et al., 2012). Others claim a parallel link between the implicit and explicit processes and knowledge emerges together with their distinct properties, like their decay in time, but overall they are responsible for the SL effect together (Liu et al., 2023). Some results also led to hypothesis that these systems are interdependent, i.e., that explicit knowledge emerges when we the processing network has enough implicit information and can form predictions. These behavioral observations prompt unclear outcomes, but we also have neural evidence regarding the phenomena.

The disruption of the frontal area functions increased SL scores, while our results indicate that the emerging gamma activity shows a positive correlation with SL scores. This controversy can be resolved by considering the results of different behavioral performance. SRT tasks measure the RT difference which is generally categorized as a measurement of implicit learning and knowledge, while the familiarity test measures the explicit recollection of an acquired regularity (R. Kim et al., 2009). While the previously discussed study found a negative relationship with the engagement of the frontal areas, another study found a correlation between the activity of the posterior regions and the RT results (Batterink, Reber, Neville, et al., 2015). Interestingly, the subsequently recorded results of the familiarity test did not show the same correlation. These results indicated that the posterior areas play a role in the implicit processes of statistical learning. Our results appearing in the frontal region of the scalp emerged as an activity correlating with the explicit knowledge of the participants. It is important to note here that the low spatial resolution and the volume-conduction phenomenon limits our ability to make great conclusions about the localization of the observed cluster.

These observations can be united under the afore-mentioned rostro-caudal or frontoparietal hypothesis (Conway, 2020; Kiebel et al., 2008). The model describes the functional connectivity of the higher-level domain-general areas, like the prefrontal cortex which is responsible for the top-down cognitive control and larger-scale learning, while the parietal areas are modality-specific, and their local computations are affected by higher-levels. The mentioned observation and the presented result can fit into this framework and can complement it with the implicit/explicit observations.

Conclusion

In the presented studies we explored the behavioral and cortical aspects of the unsupervised acquisition of temporally associated visual stimuli. We adapted a previously published paradigm that utilizes stimulus pairs and recorded participants' answers and RTs. We recreated their results and found that predictable stimuli elicited higher accuracies and lower RT. Following these observations, we modified the design to eliminate a suspected motor pattern in the stream. The modified paradigm with the same statistical regularity but lower amount of motor information yielded considerably smaller effects sizes. The individual results of Experiment 1a and 1b and their direct comparison led us to the conclusion that the original design and its results are skewed and do not reflect a reliable SL effect. Subsequently to this remark, we set our goals to modify the design and increase the SL effect. In order to achieve this aim, we increased the number of subjects and the number of presentations. Additionally, we introduced a random warm-up period at the beginning of the sequence and random ITI to reduce the monotony of the task. Based on the lack of trend in the accuracy data, we simplified the categorization task, as well. With these adjustments we managed to observe the reduction of RT and negative linear trend for predictable images without the motor pattern this time. Moreover, we could describe the learning trajectory based on the RT difference of the predictable and control images. The curve showed a logarithmic trajectory which is in line with previous findings.

After establishing the behavioral aspect of unsupervised VSL, we shifted our attention toward the cortical activities associated with SL. We adapted the design to be suitable for EEG recording. This included changing the categorization task to a detection thus eliminating the decision-making and motor activities from the recording and adding a familiarity test and the end of the image stream. After data collection, we first determined a window of interest based on the average of all trials. A window of interest emerged in the gamma range (40-70 Hz) 0.5-0.75 s after stimulus presentation. The average power within the window showed a positive correlation with the results of the familiarity test. To determine the scalp distribution of this behavior-related activity we compared subjects who exceeded the familiarity test above chance with those who did not. This comparison showed that the gamma activity spread across the frontoparietal area with a greater expanse in the frontal region. Additional analysis of this activity revealed that the observed high frequency oscillation is a non-phase locked condition-specific activity, that appears after presentation of the first member of a temporally associated stimulus pair.

The spatial and temporal distribution of the observed activity showed a great similarity with the utilization or model-based learning processes. These cortical functions are described as top-down mechanisms that control our attention, decision making and overall create goal-oriented behavior. These activities are part of a greater cortical network, called frontoparietal network. Previous results and our findings suggest that the posterior part of this network is responsible for the mostly stimulus-driven, bottom-up processes of learning that contribute towards the implicit knowledge of environmental regularity. The anterior areas are responsible for the goal-oriented top-down behavior, that modulates other cognitive functions based on the previously acquired information. Our results show that explicit knowledge shows a correlation with activities related to these top-down processes.

Acknowledgements

First, I would like to thank Prof. Dr. Ferenc Bari and Prof. Dr. Gábor Jancsó for accepting me to the Doctoral School of Theoretical Medicine and the Neurosciences Doctoral program. I’m also grateful to Prof. Dr. Gyula Sáry for allowing me to join the Department of Physiology.

I would like to thank my supervisor, Dr. Péter Kaposvári, for his guidance during my Ph.D. work and my colleagues in the laboratory, Dr. Ágnes Fehér and Dr. András Benyhe for their help and advice during my work. I am also obliged to all my colleagues in the Department of Physiology. And finally, I would like to thank my family and friends for the endless love and support they showed me during these years.

References

Aaronson, D., & Watts, B. (1987). Extensions of Grier’s computational formulas for A′ and B″ to below-chance performance. *Psychological Bulletin*, *102*(3), 439–442. https://doi.org/10.1037/0033-2909.102.3.439

Abla, D., Katahira, K., & Okanoya, K. (2008). On-line Assessment of Statistical Learning by Event-related Potentials. *Journal of Cognitive Neuroscience*, *20*(6), 952–964. https://doi.org/10.1162/jocn.2008.20058

Alamia, A., & VanRullen, R. (2019). Alpha oscillations and traveling waves: Signatures of predictive coding? *PLOS Biology*, *17*(10), e3000487. https://doi.org/10.1371/journal.pbio.3000487

Amato, M. S., & MacDonald, M. C. (2010). Sentence processing in an artificial language: Learning and using combinatorial constraints. *Cognition*, *116*(1), 143–148. https://doi.org/10.1016/j.cognition.2010.04.001

Ambrus, G. G., Vékony, T., Janacsek, K., Trimborn, A. B. C., Kovács, G., & Nemeth, D. (2020). When less is more: Enhanced statistical learning of non-adjacent dependencies after disruption of bilateral DLPFC. *Journal of Memory and Language*, *114*, 104144. https://doi.org/10.1016/j.jml.2020.104144

Arciuli, J., Torkildsen, J. von K., Stevens, D. J., & Simpson, I. C. (2014). Statistical learning under incidental versus intentional conditions. *Frontiers in Psychology*, *5*. https://www.frontiersin.org/articles/10.3389/fpsyg.2014.00747

Aslin, R. N. (2017). Statistical learning: A powerful mechanism that operates by mere exposure. *WIREs Cognitive Science*, *8*(1–2), e1373. https://doi.org/10.1002/wcs.1373

Atallah, H. E., Frank, M. J., & O’Reilly, R. C. (2004). Hippocampus, cortex, and basal ganglia: Insights from computational models of complementary learning systems. *Neurobiology of Learning and Memory*, *82*(3), 253–267. https://doi.org/10.1016/j.nlm.2004.06.004

Bastiaansen, M., & Hagoort, P. (2006). Oscillatory neuronal dynamics during language comprehension. In C. Neuper & W. Klimesch (Eds.), *Progress in Brain Research* (Vol. 159, pp. 179–196). Elsevier. https://doi.org/10.1016/S0079-6123(06)59012-0

Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J. R., De Weerd, P., Kennedy, H., & Fries, P. (2015). Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels. *Neuron*, *85*(2), 390–401. https://doi.org/10.1016/j.neuron.2014.12.018

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). *Fitting Linear Mixed-Effects Models using lme4* (arXiv:1406.5823). arXiv. https://doi.org/10.48550/arXiv.1406.5823

Batterink, L. J., & Paller, K. A. (2017). Online neural monitoring of statistical learning. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *90*, 31–45. https://doi.org/10.1016/j.cortex.2017.02.004

Batterink, L. J., Paller, K. A., & Reber, P. J. (2019). Understanding the Neural Bases of Implicit and Statistical Learning. *Topics in Cognitive Science*, tops.12420. https://doi.org/10.1111/tops.12420

Batterink, L. J., Reber, P. J., Neville, H. J., & Paller, K. A. (2015). Implicit and explicit contributions to statistical learning. *Journal of Memory and Language*, *83*, 62–78. https://doi.org/10.1016/j.jml.2015.04.004

Batterink, L. J., Reber, P. J., & Paller, K. A. (2015). Functional differences between statistical learning with and without explicit training. *Learning & Memory*, *22*(11), 544–556. https://doi.org/10.1101/lm.037986.114

Bertels, J., Boursain, E., Destrebecqz, A., & Gaillard, V. (2015). Visual statistical learning in children and young adults: How implicit? *Frontiers in Psychology*, *5*. https://www.frontiersin.org/articles/10.3389/fpsyg.2014.01541

Bertels, J., Franco, A., & Destrebecqz, A. (2012). How implicit is visual statistical learning? *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(5), 1425–1431. https://doi.org/10.1037/a0027210

Bertrand, O., & Tallon-Baudry, C. (2000). Oscillatory gamma activity in humans: A possible role for object representation. *International Journal of Psychophysiology*, *38*(3), 211–223. https://doi.org/10.1016/S0167-8760(00)00166-5

Bigdely-Shamlo, N., Kreutz-Delgado, K., Kothe, C., & Makeig, S. (2013). EyeCatch: Data-mining over Half a Million EEG Independent Components to Construct a Fully-Automated Eye-Component Detector. *Conference Proceedings : ... Annual International Conference of the IEEE Engineering in Medicine and Biology Society. IEEE Engineering in Medicine and Biology Society. Conference*, *2013*, 5845–5848. https://doi.org/10.1109/EMBC.2013.6610881

Bogaerts, L., Richter, C. G., Landau, A. N., & Frost, R. (2020). Beta-Band Activity Is a Signature of Statistical Learning. *The Journal of Neuroscience*, *40*(39), 7523–7530. https://doi.org/10.1523/JNEUROSCI.0771-20.2020

Bogaerts, L., Siegelman, N., Christiansen, M. H., & Frost, R. (2022). Is there such a thing as a 'good statistical learner'? *Trends in Cognitive Sciences*, *26*(1), 25–37. https://doi.org/10.1016/j.tics.2021.10.012

Boros, M., Magyari, L., Török, D., Bozsik, A., Deme, A., & Andics, A. (2021). Neural processes underlying statistical learning for speech segmentation in dogs. *Current Biology: CB*, *31*(24), 5512-5521.e5. https://doi.org/10.1016/j.cub.2021.10.017

Brady, T. F., Konkle, T., & Alvarez, G. A. (2009). Compression in visual working memory: Using statistical regularities to form more efficient memory representations. *Journal of Experimental Psychology: General*, *138*(4), 487–502. https://doi.org/10.1037/a0016797

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, *10*(4), 433–436. https://doi.org/10.1163/156856897X00357

Brodeur, M. B., Dionne-Dostie, E., Montreuil, T., & Lepage, M. (2010). The Bank of Standardized Stimuli (BOSS), a New Set of 480 Normative Photos of Objects to Be Used as Visual Stimuli in Cognitive Research. *PLOS ONE*, *5*(5), e10773. https://doi.org/10.1371/journal.pone.0010773

Brodeur, M. B., Guérard, K., & Bouras, M. (2014). Bank of Standardized Stimuli (BOSS) Phase II: 930 New Normative Photos. *PLOS ONE*, *9*(9), e106953. https://doi.org/10.1371/journal.pone.0106953

Buiatti, M., Peña, M., & Dehaene-Lambertz, G. (2009). Investigating the neural correlates of continuous speech computation with frequency-tagged neuroelectric responses. *NeuroImage*, *44*(2), 509–519. https://doi.org/10.1016/j.neuroimage.2008.09.015

Burgess, N., Maguire, E. A., & O'Keefe, J. (2002). The Human Hippocampus and Spatial and Episodic Memory. *Neuron*, *35*(4), 625–641. https://doi.org/10.1016/S0896-6273(02)00830-9

Busch, N. A., Debener, S., Kranczioch, C., Engel, A. K., & Herrmann, C. S. (2004). Size matters: Effects of stimulus size, duration and eccentricity on the visual gamma-band response. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, *115*(8), 1810–1820. https://doi.org/10.1016/j.clinph.2004.03.015

Busch, N. A., Groh-Bordin, C., Zimmer, H. D., & Herrmann, C. S. (2008). Modes of memory: Early electrophysiological markers of repetition suppression and recognition enhancement predict behavioral performance. *Psychophysiology*, *45*(1), 25–35. https://doi.org/10.1111/j.1469-8986.2007.00607.x

Cashdollar, N., Ruhnau, P., Weisz, N., & Hasson, U. (2017). The Role of Working Memory in the Probabilistic Inference of Future Sensory Events. *Cerebral Cortex*, *27*(5), 2955–2969. https://doi.org/10.1093/cercor/bhw138

Cavanagh, J. F., Figueroa, C. M., Cohen, M. X., & Frank, M. J. (2012). Frontal Theta Reflects Uncertainty and Unexpectedness during Exploration and Exploitation. *Cerebral Cortex*, *22*(11), 2575–2586. https://doi.org/10.1093/cercor/bhr332

Christiansen, M. H. (2019). Implicit Statistical Learning: A Tale of Two Literatures. *Topics in Cognitive Science*, *11*(3), 468–481. https://doi.org/10.1111/tops.12332

Conway, C. M. (2020). How does the brain learn environmental structure? Ten core principles for understanding the neurocognitive mechanisms of statistical learning. *Neuroscience & Biobehavioral Reviews*, *112*, 279–299. https://doi.org/10.1016/j.neubiorev.2020.01.032

Conway, C. M., Bauernschmidt, A., Huang, S. S., & Pisoni, D. B. (2010). Implicit statistical learning in language processing: Word predictability is the key. *Cognition*, *114*(3), 356–371. https://doi.org/10.1016/j.cognition.2009.10.009

Conway, C. M., & Christiansen, M. H. (2005). Modality-Constrained Statistical Learning of Tactile, Visual, and Auditory Sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *31*(1), 24–39. https://doi.org/10.1037/0278-7393.31.1.24

Crivelli-Decker, J., Hsieh, L.-T., Clarke, A., & Ranganath, C. (2018). Theta oscillations promote temporal sequence learning. *Neurobiology of Learning and Memory*, *153*, 92–103. https://doi.org/10.1016/j.nlm.2018.05.001

Cunillera, T., Càmara, E., Toro, J. M., Marco-Pallares, J., Sebastián-Galles, N., Ortiz, H., Pujol, J., & Rodríguez-Fornells, A. (2009). Time course and functional neuroanatomy of speech segmentation in adults. *NeuroImage*, *48*(3), 541–553. https://doi.org/10.1016/j.neuroimage.2009.06.069

Daw, N. D., Niv, Y., & Dayan, P. (2005). Uncertainty-based competition between prefrontal and dorsolateral striatal systems for behavioral control. *Nature Neuroscience*, *8*(12), Article 12. https://doi.org/10.1038/nn1560

Dayan, P., & Niv, Y. (2008). Reinforcement learning: The Good, The Bad and The Ugly. *Current Opinion in Neurobiology*, *18*(2), 185–196. https://doi.org/10.1016/j.conb.2008.08.003

Delorme, A., & Makeig, S. (2004). EEGLAB: An open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

den Ouden, C., Zhou, A., Mepani, V., Kovács, G., Vogels, R., & Feuerriegel, D. (2023). Stimulus expectations do not modulate visual event-related potentials in probabilistic cueing designs. *NeuroImage*, *280*, 120347. https://doi.org/10.1016/j.neuroimage.2023.120347

Denham, S. L., & Winkler, I. (2020). Predictive coding in auditory perception: Challenges and unresolved questions. *European Journal of Neuroscience*, *51*(5), 1151–1160. https://doi.org/10.1111/ejn.13802

Dennis, N. A., Howard, J. H., & Howard, D. V. (2006). Implicit sequence learning without motor sequencing in young and old adults. *Experimental Brain Research*, *175*(1), 153–164. https://doi.org/10.1007/s00221-006-0534-3

Duncan, D., & Theeuwes, J. (2020). Statistical learning in the absence of explicit top-down attention. *Cortex*, *131*, 54–65. https://doi.org/10.1016/j.cortex.2020.07.006

Evans, J. L., Saffran, J. R., & Robe-Torres, K. (2009). Statistical learning in children with specific language impairment. *Journal of Speech, Language, and Hearing Research: JSLHR*, *52*(2), 321–335. https://doi.org/10.1044/1092-4388(2009/07-0189)

Farbood, M. M., Heeger, D. J., Marcus, G., Hasson, U., & Lerner, Y. (2015). The neural processing of hierarchical structure in music and speech at different timescales. *Frontiers in Neuroscience*, *9*. https://www.frontiersin.org/articles/10.3389/fnins.2015.00157

Fedorenko, E., Duncan, J., & Kanwisher, N. (2012). Language-Selective and Domain-General Regions Lie Side by Side within Broca's Area. *Current Biology*, *22*(21), 2059–2062. https://doi.org/10.1016/j.cub.2012.09.011

Fell, J., Klaver, P., Elfadil, H., Schaller, C., Elger, C. E., & Fernández, G. (2003). Rhinal–hippocampal theta coherence during declarative memory formation: Interaction with gamma synchronization? *European Journal of Neuroscience*, *17*(5), 1082–1088. https://doi.org/10.1046/j.1460-9568.2003.02522.x

Feuerriegel, D., Churches, O., Coussens, S., & Keage, H. A. D. (2018). Evidence for spatiotemporally distinct effects of image repetition and perceptual expectations as measured by event-related potentials. *NeuroImage*, *169*, 94–105. https://doi.org/10.1016/j.neuroimage.2017.12.029

Feuerriegel, D., Vogels, R., & Kovács, G. (2021). Evaluating the evidence for expectation suppression in the visual system. *Neuroscience & Biobehavioral Reviews*, *126*, 368–381. https://doi.org/10.1016/j.neubiorev.2021.04.002

Fiser, J., & Aslin, R. N. (2001). Unsupervised Statistical Learning of Higher-Order Spatial Structures from Visual Scenes. *Psychological Science*, *12*(6), 499–504. https://doi.org/10.1111/1467-9280.00392

Fiser, J., & Aslin, R. N. (2002). Statistical learning of higher-order temporal structure from visual shape sequences. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *28*(3), 458–467. https://doi.org/10.1037/0278-7393.28.3.458

Fitzgerald, K., & Todd, J. (2018). Hierarchical timescales of statistical learning revealed by mismatch negativity to auditory pattern deviations. *Neuropsychologia*, *120*, 25–34. https://doi.org/10.1016/j.neuropsychologia.2018.09.015

Fletcher, P. C., & Frith, C. D. (2009). Perceiving is believing: A Bayesian approach to explaining the positive symptoms of schizophrenia. *Nature Reviews. Neuroscience*, *10*(1), 48–58. https://doi.org/10.1038/nrn2536

Forkstam, C., Hagoort, P., Fernandez, G., Ingvar, M., & Petersson, K. M. (2006). Neural correlates of artificial syntactic structure classification. *NeuroImage*, *32*(2), 956–967. https://doi.org/10.1016/j.neuroimage.2006.03.057

Franco, A., Gaillard, V., Cleeremans, A., & Destrebecqz, A. (2015). Assessing segmentation processes by click detection: Online measure of statistical learning, or simple interference? *Behavior Research Methods*, *47*(4), 1393–1403. https://doi.org/10.3758/s13428-014-0548-x

Frank, M. J., O'Reilly, R. C., & Curran, T. (2006). When Memory Fails, Intuition Reigns: Midazolam Enhances Implicit Inference in Humans. *Psychological Science*, *17*(8), 700–707. https://doi.org/10.1111/j.1467-9280.2006.01769.x

Frost, R., Armstrong, B. C., & Christiansen, M. H. (2019). Statistical learning research: A critical review and possible new directions. *Psychological Bulletin*, *145*, 1128–1153. https://doi.org/10.1037/bul0000210

Frost, R., Armstrong, B. C., Siegelman, N., & Christiansen, M. H. (2015). Domain generality versus modality specificity: The paradox of statistical learning. *Trends in Cognitive Sciences*, *19*(3), 117–125. https://doi.org/10.1016/j.tics.2014.12.010

Frost, R., Siegelman, N., Narkiss, A., & Afek, L. (2013). What Predicts Successful Literacy Acquisition in a Second Language? *Psychological Science*, *24*(7), 1243–1252. https://doi.org/10.1177/0956797612472207

Funahashi, S. (2017). Working Memory in the Prefrontal Cortex. *Brain Sciences*, *7*(5), Article 5. https://doi.org/10.3390/brainsci7050049

Fuster, J. M., & Bressler, S. L. (2012). Cognit activation: A mechanism enabling temporal integration in working memory. *Trends in Cognitive Sciences*, *16*(4), 207–218. https://doi.org/10.1016/j.tics.2012.03.005

Gebauer, G. F., & Mackintosh, N. J. (2007). Psychometric intelligence dissociates implicit and explicit learning. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *33*, 34–54. https://doi.org/10.1037/0278-7393.33.1.34

Gevins, A., Smith, M. E., McEvoy, L., & Yu, D. (1997). High-resolution EEG mapping of cortical activation related to working memory: Effects of task difficulty, type of processing, and practice. *Cerebral Cortex*, *7*(4), 374–385. Scopus. https://doi.org/10.1093/cercor/7.4.374

Gómez, D. M., Bion, R. A. H., & Mehler, J. (2011). The word segmentation process as revealed by click detection. *Language and Cognitive Processes*, *26*(2), 212–223. https://doi.org/10.1080/01690965.2010.482451

Gonzalez Andino, S. L., Michel, C. M., Thut, G., Landis, T., & Grave de Peralta, R. (2004). Prediction of response speed by anticipatory high-frequency (gamma band) oscillations in the human brain. *Human Brain Mapping*, *24*(1), 50–58. https://doi.org/10.1002/hbm.20056

Greve, A., Cooper, E., Kaula, A., Anderson, M. C., & Henson, R. (2017). Does prediction error drive one-shot declarative learning? *Journal of Memory and Language*, *94*, 149–165. https://doi.org/10.1016/j.jml.2016.11.001

Grier, J. B. (1971). Nonparametric indexes for sensitivity and bias: Computing formulas. *Psychological Bulletin*, *75*(6), 424–429. https://doi.org/10.1037/h0031246

Hallgató, E., Győri-Dani, D., Pekár, J., Janacsek, K., & Nemeth, D. (2013). The differential consolidation of perceptual and motor learning in skill acquisition. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *49*(4), 1073–1081. https://doi.org/10.1016/j.cortex.2012.01.002

Harlé, K. M., Zhang, S., Schiff, M., Mackey, S., Paulus, M. P., & Yu, A. J. (2015). Altered Statistical Learning and Decision-Making in Methamphetamine Dependence: Evidence from a Two-Armed Bandit Task. *Frontiers in Psychology*, *6*. https://www.frontiersin.org/articles/10.3389/fpsyg.2015.01910

Hauser, M. D., Newport, E. L., & Aslin, R. N. (2001). Segmentation of the speech stream in a non-human primate: Statistical learning in cotton-top tamarins. *Cognition*, *78*(3), B53–B64. https://doi.org/10.1016/S0010-0277(00)00132-3

Henin, S., Turk-Browne, N. B., Friedman, D., Liu, A., Dugan, P., Flinker, A., Doyle, W., Devinsky, O., & Melloni, L. (2021). Learning hierarchical sequence representations across human cortex and hippocampus. *Science Advances*, *7*(8), eabc4530. https://doi.org/10.1126/sciadv.abc4530

Herrmann, C. S., Munk, M. H. J., & Engel, A. K. (2004). Cognitive functions of gamma-band activity: Memory match and utilization. *Trends in Cognitive Sciences*, *8*(8), 347–355. https://doi.org/10.1016/j.tics.2004.06.006

Heyes, C. M., & Foster, C. L. (2002). Motor learning by observation: Evidence from a serial reaction time task. *The Quarterly Journal of Experimental Psychology A: Human Experimental Psychology*, *55A*(2), 593–607. https://doi.org/10.1080/02724980143000389

Hodapp, A., & Rabovsky, M. (2021). The N400 ERP component reflects an error-based implicit learning signal during language comprehension. *European Journal of Neuroscience*, *54*(9), 7125–7140. https://doi.org/10.1111/ejn.15462

Hsieh, L.-T., & Ranganath, C. (2014). Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *NeuroImage*, *85*, 721–729. https://doi.org/10.1016/j.neuroimage.2013.08.003

Janacsek, K., Fiser, J., & Nemeth, D. (2012). The best time to acquire new skills: Age-related differences in implicit sequence learning across the human lifespan. *Developmental Science*, *15*(4), 496–505. https://doi.org/10.1111/j.1467-7687.2012.01150.x

Janacsek, K., & Nemeth, D. (2013). Implicit sequence learning and working memory: Correlated or complicated? *Cortex*, *49*(8), 2001–2006. https://doi.org/10.1016/j.cortex.2013.02.012

Juhasz, D., Nemeth, D., & Janacsek, K. (2019). Is there more room to improve? The lifespan trajectory of procedural learning and its relationship to the between- and within-group differences in average response times. *PloS One*, *14*(7), e0215116. https://doi.org/10.1371/journal.pone.0215116

Kaposvari, P., Kumar, S., & Vogels, R. (2018). Statistical Learning Signals in Macaque Inferior Temporal Cortex. *Cerebral Cortex*, *28*(1), 250–266. https://doi.org/10.1093/cercor/bhw374

Karuza, E. A., Newport, E. L., Aslin, R. N., Starling, S. J., Tivarus, M. E., & Bavelier, D. (2013). The neural correlates of statistical learning in a word segmentation task: An fMRI study. *Brain and Language*, *127*(1), 46–54. https://doi.org/10.1016/j.bandl.2012.11.007

Kaufman, S. B., Deyoung, C. G., Gray, J. R., Jiménez, L., Brown, J., & Mackintosh, N. (2010). Implicit learning as an ability. *Cognition*, *116*(3), 321–340. https://doi.org/10.1016/j.cognition.2010.05.011

Keane, M. M., Cruz, M. E., & Verfaellie, M. (2015). Attention and Implicit Memory: Priming-Induced Benefits and Costs Have Distinct Attentional Requirements. *Memory & Cognition*, *43*(2), 216–225. https://doi.org/10.3758/s13421-014-0464-4

Kiebel, S. J., Daunizeau, J., & Friston, K. J. (2008). A Hierarchy of Time-Scales and the Brain. *PLOS Computational Biology*, *4*(11), e1000209. https://doi.org/10.1371/journal.pcbi.1000209

Kim, G., Norman, K. A., & Turk-Browne, N. B. (2017). Neural Differentiation of Incorrectly Predicted Memories. *Journal of Neuroscience*, *37*(8), 2022–2031. https://doi.org/10.1523/JNEUROSCI.3272-16.2017

Kim, R., Seitz, A., Feenstra, H., & Shams, L. (2009). Testing assumptions of statistical learning: Is it long-term and implicit? *Neuroscience Letters*, *461*(2), 145–149. https://doi.org/10.1016/j.neulet.2009.06.030

Kleiner, M., Brainard, D., Pelli, D., Ingling, A., Murray, R., & Broussard, C. (2007). What's new in psychtoolbox-3. *Perception*, *36*(14), 1–16.

Knight, R. T., Grabowecky, M. F., & Scabini, D. (1995). Role of human prefrontal cortex in attention control. *Advances in Neurology*, *66*, 21–34; discussion 34-6.

Kok, P., Jehee, J. F. M., & de Lange, F. P. (2012). Less is more: Expectation sharpens representations in the primary visual cortex. *Neuron*, *75*(2), 265–270. https://doi.org/10.1016/j.neuron.2012.04.034

Kristjánsson, A., Vuilleumier, P., Schwartz, S., Macaluso, E., & Driver, J. (2007). Neural basis for priming of pop-out during visual search revealed with fMRI. *Cerebral Cortex (New York, N.Y.: 1991)*, *17*(7), 1612–1624. https://doi.org/10.1093/cercor/bhl072

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*, 1–26. https://doi.org/10.18637/jss.v082.i13

Lavenex, P., & Amaral, D. G. (2000). Hippocampal-neocortical interaction: A hierarchy of associativity. *Hippocampus*, *10*(4), 420–430. https://doi.org/10.1002/1098-1063(2000)10:4<420::AID-HIPO8>3.0.CO;2-5

Lengyel, G., Nagy, M., & Fiser, J. (2021). Statistically defined visual chunks engage object-based attention. *Nature Communications*, *12*(1), Article 1. https://doi.org/10.1038/s41467-020-20589-z

Lengyel, G., Žalalytė, G., Pantelides, A., Ingram, J. N., Fiser, J., Lengyel, M., & Wolpert, D. M. (2019). Unimodal statistical learning produces multimodal object-like representations. *eLife*, *8*, e43942. https://doi.org/10.7554/eLife.43942

Liu, H., Forest, T. A., Duncan, K., & Finn, A. S. (2023). What sticks after statistical learning: The persistence of implicit versus explicit memory traces. *Cognition*, *236*, 105439. https://doi.org/10.1016/j.cognition.2023.105439

Lungu, O. V., Wächter, T., Liu, T., Willingham, D. T., & Ashe, J. (2004). Probability detection mechanisms and motor learning. *Experimental Brain Research*, *159*(2), 135–150. https://doi.org/10.1007/s00221-004-1945-7

Manahova, M. E., Mostert, P., Kok, P., Schoffelen, J.-M., & de Lange, F. P. (2018). Stimulus Familiarity and Expectation Jointly Modulate Neural Activity in the Visual Ventral Stream. *Journal of Cognitive Neuroscience*, *30*(9), 1366–1377. https://doi.org/10.1162/jocn_a_01281

Mandikal Vasuki, P. R., Sharma, M., Ibrahim, R., & Arciuli, J. (2017a). Statistical learning and auditory processing in children with music training: An ERP study. *Clinical Neurophysiology*, *128*(7), 1270–1281. https://doi.org/10.1016/j.clinph.2017.04.010

Mandikal Vasuki, P. R., Sharma, M., Ibrahim, R. K., & Arciuli, J. (2017b). Musicians' Online Performance during Auditory and Visual Statistical Learning Tasks. *Frontiers in Human Neuroscience*, *11*. https://www.frontiersin.org/articles/10.3389/fnhum.2017.00114

Mayr, U. (1996). Spatial attention and implicit sequence learning: Evidence for independent learning of spatial and nonspatial sequences. *Journal of Experimental Psychology:*

Learning, Memory, and Cognition, *22*(2), 350–364. https://doi.org/10.1037/0278-7393.22.2.350

McNealy, K., Mazziotta, J. C., & Dapretto, M. (2006). Cracking the Language Code: Neural Mechanisms Underlying Speech Parsing. *Journal of Neuroscience*, *26*(29), 7629–7639. https://doi.org/10.1523/JNEUROSCI.5501-05.2006

Misyak, J. B., & Christiansen, M. H. (2012). Statistical Learning and Language: An Individual Differences Study. *Language Learning*, *62*(1), 302–331. https://doi.org/10.1111/j.1467-9922.2010.00626.x

Moorselaar, D. van, & Slagter, H. A. (2019). Learning What Is Irrelevant or Relevant: Expectations Facilitate Distractor Inhibition and Target Facilitation through Distinct Neural Mechanisms. *Journal of Neuroscience*, *39*(35), 6953–6967. https://doi.org/10.1523/JNEUROSCI.0593-19.2019

Moser, J., Batterink, L., Li Hegner, Y., Schleger, F., Braun, C., Paller, K. A., & Preissl, H. (2021). Dynamics of nonlinguistic statistical learning: From neural entrainment to the emergence of explicit knowledge. *NeuroImage*, *240*, 118378. https://doi.org/10.1016/j.neuroimage.2021.118378

Musz, E., Weber, M. J., & Thompson-Schill, S. L. (2015). Visual statistical learning is not reliably modulated by selective attention to isolated events. *Attention, Perception, & Psychophysics*, *77*(1), 78–96. https://doi.org/10.3758/s13414-014-0757-5

Nakajima, M., Schmitt, L. I., & Halassa, M. M. (2019). Prefrontal Cortex Regulates Sensory Filtering through a Basal Ganglia-to-Thalamus Pathway. *Neuron*, *103*(3), 445-458.e10. https://doi.org/10.1016/j.neuron.2019.05.026

Nemeth, D., Janacsek, K., & Fiser, J. (2013). Age-dependent and coordinated shift in performance between implicit and explicit skill learning. *Frontiers in Computational Neuroscience*, *7*. https://www.frontiersin.org/articles/10.3389/fncom.2013.00147

Ohla, K., Busch, N. A., & Herrmann, C. S. (2007). Early electrophysiological markers of visual awareness in the human brain. *NeuroImage*, *37*(4), 1329–1337. https://doi.org/10.1016/j.neuroimage.2007.06.010

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2010). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, *2011*, e156869. https://doi.org/10.1155/2011/156869

Parks, J., Askew, N., Creagh-Grave, J., & Nyerges, G. (2020). Presence and abundance of antibiotic resistance genes at an organic goat dairy farm. *International Journal of Undergraduate Research and Creative Activities*, *12*(1), Article 1. https://doi.org/10.7710/2168-0620.0309

Pearce, M. T., Ruiz, M. H., Kapasi, S., Wiggins, G. A., & Bhattacharya, J. (2010). Unsupervised statistical learning underpins computational, behavioural, and neural manifestations of musical expectation. *NeuroImage*, *50*(1), 302–313. https://doi.org/10.1016/j.neuroimage.2009.12.019

Pellicano, E., & Burr, D. (2012). When the world becomes ‘too real’: A Bayesian explanation of autistic perception. *Trends in Cognitive Sciences*, *16*(10), 504–510. https://doi.org/10.1016/j.tics.2012.08.009

Pelucchi, B., Hay, J. F., & Saffran, J. R. (2009). Statistical Learning in a Natural Language by 8-Month-Old Infants. *Child Development*, *80*(3), 674–685. https://doi.org/10.1111/j.1467-8624.2009.01290.x

Perfors, A., & Kidd, E. (2022). The Role of Stimulus-Specific Perceptual Fluency in Statistical Learning. *Cognitive Science*, *46*(2), e13100. https://doi.org/10.1111/cogs.13100

Perkovic, S., & Orquin, J. L. (2018). Implicit Statistical Learning in Real-World Environments Leads to Ecologically Rational Decision Making. *Psychological Science*, *29*(1), 34–44. https://doi.org/10.1177/0956797617733831

Perruchet, P., & Pacton, S. (2006). Implicit learning and statistical learning: One phenomenon, two approaches. *Trends in Cognitive Sciences*, *10*(5), 233–238. https://doi.org/10.1016/j.tics.2006.03.006

Pinto, D., Prior, A., & Zion Golumbic, E. (2022). Assessing the Sensitivity of EEG-Based Frequency-Tagging as a Metric for Statistical Learning. *Neurobiology of Language*, *3*(2), 214–234. https://doi.org/10.1162/nol_a_00061

Poldrack, R. A., & Rodriguez, P. (2004). How do memory systems interact? Evidence from human classification learning. *Neurobiology of Learning and Memory*, *82*(3), 324–332. https://doi.org/10.1016/j.nlm.2004.05.003

Pulvermüller, null, Keil, null, & Elbert, null. (1999). High-frequency brain activity: Perception or active memory? *Trends in Cognitive Sciences*, *3*(7), 250–252. https://doi.org/10.1016/s1364-6613(99)01344-3

Qi, Z., Sanchez Araujo, Y., Georgan, W. C., Gabrieli, J. D. E., & Arciuli, J. (2019). Hearing Matters More Than Seeing: A Cross-Modality Study of Statistical Learning and Reading Ability. *Scientific Studies of Reading*, *23*(1), 101–115. https://doi.org/10.1080/10888438.2018.1485680

Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*(1), Article 1. https://doi.org/10.1038/4580

Raviv, L., & Arnon, I. (2018). The developmental trajectory of children's auditory and visual statistical learning abilities: Modality-based differences in the effect of age. *Developmental Science*, *21*(4), e12593. https://doi.org/10.1111/desc.12593

Reber, A. S. (1967). Implicit learning of artificial grammars. *Journal of Verbal Learning and Verbal Behavior*, *6*(6), 855–863. https://doi.org/10.1016/S0022-5371(67)80149-X

Reber, A. S. (1993). *Implicit learning and tacit knowledge: An essay on the cognitive unconscious* (pp. xii, 188). Oxford University Press.

Reber, P. J., Gitelman, D. R., Parrish, T. B., & Mesulam, M. M. (2003). Dissociating Explicit and Implicit Category Knowledge with fMRI. *Journal of Cognitive Neuroscience*, *15*(4), 574–583. https://doi.org/10.1162/089892903321662958

Richards, B. A., Xia, F., Santoro, A., Husse, J., Woodin, M. A., Josselyn, S. A., & Frankland, P. W. (2014). Patterns across multiple memories are identified over time. *Nature Neuroscience*, *17*(7), Article 7. https://doi.org/10.1038/nn.3736

Richter, D., & de Lange, F. P. (2019). Statistical learning attenuates visual activity only for attended stimuli. *eLife*, *8*, e47869. https://doi.org/10.7554/eLife.47869

Robertson, E. M., & Pascual-Leone, A. (2001). Aspects of sensory guidance in sequence learning. *Experimental Brain Research*, *137*(3), 336–345. https://doi.org/10.1007/s002210000673

Rungratsameetaweemana, N., Itthipuripat, S., Salazar, A., & Serences, J. T. (2018). Expectations Do Not Alter Early Sensory Processing during Perceptual Decision-Making. *The Journal of Neuroscience*, *38*(24), 5632–5648. https://doi.org/10.1523/JNEUROSCI.3638-17.2018

Saffran, J. R., Aslin, R. N., & Newport, E. L. (1996). Statistical Learning by 8-Month-Old Infants. *Science*, *274*(5294), 1926–1928. https://doi.org/10.1126/science.274.5294.1926

Saffran, J. R., Johnson, E. K., Aslin, R. N., & Newport, E. L. (1999). Statistical learning of tone sequences by human infants and adults. *Cognition*, *70*(1), 27–52. https://doi.org/10.1016/S0010-0277(98)00075-4

Saffran, J. R., Newport, E. L., Aslin, R. N., Tunick, R. A., & Barrueco, S. (1997). Incidental Language Learning: Listening (and Learning) Out of the Corner of Your Ear. *Psychological Science*, *8*(2), 101–105. https://doi.org/10.1111/j.1467-9280.1997.tb00690.x

Sanders, L. D., Newport, E. L., & Neville, H. J. (2002). Segmenting nonsense: An event-related potential index of perceived onsets in continuous speech. *Nature Neuroscience*, *5*(7), Article 7. https://doi.org/10.1038/nn873

Schadow, J., Lenz, D., Dettler, N., Fründ, I., & Herrmann, C. S. (2009). Early gamma-band responses reflect anticipatory top-down modulation in the auditory cortex. *NeuroImage*, *47*(2), 651–658. https://doi.org/10.1016/j.neuroimage.2009.04.074

Schadow, J., Lenz, D., Thaerig, S., Busch, N. A., Fründ, I., & Herrmann, C. S. (2007). Stimulus intensity affects early sensory processing: Sound intensity modulates auditory evoked gamma-band activity in human EEG. *International Journal of Psychophysiology*, *65*(2), 152–161. https://doi.org/10.1016/j.ijpsycho.2007.04.006

Schadow, J., Lenz, D., Thaerig, S., Busch, N. A., Fründ, I., Rieger, J. W., & Herrmann, C. S. (2007). Stimulus intensity affects early sensory processing: Visual contrast modulates evoked gamma-band activity in human EEG. *International Journal of Psychophysiology*, *66*(1), 28–36. https://doi.org/10.1016/j.ijpsycho.2007.05.010

Sebastian, A., Konken, A. M., Schaum, M., Lieb, K., Tüscher, O., & Jung, P. (2021). Surprise: Unexpected Action Execution and Unexpected Inhibition Recruit the Same Fronto-Basal-Ganglia Network. *Journal of Neuroscience*, *41*(11), 2447–2456. https://doi.org/10.1523/JNEUROSCI.1681-20.2020

Seitz, A. R., Kim, R., van Wassenhove, V., & Shams, L. (2007). Simultaneous and Independent Acquisition of Multisensory and Unisensory Associations. *Perception*, *36*(10), 1445–1453. https://doi.org/10.1068/p5843

Sherman, B. E., Graves, K. N., & Turk-Browne, N. B. (2020). The prevalence and importance of statistical learning in human cognition and behavior. *Current Opinion in Behavioral Sciences*, *32*, 15–20. https://doi.org/10.1016/j.cobeha.2020.01.015

Shufaniya, A., & Arnon, I. (2018). Statistical Learning Is Not Age-Invariant During Childhood: Performance Improves With Age Across Modality. *Cognitive Science*, *42*(8), 3100–3115. https://doi.org/10.1111/cogs.12692

Siegelman, N., Bogaerts, L., Kronenfeld, O., & Frost, R. (2018). Redefining "Learning" in Statistical Learning: What Does an Online Measure Reveal About the Assimilation of Visual Regularities? *Cognitive Science*, *42*(S3), 692–727. https://doi.org/10.1111/cogs.12556

Siegelman, N., & Frost, R. (2015). Statistical learning as an individual ability: Theoretical perspectives and empirical evidence. *Journal of Memory and Language*, *81*, 105–120. https://doi.org/10.1016/j.jml.2015.02.001

Smittenaar, P., FitzGerald, T. H. B., Romei, V., Wright, N. D., & Dolan, R. J. (2013). Disruption of Dorsolateral Prefrontal Cortex Decreases Model-Based in Favor of Model-free Control in Humans. *Neuron*, *80*(4), 914–919. https://doi.org/10.1016/j.neuron.2013.08.009

Spearman, C. (1904). "General intelligence," objectively determined and measured. *The American Journal of Psychology*, *15*(2), 201–293. https://doi.org/10.2307/1412107

Steinmetz, P. N., Roy, A., Fitzgerald, P. J., Hsiao, S. S., Johnson, K. O., & Niebur, E. (2000). Attention modulates synchronized neuronal firing in primate somatosensory cortex. *Nature*, *404*(6774), 187–190. https://doi.org/10.1038/35004588

Sterzer, P., Adams, R. A., Fletcher, P., Frith, C., Lawrie, S. M., Muckli, L., Petrovic, P., Uhlhaas, P., Voss, M., & Corlett, P. R. (2018). The Predictive Coding Account of Psychosis. *Biological Psychiatry*, *84*(9), 634–643. https://doi.org/10.1016/j.biopsych.2018.05.015

Strube, A., Rose, M., Fazeli, S., & Büchel, C. (2021). Alpha-to-beta- and gamma-band activity reflect predictive coding in affective visual processing. *Scientific Reports*, *11*(1), Article 1. https://doi.org/10.1038/s41598-021-02939-z

Summerfield, C., & de Lange, F. P. (2014). Expectation in perceptual decision making: Neural and computational mechanisms. *Nature Reviews Neuroscience*, *15*(11), Article 11. https://doi.org/10.1038/nrn3838

Summerfield, C., & Koechlin, E. (2008). A Neural Representation of Prior Information during Perceptual Inference. *Neuron*, *59*(2), 336–347. https://doi.org/10.1016/j.neuron.2008.05.021

Tallon-Baudry, C., Bertrand, O., Delpuech, C., & Pernier, J. (1996). Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *16*(13), 4240–4249. https://doi.org/10.1523/JNEUROSCI.16-13-04240.1996

Tiitinen, H. T., Sinkkonen, J., Reinikainen, K., Alho, K., Lavikainen, J., & Näätänen, R. (1993). Selective attention enhances the auditory 40-Hz transient response in humans. *Nature*, *364*(6432), Article 6432. https://doi.org/10.1038/364059a0

Timmann, D., Drepper, J., Frings, M., Maschke, M., Richter, S., Gerwig, M., & Kolb, F. P. (2010). The human cerebellum contributes to motor, emotional and cognitive associative learning. A review. *Cortex; a Journal Devoted to the Study of the Nervous System and Behavior*, *46*(7), 845–857. https://doi.org/10.1016/j.cortex.2009.06.009

Todorovic, A., van Ede, F., Maris, E., & de Lange, F. P. (2011). Prior expectation mediates neural adaptation to repeated sounds in the auditory cortex: An MEG study. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *31*(25), 9118–9123. https://doi.org/10.1523/JNEUROSCI.1425-11.2011

Toro, J. M., & Trobalón, J. B. (2005). Statistical computations over a speech stream in a rodent. *Perception & Psychophysics*, *67*(5), 867–875. https://doi.org/10.3758/BF03193539

Tóth, B., Janacsek, K., Takács, Á., Kóbor, A., Zavecz, Z., & Nemeth, D. (2017). Dynamics of EEG functional connectivity during statistical learning. *Neurobiology of Learning and Memory*, *144*, 216–229. https://doi.org/10.1016/j.nlm.2017.07.015

Turk-Browne, N. B., Jungé, J. A., & Scholl, B. J. (2005). The Automaticity of Visual Statistical Learning. *Journal of Experimental Psychology: General*, *134*(4), 552–564. https://doi.org/10.1037/0096-3445.134.4.552

Turk-Browne, N. B., Scholl, B. J., Chun, M. M., & Johnson, M. K. (2009). Neural Evidence of Statistical Learning: Efficient Detection of Visual Regularities Without Awareness. *Journal of Cognitive Neuroscience*, *21*(10), 1934–1945. https://doi.org/10.1162/jocn.2009.21131

Turk-Browne, N. B., Scholl, B. J., Johnson, M. K., & Chun, M. M. (2010). Implicit Perceptual Anticipation Triggered by Statistical Learning. *Journal of Neuroscience*, *30*(33), 11177–11187. https://doi.org/10.1523/JNEUROSCI.0858-10.2010

Uhrig, L., Dehaene, S., & Jarraya, B. (2014). A Hierarchy of Responses to Auditory Regularities in the Macaque Brain. *Journal of Neuroscience*, *34*(4), 1127–1132. https://doi.org/10.1523/JNEUROSCI.3165-13.2014

Ullman, M. T. (2004). Contributions of memory circuits to language: The declarative/procedural model. *Cognition*, *92*(1), 231–270. https://doi.org/10.1016/j.cognition.2003.10.008

Van Petten, C., & Luka, B. J. (2012). Prediction during language comprehension: Benefits, costs, and ERP components. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, *83*(2), 176–190. https://doi.org/10.1016/j.ijpsycho.2011.09.015

van Witteloostuijn, M., Boersma, P., Wijnen, F., & Rispens, J. (2021). The contribution of individual differences in statistical learning to reading and spelling performance in children with and without dyslexia. *Dyslexia*, *27*(2), 168–186. Scopus. https://doi.org/10.1002/dys.1678

Verneau, M., van der Kamp, J., Savelsbergh, G. J. P., & de Looze, M. P. (2014). Age and Time Effects on Implicit and Explicit Learning. *Experimental Aging Research*, *40*(4), 477–511. https://doi.org/10.1080/0361073X.2014.926778

Virag, M., Janacsek, K., Horvath, A., Bujdoso, Z., Fabo, D., & Nemeth, D. (2015). Competition between frontal lobe functions and implicit sequence learning: Evidence from the long-term effects of alcohol. *Experimental Brain Research*, *233*(7), 2081–2089. https://doi.org/10.1007/s00221-015-4279-8

White, P. M., & Yee, C. M. (2006). P50 sensitivity to physical and psychological state influences. *Psychophysiology*, *43*(3), 320–328. https://doi.org/10.1111/j.1469-8986.2006.00408.x

Willingham, D. B., Nissen, M. J., & Bullemer, P. (1989). On the development of procedural knowledge. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *15*(6), 1047–1060. https://doi.org/10.1037/0278-7393.15.6.1047

Winkler, I., Brandl, S., Horn, F., Waldburger, E., Allefeld, C., & Tangermann, M. (2014). Robust artifactual independent component classification for BCI practitioners. *Journal of Neural Engineering*, *11*(3), 035013. https://doi.org/10.1088/1741-2560/11/3/035013

Winkler, I., Haufe, S., & Tangermann, M. (2011). Automatic Classification of Artifactual ICA-Components for Artifact Removal in EEG Signals. *Behavioral and Brain Functions*, *7*(1), 30. https://doi.org/10.1186/1744-9081-7-30

Zaehle, T., Fründ, I., Schadow, J., Thärig, S., Schoenfeld, M., & Herrmann, C. (2009). Inter- and intra-individual covariations of hemodynamic and oscillatory gamma responses in the human cortex. *Frontiers in Human Neuroscience*, *3*. https://www.frontiersin.org/articles/10.3389/neuro.09.008.2009

Zeileis, A., & Hothorn, T. (2002). *Diagnostic Checking in Regression Relationships*. *2*.

Zhou, F., Wong, V., & Sekuler, R. (2007). Multi-sensory integration of spatio-temporal segmentation cues: One plus one does not always equal two. *Experimental Brain Research*, *180*(4), 641–654. https://doi.org/10.1007/s00221-007-0897-0

Zhou, Y. J., Pérez-Bellido, A., Haegens, S., & de Lange, F. P. (2020). Perceptual Expectations Modulate Low-Frequency Activity: A Statistical Learning Magnetoencephalography Study. *Journal of Cognitive Neuroscience*, *32*(4), 691–702. https://doi.org/10.1162/jocn_a_01511

Zießler, M. (1994). The impact of motor responses on serial-pattern learning. *Psychological Research*, *57*(1), 30–41. https://doi.org/10.1007/BF00452993

Zwart, F. S., Vissers, C. Th. W. M., Kessels, R. P. C., & Maes, J. H. R. (2019). Procedural learning across the lifespan: A systematic review with implications for atypical development. *Journal of Neuropsychology*, *13*(2), 149–182. https://doi.org/10.1111/jnp.12139