

Past, present and prediction: understanding the neural basis of prediction and its effect on memory processing

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Table of contents

Table of contents ..... **ii**

Declaration ..... **i**

Contextual statement ..... **ii**

Manuscript information and author contributions ..... **iii**

Abbreviations ..... **vi**

List of figures ..... **vii**

List of tables ..... **ix**

Abstract ..... **x**

Chapter 1 ..... **1**

1.1. From bottom-up to top-down 1

1.2. Enter predictive coding 2

1.3. Prediction and memory 6

1.4. Neurophysiological research informing the effect of prediction on memory 10
1.4.1. Prediction in language 10
1.4.2. Memory processing and the N400 13
1.4.3. Oscillatory activity, subsequent memory and prediction 15

1.5. The role of individual neural variability in prediction and memory processing 17
1.5.1. Individual alpha frequency (IAF) 18
1.5.2. 1/*f* aperiodic slope 19

1.6. Thesis overview 21

Chapter 2 ..... **23**

ABSTRACT 23

2.1. Introduction 24
2.1.1. Prediction in language as revealed by the N400 component 24
2.1.2. The influence of individual neural factors on prediction 25
2.1.3. Pre-stimulus event-related potentials (ERPs) may provide insight into linguistic prediction 26
2.1.4. The present study 27

2.2. Methods 27
2.2.1. Original study 27
2.2.2. Participants 27
2.2.3. Data Processing 28
2.2.4. ERP analysis 29
2.2.5. Individual alpha frequency and aperiodic 1/*f* slope estimation 30

2.2.6. Statistical analysis 31
2.2.7. Exploratory surprisal analyses 33
2.3. Results 35
2.3.1. SPP effects 35
2.3.2. N400 ERP effects 37
2.3.3. Results of models with surprisal 39
2.3.4. Correlational models 42
2.4. Discussion 43
2.4.1. The SPP may be a limited index of prediction during natural language processing 43
2.4.2. N400 effects at the article are variable and offer mixed results for prediction 44
2.4.3. Predictive processing depends on prior contextual information 45
2.4.4. Individual alpha frequency (IAF) modulates predictive processing during language comprehension 47
2.4.5. Conclusion 48
Interim summary 49
Chapter 3 50
ABSTRACT 50
3.1. Introduction 51
3.1.1. Predictions rely on memories of statistical relationships 51
3.1.2. Predictive processing influences memory encoding 52
3.1.3. Predictability and the N400 event-related potential (ERP) 53
3.1.4. The role of individual neural variability 54
3.1.5. The present study 54
3.2. Materials and methods 54
3.2.1. Participants 54
3.2.2. Stimuli and task 55
3.2.2.1. Outdoor scene task 55
3.2.2.2. Pilot testing 56
3.2.3. EEG measures 57
3.2.4. Experimental design and procedure 57
3.3. Data analysis 59
3.3.1. d-prime (d') calculation 59
3.3.2. EEG data processing 59
3.3.3. ERP generation 60
3.3.4. Individual metrics 60
3.3.5. Statistical analysis 61
3.4. Results 63
3.4.1. Descriptive statistics 63
3.4.2. Linear mixed model results of primary analyses 63
3.4.2.1. Behavioural results 63
3.4.2.2. N400 results 64
3.4.2.3. Combined N400 and behavioural results 66
3.4.3. Exploratory late positivity models 67
3.4.3.1. Late positivity results 68

3.4.3.2. Combined behavioural and late positivity results 69
3.5. Discussion 69
3.5.1. Changes in precision may influence the extent of memory encoding 70
3.5.2. The relationship between N400 amplitude and memory processing 71
3.5.3. The effect of N400 amplitude on memory is modulated by individual alpha frequency (IAF) 72
3.5.4. The significance of late ERP activity for memory encoding 73
3.5.5. Conclusion 74

Interim summary 76

Chapter 4 77

ABSTRACT 77

4.1. Introduction 78
4.1.1. The relationship between oscillations, memory, and prediction 78
4.1.2. The importance of the N400 event-related potential (ERP) for understanding the effect of predictive processing on memory 80
4.1.3. Individual alpha frequency (IAF) 81
4.1.4. The present study 82

4.2. Methods 82
4.2.1. Original study 82
4.2.2. Participants 84

4.3. Data analysis 85
4.3.1. Electroencephalography (EEG) data processing 85
4.3.2. Metrics from the original study 85
4.3.3. Time frequency analysis 85
4.3.4. In-task 1/*f* aperiodic activity 86
4.3.5. Subsequent memory 87
4.3.6. Statistical analysis of hypothesized effects 87

4.4. Results 88
4.4.1. Behavioural results from the memory recognition test 88
4.4.2. Visualizing Oscillatory Activity and ERP Patterns 89
4.4.3. Linear mixed model results of primary analyses 92
4.4.3. Exploratory correlation analysis 94

4.5. Discussion 96
4.5.1. Theta power alone does not relate to subsequent memory 96
4.5.2. IAF may modulate the relationship between prediction and memory encoding 97
4.5.3. The effect of alpha power on memory encoding does not relate to the N400 99
4.5.4. Conclusion 100

Interim summary 101

Chapter 5 102

5.1. Summary of findings and contributions of the research 103

5.2. Implications of the present results for understanding the relationship between prediction and memory processing 104
5.2.1. Understanding how predictability drives memory encoding 105

5.2.2. A potential U-shaped relationship between prediction and memory 106
5.2.3. The N400 as an implicit learning signal 108
5.2.4. A dual mechanism for memory processing 110
5.2.4.1. An implicit mechanism 110
5.2.4.2. An explicit mechanism 111
5.2.3.3. On the distinction between the implicit and explicit systems 113
5.2.5. A role for individual neural variability as measured via IAF 115
5.2.5.1. Explaining the effect of IAF from the perspective of a dual mechanism 115
5.3. Implications for the predictive coding theory 118
5.4. Implications for real-world functioning 120
5.5. Challenges and future directions 122
5.6. Conclusion 124

Reference list 126

Supplementary material 154
Chapter 2: Supplementary material A (2A) Model comparison tables 154
Chapter 2: Supplementary material B (2B) Statistical model outputs 156
Chapter 2: Supplementary material C (2C) Statistical outputs of SPP models with surprisal 166
Chapter 2: Supplementary material D (2D) 178
Chapter 3: Supplementary material A (3A) 181
Chapter 4: Supplementary material A (4A) 190

Appendices 196
Appendix A: Permissions 196
Appendix B: Statements of authorship 208

Declaration

This thesis presents work carried out by myself and does not incorporate without acknowledgement any material previously submitted for a degree or diploma in any university; to the best of my knowledge it does not contain any materials previously published or written by another person except where due reference is made in the text; and all substantive contributions by others to the work is presented, including jointly authored publications, are clearly acknowledged.



Sophie Louise Jano
30th September 2024

Contextual statement

This thesis is submitted as a 'Thesis Containing Published Research' in accordance with the University of South Australia's Academic Regulations for Higher Degrees by Research Clause 16.1.1.b. This presentation method allows students to submit a combination of conventional chapters and publications. It is required that publications be produced, published or accepted for publication in peer-reviewed journals or conference proceedings during the student's candidature. The requirements of a 'Thesis Containing Published Research' are as follows:

- Each publication must be peer reviewed and recognised for the University's publication collection
- Each publication must be published or accepted for publication pending revisions for publication in significant journals, books, and/or conference proceedings relevant to the discipline. The Associate Dean: Research Education (or equivalent) will have a list of journals and conferences that meet the University's requirement for ranked journals and conferences in the relevant Field of Research
- Conference papers published in conference proceedings and book chapters can only be included where there is evidence of peer review of the full work
- For publications that have been accepted for publication pending revisions, the principal supervisor must provide written confirmation that revisions required by referees and/or the editor have been made. This confirmation must be incorporated in an appendix to the thesis
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Manuscript information and author contributions

Jano, S., Cross, Z. R., Chatburn, A., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2024). Prior Context and Individual Alpha Frequency Influence Predictive Processing during Language Comprehension. *Journal of Cognitive Neuroscience*, *36*(9), 1-39. https://doi.org/10.1162/jocn_a_02196

This is a published manuscript that advances understandings of prediction during language processing, critically positioning it within the broader cognitive neuroscience literature. The findings of this paper inform the neurophysiological activity underlying prediction, contributing to the central ideas explored throughout the thesis.

Contributions according to the contributor role taxonomy (CRediT)
S.J: Conceptualisation, methodology, formal analysis, data curation, writing – original draft preparation, writing – review and editing, visualisation. **Z.C:** Conceptualisation, methodology, formal analysis, writing – review and editing, supervision. **A.C:** Conceptualisation, methodology, writing – review and editing, supervision. **M.S:** Conceptualisation, methodology, writing – review and editing, supervision. **I.B:** Conceptualisation, methodology, formal analysis, writing – review and editing, supervision.

Jano, S., Chatburn, A., Cross, Z., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2024). How predictability and individual alpha frequency shape memory: Insights from an event-related potential investigation. *Neurobiology of Learning and Memory, 108006*. https: //doi.org/10.1016/j.nlm.2024.108006

This manuscript has recently been published in the Neurobiology of Learning and Memory journal. It describes an electroencephalography experiment on predictability and memory, providing key insights into the core themes of the present thesis.

Contributions according to the contributor role taxonomy (CRediT)
S.J: Conceptualisation, methodology, investigation, project administration, formal analysis, data curation, writing – original draft, writing – review and editing, visualisation. **A.C:** Conceptualisation, methodology, writing – review and editing, supervision. **Z.C:** Conceptualisation, methodology, writing – review and editing, supervision. **M.S:** Conceptualisation, methodology, writing – review and editing, supervision. **I.S:** Conceptualisation, methodology, formal analysis, writing – review and editing, supervision, project administration.

Jano, S., Schlesewsky, M., Chatburn, A., Coussens, S., Cross, Z. R., & Bornkessel-Schlesewsky, I. (2024). *Predictive influences on memory encoding: investigating oscillations and the N400 event-related potential component*. bioRxiv. https://doi.org/10.1101/2024.09.27.615404

This paper is critically placed within the context of the thesis to examine how nuanced changes in prediction-related neurophysiological activity relate to subsequent memory performance. As such, it provides novel insight informing the overarching research questions.

Contributions according to the contributor role taxonomy (CRediT)

S.J: Conceptualisation, methodology (concerning analysis of data), project administration, formal analysis, data curation, writing – original draft, writing – review and editing, visualisation. **M.S:** Conceptualisation, methodology (concerning analysis of data), supervision. **A.C:** Writing – review and editing, supervision. **S.C:** Methodology (concerning analysis of data). **Z.C:** writing – review and editing, supervision. **I.B:** Conceptualisation, methodology (concerning analysis of data), supervision.

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Abbreviations

AMTL anterior medial temporal lobe

BOLD blood-oxygen-level-dependent

BIDS brain imaging data structure

CoG centre of gravity

EEG electroencephalography

EOG electrooculogram

ERN error-related negativity

ERP event-related potential

FFT fast Fourier transform

FMT frontal midline theta

FOOOF fitting Oscillations & One Over f

FRN feedback-related negativity

GPT-2 Generative Pre-Trained Transformer 2

IAF individual alpha frequency

ICA independent component analysis

IRASA Irregular Resampling Auto-Spectral Analysis

LMM linear mixed-effects model

LRT likelihood ratio test

LTP long-term potentiation

MEG magnetoencephalography

MMN mismatch negativity

mPFC medial prefrontal cortex

MTL medial temporal lobe

PAF peak alpha frequency

PSD power spectral density

RPE reward prediction error

SLIMM schema-linked interactions between medial prefrontal and medial temporal lobe

SPEAR separate phases of encoding and retrieval

SPM synaptic plasticity and memory hypothesis

SPN stimulus preceding negativity

SPP semantic prediction potential

List of figures

Figure 1.1. Example schematic of the hierarchical predictive coding framework.....6
Figure 1.2. Schematic of pattern separation and pattern completion.....9
Figure 1.3. Depicting typical N400 trends.....12
Figure 1.4. Power spectral density (PSD) plot depicting the 1/*f* slope and individual alpha frequency (IAF).....20
Figure 2.1. The number of participants at each stage of the data analysis.....28
Figure 2.2. SPP ERP grand average plots for articles according to between-sentences article cloze probability.....34
Figure 2.3. Grand average ERP plots for noun words according to noun cloze probability...36
Figure 2.4. Linear mixed model results depicting the effect of noun cloze probability on SPP amplitude.....37
Figure 2.5. Grand average ERP plots of N400 effects for articles according to article cloze probability.....38
Figure 2.6. Linear mixed model results for N400 effects.....39
Figure 2.7. Grand average N400 ERP plots for articles according to article surprisal.....40
Figure 2.8. Grand average N400 ERP plots for nouns according to noun surprisal.....41
Figure 2.9. Linear mixed model results of article surprisal effects.....42
Figure 2.10. Spearman correlations depicting the relationship between cloze probability and surprisal.....43
Figure 3.1. Schematic of the outdoor scene task.....57
Figure 3.2. Behavioural data showing d' performance.....64
Figure 3.3. Grand average plots depicting mean ERP activity according to image condition, sagitallity and laterality.....65
Figure 3.4. Grand average plots depicting mean ERP activity according to image position..66
Figure 3.5. The modelled effect of image position on N400 amplitude, and the interaction between N400 amplitude and IAF on d'.....67
Figure 3.6. The modelled effect of image position and condition on late positivity amplitude, and the effect of late positivity amplitude on d'.....69
Figure 4.1. Adapted from Jano, Chatburn, and colleagues (2024) showing the outdoor scene task.....84
Figure 4.2. Boxplots depicting hit rates and miss rates between predictable and unpredictable image conditions.....89
Figure 4.3. Time-frequency heat maps according to condition.....90
Figure 4.4. Time-frequency heat maps according to memory hits and misses.....91
Figure 4.5. Grand average ERP amplitude at frontal channels according to time and subsequent memory performance.....92
Figure 4.6. Linear mixed-effects model results of the relationship between alpha oscillatory power, image position, image condition, and IAF.....93

Figure 4.7. Linear mixed-effects model results depicting the relationship between theta power, N400 amplitude, memory recognition, and IAF 95
Figure 4.8. The correlation between IAF and hit rate 95
Figure 5.1. Schematic of the schema-linked interactions between medial prefrontal and medial temporal lobe (SLIMM) model 107
Figure 5.2. Schematic of the proposed relationship between prediction, IAF and memory. 117

List of tables

Table 2.1. The mean number of trials per condition that were entered into the ICA 29
Table 2.2. Linear mixed-effects models for primary analyses 32
Table 2.3. Example sentence demonstrating the cloze probability values for both the unexpected and expected continuations 33
Table 2.4. Exploratory linear mixed-effects model structures 35
Table 3.1. Linear mixed-effects model structures 62
Table 3.2. Mean d' scores per image condition and position 63
Table 3.3. Linear mixed-effects model structures for exploratory models 68
Table 4.1. Linear mixed-effects model structures 88
Table 5.1. Frequently cited distinctions between implicit and explicit memory 110

Abstract

The brain may be constantly involved in inferring upcoming information from prior experience. To do so, it likely draws on representations in memory and learnt understandings of the world. However, there is room for further clarification into the neural dynamics, the sources of individual variability, and the theoretical intricacies that contribute to this relationship. This doctoral thesis aims to explore the neurophysiological underpinnings of predictive processing to understand the association between prediction and memory. It harnesses existing theoretical and empirical knowledge to expand upon the literature and to unite perspectives across subfields of cognitive neuroscience.

Chapter 1 begins with an introduction to the principles underpinning predictive processing, and subsequently leads into a discussion of the link between prediction and memory. It introduces the importance of individual neural variability for this relationship, stemming from the experience-dependent nature of prediction. Chapter 2 describes a reanalysis of a large-scale linguistic study, which provides evidence for the prediction of detailed linguistic attributes. This analysis was integral to understanding prediction as a unified mechanism, and for shedding light on the event-related potential (ERP) activity that may index predictive processing. From here, Chapter 3 applies this knowledge to an electroencephalography experiment to track changes in predictive processing in a non-linguistic context. Neural activity associated with prediction was related to later remembering for certain individuals, suggesting that predictability can influence memory formation. Chapter 4 extends upon this experiment by combining an analysis of ERP activity and subsequent memory with oscillatory patterns. This study ultimately highlights the complex relationship between prediction and memory, suggesting that the two may not always be mutually exclusive. Finally, Chapter 5 interprets the findings in light of their contribution to the literature. It relates prediction to a familiar dual memory system and discusses the broader implications of the results and suggestions for forthcoming research.

Collectively, the findings of the current thesis provide evidence for the electrophysiological markers that contribute to subsequent memory recognition and to prediction during language comprehension. They also offer unique perspectives on the importance of individual neural factors for this relationship, suggesting that individuals may differ in the degree to which implicit predictions can be seen to drive explicit memory. Ultimately, this thesis emphasises the interconnectedness between prediction and memory, in conjunction with the variability associated with this relationship.

Chapter 1

General introduction

The brain is exceptionally intricate and adaptive, exerting widespread control over bodily functions such as respiration and heart rate, whilst giving rise to the emergence of higher-order cognitive phenomena like consciousness and theory of mind. It can rapidly and expertly integrate a myriad of stimuli to interpret the external environment, facilitating fine-tuned adjustments of behaviour in accordance with our sensations. Although these are only a few of the many functions exerted by the human brain, there is no question that this organ plays a focal role in defining each individual's experience of 'life' in all its richness. Consequently, the scientific emphasis on understanding the brain and its inner workings is not surprising. However, whilst the field of cognitive neuroscience has made significant advances towards studying the brain and its cognitive phenomena, many aspects of cognitive processing remain somewhat illusive. Moreover, an agreed-upon unitary theory of brain functioning is currently lacking. However, notions that rely on the brain's capacity to predict upcoming information (Friston, 2010; Huang & Rao, 2011; Rao & Ballard, 1999) may provide promising answers to some of the questions that have previously been posed, and to those yet to come. The present thesis broadly seeks to investigate the neural basis of *prediction* and its effects on learning and memory, to shed light on the strong interconnectedness between past, present and future. If the brain is a prediction machine (A. Clark, 2013; Friston, 2008; Van Berkum, 2010), then an investigation into how predictions shape memory is necessary to understand how the brain learns and adapts to its environment. This chapter begins with an introduction to prediction in the brain, including a discussion of the predictive coding theory, Bayesian Inference, and the Free Energy Principle. The second half of this chapter is devoted to the electrophysiological underpinnings of prediction and finally, to predictions' influence over what is learnt and used for the future (i.e., memory). However, in order to describe prediction, it is imperative to first introduce the broad notions of bottom-up and top-down processing.

1.1. From bottom-up to top-down

Traditional models of perception proposed that percepts were incrementally built from external sensory information in a bottom-up manner (for summaries see Engel et al., 2001; A. Clark, 2014, p. 23). For example, when light hits the retina, photoreceptors in the eye transduce that information into a neural signal that is conducted along the optic nerve before eventually reaching the occipital cortex where the information is processed (Riener, 2019). This (albeit simplified) example of visual processing implies that perception occurs in a series of incremental, unidirectional steps and does not formally consider the importance of contextual knowledge for this process (Riener, 2019). This is in contrast to an argument put forth by Hermann Von Helmholtz, who suggested that visual stimuli are so inherently complex and

vague that it would be difficult to interpret such information in a purely bottom-up manner (Kersten et al., 2004). As such, Helmholtz surmised that some form of prior knowledge must be applied when interpreting a sensory stimulus (Kersten et al., 2004). This appears especially probable given that the brain must rapidly process information to function efficiently (Press et al., 2020; Press & Yon, 2019). Today, it is generally accepted that what one perceives is not a linear and completely accurate representation of the external environment (Riener, 2019). Instead, perception involves the dynamic interplay of both bottom-up mechanisms relating to the transduction of external sensory stimuli, and top-down processes pertaining to the internally driven influence of prior knowledge, goals, experiences and expectations (Dijkstra et al., 2017; Gordon et al., 2019; Mechelli et al., 2004; Riener, 2019). It is this multifaceted and iterative interaction that may thus underlie the brain's ability to rapidly adapt to a complex and ever-changing environment (Press & Yon, 2019).

Numerous studies emphasise the importance of top-down processing for perception, with top-down expectations influencing perception in the face of ambiguous information (Bar, 2004; Toppino, 2003) and being shown to enhance neural representations of sensory inputs (Kok et al., 2012). Other research demonstrates the effects of selective attention on pain perception (Hauck et al., 2015), of prior knowledge in affecting speech perception (Sohoglu et al., 2012), and of attention and emotional cues on the perception of threats (Sussman et al., 2016). Early research by Darley and Gross (1983) also highlights the role of top-down processing in the perpetuation of stereotypes, as participants rated a child's abilities as poorer when they were told that the child came from a low versus a high socioeconomic background. Therefore, as the application of internal goals, knowledge and experiences to incoming information will affect the interpretation of that information, top-down processing likely has implications for a wide array of cognitive and behavioural phenomena, such as learning, biases, memory, social interactions, and even mental illnesses (e.g., anxiety; Sussman et al., 2016). Consequently, the importance of understanding how individuals apply such expectations to interpret environmental information transcends theoretical knowledge to influence functioning in everyday life. It is this notion of top-down and bottom-up processing that forms a basis for understanding prediction in the brain (Bastos et al., 2012; Rauss & Pourtois, 2013).

1.2. Enter predictive coding

Humans are remarkably adept at not only anticipating simple sensory stimuli (e.g., the feeling of the pavement as we are about to take a step), but also at predicting complex events far into the future (e.g., planning one's career trajectory). This general capacity for prediction has been operationalised more formally via the predictive processing framework, which is growing as an explanatory mechanism within the field of cognitive neuroscience (Hohwy, 2020). Whilst prediction as a broader concept may encompass many theories, one such process theory known as predictive coding is particularly prominent and provides a specific computational strategy for the implementation of prediction in the brain (Friston, 2005; Hohwy, 2020). Predictive coding proposes that the brain constructs generative models of the environment that are applied to incoming sensory inputs to predict their causes (A. Clark, 2013; Friston, 2005; Huang & Rao, 2011; Rao & Ballard, 1999). Such predictive models may be likened with top-down

processes, in that the application of a predictive model constitutes a top-down (feedback) transmission that is compared with the bottom-up (feedforward) inputs along a series of neuronal connections (Bastos et al., 2012; Friston, 2005; Rao & Ballard, 1999). As such, the theory draws largely on the processing hierarchies in the brain, being able to explain brain functioning at both a basic sensory level and pertaining to higher-order representations (Bastos et al., 2012; Friston, 2005; Shipp, 2016). Therefore, predictive coding (and the broader framework of predictive processing) may play an important role in the unification of functioning across various domains (A. Clark, 2013). Given the theory's neurobiological basis and its specificity, the present thesis focusses heavily on predictive coding as a model to understand prediction in the brain. From here, it is imperative to introduce in more detail the assumptions of the predictive coding theory.

Predictive coding places causal inference at the heart of perceptual processing, such that perception relies on the brain's ability to interpret the cause of a given sensation (Friston et al., 2006; Hobson & Friston, 2012; Hohwy, 2013, 2020; Rao & Ballard, 1999; Spratling, 2017). The theory emphasises the *inverse* nature of perception by suggesting that when the brain receives a sensation, to interpret it, it must infer the hidden causes of the sensory input that it is receiving (i.e., the factors that lead to that input; Hohwy, 2020; Rao & Ballard; 1999; Spratling, 2017). It does this by relating the sensory information to a generative or forward model (i.e., a model that generates the sensory information; Parr et al., 2022, p. 16; A. Clark, 2014, p. 26). Predictive coding is grounded in Bayesian inference (or Bayes' rule), suggesting that the generative model is comprised of the *prior probability* (the probability of the hypothesis itself independent of its fit to the sensory input), and the *likelihood* (the probability that the hypothesis explains the causes of the given sensory information; Friston, 2010; Hohwy, 2013, p. 17; Parr et al., 2022, p. 17). This information is then used to update the *posterior probability* (the probability of the sensory data's causes, weighted by prior experience; Friston, 2010; Rao et al., 2002). Consequently, the brain is proposed to select the strongest prediction (i.e., the one with the highest posterior probability), when inferring the causes of sensory information (Hohwy, 2013, pg. 36). To summarise, the brain predicts upcoming inputs based on prior beliefs and the probability that the prediction explains the sensory input in question. But what happens if the sensory information is incongruent with the prediction? This can be explained via a consideration of free energy and prediction error.

The Bayesian brain is situated within the Free Energy Principle, which suggests that biological systems "resist a tendency to disorder" (Friston et al., 2006; Friston, 2009, p. 293, 2010, p. 127). This disorder is equated to free energy, which under simple derivations, reflects the difference between the actual sensory data and the prediction of that data (i.e., the prediction error; Friston, 2009, 2010). The brain is proposed to reduce free energy in the system by predicting the causes behind the sensory data, whilst only representing that data (in the form of a prediction error) if the prediction is unsuccessful in anticipating the sensory stimulus (Friston, 2010; Huang & Rao, 2011; Rao & Ballard, 1999). In this case, prediction errors are used to update the predictive model (Friston, 2010; Rao & Ballard, 1999). On the other hand, accurate sensory predictions are proposed to lead to the silencing of prediction error-encoding neuronal populations by top-down predictions, which 'explain away' the error relating to a

stimulus and consequently reduce free energy (Friston, 2005, 2010). This process is supposedly implemented by two neuronal populations; one that encodes the prediction error relating to a signal, and another that represents the expectation of the sensory data's causes (Jehee & Ballard, 2009; Rao & Ballard, 1999). While this process of 'explaining away' errors may imply that accurately predicted (i.e., redundant) information is not represented in the brain, predictions may also sharpen sensory representations by reducing brain activity at lower levels that is incongruent with the higher-level prediction (for discussion see Friston, 2005; Kersten et al., 2004; Kok et al., 2012). Regardless of how error signals are managed however, prediction may be integral for optimising sensory processing and energy expenditure. Furthermore, while the brain may reduce prediction errors by updating predictions, it may also minimise error via *active inference*, where the individual can instead act to sample the environment to promote sensations that fit the predicted outcome (e.g., by moving toward a predicted object so that it comes into view; A. Clark, 2013; Friston et al., 2011; Friston et al., 2010; Parr et al., 2022). Consequently, theories of active inference take into account the agency of an organism (Hohwy, 2013), whilst uniting perception and action with the common goal of error minimisation (Parr et al., 2022, p. 25). When considering the relationship between prediction, Bayesian inference, free energy and active inference, a highly dynamic picture of predictive processing begins to emerge. Such a process would likely require flexible and adaptable neural architecture, hence prediction's proposed dependence on the hierarchical circuitry in the brain (Bastos et al., 2012; Friston, 2005).

The application of a predictive model is proposed to occur at each level of the cortical hierarchy, where predictions at one level anticipate the nature of the incoming stimulus at the next (Huang & Rao, 2011; Rao & Ballard, 1999). If the sensory information at one level is incongruent with the prediction, the residual prediction error is sent upwards in a feedforward manner to correct the original prediction (Huang & Rao, 2011; Rao & Ballard, 1999) Interestingly, whilst lower levels of the hierarchy represent stimuli at rapid time scales, higher levels code for information that changes across longer temporal scales (Parr et al., 2022). Hierarchical predictive processing is most intuitive to explain in the context of the visual system, which is hierarchically organised such that cells in lower-order visual regions of the cortex code for basic stimulus properties, whilst cells in higher-order regions represent more complex attributes (Hegdé & Van Essen, 2000; Hubel & Wiesel, 1968). Here, it is helpful to borrow Noë's (2004) example of a cat partially hidden behind a picket fence (originally used to highlight how objects can be experienced as perceptual wholes by the system, but also useful in describing hierarchical predictive processing; see also Hohwy, 2013's use of this example). When in this scenario (*Figure 1.1)*, the brain may apply a lower-level visual prediction that concerns the colours, edges and line orientations associated with a cat (Huang & Rao, 2011; Rao & Ballard, 1999). As the receptive fields of the neurons at these lower levels may operate on shorter timescales (Huang & Rao, 2011), such attributes are likely to be processed rapidly by the sensory system. At higher levels, the brain may predict information that changes at a slower time course and that provides the context within which lower-level perceptual information fluctuates (e.g., a cat's direction of movement or its likely behaviour; Kiebel et al., 2008). If the animal moved from behind the fence, and was revealed instead to be a dog, prediction errors may cascade from lower levels (as colours and line orientations may be

inconsistent with representations of a cat), to higher-order areas (Huang & Rao, 2011; Rao & Ballard, 1999), allowing the system to process this incongruent shape wholly and semantically as a dog. Whilst the basic principles used in this example can be applied to a myriad of situations (for a discussion of extra-classical receptive field effects in the visual cortex, see Rao & Ballard, 1999), they may also provide a theoretical explanation behind the brain's adeptness for efficient environmental adaptation. Hierarchical predictive coding notions explain how the brain reduces redundancy whilst extending upon the basic notions of top-down versus bottom-up processing (Huang & Rao, 2011). This renders predictive coding an attractive mechanism to explain cognitive processing, and as such, its proposal as a unifying theory of brain functioning is unsurprising (Friston, 2010; Huang & Rao, 2011).

Predictive coding provides a seemingly straightforward framework of cognitive processing, and as such, it is thought to underlie general brain functioning (Huang & Rao, 2011). Evidence for prediction is provided by research in many fields ranging from visual perception (Rao & Ballard, 1999), object recognition (Bar, 2004), action perception (Kilner et al., 2007), theory of mind (Koster-Hale & Saxe, 2013), self-recognition (Apps & Tsakiris, 2014), and beyond to clinical contexts (e.g., Horga et al., 2014; Von Der Lühe et al., 2016). The universality of prediction is also furthered by the wide range of cognitive theories that are arguably synonymous for prediction or that at least in part draw on notions within the predictive processing framework. For example, the theory of optimal feedback control explains voluntary motor behaviour as involving the integration of sensory feedback signals with an 'efferent copy' (i.e., a forward internal model; Scott, 2004). Myers and colleagues (2015) also discuss the notion of a 'sensory template' – a framework to which the brain compares incoming sensory information. Furthermore, prior to the formal conceptualisation of predictive coding in the brain, many proposed a feed-forward/feedback relationship in the neural hierarchy, such that higher-order areas coded for hypotheses or expectations, which were then reconciled with the neural signals in lower-order areas representing the sensory stimulus itself (Mumford, 1992). As such, despite variations in the specific terms used, the above theories have in common the notion that the brain applies some form of model to interpret the incoming data. As multiple subfields have come to accept prediction (or its variants) as a significant influence on perception and cognition, it is imperative to understand the consequences of this process for learning and memory processing.

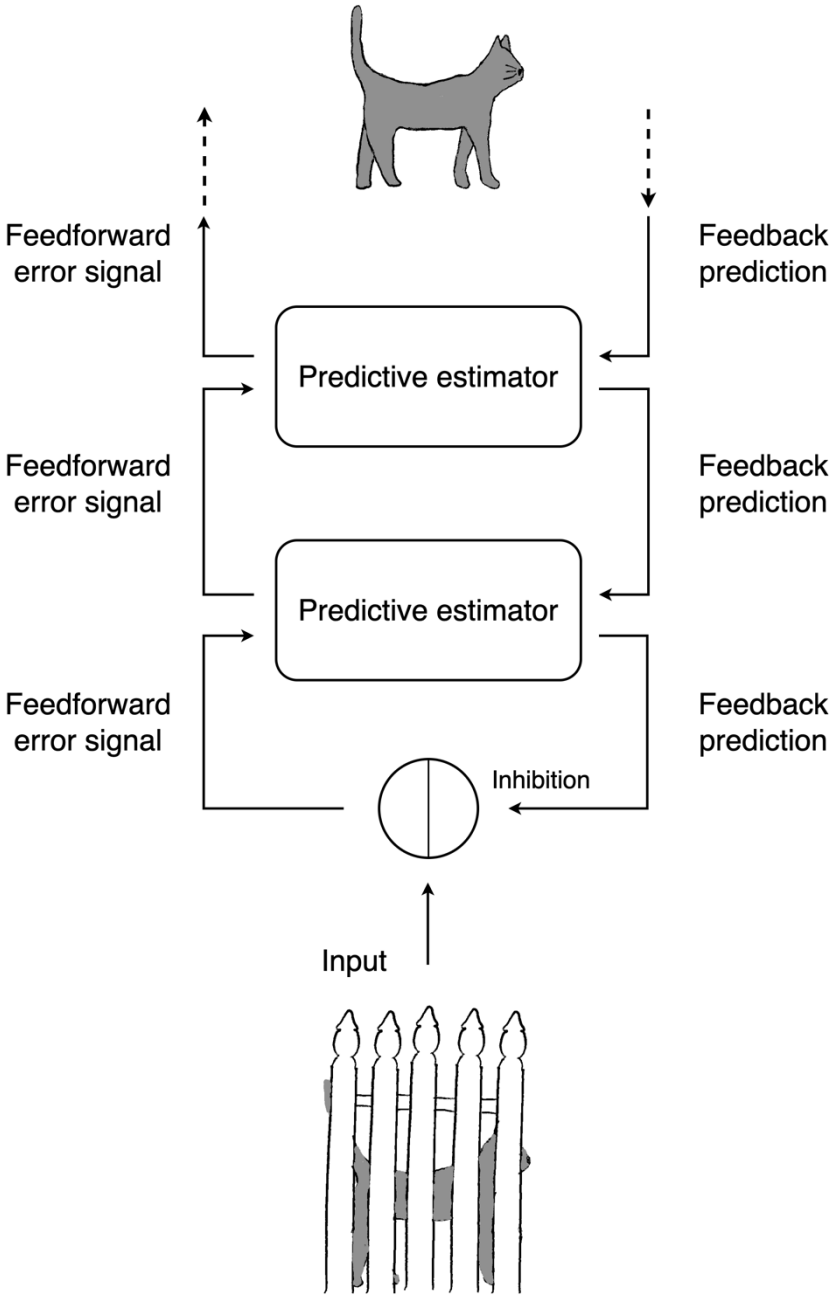


Figure 1.1. *Schematic of the hierarchical predictive coding framework in the visual system adapted from Rao and Ballard (1999, Figure 1A) with permission from Springer Nature. Each level of the hierarchy predicts the sensory information at the lower level, with these predictions being sent via feedback connections. Error signals from the sensory input are carried forward to the predictive estimator to adjust the prediction.*

1.3. Prediction and memory

An investigation into the consequences of prediction for learning may provide a more holistic picture of cognitive processing, shedding light on how expectations shape understandings of the world. It has been proposed that the function of memory is not purely to remember the past, but also to anticipate events in the future (Kveraga et al., 2007; Schacter et al., 2008). Given

that widespread hippocampal and neocortical networks appear devoted to memory processing (for a review see Sekeres et al., 2018), it appears likely that memory has an adaptive purpose beyond mere reminiscence. The relationship between memory and prediction appears two-fold. On one hand, predictions purportedly draw on memories of past experience (Bar, 2007; Barron et al., 2020; Schacter et al., 2008), whilst on the other hand, predictions can influence the extent to which new information is incorporated into memory (Hubbard et al., 2019; Sherman et al., 2022; Sherman & Turk-Browne, 2020). According to Barron and colleagues (2020), prediction and memory recall rely on the same underlying hippocampal mechanism; a notion that is supported by prior research demonstrating the predictive capacity of the hippocampus. Rodent studies show that hippocampal place cells fire for a region in space ahead of time, only after a rodent has acquired experience of the track (Lisman & Redish, 2009). This anticipatory neural activity, coupled with the reliance of episodic memory on the hippocampus (Burgess et al., 2002; Rolls, 2010), may therefore suggest that predictions engage memory retrieval processes as current sensory information is compared with a representation of past experience. This is compatible with neuropsychological research, where patients with hippocampal damage (and associated amnesia) also exhibited an impaired ability to imagine new future experiences (Hassabis et al., 2007). This process of imagining the future may arguably rely on predictive processing, supporting the suggestion that prediction and memory recall recruit the hippocampus (Barron et al., 2020) and are functionally similar (Schoknecht et al., 2022). Ultimately, whilst episodic memory recall has been likened with the process of "mental time travel" (Tulving, 2002, pg. 2), the same may apply to prediction, as past experiences are revisited in the process of anticipating future states.

The relationship between memory retrieval and prediction has been used to inform understandings of how predictions shape memory encoding. In particular, the engagement of memory retrieval mechanisms during prediction has been proposed to interfere with the encoding of new information into memory (Sherman et al., 2022; Sherman & Turk-Browne, 2020). This could occur because hippocampal resources are limited, causing retrieval and encoding to compete (Sherman & Turk-Browne, 2020). An alternative (but not necessarily mutually exclusive) proposal suggests that the brain encodes predictable information in a shallow manner, such that it verifies consistency with the prediction without having to process the input in detail (Hubbard et al., 2019; Van Berkum, 2010). In support of this notion is research demonstrating faster processing of words in congruent versus incongruent contexts (West & Stanovich, 1978). Eye-tracking research, which shows that individuals fixate less on words that are strongly constrained by the prior linguistic context (Ehrlich & Rayner, 1981), also provides evidence to suggest that predictable information is processed more shallowly. This is complementary to predictive coding accounts (described above), which suggest that accurate predictions reduce free energy in the system by 'explaining away' activity at error-encoding neurons (Friston, 2005, 2010). Here, it is possible that the silencing of error-encoding neurons in the face of predictable information is accompanied by shallower processing of that information, and subsequently, poorer memory. Although such a strategy may facilitate adaptive processing, it may also explain the poorer memory observed for low (versus high) prediction error-eliciting stimuli (e.g., Greve et al., 2017) and for items that are *predictive* of upcoming information (e.g., Sherman & Turk-Browne, 2020).

The trade-off between prediction and memory encoding is further supported by research demonstrating enhanced memory for unpredictable stimuli. For example, a study by Corley and colleagues (2007) manipulated the predictability of target words (e.g., 'nails') by situating the words within predictable and unpredictable contexts (e.g., 'Everyone's got bad habits and mine is biting my *nails*' versus 'That drink's too hot; I have just burnt my *nails*', respectively). They observed a memory recognition benefit for target words in unpredictable versus predictable contexts, suggesting that unpredictable content is prioritised during memory encoding (Corley et al., 2007). However, it is important to note that a plausibility confound might arise here from the implausibility of burning one's fingernails, highlighting the importance of separating predictability from plausibility. The complexity of the relationship between prediction and memory is also highlighted by research by Haeuser and Kray (2023), who employed a self-paced reading task with predictable and unpredictable article-noun continuations. Crucially, in the unpredictable condition, the articles that preceded the nouns provided a clue to suggest that the sentence was not unfolding in a predictable manner (Haeuser & Kray, 2023). The authors observed better subsequent memory recognition for predictable versus unpredictable nouns (Haeuser & Kray, 2023). However, individuals with better *overall* memory for nouns at test demonstrated slower reading of pre-nominal words in the unpredictable condition during learning; a behaviour that was thought to reflect the early disconfirmation of predictions (Haeuser & Kray, 2023). This provides partial support for the notion that early prediction errors promote the formation of a distinct memory representation, thus affording better retrieval at a later point in time (Haeuser & Kray, 2023). Mechanistically, this is compatible with the suggestion that prediction errors promote *pattern separation* (Barron et al., 2020; Mack et al., 2018), where new memories are formed and stored as independent traces (Yassa & Stark, 2011; see *Figure 1.2*). In contrast, prediction and memory retrieval may both involve *pattern completion* (Barron et al., 2020; Mack et al., 2018; Sherman & Turk-Browne, 2020), where a memory trace is recalled or 'completed' from an associated cue (Rolls, 2013). Whilst the former may lead to episodically rich memory representations (Ngo et al., 2021), the latter may engender processes relating to memory generalisation (Libby et al., 2019). Such generalisation may discourage memory accuracy, potentially explaining why memory is often poorer for predictable stimuli, and better for unpredictable items that elicit prediction error.

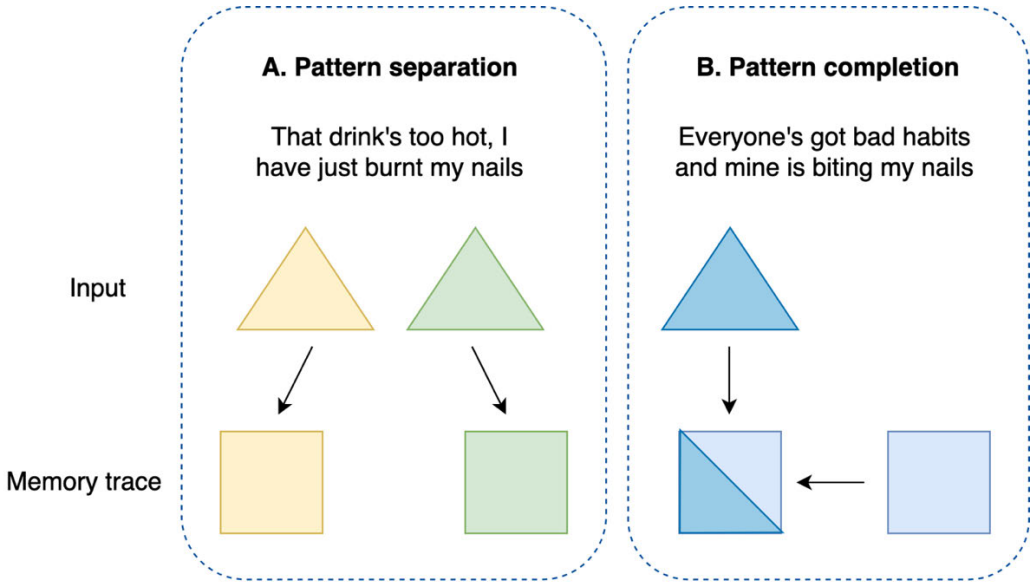


Figure 1.2. *Based in part on Yassa and Stark (2011) with examples from Corley and colleagues (2007).* **(A) Pattern separation:** *When exposed to a prediction error-eliciting stimulus, the hippocampus may store the information as dissociated, episodically detailed traces.* **(B) Pattern completion:** *When faced with information that is predictable and congruent with the broader context, the hippocampus may 'complete' an existing memory trace with the new information, storing it as a unified, generalised trace.*

The effect of prediction on memory is not limited to the linguistic realm, with research in other settings also demonstrating a memory benefit for prediction error-eliciting information. In reward contexts, reward prediction errors (RPE's) represent the discrepancy between an expected and an actual reward (Ergo et al., 2020; Rouhani et al., 2018). Prior research shows that RPE's can positively influence memory and learning (Jang et al., 2019; Rouhani et al., 2018; Rouhani & Niv, 2021), whilst also contributing to the segmentation of events in memory (Rouhani et al., 2020). Other behavioural research demonstrates enhanced memory for surprising, incongruent, or bizarre information (Greve et al., 2017; Michelon et al., 2003; Worthen & Roark, 2002). Given that this information is likely to elicit prediction error, this may provide evidence for a prediction error-based mechanism underlying learning. The notion that prediction errors drive memory encoding is also consistent with neuroimaging research by Sinclair and colleagues (2021), who elicited prediction errors by interrupting videos prior to their predictable endings. This was shown to disrupt hippocampal activity, with this disruption being correlated with the extent of memory updating (Sinclair et al., 2021). Together, these results point towards a role for prediction error in memory encoding, implying that during learning, the brain prioritises the information that can make a novel contribution to its world view. On the other hand, when information is consistent with a prediction, the brain may focus on relating the content to associated representations, thus allowing it to conserve encoding resources. Such a mechanism may contribute not only to memory inaccuracies but could have consequences for social cognition, along with the development of stereotypes and other biases in one's world view (Westra, 2019). Consequently, an understanding of the effect of prediction on memory is important in illuminating the deeper aspects of human experience.

Prior research ultimately highlights the interconnectedness between prediction and memory; a relationship that may provide an intersection between the past and the future. Whilst the potential trade-off between prediction and memory encoding appears intuitive at a first glance (Hubbard et al., 2019; Sherman et al., 2022; Sherman & Turk-Browne, 2020), other literature highlights the complexity of this relationship by demonstrating memory enhancements for predictable, high frequency, or contextually related stimuli (e.g., G. Fernández et al., 1998, 2002; Gronau & Shachar, 2015; Turan et al., 2023). Furthermore, differential task demands appear to contribute to these mixed findings, with some studies employing incidental encoding designs (e.g., Rouhani & Niv, 2021; Sherman & Turk-Browne, 2020), and others using intentional encoding paradigms, where participants are instructed to memorise the material (e.g., G. Fernández et al., 1998, 2002; Gronau & Shachar, 2015). Similarly, whilst some experiments explicitly ask participants to predict upcoming information (e.g., Turan et al., 2023), active prediction may differ from the predictions that should be constantly occurring (for discussion see Brod et al., 2022; Rabovsky & McRae, 2014), providing a potential explanation for the variable outcomes in the prior literature. Importantly, while behavioural performance may vary, an investigation into the neurophysiological activity underlying prediction may facilitate more direct investigations into the effect of prediction on memory. An ideal candidate to gauge the brain activity associated with prediction could be language, as it has a clear structure, is often inherently understood by its speakers, and can be easily manipulated. Moreover, as language is learnt across the lifespan, and as it is based on sequential probabilities, it likely affords prior expectations that constrain predictive processing. Consequently, theories of language processing are becoming increasingly accepting of prediction as an important mechanism (e.g., Kuperberg & Jaeger, 2016; Pickering & Garrod, 2013), emphasising its applicability to multiple domains.

1.4. Neurophysiological research informing the effect of prediction on memory

1.4.1. Prediction in language

Prediction-based accounts of language view the anticipation of upcoming linguistic information as integral for language processing (e.g., Kuperberg & Jaeger, 2016; Pickering & Garrod, 2013; Van Berkum, 2010). For example, Pickering and Garrod (2013) suggest that during language production, the speaker constructs a forward model of their anticipated speech, which is compared to the actual speech (Pickering & Garrod, 2013). On the other hand, when comprehending language, listeners are proposed to covertly imitate the speaker's present speech (Pickering & Garrod, 2013). This allows for the generation of a forward model that affords a prediction about upcoming linguistic information, in a similar manner to the process applied during language production (Pickering & Garrod, 2013). As such, the framework places action at the heart of both language production and comprehension, integrating the two processes and drawing on notions of efference copies (Pickering & Garrod, 2013). In other literature, Kuperberg and Jaeger (2016) describe language processing from the perspective of Bayesian inference, proposing that hierarchical generative models facilitate the prediction of upcoming linguistic content. The importance of prediction for language research is further

reiterated by empirical findings (e.g., relating to speech perception), which can be explained from the perspective of the predictive coding framework (Sohoglu et al., 2012).

Much of the research informing the relationship between prediction and language stems from event-related potentials (ERPs), often derived from electroencephalography (EEG) or magnetoencephalography (MEG) studies (Luck, 2014). ERPs represent summed neuronal activity in response to a particular stimulus or event, rendering them useful for relating cognitive and behavioural phenomena to brain functioning (Luck, 2014). An ERP with particular ties to prediction in language is the N400; a negativity that arises between approximately 200 to 600ms post-stimulus onset, and peaks around 400ms (Kutas & Federmeier, 2011; Kutas & Hillyard, 1980b). In the classic study by Kutas & Hillyard (1980b), when participants were presented with unexpected sentence endings, such as *"He spread the warm bread with socks,"* the N400 amplitude following the unexpected word 'socks' increased (i.e., became more negative). This, and replications of this finding with similar paradigms (e.g., Federmeier & Kutas, 1999; Kutas & Hillyard, 1980a, 1984), highlighted the strong relationship between the N400 and word expectancy (see *Figure 1.3A*). This was further emphasised by research demonstrating a graded relationship between the amplitude of the N400 and word predictability (e.g., DeLong et al., 2005; Federmeier et al., 2007; Wlotko & Federmeier, 2012; see *Figure 1.3B* for a schematic of this relationship), suggesting that the magnitude of the component may inform the extent to which an item is predicted. However, there is some debate regarding the extent to which the N400 reflects processes relating to linguistic prediction, with other research suggesting that the N400 captures processes relating to the integration of information with prior context (Van Berkum et al., 1999; Brown & Hagoort, 1993; Chwilla & Kolk, 2000). This debate on the role of the N400 ties in with a broader debate concerning the role of prediction in language processing more generally. According to Van Berkum (2010), the prevailing belief within the psycholinguistic field for a time was that language processing was so unique that it must depend on its own specialised mechanisms. This was furthered by the proposal that the sheer number of potential linguistic continuations within a sentence could render prediction a costly mechanism of language processing (Jackendoff, 2002; for discussion see Van Petten & Luka, 2012). However, research on the N400 has provided evidence for both prediction and integration perspectives (e.g., Brown & Hagoort, 1993; DeLong et al., 2005; Wicha et al., 2004), prompting the proposal that the N400 reflects the prediction error associated with a stimulus (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019; Eddine et al., 2024; Hodapp & Rabovsky, 2021). This is supported by studies in the computational domain, which have defined the N400 in terms of the difference between a model's state and an ideal input state (for a review see Eddine et al., 2022, 2024). While in some cases this difference is directly operationalized as a form of prediction error (e.g., Fitz & Chang, 2019; Rabovsky & McRae, 2014), other models define this as a change-in-state related to the model updating process (e.g., Rabovsky et al., 2018; for a review see Eddine et al., 2022, 2024). Such models simulated a range of N400 phenomena successfully, suggesting that the N400 mirrors the processes relating to prediction error and model adaptation (Eddine et al., 2024; Rabovsky et al., 2018; Rabovsky & McRae, 2014).

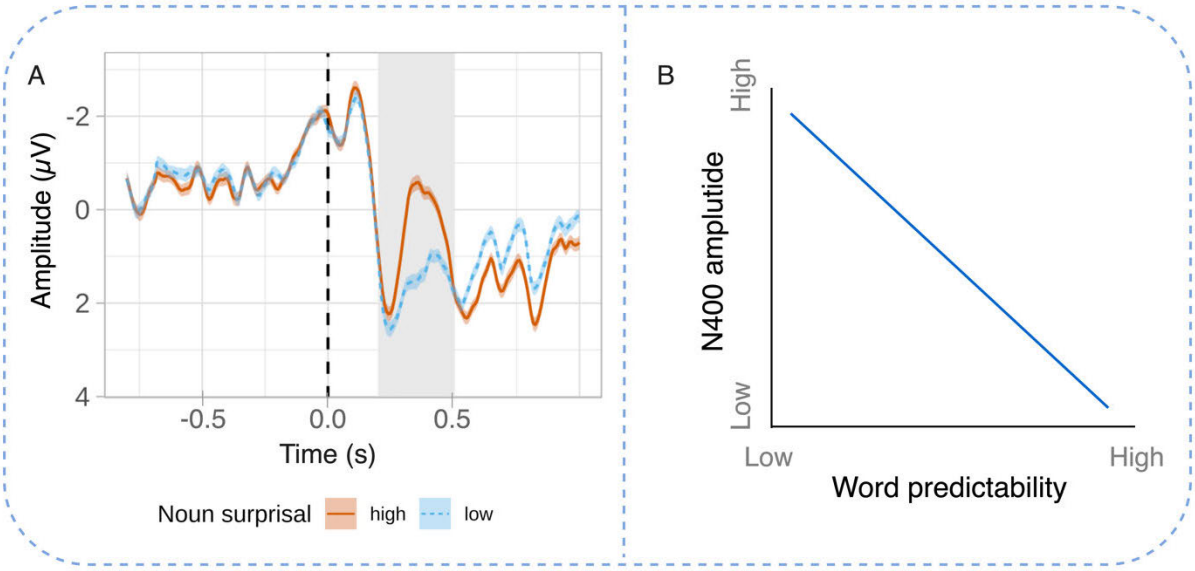


Figure 1.3. (A) *Grand average event-related potential (ERP) plot) depicting a typical N400 effect adapted from Jano, Cross, and colleagues (2024) with permission from MIT Press. Highly surprising (unpredictable) nouns (red) are associated with a greater N400 amplitude than predictable nouns with low surprisal (blue).* **(B)** *Schematic of the typical graded negative relationship between the amplitude of the N400 and word predictability.*

The conceptualisation of the N400 as reflecting prediction error has been extended upon by Bornkessel-Schlesewsky and Schlesewsky (2019), who define the component as an index of precision-weighted prediction error, with precision in this context referring to the inverse of variance (Feldman & Friston, 2010; Friston, 2005). According to predictive coding perspectives, the size of the error signal is proportionate to the amount of precision that the stimulus is deemed to have, such that higher precision is indicative of lower variance and more certainty in the signal (Feldman & Friston, 2010). Evidence for the precision-weighted prediction error notion of the N400 partially stems from cases in which an anomaly is presented but no N400 effect is observed (Bornkessel-Schlesewsky & Schlesewsky, 2019; Tune et al., 2014). For instance, when presented with sentences that include an anomaly at the borderline of awareness, such as '*After an air crash, where should the survivors be buried?'* many people fail to notice the anomalous word *survivors* (Barton & Sanford, 1993). In a study by Tune and colleagues (2014), an increased N400 to borderline anomalies was observed for native German speakers, whilst the effect was absent for native English speakers. These findings were interpreted in light of the weighting given to top-down and bottom-up linguistic cues; native English speakers rely heavily on top-down cues such as word order during language comprehension and thus a subtler incongruity may be insufficient to produce a prediction error signal (Tune et al., 2014). In contrast, native German speakers rely more on the inherent bottom-up properties of a word, potentially rendering a subtle conflict more relevant and thus more likely to incite an expectancy violation (Tune et al., 2014). This is highly compatible with predictive coding accounts, which suggest that predictive processing involves a first-order prediction (concerning the anticipated input itself), and a second-order prediction that anticipates the certainty or precision of the information (Hohwy, 2013; Kanai et al., 2015). In

other words, one must not only know what to predict but must also understand which errors are most useful for predictive model updating (Van De Cruys et al., 2014). Tune and colleagues' (2014) study may therefore suggest that stimulus precision weightings and the extent to which information is used for model updating differs cross-linguistically.

Whilst the N400 may reflect a precision-weighted prediction error, computational modelling research by Eddine and colleagues (2024) has linked the component to lexical-semantic prediction error in particular. However, Eddine and colleagues (2024) emphasise that their model was based on a more general predictive coding algorithm drawing on research from the visual system (e.g., Rao & Ballard, 1999), relating the N400 to prediction as a generalised mechanism. This is compatible with prior research demonstrating N400 effects in domains such as arithmetic, visual perception, action, and in relation to the uncanny valley effect (e.g., Amoruso et al., 2013; Niedeggen et al., 1999; Reid & Striano, 2008; Sitnikova et al., 2008; Urgen et al., 2018). For example, Proverbio and Riva (2009) presented participants with scenes depicting congruent actions (e.g., a man tying a shoelace) and scenes showing incongruent actions (e.g., a woman cutting bread with a saw). They observed greater N400 amplitudes in response to the incongruent pictures (Proverbio & Riva, 2009). This finding demonstrates a more general role for the N400, possibly related to meaning processing (Amoruso et al., 2013; Kutas & Federmeier, 2011). Consequently, the N400's links to prediction may provide a useful method for tracking real-time predictive processing in the brain, both in linguistic and non-linguistic contexts, as well as in relation to memory.

1.4.2. Memory processing and the N400

Given the strong correlations between the amplitude of the N400 ERP and stimulus predictability (e.g., DeLong et al., 2005; Federmeier et al., 2007; Wlotko & Federmeier, 2012), an analysis of this component may provide insight into the extent to which a stimulus evokes prediction error and subsequent memory updating. Further, when considering that prediction errors may serve as the 'currency' of the brain (Cavanagh & Frank, 2014), a measure of prediction error could be a more direct way to capture predictive processing's relationship to memory, potentially extending beyond research in the behavioural domain. For these reasons, the N400 could be an ideal candidate for gauging the neural patterns associated with prediction and memory; a suggestion that has been embraced by prior literature (e.g., Hodapp & Rabovsky, 2021, 2024).

Previous research comparing N400 activity during learning with subsequent memory in study/test paradigms is limited and is primarily constrained to the language domain. This literature broadly provides support for a positive relationship between the magnitude of the N400 component and later remembering, with greater N400 amplitudes being associated with enhanced implicit memory performance (Hodapp & Rabovsky, 2021), and stronger ERP old/new effects related to familiarity memory at test (Meyer et al., 2007). Research by Klimesch, Schimke, and colleagues (1996) also shows that when behavioural memory performance was tested via free recall, subsequently recalled words were those that elicited larger (more negative) N400 amplitudes during learning than subsequently forgotten words. In another subsequent memory paradigm, Fernández and colleagues (2002) recorded EEG from

depth electrodes in nine epilepsy patients whilst they learnt high and low-frequency nouns, after which their recall of the nouns was tested. The authors observed increased (more negative) amplitudes in the anterior medial temporal lobe (AMTL)-N400 ERP for subsequently remembered high-frequency words versus subsequently forgotten high-frequency words (Fernández et al., 2002). Given that AMTL-N400 effects in previous literature bear similarities to scalp-recorded N400 trends (Nobre & McCarthy, 1995), this finding may imply that the size of the N400 is proportional to the extent of memory encoding (with larger amplitudes corresponding to stronger information uptake). However, the AMTL-N400 was more pronounced for high versus low frequency words, which were also better remembered overall (Fernández et al., 2002). While word frequency and predictability may be separable linguistic attributes, the two appear to modulate the N400 in a similar fashion, demonstrating inverse relationships with the amplitude of the N400 component (Dambacher et al., 2006). From this, it may be argued that low frequency stimuli are less predictable than high frequency stimuli and should elicit greater N400 amplitudes. However, this is difficult to consolidate with Fernández and colleagues' (2002) findings, suggesting that the extent to which the AMTL-N400 specifically reflects a prediction error in this context is unclear. External to the subsequent memory literature, Hodapp and Rabovsky (2024) employed a repetition paradigm, where unexpected critical words were repeated either in their original sentence context, or in a new context. N400 amplitudes decreased when the word was repeated in the same sentence context (for further discussion of constraint effects see Hodapp & Rabovsky, 2024). This reduction in the N400 provides evidence for sentence-level adaptation of the predictive model, which may also imply that the content was incorporated into memory (Hodapp & Rabovsky, 2024).

Although research on the N400's relationship to subsequent memory is sparse, it generally suggests that enhanced N400 amplitudes are associated with stronger memory encoding. Interestingly, whilst the N400 receives attention in the memory literature, much of this work focusses on a related, frontally distributed component known as the FN400 (e.g., Chen & Caplan, 2017; Curran, 2000). The FN400 is primarily associated with memory familiarity (Curran, 2000), although its distinction from the N400 remains a topic of debate (see Bridger et al., 2012; Stróżak et al., 2016; Voss & Federmeier, 2011). Nevertheless, given that reductions in the N400 amplitude have been interpreted to reflect enhanced learning (Hodapp & Rabovsky, 2024; Mestres-Missé et al., 2007), attenuated N400 amplitudes to a stimulus at test may suggest that participants are less 'surprised' by the stimulus because it has already been encoded. Importantly, while research measuring the N400 (and the FN400) at test cannot directly inform the extent to which a stimulus elicits prediction error and memory updating upon first exposure, it points toward a dual role for the component in memory processing more generally. On one hand, the size of the N400 may provide a measure of the degree of memory encoding elicited by an item in real-time. On the other hand, it may also gauge recognition processing, with N400 suppressions implying that encoding has already taken place. Importantly, both effects align with the idea that stimuli initially generating a prediction error (and a larger N400) become encoded, resulting in a reduced N400 amplitude upon future encounters. Moreover, whilst the literature is primarily weighted towards investigating N400-like components at test, analyses during learning present an interesting opportunity to delve

deeper into the role of neurophysiological activity in memory formation (hence the growing popularity of N400-subsequent memory analyses in recent research e.g., Hodapp & Rabovsky, 2021). Therefore, event-related patterns may fluctuate with the degree of stimulus predictability and thus shed light on the effect of prediction on memory encoding.

Importantly, despite the N400 potentially serving as a prediction error signal (Bornkessel-Schlesewsky & Schlesewsky, 2019; Eddine et al., 2024; Hodapp & Rabovsky, 2021), it is unclear whether prediction error and model updating are one and the same. Prior research suggests that the N400 corresponds to a prediction error that drives updates to a probabilistic representation of meaning (Rabovsky et al., 2018). This potentially implies that prediction errors and model updating are interconnected but distinct. On the other hand, it is also possible that error and updating comprise one unified mechanism; a discussion that has relevance for understanding the functional significance of ERPs for learning. Therefore, an investigation into the neural activity related to memory *encoding* alongside an analysis of the N400 ERP may also capture the subtleties underpinning the relationship between prediction error and adaptation.

1.4.3. Oscillatory activity, subsequent memory and prediction

While the extent of memory encoding induced by prediction may be gauged after-the-fact via behavioural memory recognition performance, memory encoding may also be measured in the moment. Although event-related activity is transient and temporally precise, periodic oscillations in the EEG signal fluctuate on longer timescales in a rhythmic, synchronised manner and may thus inform the nature of information communication in the brain (Buzsáki & Draguhn, 2004; Luck, 2014; Schnitzler & Gross, 2005). Synchronised fluctuations in neuronal excitability give rise to "waves" of activity known as oscillations (Fries, 2005; Luo & Guan, 2018). The rhythmicity of oscillations regulates the likelihood of neuronal firing (Fries, 2005), with oscillations proposed as a potential mechanism underlying the brain's ability to communicate (Fries, 2005; Schnitzler & Gross, 2005) and represent information (Buzsáki & Draguhn, 2004). While the functional significance of oscillatory activity is still under debate due to its complex and dynamic nature, such activity is frequently linked to memory processing (Hanslmayr et al., 2009; Hsieh & Ranganath, 2014; Luo & Guan, 2018), and prediction (Alamia & VanRullen, 2019; Arnal & Giraud, 2012), potentially providing real-time insight into the extent to which predictions influence memory encoding.

Oscillations within the theta frequency range (~4–7Hz; Hanslmayr et al., 2009) appear particularly relevant for memory processing, with theta power being greater (i.e., more synchronised) for subsequently remembered as opposed to forgotten content (Hanslmayr et al., 2009; Klimesch, Doppelmayr, Schimke, et al., 1997; Osipova et al., 2006; White et al., 2013). For example, Osipova and colleagues (2006) employed a study/test declarative memory paradigm, where participants were exposed to realistic images of landscapes and buildings, after which their memory for the images was tested. They recorded MEG throughout and observed that increased theta power to items during learning was associated with better remembering at test (Osipova et al., 2006). While this may highlight a crucial role for theta power in memory encoding, the authors also observed increased theta power during memory

retrieval, suggesting that such activity may underlie both encoding and retrieval processes (Osipova et al., 2006). This is compatible with the proposal that encoding and retrieval are separated by the phase of the theta rhythm, with encoding occurring during the trough, and retrieval being promoted during the peak (Hasselmo et al., 2002 in Hasselmo, 2005). As such, rhythmic changes in theta activity may support memory processing more generally, rendering theta activity a useful correlate for tracking the effects of prediction on memory uptake.

Not only is activity in the theta band frequently related to memory, but the relationship between alpha oscillations (~8–12Hz; Hanslmayr et al., 2009) and inhibitory processing may also render alpha waves relevant for the present investigation. Alpha rhythms dominate the human EEG and become suppressed (i.e., desynchronised) with increasing task demands and upon opening the eyes, versus closing them (Alamia & VanRullen, 2019; Berger, 1929; Klimesch, 1999). Prior research in the attentional domain has demonstrated enhanced alpha power in hemispheres responsible for processing distractor items (Kelly et al., 2006; Thut et al., 2006) and alpha suppression in regions involved in processing attended stimuli (Sauseng et al., 2005). As such, the alpha rhythm may be linked to top-down processes associated with inhibition (Jensen & Mazaheri, 2010; Kelly et al., 2006). This is congruent with the alpha synchronisation that has been observed during eyes closed periods, which may reflect visual suppression (Toscani et al., 2010). In contrast, a reduction in this inhibitory mechanism via alpha desynchronisation is associated with enhanced attention towards a stimulus (Janssens et al., 2018; Sauseng et al., 2005). Attention plays a crucial role in selecting information for memory encoding (Chun & Turk-Browne, 2007), suggesting that alpha power modulates attentional processing and the extent to which information is encoded. Given that decreased alpha power during learning is associated with better memory retention at test (e.g., Hanslmayr et al., 2009; Sederberg et al., 2003), the link between alpha suppression and enhanced attention may explain its connection to memory processing.

The relationship between alpha activity and memory may also be furthered by predictive coding accounts, which suggest that attention reflects an estimate of the precision related to a stimulus (Feldman & Friston, 2010). Precision is represented via synaptic gain, where greater precision corresponds to increased gain, translating to greater receptivity of prediction error-encoding neurons to sensory input (Friston, 2008 in Feldman & Friston, 2010; Friston; 2009; Pertermann et al., 2019). If alpha power regulates attentional fluctuations, desynchronisation in the alpha band may direct attention toward the sensory stimuli, increasing its precision-weighting. This increase in precision (and neural gain) may enhance the likelihood that the information will be processed and represented by the system, potentially explaining the links between alpha power and later remembering (Friston, 2009; Hohwy, 2012). Therefore, oscillatory activity in the alpha and theta bands may be useful for capturing the extent of memory encoding in prediction contexts beyond behavioural subsequent memory effects. The relevance of such activity for this investigation is further emphasised by research demonstrating correlations between oscillatory patterns and stimulus predictability.

Oscillatory fluctuations in the theta and alpha bands are not only related to memory encoding but may be relevant for predictive processing. Prior research demonstrates increased theta

synchrony in response to prediction errors (Cavanagh et al., 2010; Mas-Herrero & Marco-Pallarés, 2014) and incongruent information (Dini et al., 2022). Alpha rhythms also appear important for prediction, with Alamia and VanRullen (2019) observing the natural generation of alpha activity in a simulated predictive coding model of the visual cortex. Using a multi-level version of the same model, they subsequently observed both forward (bottom-up) travelling waves when processing sensory input, and backward (top-down) waves when sensory input was absent (Alamia & VanRullen, 2019). Consequently, the authors concluded that "it may simply not be possible for a biological brain, in which communication delays are non-negligible, to implement predictive coding without also producing alpha-band reverberations" (Alamia & VanRullen, 2019, p. 11). Therefore, as oscillatory patterns in both the alpha and theta frequency bands have been linked to memory and prediction, such activity may provide a means to measure the extent to which the two processes are related. Further, few studies have compared the relationship between oscillatory and N400 activity during learning or study periods with subsequent memory outcomes. If engaging in an analysis of all three components in unison, the N400 or FN400 is typically investigated at test as a measure of memory recognition (e.g., Chen & Caplan, 2017; Ordin et al., 2020). However, if the N400 serves as a prediction error signal, and if alpha and theta oscillations underlie memory encoding, an analysis of these components during learning may provide electrophysiological evidence for a prediction error-based learning mechanism in the brain. This may also illuminate the mixed nature of the behavioural literature on prediction and memory, which may be explained by variability at the neurophysiological level. Stepping back, this additionally highlights the importance of considering other sources of diversity when delving deeper into the connection between prediction and memory. Namely, variability at the *individual* level may further contribute to the conflicting behavioural evidence, particularly considering the experience-dependent nature of prediction (den Ouden et al., 2012; Friston, 2005). As such, the following section turns to a discussion of individual neural variability and its relevance for understanding the connection between prediction and memory.

1.5. The role of individual neural variability in prediction and memory processing

While predictions rest heavily upon the hardware of the brain (being established through the brain's hierarchical circuitry; Bastos et al., 2012; Friston, 2005), they are also based on statistical patterns gleamed from previous experience (den Ouden et al., 2012). This may render predictions inherently unique to the individual, implying that one person's predictions about an event could differ significantly from another's. This was emphasised by Tune and colleagues' (2014) study, where cross-linguistic differences in the N400 response to borderline anomalies may imply that prior linguistic experience influences the extent to which a stimulus evokes a prediction error. Research by Troyer and Kutas (2020) similarly demonstrates that an individual's knowledge of Harry Potter influences N400 effects in response to contextually supported and unsupported words within Harry Potter-related sentences. As previous literature also suggests that prior knowledge influences perception (Sohoglu et al., 2012), it may be important to consider prediction not only as a domain-general mechanism, but as a process that moulds to the individual. Andy Clark (2014, p. 36) provides a helpful example to illustrate how predictions shape perceptual processing:

> "It is intuitively obvious that, for example, a familiar song played using a poor radio receiver will sound much clearer than an unfamiliar one... The clear-sounding percept, after all, is constructed in just the same way as the fuzzy-sounding percept, albeit using a better set of top-down predictions... That is to say – or so I would suggest – the familiar song *really does* sound clearer."

To extend upon this example and consider that different individuals are often familiar with different music, it becomes evident that even something as simple as music experience may influence perception in the moment. When also acknowledging that other environmental aspects vary significantly between individuals, one can naturally see how these differences may manifest into diverse understandings of the world. Anecdotally, we often encounter scenarios where two individuals involved in the same event report varied interpretations of the situation after-the-fact. Such outcomes may arise from the uniqueness of experience, which may shape what is predicted and in turn, how the sensory information is perceived. However, while it may be impossible to capture how the specific life experiences of an individual affect prediction in an experimental context, neural activity is arguably a product of both genetic makeup and environmental nurture (Meaney, 2001). As such, between-subject neural differences may partially capture the variability relating to prediction that may stem from nurture- and nature-based factors. This may consequently provide a more holistic picture of how predictions shape learning and our experiential reality.

1.5.1. Individual alpha frequency (IAF)

Not only are task-related, intraindividual shifts in alpha activity relevant for memory processing, but characteristics of the alpha rhythm demonstrate interindividual variance that may be related to cognition (Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013; for a review see Klimesch, 1999), and predictive processing (Kurthen et al., 2020). Specifically, individual alpha frequency (IAF; the predominant frequency within the alpha frequency band; Corcoran et al., 2018; Klimesch, 1999) could provide a marker of cognitive performance at the trait level (Grandy, Werkle-Bergner, Chicherio, Schmiedek et al., 2013). IAF is typically calculated during an eyes-closed resting period (Corcoran et al., 2018, e.g., Dziego et al., 2023; Klimesch et al., 1990; Samaha & Postle, 2015) and is often observed as a peak in the power spectrum (see *Figure 4*). It demonstrates strong test-retest reliability and is not altered by cognitive training, suggesting that the component may be relatively stable within the individual (Grandy, Werkle-Bergner, Chicherio, Schmiedek et al., 2013). Faster alpha oscillations give rise to a higher IAF, with high IAFs being associated with enhanced memory performance (Klimesch et al., 1990, 1993), better general intelligence (Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013), faster information processing (Surwillo, 1961, 1963), and more fine-grained temporal windows for visual perception (Cecere et al., 2015; Samaha & Postle, 2015).

While previous literature establishes the importance of IAF for cognitive functioning, other research also alludes to its relevance for predictive processing. For example, Kurthen and colleagues (2020) measured the P600 ERP while older adults listened to sentences of varying syntactic structure, some of which contained an ambiguity that required reanalysis. High IAF

individuals exhibited stronger P600 effects than those with a low IAF, implying that they were more inclined to reanalyse sentences with an ambiguity (Kurthen et al., 2020). Kurthen and colleagues (2020) interpreted this result from a predictive coding perspective, suggesting that high IAF individuals demonstrated a stronger tendency to update their predictive model of the sentence. Mechanistically, this greater inclination towards model updating may stem from the shorter temporal processing windows that could accompany a high IAF (Samaha & Postle, 2015). Shorter windows may increase the amount of sensory information that is processed by the system (Samaha & Postle, 2015), which may in turn result in a stronger reliance on the bottom-up sensory information (a suggestion proposed but not supported by the results of Bornkessel-Schlesewsky, Sharrad, et al., 2022). This highlights the potential complexity surrounding the relationship between IAF and predictive processing. At the very least, inter-individual changes in IAF across the lifespan appear to mirror the proposed need for model updating at different stages of life (Klimesch, 1999; Moran et al., 2014). IAF exhibits a somewhat inverted U-shaped pattern across the lifespan, increasing towards young adulthood and decreasing again during older adulthood (for a review, see Klimesch, 1999). Similarly, Moran and colleagues (2014) suggest that with aging comes an optimisation of predictive models, such that models become more accurate but also more generalised. Consequently, older adulthood may be characterised by a stronger reliance on a top-down prediction and a reduced need for model updating (Moran et al., 2014), which may be accompanied by decreases in IAF (Klimesch, 1999). As such, whilst research on the relationship between IAF and prediction is in its infancy, oscillatory resting-state dynamics such as IAF may shed light on individual prediction tendencies and their role in model updating and learning.

1.5.2. 1/f aperiodic slope

So far, the importance of oscillatory activity in the time frequency domain for understanding prediction and memory has been highlighted. However, the complex and dynamic nature of the EEG spectrum renders it important to investigate non-periodic components in prediction contexts, such as the 1/*f* aperiodic slope. The EEG spectrum can be separated into periodic (oscillatory) and aperiodic (noise-like) components (Donoghue, Haller, et al., 2020; He, 2014). The aperiodic component conforms to a power-law function, where increases in power are associated with decreases in frequency (*f*; Buzsáki & Draguhn, 2004; Donoghue, Haller, et al., 2020; He, 2014). This power-law relationship is expressed as the "1/*f* component," which is considered "scale-free" as it occurs independently of specific timescales or frequencies (He, 2014). According to Buzsáki and Draguhn (2004), the inverse relationship between power and frequency that characterises the 1/*f* component emerges from the anatomical structure of neuronal networks, which is restricted by the speed of axon conduction and synaptic transmission. High frequency oscillations are faster, and due to the limits on neuronal communication, must occur across smaller, local networks (Buzsáki & Draguhn, 2004). In contrast, slow frequency oscillations can employ neurons that span more widespread populations, resulting in greater power at slower frequencies (Buzsáki & Draguhn, 2004). Therefore, the 1/*f* component may capture the broadband dynamics that underlie brain functioning (He, 2014), with the exponent of this relationship (the 1/*f* slope; see *Figure 1.4*) appearing functionally significant for understandings of cognition (e.g., Ouyang et al., 2020; Voytek et al., 2015). Moreover, as the component is often computed at rest (similarly to IAF,

e.g., Bornkessel-Schlesewsky, Sharrad, et al., 2022; Dziego et al., 2023; He, 2014), and as it demonstrates consistency at the single-subject level (Demuru & Fraschini, 2020), it may be useful for understanding the interindividual variability associated with prediction.

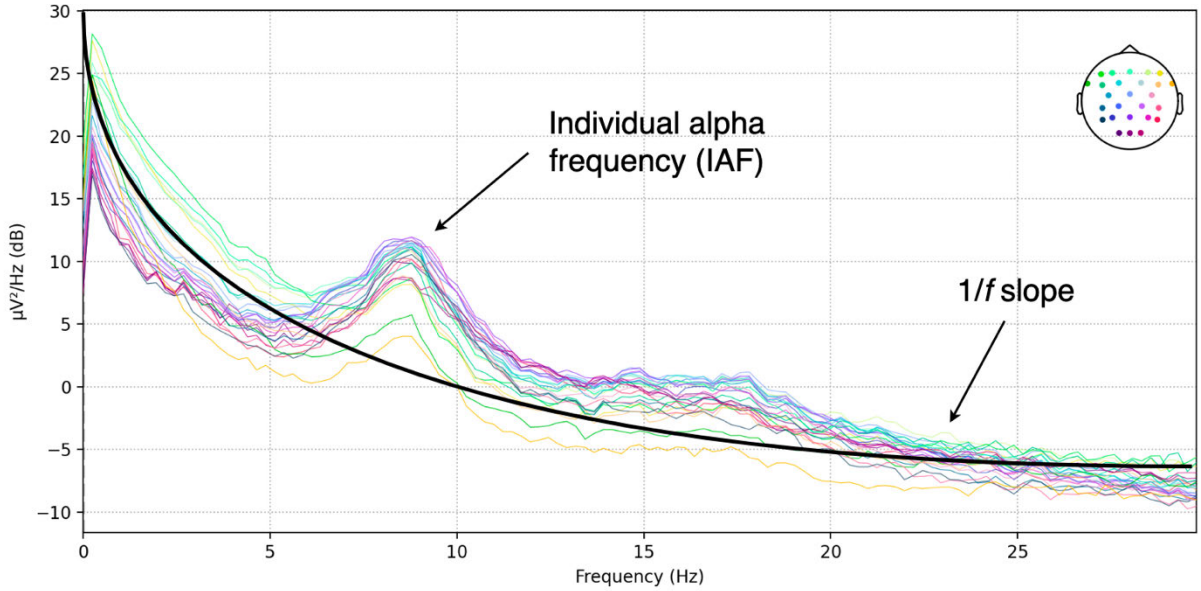


Figure 1.4. *Power spectral density (PSD) plot of electroencephalographic (EEG) power (y axis) according to frequency (x axis), with coloured lines representing activity at each EEG channel. The individual alpha frequency manifests as a peak at approximately 8.5Hz (in this example). This peak is observable above the 1/f slope, which captures the strength of the negative relationship between EEG power and frequency (the power-law relationship).*

The steepness of the 1/*f* slope is generally positively correlated with cognitive performance, with steeper slopes being associated with better visual working memory (Voytek et al., 2015), cognitive processing speed (Ouyang et al., 2020), and visuomotor performance (although this may be dependent on the level of perceptual demand; Immink et al., 2021). However, other research employing a semi-naturalistic simulation task demonstrated enhanced performance during learning for individuals with flatter versus steeper 1/*f* slopes (Dziego et al., 2023), highlighting the need for further research on 1/*f* and performance across a range of cognitive domains. In prediction contexts, steeper 1/*f* slopes have been related to faster model updating, as evidenced by enhanced adaptation of the N400 to intra-experimental surprisal (Bornkessel-Schlesewsky, Sharrad, et al., 2022). Additionally, Cross, Corcoran, and colleagues (2022) examined flexible versus fixed word-order sentence processing and measured task-related changes in the 1/*f* slope. Flexible word-order sentences were associated with steeper slopes as compared to fixed word-order sentences (Cross, Corcoran, et al., 2022). As the flexible word-order sentences may elicit prediction errors in native English speakers (who rely on word-order cues), this supports 1/*f*'s functional relevance for predictive processing (Cross, Corcoran, et al., 2022). Finally, research by Dave and colleagues (2018) examined on-task changes in 1/*f* during sentence comprehension and observed stronger N400 effects reflecting prediction for those with steeper 1/*f* slopes. These findings broadly provide evidence to suggest that the 1/*f* component could capture some of the variability relating to prediction. However, the limited prior research on 1/*f* and prediction highlights the need for further investigation. Nevertheless,

the stability of the component, and its proposed role as an 'EEG fingerprint' (Demuru & Fraschini, 2020) emphasises its potential utility for investigating how the influence of prediction on memory differs between individuals.

1.6. Thesis overview

The present thesis delves into the strong interconnectedness between past, present and future, and aims to investigate 1) the effect of prediction on memory processing, 2) the neural underpinnings of this relationship, and 3) how individual neural variability contributes to these mechanisms. While most research examining the effect of prediction on memory encoding is restricted to the behavioural domain, an analysis of the electrophysiological activity that contributes to this relationship may more clearly delineate the connection between these two processes. Furthermore, this thesis seeks to understand prediction as a potential ubiquitous mechanism underlying cognition (Friston, 2010; Huang & Rao, 2011). Additionally, while prediction may be collective to the human experience, it could also be inherently unique to the individual, with these individual prediction tendencies contributing to the variability surrounding the effect of prediction on memory. This thesis begins with an analysis of the neural activity associated with prediction during language processing. It subsequently progresses towards an investigation into the effect of prediction on memory in a context external to language, capitalising on the sequential dependencies that underlie prediction more generally. The thesis takes a novel approach by considering between-subject neural variability throughout, shedding light on the conditions that promote predictive model updating and memory encoding.

The body of this thesis is comprised of three chapters detailing the work described above, followed by a general discussion chapter. Chapter 2 describes a reanalysis of a large-scale replication study, which aimed to examine the ERP activity related to prediction, and the significance of prediction for language comprehension (Jano, Cross, et al., 2024; published in the *Journal of Cognitive Neuroscience*). The results revealed a role for prior context and IAF in modulating the extent of prediction in language, supporting perspectives that view prediction as integral to language processing.

Chapter 3 reports on an EEG experiment that examined the effect of prediction on memory encoding (Jano, Chatburn, et al., 2024; published in the *Neurobiology of Learning and Memory* journal). Participants were exposed to sequential relationships (some of which encouraged prediction) and were subsequently tested on their memory for the individual items. This study extended upon the work described in Chapter 2, as it applied an analysis of the ERP activity relating to prediction to a non-linguistic context. While the behavioural results provided initial insights, the ERP findings more clearly elucidated the underlying effects at play, potentially suggesting that IAF modulates the relationship between predictability and memory encoding.

Chapter 4 describes a reanalysis of the data from the experimental study detailed in Chapter 3 (Jano, Schlesewsky, et al., 2024; *BioRxiv preprint*). This analysis sought to delve deeper into the effect of prediction on memory, by examining the how the relationship between ERP and

oscillatory activity during prediction influences subsequent memory performance at test. This analysis was specifically conducted on an item-specific level to capture the nuanced, event-related changes that contribute to memory encoding. Oscillations were measured to gauge the extent of information transfer into long-term memory. Broadly, the results suggest that memory encoding can occur independently of the level of prediction error (potentially indexed by the N400), highlighting the complex relationship between prediction and memory.

Finally, Chapter 5 concludes the thesis with a discussion of the findings described above and their significance for understandings of prediction and memory processing. The data are framed in the context of the predictive coding theory and with regard to a well-recognised (though somewhat debated) dual memory system that has been proposed in prior literature. Consequently, this discussion serves to illuminate the contribution of the present research to the field of cognitive neuroscience more broadly, shedding light on prediction's importance for information uptake.

Chapter 2

Prior context and individual alpha frequency influence predictive processing during language comprehension

ABSTRACT

The extent to which the brain predicts upcoming information during language processing remains controversial. To shed light on this debate, the present study reanalysed Nieuwland and colleagues' (2018) replication of DeLong and colleagues (2005). Participants (N = 356) viewed sentences containing articles and nouns of varying predictability, while their EEG was recorded. We measured ERPs preceding the critical words (namely the semantic prediction potential), in conjunction with post-word N400 patterns and individual neural metrics. ERP activity was compared with two measures of word predictability: cloze probability and lexical surprisal. In contrast to prior literature, semantic prediction potential amplitudes did not increase as cloze probability increased, suggesting that the component may not reflect prediction during natural language processing. Initial N400 results at the article provided evidence against phonological prediction in language, in line with Nieuwland and colleagues' findings. Strikingly however, when the surprisal of the prior words in the sentence was included in the analysis, increases in article surprisal were associated with increased N400 amplitudes, consistent with prediction accounts. This relationship between surprisal and N400 amplitude was not observed when the surprisal of the two prior words was low, suggesting that expectation violations at the article may be overlooked under highly predictable conditions. Individual alpha frequency also modulated the relationship between article surprisal and the N400, emphasising the importance of individual neural factors for prediction. The present study extends upon existing neurocognitive models of language and prediction more generally, by illuminating the flexible and subject-specific nature of predictive processing.

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Jano, S., Cross, Z.R., Chatburn, A., Schlesewsky, M., & Bornkessel-Schlesewsky, I. (2024). Prior Context and Individual Alpha Frequency Influence Predictive Processing during Language Comprehension. *Journal of Cognitive Neuroscience*, *36*(9), 1-39. https://doi.org/10.1162/jocn_a_02196

2.1. Introduction

The question of how the brain converts sensory information into abstract meaning has led to the proposal of prediction as a core mechanism underlying perception (Bar, 2011; Friston, 2005, 2010; Friston & Kiebel, 2009; Press et al., 2020). This is the major assumption of the predictive coding theory, which suggests that prior experiences are used to form generative models (Friston, 2005; Friston & Kiebel, 2009). These models are applied to predict incoming sensory inputs, thus reducing processing effort and facilitating environmental adaptation (A. Clark, 2013; Friston, 2010; Hohwy, 2013). Although prediction is largely accepted as an explanatory mechanism within numerous cognitive domains (Apps & Tsakiris, 2014; Horga et al., 2014; Koster-Hale & Saxe, 2013), a longstanding debate remains within the cognitive neuroscience of language between prediction-based and integrationist theories of language processing (cf., for example, Ferreira & Chantavarin, 2018). Prediction theories propose that the brain anticipates upcoming linguistic content in a top-down manner, whilst integrationist theories argue that language comprehension proceeds via the bottom-up integration of linguistic units with the prior context (for summaries and discussion see Kuperberg & Jaeger, 2016; Mantegna et al., 2019; Van Petten & Luka, 2012). Although seemingly specific to language, this debate could have important implications for existing understandings of prediction as a ubiquitous cognitive mechanism (Friston, 2010; Kveraga et al., 2007), particularly if linguistic prediction does not occur. As such, clarifying the role of prediction in language processing could provide insight into whether predictive processing is indeed fundamental to general cognition as has been argued (Friston, 2010; Kveraga et al., 2007).

2.1.1. Prediction in language as revealed by the N400 component

As prediction and integration in language are notoriously difficult to disentangle empirically, the debate surrounding their role in linguistic processing has hinged prominently on an influential study by DeLong and colleagues (2005). DeLong and colleagues investigated the N400 event-related potential (ERP), which has been linked to prediction errors in language (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019; Hodapp & Rabovsky, 2021; Rabovsky et al., 2018). By the nature of its design, their experiment sought to exclude an integration-based explanation of purported prediction effects, by capitalising on the English regularity whereby the indefinite articles ‘a’ and ‘an’ precede words beginning with a consonant, and beginning with a vowel, respectively (e.g., “a kite” or “an airplane”). DeLong and colleagues (2005) observed larger N400 amplitudes time-locked to the article preceding unpredictable (versus predictable) nouns (e.g., “The day was breezy, so the boy went outside to fly *an* …”; the article “an” rules out the predictable continuation “kite”). As the indefinite articles ‘a/an’ have the same meaning, this observation is difficult to reconcile with integrationist views of the N400, which postulate that N400 differences reflect the ease with which a word’s meaning can be integrated with its preceding context (Van Berkum et al., 1999; Brown & Hagoort, 1993; Chwilla & Kolk, 2000). Moreover, the N400 effect was graded in accordance with how predictable the article word was, suggesting that language comprehension involves the prediction and pre-activation of words down to the highly detailed level of speech sounds. This assumption is highly compatible with predictive coding approaches, where predictions are proposed to activate a representation of the anticipated stimulus at multiple levels of the cortical

hierarchy (Rao & Ballard, 1999; Rauss & Born, 2017). Therefore, although there are various definitions for prediction (for discussion see Kuperberg & Jaeger, 2016), such N400-article analyses have the potential to provide evidence for the prediction of form-based linguistic attributes.

The investigation by DeLong and colleagues (2005) suggests that prediction serves as a likely mechanism for linguistic processing. This is supported by research which has observed similar ERP effects time-locked to adjectives (Van Berkum et al., 2005) and gender-marked determiners (Wicha et al., 2004) preceding a noun, as well as prior to sign onset in sign language (Hosemann et al., 2013; Krebs et al., 2019). However, other studies have observed differential patterns (for discussion see Ito et al., 2017; Schoknecht et al., 2022), including a large-scale direct replication study by Nieuwland and colleagues (2018), who analysed data from 356 participants using the same stimuli as in DeLong and colleagues (2005). In contrast to DeLong and colleagues, Nieuwland and colleagues did not observe a more pronounced N400 following unpredictable articles. Accordingly, they suggested that, although the brain may predict upcoming contextual or semantic information, this may not extend to form-based linguistic characteristics such as speech sounds (Nieuwland et al., 2018). Therefore, the extent of prediction in language is currently unclear and may be subject to significant variability. Consequently, the mixed nature of the literature renders it important to examine other sources of variability that may influence predictive processing.

2.1.2. The influence of individual neural factors on prediction

An investigation of variability at the individual level may provide insight into linguistic prediction, with such variability capturing effects over and above group-level contrasts in previous studies (e.g., Roehm et al., 2013). Although individual neural differences were not considered by DeLong and colleagues (2005), nor by Nieuwland and colleagues (2018), such activity could contribute to understandings of prediction in language, particularly if prediction tendencies differ between individuals. A potential neurobiological marker that may relate to individual differences in prediction is the individual alpha frequency (IAF), the individual peak frequency within the alpha rhythm (Corcoran et al., 2018; Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013; Klimesch, 1999). The link between IAF and prediction primarily stems from IAF's role as a trait-like marker of information processing, where those with a high IAF were shown to have faster reaction times (Klimesch, Doppelmayr, Schimke, et al., 1996; Surwillo, 1961, 1963) and improved discrimination of rapidly presented stimuli (Samaha & Postle, 2015). Enhanced information processing in high versus low IAF individuals may therefore translate to a stronger reliance on bottom-up perceptual information as opposed to a top-down model, resulting in more frequent model updating (in line with findings from Kurthen et al., 2020; however, see Bornkessel-Schlesewsky, Sharrad, et al., 2022 for a stronger tendency to adjust predictions in low IAF individuals). As such, IAF may influence predictive processing and the extent to which sensory information is used to adjust predictions.

Despite periodic oscillatory components such as IAF traditionally being linked to cognitive processing, the importance of considering the aperiodic noise-like activity (particularly the $1/f$ slope of the distribution) that underlies the EEG spectra has been recently emphasised in the

literature (Cross, Corcoran, et al., 2022; Demuru & Fraschini, 2020; Dziego et al., 2023; Immink et al., 2021; Merkin et al., 2023; Ouyang et al., 2020; Voytek et al., 2015; Voytek & Knight, 2015). Although prior literature has ignored or dismissed this activity as noise (Donoghue, Haller, et al., 2020), the 1/*f* component has been shown to predict information processing speeds (Ouyang et al., 2020), and to mediate the relationship between age and cognitive functioning (Pathania et al., 2022; Voytek et al., 2015), suggesting that it may be relevant for cognition. Regarding prediction in language, steeper 1/*f* slopes may be linked to prediction error processing (Cross, Corcoran, et al., 2022), and have been associated with stronger N400 effects (Dave et al., 2018), and a greater tendency to update a predictive model (Bornkessel-Schlesewsky, Sharrad, et al., 2022). Therefore, by analysing the role of the 1/*f* slope in Nieuwland and colleagues' (2018) dataset, it may be possible to capture the individual variability relating to prediction, contributing insight to the extent of prediction in language and the role of inter-subject variability in predictive processing.

2.1.3. Pre-stimulus event-related potentials (ERPs) may provide insight into linguistic prediction

Whilst an analysis of individual factors may shed light on prediction, pre-stimulus ERP activity may also probe predictive processing more directly than post-word N400 patterns. Pre-stimulus ERPs have been proposed to reflect the transient, time-locked activity associated with anticipation (Grisoni et al., 2016, 2017, 2019, 2021). Such components are generally negative-going deflections with frontal topographies and larger amplitudes preceding predictable information (Grisoni et al., 2021; León-Cabrera et al., 2019). Of note is the semantic prediction potential (SPP), which exhibits greater amplitudes in the interval preceding predictable versus unpredictable critical words, whilst demonstrating topographical variance in accordance with the meaning of each word (Grisoni et al., 2017, 2021). This provides evidence not only for prediction but for the pre-activation of the semantic characteristics of a word before it arises (Grisoni et al., 2017, 2021). Such correlates also strongly resemble the stimulus preceding negativity (SPN) ERP (León-Cabrera et al., 2019), a component associated with the subjective appraisal of prediction accuracy (Ono et al., 2021), and with feedback anticipation during reinforcement learning (Brunia et al., 2011; Morís et al., 2013). As such, whilst the absence of an N400 effect at the article (as observed in Nieuwland and colleagues' original analysis) was considered as evidence against the prediction of detailed linguistic features, a relationship between SPP amplitude and word predictability in the pre-stimulus window may provide alternative support for prediction in language, at least at the semantic level. Further, the SPP has been investigated in contexts alongside the N400 component, with high (versus low) constraint sentences eliciting larger pre-word SPP amplitudes and smaller N400 amplitudes (Grisoni et al., 2021). This inverse relationship between the N400 and the SPP may be due to the predictable nature of the words in the high-constraint sentences, which likely facilitates strong predictions (as evidenced by larger SPPs) whilst eliciting fewer prediction violations (potentially reflected in decreased N400 amplitudes; Grisoni et al., 2021). Consequently, this relationship between the SPP and the N400, and the correlations between the SPP and word predictability, highlight the potential utility of the component for understandings of prediction in language.

2.1.4. The present study

The current study aimed to investigate the extent of prediction in language and the role of individual neural differences in predictive processing. To do so, we analysed the event-related activity preceding the critical words in the Nieuwland and colleagues (2018) data (i.e., the SPP), in conjunction with the 1/*f* aperiodic slope and IAF. Such an analysis has the potential to shed light on the discrepancies in findings between DeLong and colleagues (2005) and Nieuwland and colleagues (2018), while concomitantly deepening existing understandings of prediction as a general cognitive mechanism (Friston, 2010). It was hypothesised that increases in article and noun predictability would be associated with greater pre-stimulus SPP amplitudes, and that this would be modulated by IAF and the 1/*f* slope. Additionally, although not the original focus of the study, we report analyses of the N400 component to maintain consistency with Nieuwland and colleagues' (2018) investigation. After initial plots revealed differences in ERP activity at earlier stages of the sentence, we also conducted exploratory analyses including prior word surprisal, shedding light on the role of prior context in prediction.

2.2. Methods

2.2.1. Original study

The present study involved a reanalysis of Nieuwland and colleagues (2018), which included 356 participants (females = 222, mean age = 19.8 years) who were all right-handed native English speakers. Participants were recruited across nine different laboratories and the sample size was chosen to ensure that each laboratory's sample equated approximately to that of DeLong and colleagues (2005), who included 32 participants in total (Nieuwland et al., 2018). Participants provided informed consent for the use of their data, and ethical approval for each laboratory was sought in accordance with the requirements of the specific institution (Nieuwland et al., 2018). Cloze probability (the probability that a word will be chosen as the likely continuation based on the prior sentence context; Taylor, 1953) was used as an index of stimulus predictability. The materials consisted of 80 sentences with two cloze probability continuations: a more-expected article/noun combination (e.g., "…the boy went outside to fly *a kite*") and a less-expected article/noun combination (e.g., "…the boy went outside to fly *an airplane*"). Words within each sentence were presented for 200ms sequentially on a computer screen and separated by a 300ms interstimulus interval during which participants viewed a blank screen. Following 25% of sentences, participants answered a yes/no comprehension question. EEG was recorded throughout the study to enable an analysis of the event-related activity in response to articles and nouns. For a detailed description of the study protocol and materials, the reader is directed to Nieuwland and colleagues (2018).

2.2.2. Participants

Data for 356 participants were originally obtained from the Open Science Framework (OSF) repository (see https://osf.io/eyzaq/). Five participants were removed prior to the Brain Imaging Data Structure (BIDS) conversion (see *Data processing* section) due to incomplete files, answering questions randomly or due to being a non-native English speaker. As such, the BIDS conversion was completed for 351 participants. Subsequent pre-processing and epoching led to the removal of 18 more participants (ten due to trigger issues that could not be resolved,

and eight participants due to excessive signal noise). As such, data for 333 participants were epoched, with four participants being excluded due to a lack of trials.

Seventeen participants were also identified as having an insufficient number of epochs for the calculation of the aperiodic (1/*f*) slope and IAF (less than 16 trials). As all analyses included individual factors, these participants were excluded from the final sample, taking the final sample size to 312 (females = 194, mean age = 22.4 years). See *Figure 2.1* for a schematic of participants at each stage of the data analysis pipeline.

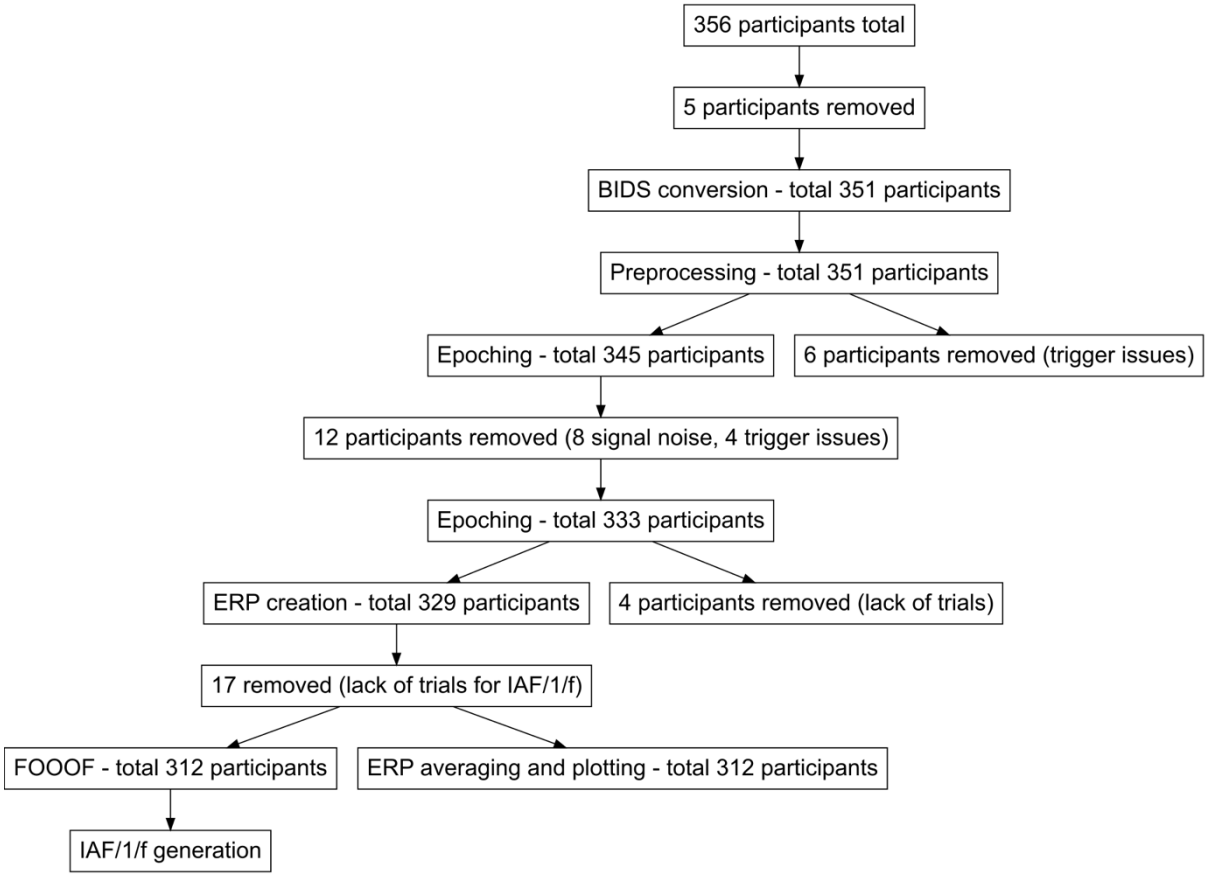


Figure 2.1. *The number of participants at each stage of the data analysis, including the number removed and reasons for removal.*

2.2.3. Data Processing

Data were first converted to the Brain Imaging Data Structure (BIDS) using the *MNE-BIDS* package (Appelhoff et al., 2019) in MNE-Python (Gramfort et al., 2013), to account for file structure variations as a result of the differing EEG systems used across the laboratories. As files with the .cnt extension were unsupported by the BIDS package in Python (MNE-BIDS 0.10 Documentation, 2022), such files were converted to the Brainvision Core Data format (Brain Products Gmbh) prior to the BIDS conversion using MATLAB (MathWorks, Natick, Massachusetts, USA). As most raw files encompassed both the experimental session and the control session, each file was then cropped to exclude the control session, as this was not of interest to the present analysis.

Data were then re-sampled to either 250Hz or 256Hz, depending on the original sampling rate, which ranged from 250Hz to 2048Hz between laboratories. Resampling occurred at an equal interval to avoid data loss when epoching (Gramfort et al., 2013), hence the two sampling frequencies. Therefore, the final sample consisted of 184 participants with data sampled at 250Hz, and 145 participants with sampling rates of 256Hz. This is not expected to have affected the single-trial ERP analyses, as samples were averaged across time intervals of interest and slight discrepancies in the number of samples per window should not introduce significant variability. Following resampling, the EEG data were re-referenced to linked mastoids, while EOGs were set as Fp1 and Fp2 across laboratories. For laboratories that used the alphabetized Biosemi system (https://www.biosemi.com/), EOG channels were those closest to Fp1 and Fp2 (i.e., C29 and C16, respectively). The data were filtered using a bandpass filter that ranged from 0.1 to 30Hz.

To conduct an independent component analysis (ICA), temporary epochs around events of interest were first generated. Rejection thresholds were then computed from the epochs using the *Autoreject* package in MNE-Python (Jas et al., 2017), to be included in the ICA for the detection and removal of ocular artefacts. This procedure is argued to lead to more precision in the ICA, as thresholds are tailored specifically depending on the activity in segments of interest (Jas et al., 2017). The ICA was then fit to a 1Hz high pass filtered copy of the temporary epochs, to minimise the influence of noise from the inter-trial intervals. Subsequently, the ICA was applied to the raw data (see *Table 1* for average number of trials per condition). Following this, channels marked as bad were interpolated using spherical splines and the raw data were epoched around events of interest into segments ranging from -800ms to 1000ms (1.8 seconds total). The *Autoreject* function (Jas et al., 2017) was then applied to repair or remove bad epochs (average percentage of epochs rejected across the final 312 participants = 8.96%).

Table 2.1. *Demonstrating the mean number of trials per condition that were entered into the ICA, with standard deviations (SD) in brackets.*

Expected articles	Unexpected articles	Expected nouns	Unexpected nouns	Article-1*
39.97 (0.29)	39.98 (0.20)	39.97 (0.30)	38.96 (1.01)	79.98 (0.15)

**The article-1 window (-300 to 0ms preceding the word before the article) was used as a baseline period.*

2.2.4. ERP analysis

Event-related activity was extracted within the SPP and N400 time windows on a trial-by-trial basis. The SPP window ranged from -300 to 0ms prior to the article and noun words, to encompass the length of the interstimulus intervals. The N400 time window ranged from 200ms to 500ms post-stimulus onset, in line with Nieuwland and colleagues (2018). To control for differences in neural activity unrelated to the experimental manipulation, epochs were also generated around the word preceding the article. The inter-stimulus interval (-300 to 0ms) preceding the word before the article (the article-1 word) was chosen as a baseline period due to its temporal proximity to the trials of interest, and because the SPP activity preceding the articles and nouns could not be used since it was the focus of the present investigation. This

pre-article-1 word baseline window was not used for traditional baseline correction, but rather the mean amplitude across this window was entered as a covariate into the statistical models of SPP effects involving both the article and the noun that followed (in line with Alday, 2019). For N400 analyses at the article, activity in the pre-article window itself (-300 to 0ms preceding the article) was used as the "baseline" period, whilst for noun N400 analyses, activity in the pre-noun window (-300 to 0ms preceding the noun) was used. This activity was similarly included as a covariate for statistical modelling, and according to Alday (2019), does not need to be further interpreted once controlled for (i.e., it serves as a covariate of no interest).

To generate ERPs, MNE-Python (Gramfort et al., 2013) was used to calculate the mean ERP amplitude across time windows of interest. Due to differing EEG systems, one laboratory lacked channels that directly corresponded to a common 10-20 channel shared by the other laboratories. As such, a region-based approach was taken whereby SPP event-related activity was analysed over frontal regions, in line with previous research (León-Cabrera et al., 2017, 2019; Morís et al., 2013). For N400 analyses, we included the channels that were used in the original study (Cz, C3, C4, Pz, P3, and P4). However, the laboratory that used the alphabetized system did not have channels that directly corresponded to P3 and P4, and thus the closest channels were used (A7 and B4, respectively). ERP grand average plots were created using *ggplot2* in *R version 4.1.1* (Wickham, 2016). Due to the differing sampling intervals, the timing of the samples for four laboratories was adjusted by a maximum of four milliseconds to match the timing of the other laboratories. This was done for visualisation purposes only. Additionally, for ease of visualisation, channel-specific ERP plots include data from the alphabetized Biosemi channel that was closest to the shared 10-20 channel nomenclature.

2.2.5. Individual alpha frequency and aperiodic 1/f slope estimation

Individual alpha frequency (IAF) and the aperiodic 1/*f* slope were calculated at the individual level using the *Fitting Oscillations & One Over f (FOOOF)* package (version 1.0.0) in MNE-python (Gramfort et al., 2013). Epochs were first generated around the between sentence intervals as during this time, participants should not have been actively engaged in the task (in exception is the 25% of trials that included a comprehension question, which were removed), and thus task-related effects were likely reduced. Epochs ranged from 200ms after the final word (when the presentation of the final word had ended), to 2.2 seconds, to ensure a sufficient number of samples to obtain reliable estimates. As the between-sentences intervals were self-paced, trials in which the intervals were shorter than 2.2 seconds were removed from the analysis. Similarly to the treatment of task-related epochs, the *Autoreject* function (Jas et al., 2017) was then applied to the between-sentences epochs to repair or remove bad trials.

Following epoching, the *FOOOF* algorithm was fit to power spectral density estimates derived from each channel of interest, per epoch (Donoghue, Haller, et al., 2020). Channels Oz, O1, and O2 were selected, as alpha activity is prominent over occipital regions (Grandy, Werkle-Bergner, Chicherio, Schmiedek, et al., 2013), and as prior research suggests that the relationship between 1/*f* and cognitive processing may be similar across the scalp (Ouyang et al., 2020). For the laboratory with the alphabetized system, the channels closest to Oz, O1 and O2 were used (A23, A15 and A28, respectively). Parameterization of the power spectra

occurred across a frequency range of 1–30Hz. Settings for the *FOOOF* algorithm included a peak width limit of 2 to 8, a maximum peak number of four, the minimum peak height as 0.0, a peak threshold of 2.0, and a fixed aperiodic mode. To obtain individual metrics, activity across the three channels was averaged across all epochs, resulting in single-subject slope and offset values. IAF estimates were calculated by selecting peaks within the 7–13Hz range and averaging over the activity across each channel and epoch to obtain a single IAF value per participant.

2.2.6. Statistical analysis

Statistical model structures for the primary analyses are presented in *Table 2.2.* To examine effects of interest whilst accounting for random effects, linear mixed-effects models (LMMs) were computed using the *Lme4* package in R version 4.2.2 (Bates et al., 2015). P-values were calculated using the *summary* function from the *lmerTest* package, which is based on Satterthwaite's degrees of freedom (Kuznetsova et al., 2017). The alpha level was set at 0.05 and all predictor variables were scaled and centred. Note that for the main analyses, IAF and the 1/*f* slope were included in the same models, specifying different interaction terms, as the relationship between the two factors was not a primary interest of the study. The model fits of these combined models also were either better or did not significantly differ from separate models for IAF and 1/*f*, as measured by the Akaike criterion (see *Supplementary material 2A.1* for Akaike criterion values).

Primary and exploratory surprisal models (described in the *Exploratory surprisal analyses* section) initially failed to converge with complex random effects structures (i.e., random intercepts of item, subject and channel, and by-item and by-subject random slopes). To simplify the model structures, ERP activity was averaged over channels of interest, allowing for the removal of random intercepts of channel. However, the models either failed to converge, or exhibited singular fits, when random slopes according to all predictors were included. To avoid overfitting, by-subject and by-item random slopes according to the primary predictor of interest (critical word cloze or critical word surprisal) were instead included (for a discussion of model overspecification resulting from maximal LMM structures, see Bates et al., 2018). However, one model (Model 1) failed to converge with random slopes, which were omitted. To determine whether the inclusion of random slopes improved goodness of fit, models that converged with random slopes were compared with and without the random slopes using likelihood ratio tests (LRTs). The LRTs revealed that for all models (excluding Model 3), the inclusion of random slopes significantly improved the model fit (see *Supplementary material 2A.2.* for LRT results). Model 3 also initially only exhibited a non-singular fit with by-item, not by-subject random slopes. However, because the by-item random slopes did not improve the model fit, they were removed.

Table 2.2. *Linear mixed-effects models for primary analyses with outcome variables, covariates, fixed and random effects. Note that IAF and 1/f were included as separate interaction terms, such that in model 1 for example, the interaction of cloze*IAF was examined independently from the interaction of cloze*1/f slope.*

Model	Outcome	Covariates	Fixed effects	Separate interaction terms	Random intercepts	Random slopes
1	**Pre-article** SPP amplitude (-300 to 0ms)	Article-1 word ERP amplitude (-300 to 0ms)	Between-sentences article cloze probability	1/*f* slope IAF	+ Subject + item	
2	**Pre-noun** SPP amplitude (-300 to 0ms)	Article-1 word ERP amplitude (-300 to 0ms)	Noun cloze probability	1/*f* slope IAF	+ Subject + item	By-subject and by-item according to cloze
3	**Post-article** N400 amplitude (200 to 500ms)	Pre-article ERP amplitude (-300 to 0ms)	Article cloze probability	1/*f* slope IAF	+ Subject + item	
4	**Post-noun** N400 amplitude (200 to 500ms)	Pre-noun ERP amplitude (-300 to 0ms)	Noun cloze probability	1/*f* slope IAF	+ Subject + item	By-subject and by-item according to cloze

When investigating the effect of word predictability (operationalized as cloze probability) on the SPP time-locked to articles (Model 1), cloze probability was contrasted between-sentences, as opposed to between expected and unexpected sentence conditions. This is because, prior to the article, the sentence contexts were identical. The likely continuation (the expected article cloze value for that sentence) was taken as the cloze metric for both versions of the sentence (see *Table 2.3* for an example). In contrast, when measuring SPP effects time-locked to the nouns, the original noun cloze values for both expected and unexpected continuations were applied because the sentences arguably differed once participants had been exposed to the article variation.

The model effects were plotted using the *ggplot2* package (Wickham, 2016), with 83% confidence intervals to enable visual identification of statistical effects. For plots in which variables are presented dichotomously (e.g., high/low), this distinction was categorised according to the first and third quartiles.

Table 2.3. *Example sentence demonstrating the cloze probability values (in brackets) for both the unexpected and expected continuations. Note that prior to the article, the sentence versions are identical, thus justifying the application of the expected article cloze value (82) to all versions of the sentence when analysing pre-stimulus effects time-locked to articles.*

Sentence beginning	Expected article	Unexpected article	Expected noun	Unexpected noun
The old wives' tale says that if you want to keep the doctor away then you should eat	an (82)	a (0)	apple (97)	carrot (0)

2.2.7. Exploratory surprisal analyses

Early ERP grand average plots revealed event-related differences according to between-sentences cloze probability at earlier stages of the sentence (see *Figure 2.2*). This sparked interest regarding the accumulation of predictions over time, and of how the predictability of the prior words in the sentence may influence later predictions. Additional exploratory LMMs were thus included to analyse whether the surprisal of the preceding words interacted with the surprisal of the articles to influence ERP amplitudes time-locked to the articles. The raw surprisal values of the two preceding words (article-2 and article-1) and of the critical articles were included in the statistical models. To maintain consistency with our cloze models, LMMs were also computed investigating the effect of article/noun surprisal alone on ERP amplitude time-locked to the articles and nouns, respectively (see *Table 2.4* for exploratory model structures). IAF and the 1/*f* slope were included in all exploratory statistical models, and random effects were structured similarly to the original models. Note that although we ran SPP models with surprisal, the results either did not differ to those of cloze or did not reveal interactions with the surprisal of the critical word. Therefore, for simplicity's sake, we do not report the results of these models or specify their structures in *Table 2.4*, although the model outputs are presented in *Supplementary material 2C*. Additionally, because an N400 effect at the noun could not directly provide evidence for phonological prediction in the same manner as effects at the article (where a relationship between N400 amplitude and word predictability may index prediction for the upcoming noun), we did not deem it necessary to examine prior word surprisal in this context. Rather, analyses at the noun were primarily included as a sanity check and for completeness. Therefore, to reduce complexity, we do not report N400 effects at the noun with prior word surprisal. Finally, Pearson correlations were calculated to examine the relationship between cloze probability and surprisal for the two respective word types.

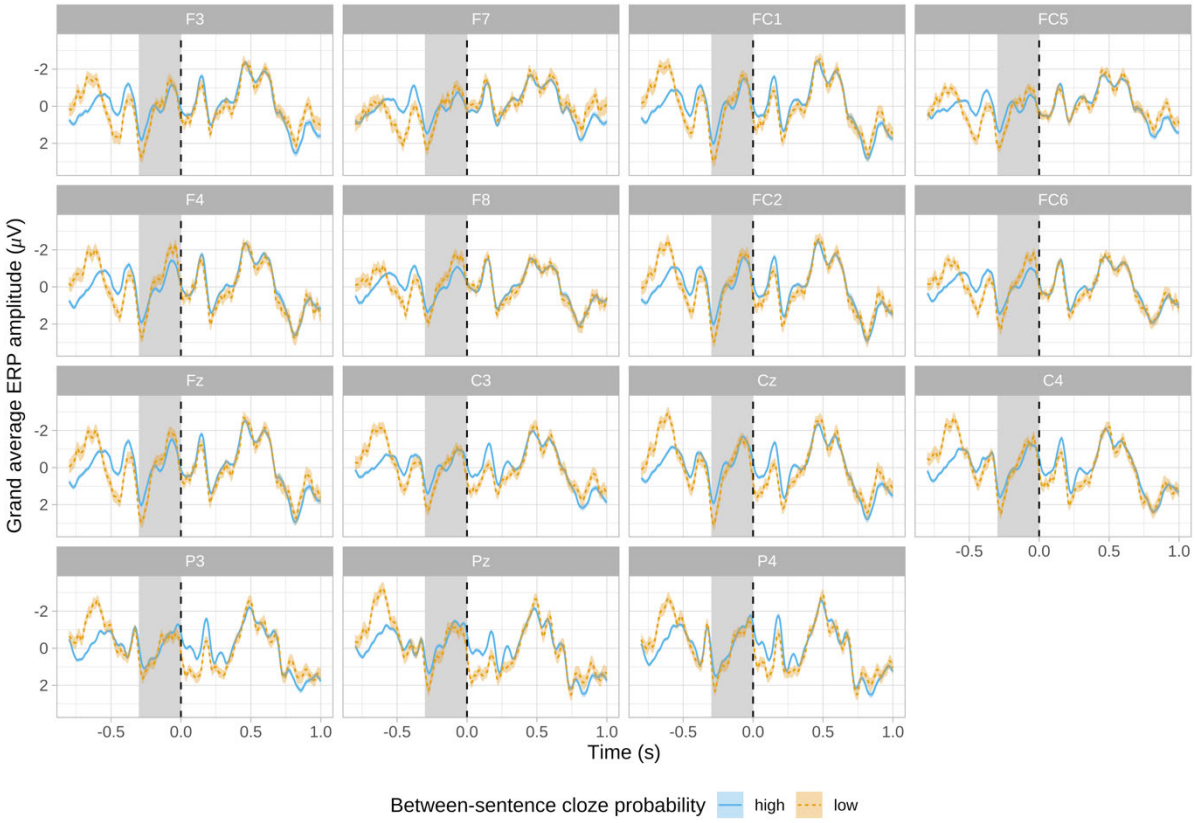


Figure 2.2. *SPP ERP grand average plots for articles over channels of interest according to between-sentences article cloze probability (n = 312) to gauge SPP effects. Blue lines represent high article cloze probability (>50%) whilst orange dashed lines reflect low article cloze probability (<50%). Blue and orange shading reflects the standard errors for each condition. The SPP window is shaded grey, and the black dashed line depicts the onset of the article word. Note that the plot depicts non-baseline corrected ERP activity.*

Lexical surprisal was calculated using an open artificial intelligence model known as Generative Pre-Trained Transformer-2 (GPT-2; Radford et al., 2019) using the *Transformers* package in Python (Wolf et al., 2020). Surprisal in a linguistic context is calculated based on the probability of a given word in a linguistic corpus or database, whereby a higher surprisal value corresponds to lower predictability of a word within, for example, a sentence (Frank et al., 2013). GPT-2 is trained on a large corpus of English texts to traditionally predict upcoming words in a sentence, hence its efficacy in calculating surprisal (Radford et al., 2019). This measure was specifically used as the original experiment lacked cloze probability values of the prior words (Nieuwland et al., 2018).

Table 2.4. *Exploratory linear mixed-effects model structures with outcome variables, covariates, fixed and random effects.*

Model	Outcome	Covariates	Fixed effects	Separate interaction terms	Random intercepts	Random slopes
5	**Post-article** N400 amplitude (200 to 500ms)	Pre-article ERP amplitude	Article surprisal	IAF 1/*f*	+ Subject + item	By-subject and by-item according to article surprisal
6a	**Post-article** N400 amplitude (200 to 500ms)	Pre-article ERP amplitude	Article surprisal Article-1 surprisal Article-2 surprisal 1/*f*		+ Subject + item	By-subject and by-item according to article surprisal
6b	**Post-article** N400 amplitude (200 to 500ms)	Pre-article ERP amplitude	Article surprisal Article-1 surprisal Article-2 surprisal IAF		+ Subject + item	By-subject and by-item according to article surprisal
7	**Post-noun** N400 amplitude (200 to 500ms)	Pre-noun ERP amplitude	Noun surprisal	IAF 1/*f*	+ Subject + item	By-subject and by-item according to noun surprisal

2.3. Results

Statistical model outputs are presented in *Supplementary material 2B.* Nieuwland and colleagues' data used in the present analysis is publicly available at https://osf.io/eyzaq/, whilst our data analysis scripts to replicate this investigation are publicly available at https://osf.io/b7txn/.

2.3.1. SPP effects

SPP ERP grand average plots time-locked to articles are shown in *Figure 2.2,* and ERP effects for nouns are shown in *Figure 2.3.* It was hypothesized that SPP amplitude directly preceding the articles would become larger (i.e., more negative) as article predictability increased, and

that this relationship would be influenced by IAF and the 1/*f* slope (tested via Model 1). The main effect of *between-sentences article cloze probability* on pre-article SPP amplitude was nonsignificant (p = .620, β = 0.06, *SE* = 0.13, 95% CI [-0.18, 0.31]), similarly to the interaction of *between-sentences article cloze probability* and *IAF* on pre-article SPP amplitude (p = .748, β = -0.03, *SE* = 0.08, 95% CI [-0.19, 0.13]). The effect of *between-sentences article cloze* and *1/f slope* on SPP amplitude preceding the articles was also nonsignificant (p = .720, β = -0.03, *SE* = 0.08, 95% CI [-0.19, 0.13]). Therefore, there were no detectable effects of article cloze probability and individual factors on SPP activity before the articles.

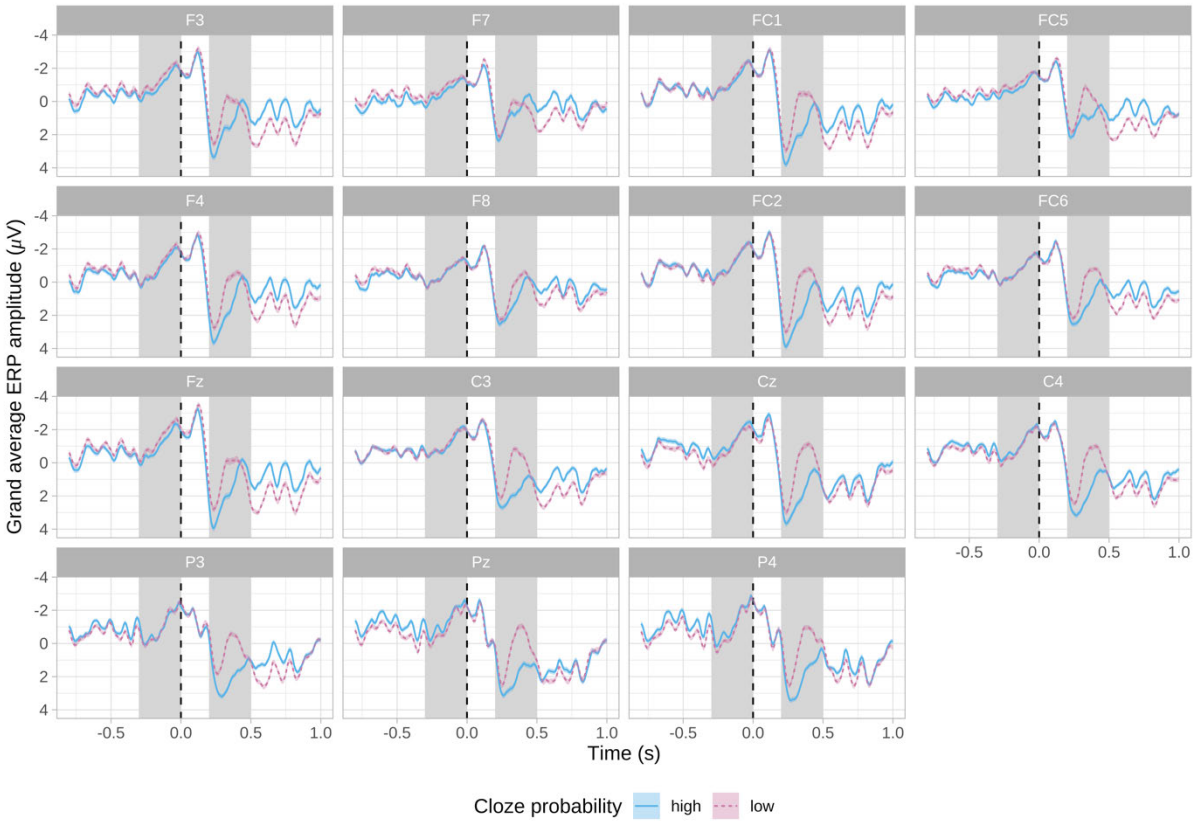


Figure 2.3. *Grand average ERP plots for noun words over channels of interest according to noun cloze probability (n = 312). Blue lines represent high noun cloze probability (>50) whilst magenta dashed lines reflect low noun cloze probability (<50). Blue and magenta shading reflects the standard errors for the respective conditions. The SPP window and the N400 window are denoted via grey shading, and the black dashed line depicts the onset of the noun word. Note that the plot depicts non-baseline corrected ERP activity.*

Model 2 addressed the hypothesis that increases in noun cloze probability would lead to greater (i.e., more negative) SPP amplitudes directly preceding the nouns, and that this would be modulated by IAF or the aperiodic 1/*f* slope. The model demonstrated a significant main effect of *noun cloze probability* on pre-noun SPP amplitude (p = .038, β = 0.11, *SE* = 0.05, 95% CI [0.01, 0.21]), such that increases in noun cloze probability were associated with decreased (i.e., less negative) SPP amplitudes preceding the nouns (see *Figure 2.4*). The interaction between *noun cloze* and *IAF* on pre-noun SPP amplitude was non-significant (p = .220, β = -0.05, *SE* = 0.04, 95% CI [-0.12, 0.03]), similarly to the effect of *noun cloze* and *1/f slope* (p = .919, β = -

0.00, *SE* = 0.04, 95% CI [-0.08, 0.07]). As such, we did not detect a modulatory effect of individual factors on the relationship between cloze and the SPP.

To further quantify the effects of cloze probability on SPP amplitude, we ran exploratory Bayesian sensitivity analyses, as recommended by an anonymous reviewer (described in *Supplementary material 2D*). Broadly, the results provided additional evidence against an effect of cloze probability on SPP amplitude.

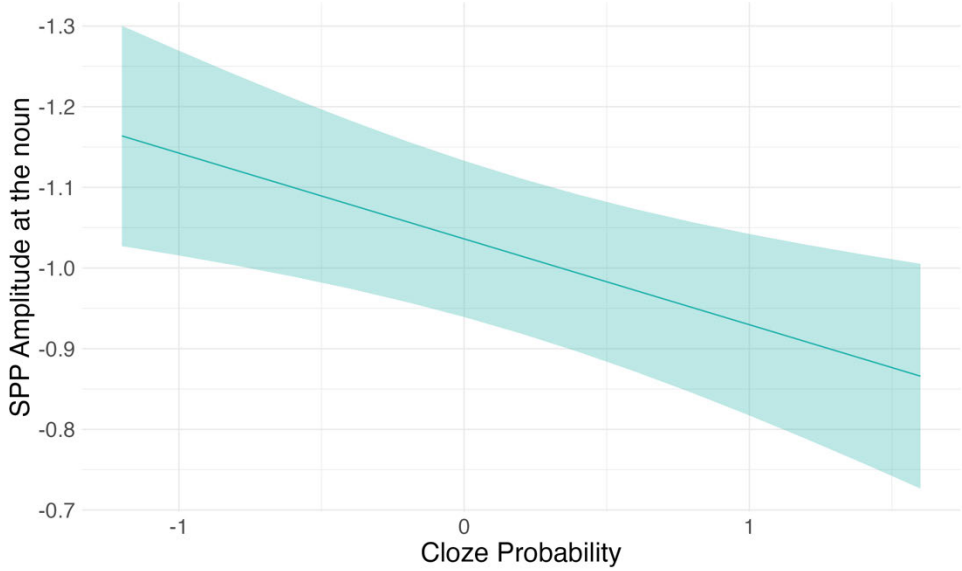


Figure 2.4. *Linear mixed model results depicting the effect of noun cloze probability (scaled and centered) on SPP amplitude time-locked to the nouns (p = .038, β = 0.11, SE = 0.05, 95% CI [0.01, 0.21]). Lines represent model fit, with shading depicting the 83% confidence intervals.*

2.3.2. N400 ERP effects

N400 grand average ERPs time-locked to articles are presented in *Figure 2.5*. To examine whether individual neural factors influence the relationship between article cloze probability and N400 amplitude directly following the article, Model 3 was fitted. The model revealed a significant effect of *article cloze probability* on N400 amplitude time-locked to the article ($p < .001$, β = -0.14, *SE* = 0.03, 95% CI [-0.20, -0.07]), such that as article cloze increased, post-article N400 amplitudes increased (i.e., became more negative; see *Figure 2.6A*). The interaction between *article cloze* and *IAF* was nonsignificant ($p = .937$, β = 0.00, *SE* = 0.03, 95% CI [-0.06, 0.07]), as was the interaction between *article cloze* and *1/f slope* ($p = .512$, β = -0.02, *SE* = 0.03, 95% CI [-0.09, 0.04]).

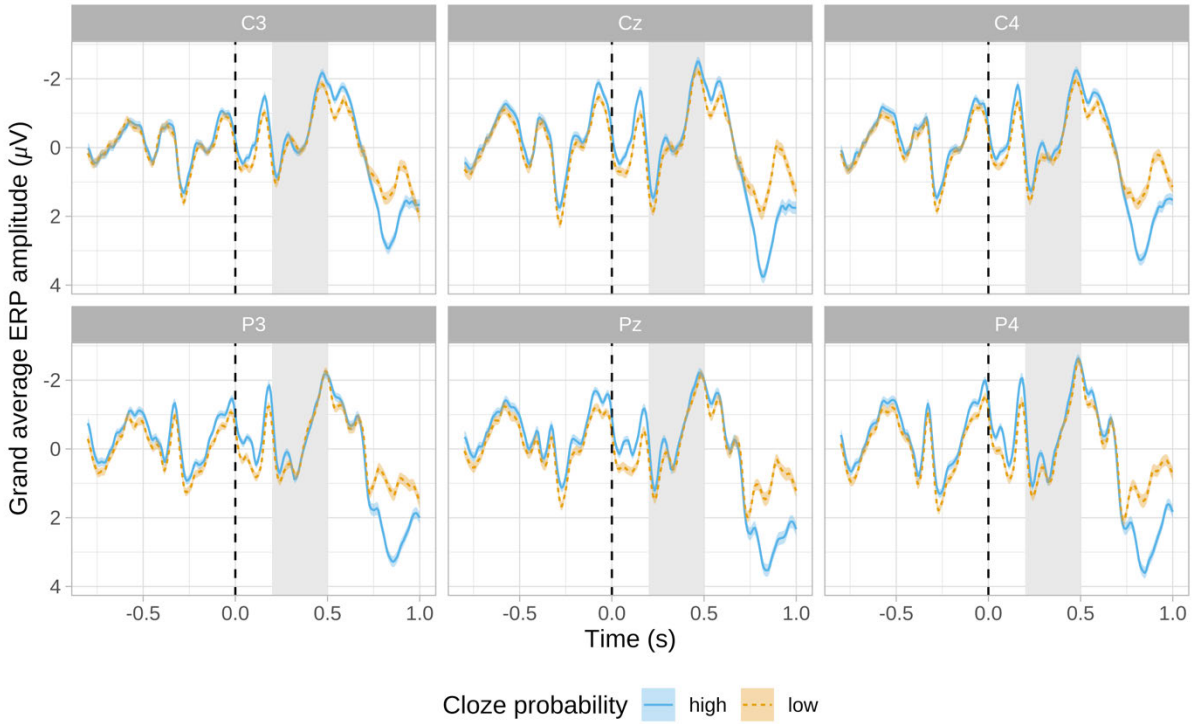


Figure 2.5. *Grand average ERP plots of N400 effects for articles over channels of interest, according to article cloze probability (n = 312). Blue lines represent high article cloze probability (>50) whilst orange dashed lines reflect low article cloze probability (<50). Blue and orange shading depicts the standard errors for the two conditions. The N400 window is depicted via grey shading, and the black dashed line represents the onset of the article word. Note that the plot depicts non-baseline corrected ERP activity.*

The effect of noun cloze probability, IAF and 1/*f* slope on the N400 amplitude following the nouns was explored in Model 4. The model detected a significant main effect of *noun cloze probability* on N400 amplitude time-locked to the noun ($p < .001$, $\beta = 0.71$, $SE = 0.07$, 95% CI [0.56, 0.85]), where increases in noun cloze probability were associated with decreased (i.e., less negative) post-noun N400 amplitudes (see *Figure 2.6B*). The interaction between *noun cloze* and *IAF* on post-noun N400 amplitude did not reach significance ($p = .395$, $\beta = -0.03$, $SE = 0.04$, 95% CI [-0.11, 0.04]). The effect of *noun cloze* and *1/f slope* was also nonsignificant ($p = .127$, $\beta = 0.06$, $SE = 0.04$, 95% CI [-0.02, 0.13]). Therefore, whilst cloze probability influenced N400 amplitudes following the articles and nouns, this relationship was not modulated by individual factors.

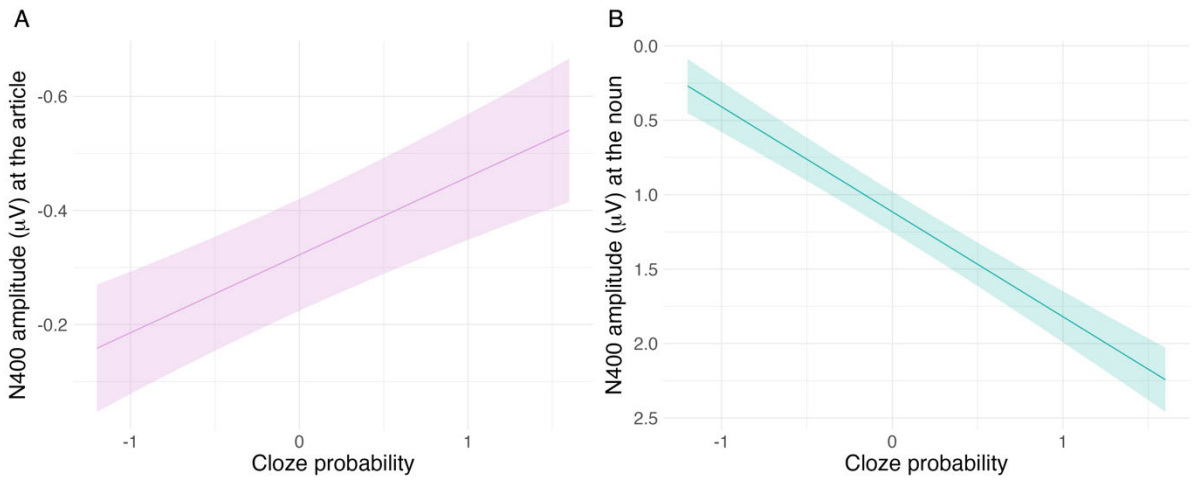


Figure 2.6. *Linear mixed model results for N400 effects.* **(A)** *The effect of article cloze probability (scaled and centered) on N400 amplitude time-locked to articles ($p < .001$, $\beta = -0.14$, $SE = 0.03$, 95% CI [-0.20, -0.07]).* **(B)** *The effect of noun cloze probability (scaled and centered) on N400 amplitude time-locked to nouns ($p < .001$, $\beta = 0.71$, $SE = 0.07$, 95% CI [0.56, 0.85]). Shading in both plots reflects 83% confidence intervals and lines indicate model fit.*

2.3.3. Results of models with surprisal

As described above, whilst we ran SPP models with surprisal, the results either yielded the same outcomes as the cloze probability models or did not reveal interactions with the surprisal of the critical word. Therefore, for simplicity's sake, the models are not reported here although the outputs are presented in *Supplementary material 2C*.

Grand average N400 ERPs according to article surprisal are presented in *Figure 2.7,* whilst grand averages according to noun surprisal are shown in *Figure 2.8.* To determine whether article surprisal influenced the N400 amplitude directly following the article, Model 5 was computed, revealing a nonsignificant main effect of *article surprisal* on post-article N400 amplitude ($p = .124$, $\beta = -0.08$, $SE = 0.05$, 95% CI [-0.18, 0.02]). The interaction between *article surprisal* and *IAF* on N400 amplitude time-locked to the articles was nonsignificant ($p = .557$, $\beta = -0.02$, $SE = 0.04$, 95% CI [-0.09, 0.05]). The effect of *article surprisal* and *1/f slope* also did not reach significance ($p = .671$, $\beta = -0.02$, $SE = 0.04$, 95% CI [-0.09, 0.06]). Therefore, article surprisal, IAF and 1/*f* slope did not interact to influence the amplitude of the N400 component following the articles.

To investigate the role of prior surprisal in prediction, Model 6a was fitted with article, a-1 and a-2 surprisal, and the 1/*f* slope. A significant interaction effect between *article surprisal*, *a-1 surprisal* and *a-2 surprisal* on post-article N400 amplitude was detected ($p = .035$, $\beta = 0.11$, $SE = 0.05$, 95% CI [0.01, 0.22]). In most cases, increases in article surprisal were associated with increased (i.e., more negative) N400 amplitudes following the articles. However, this relationship was not observed when a-2 and a-1 surprisal were low (see *Figure 2.9A*). Model 6b predicted N400 amplitude from article, a-1 and a-2 surprisal, and IAF, which led to a significant interaction between *article surprisal, a-2 surprisal* and *IAF* on post-article N400

amplitude (p = .045, β = -0.07, SE = 0.04, 95% CI [-0.15, -0.00]). While increases in article surprisal were associated with larger (i.e., more negative) N400 amplitudes after the articles, this relationship was strongest for high IAF individuals when a-2 surprisal was high (see *Figure 2.9B*).

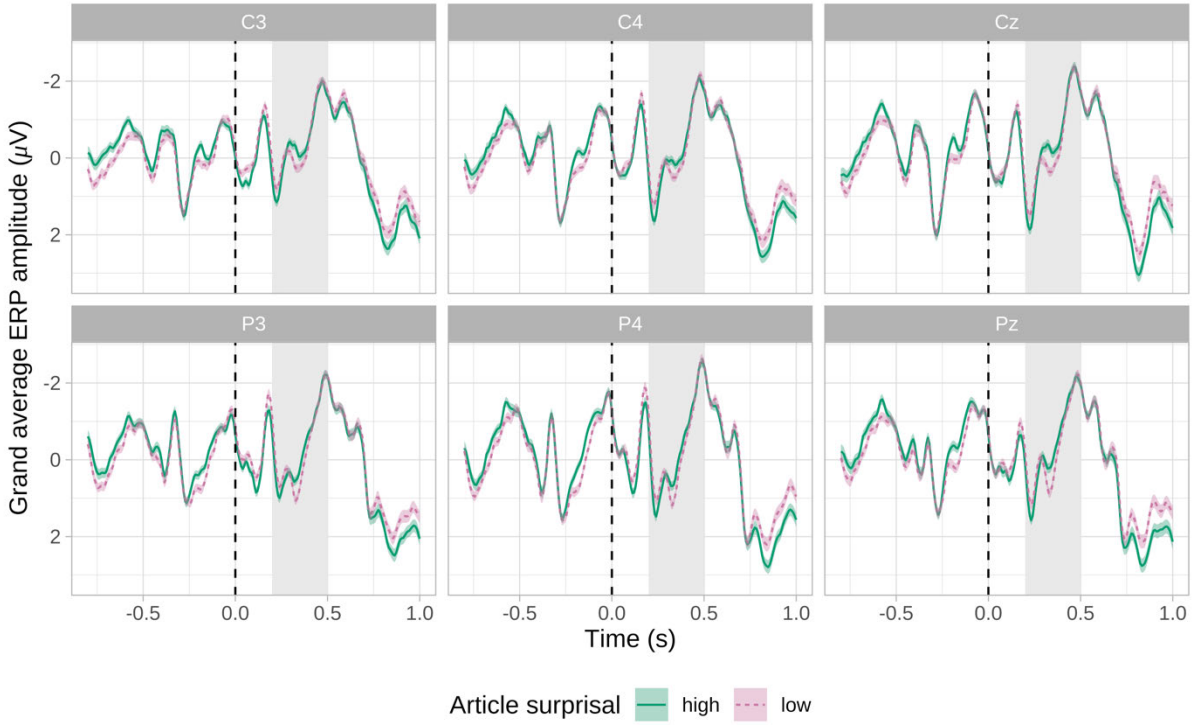


Figure 2.7. *Grand average N400 ERP plots for articles over channels of interest, according to article surprisal (n = 312). Green lines represent high article surprisal (>4.08; the mean article surprisal value) whilst magenta dashed lines reflect low article surprisal (<4.08). Green and magenta shading depicts the standard errors for the two conditions. The N400 window is depicted via grey shading, and the black dashed line represents the onset of the article. Note that the plot depicts non-baseline corrected ERP activity.*

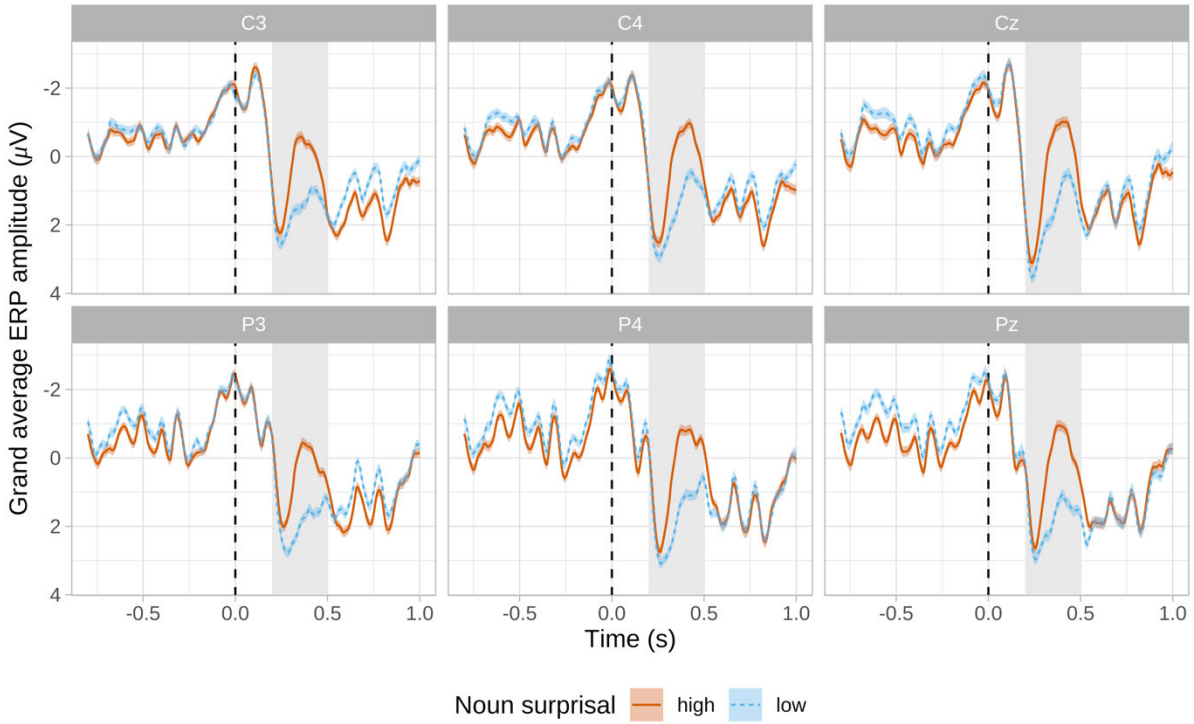


Figure 2.8. *Grand average N400 ERP plots for nouns over channels of interest, according to noun surprisal (n = 312). Red lines represent high noun surprisal (>5.8; the mean noun surprisal value) whilst blue dashed lines reflect low noun surprisal (<5.8). Red and blue shading depicts the standard errors for the two conditions. The N400 window is depicted via grey shading, and the black dashed line represents the onset of the noun. Note that the plot depicts non-baseline corrected ERP activity.*

The effect of noun surprisal on N400 amplitude time-locked to the nouns was investigated via Model 7. A significant main effect of *noun surprisal* on post-noun N400 amplitude was observed ($p < .001$, $\beta = -0.79$, $SE = 0.12$, 95% CI [-1.03, -0.55]), such that greater noun surprisal values were associated with larger (i.e., more negative) N400 amplitudes following the nouns.

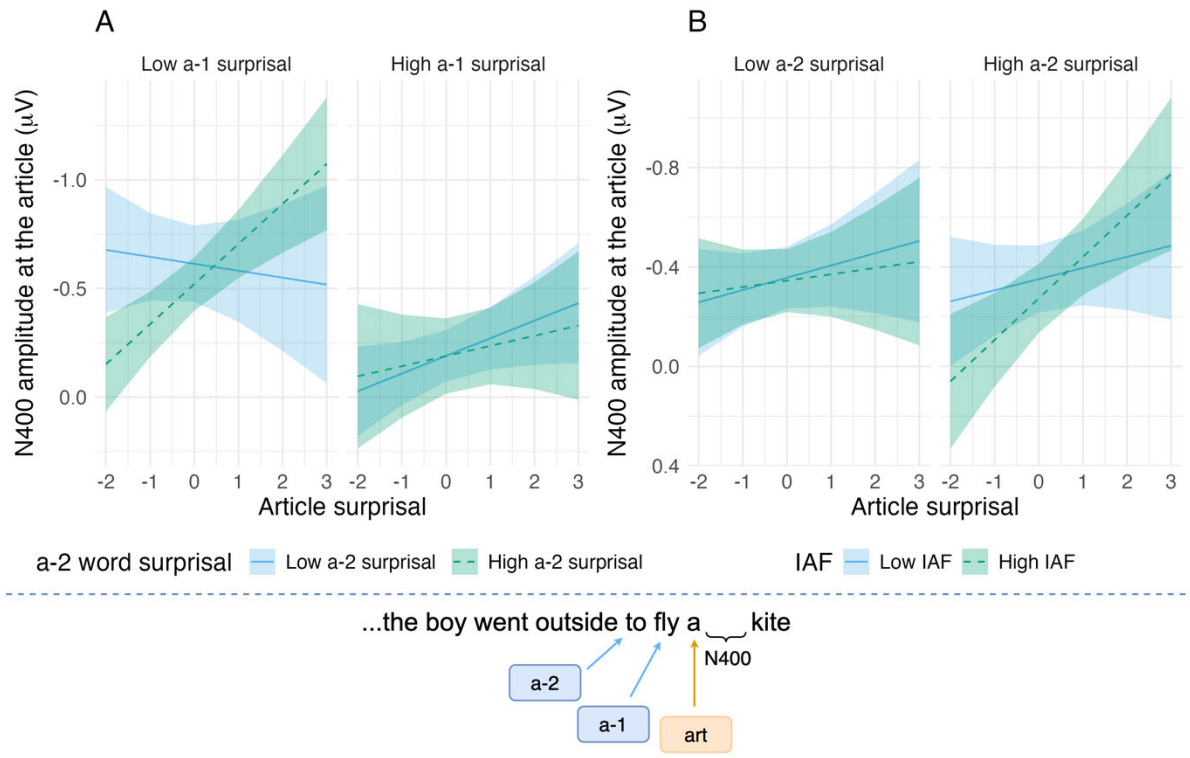


Figure 2.9. *Linear mixed model results of article surprisal effects.* **(A)** *N400 amplitude following the articles, predicted by article-2 (a-2), article-1 (a-1), and article surprisal (p = .035, β = 0.11, SE = 0.05, 95% CI [0.01, 0.22]).* **(B)** *N400 amplitude time-locked to articles, predicted by article-2 (a-2) surprisal, article surprisal and IAF (p = .045, β = -0.07, SE = 0.04, 95% CI [-0.15, -0.00]). Shading in both plots reflects 83% confidence intervals, lines indicate model fit, and the dichotomisation of variables is for visualisation purposes only. Note that both plots depict scaled and centered predictors.*

2.3.4. Correlational models

Shapiro-Wilk tests revealed that article cloze probability and article surprisal were not normally distributed, and as such, a Spearman correlation was computed to examine the relationship between the two variables. The test revealed a significant but weak correlation ($r(158) = -.25$, $p = .001$), such that increases in article cloze were associated with decreases in article surprisal (see *Figure 2.10A*). A second Spearman correlation was calculated to determine the relationship between noun surprisal and noun cloze probability, after Shapiro-Wilk tests revealed that both variables also did not conform to a normal distribution. Noun surprisal and noun cloze probability were significantly negatively correlated ($r(157) = -.63$, $p < .001$), with increases in noun cloze associated with decreases in noun surprisal (see *Figure 2.10B*). Finally, we examined the correlation between the 1/*f* slope and IAF using a Spearman correlation, as these variables were not normally distributed. The test revealed a significant but weak negative correlation between the two variables ($r(310) = -.17$, $p < .01$), such that increases in IAF were associated with decreased (flatter) 1/*f* slopes.

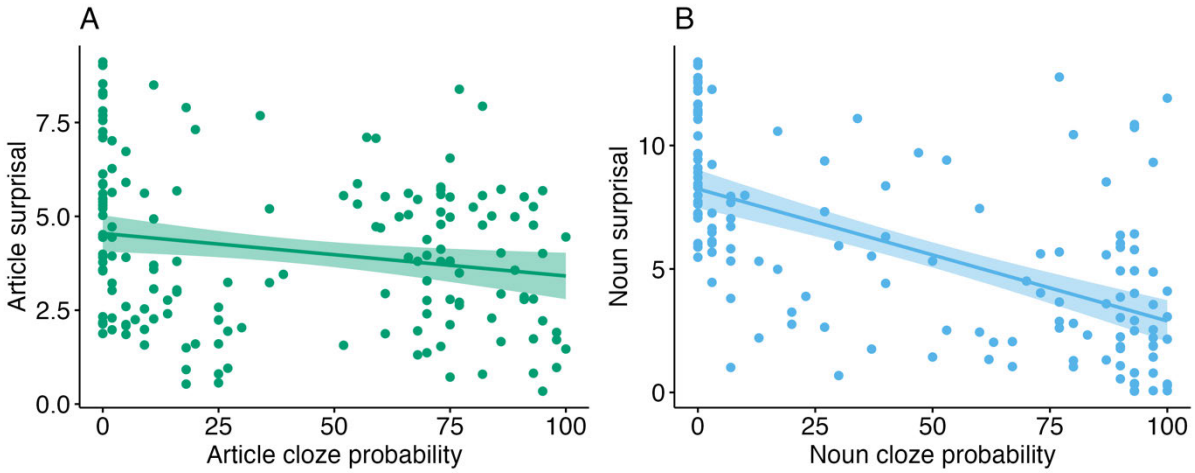


Figure 2.10. *Spearman correlations depicting the relationship between cloze probability and surprisal.* **(A)** *The relationship between article cloze probability and article surprisal (r(158) = -.25, p = .001).* **(B)** *The relationship between noun cloze probability and noun surprisal (r(157) = -.63, p <.001).*

2.4. Discussion

The present study sought to investigate the degree to which prediction underlies linguistic processing via an analysis of individual neural differences and ERP activity in Nieuwland and colleagues' (2018) data. Our analysis did not reveal a positive relationship between word predictability and the magnitude of the SPP as was hypothesized. This may question the extent to which the SPP reflects prediction during natural language processing. Initial N400 models time-locked to articles demonstrated increases in N400 amplitude as article cloze probability increased, whilst article surprisal and post-article N400 amplitudes were not significantly related. At a first glance, this may be taken to suggest that the brain does not predict the phonological form of an upcoming noun, in line with Nieuwland and colleagues' original findings. However, evidence for prediction arose when prior surprisal was considered, such that N400 amplitudes following the articles increased as article surprisal increased. This relationship was not observed when the surprisal of the two prior words was low but was strengthened for high IAF individuals when article-2 surprisal was high. Broadly, our reanalysis contributes novel insights to the debate surrounding prediction in language, by suggesting that prediction during linguistic comprehension depends on contextual and individual factors. This emphasises the adaptive and between-subject nature of prediction, whilst highlighting the variability that surrounds predictive processing at the article.

2.4.1. The SPP may be a limited index of prediction during natural language processing

It was hypothesized that SPP amplitudes would increase (i.e., become more negative) as words became more predictable, reflecting anticipatory processing during linguistic comprehension. However, our analyses in the pre-stimulus window did not reveal a significant effect of article cloze probability on pre-article SPP amplitude, whilst SPP amplitudes preceding the nouns decreased (i.e., became more positive) as noun cloze probability increased. These findings are inconsistent with prior literature, which demonstrates a positive relationship between the

magnitude of the SPP/SPN and word predictability (Grisoni et al., 2017, 2021; León-Cabrera et al., 2017, 2019). Although at face level, these findings might be taken to suggest that participants were not predicting upcoming semantic information, the results may be further illuminated by considering paradigm-specific effects.

As the SPP is proposed to reflect the prediction of semantic information (Grisoni et al., 2021; Pulvermüller & Grisoni, 2020), the observed null article finding may be explained by the overlap in meaning between the articles 'a' and 'an,' resulting in a similar semantic prediction between the two. Alternatively, the noun effect may suggest that SPP analyses were influenced by the temporal overlap between the pre-stimulus and N400 windows following the prior words. Most studies observing SPP/SPN effects employed intervals preceding the critical words of 1000ms or longer to capture activity independent of ERP components following the prior word (Grisoni et al., 2017, 2021; León-Cabrera et al., 2017, 2019). In contrast, the present study included interstimulus intervals of 300ms, which overlapped with the prior word's N400 window. To test whether the N400 following the prior words was probed in our SPP analyses, we also ran the SPP models whilst controlling for prior word surprisal (for model outputs, see *Supplementary material 2C*). This did not influence the results, likely because whilst the windows for the two components overlapped, the topographies differed (frontal for the SPP and centroparietal for the N400). Further, the relationship between critical word predictability (as measured by both cloze and surprisal) and SPP amplitude was not influenced by prior word surprisal or individual factors. This is in contrast with the N400 patterns at the article, which may provide evidence for probabilistic prediction under certain circumstances. Therefore, as an SPP effect in the expected direction was absent even after including factors that influenced prediction (as evidenced by the N400 effects), this may suggest that the SPP does not reflect naturalistic linguistic prediction. This raises the question of whether the longer intervals in other studies encourage prediction to a greater extent, or whether they give rise to a process that differs from natural language comprehension. Supporting this enquiry is a study by Kaan and Carlisle (2014), which presented participants with predictable and random letter strings and varied the length of the delay between the letters. The authors observed a negativity resembling the SPN/SPP only during longer delay trials, which was larger (more negative) for predictable versus random sequences (Kaan & Carlisle, 2014). This further supports the notion that such pre-stimulus negativities may manifest in the presence of longer delays, rendering the extent to which they mirror predictive processes unclear. Ultimately, while we sought to gauge prediction more directly via an analysis of the SPP, effects relating to the N400 may contribute more strongly to understandings of prediction in language.

2.4.2. N400 effects at the article are variable and offer mixed results for prediction

Initial article analyses revealed that as article cloze probability increased, N400 amplitudes following the articles became larger (i.e., more negative), questioning the extent to which the brain predicts upcoming linguistic information. This result opposes both DeLong and colleagues (2005), who found the reversed effect, and Nieuwland and colleagues (2018), whose N400-article analysis did not reach significance (although the trend was detected in some laboratories in Nieuwland and colleagues' replication analysis). Differences in the data analysis pipeline between our analysis and Nieuwland and colleagues' (2018) study may have

contributed to the differential results. Variations in pre-processing steps and our inclusion of pre-stimulus activity as a model covariate (which is shown to improve statistical power over baseline correction; Alday, 2019), may provide a potential explanation for this outcome. Interestingly, the results at the article differed depending on whether surprisal or cloze probability was used, highlighting the potential discrepancy between the two measures in their ability to gauge the predictability of function words such as articles.

When article surprisal was used to operationalize word predictability as opposed to article cloze probability, the N400 effect no longer reached significance. This is in line with Nieuwland and colleagues' original analysis, suggesting that phonological prediction in language may be limited. On the other hand, it is inconsistent with Yan and colleagues' (2017) reanalysis of Nieuwland and colleagues (2018), which revealed increases in the N400 as article surprisal increased (supporting phonological prediction in language). However, whilst we calculated surprisal using corpus-derived GPT-2 models, Yan and colleagues (2017) used the log-transformation of cloze as a measure of surprisal. Consequently, the mixed results at the article may in part arise from the use of differential word predictability metrics; a suggestion that is supported by the weak negative correlation between article cloze probability and article surprisal observed in the present analysis. Cloze probability and GPT-2 measures appear to model N400 patterns slightly differently, particularly at the lower end of the predictability spectrum (Szewczyk & Federmeier, 2022). Whilst cloze is limited in modelling N400 effects to unexpected words with cloze probabilities closer to zero, GPT-2 measures may explain more variance in N400 amplitudes here due to their reliance on the log scale (Szewczyk & Federmeier, 2022). Other research however suggests that cloze probability is a better predictor of N400 amplitude than GPT-2 surprisal (Michaelov et al., 2022). Interestingly, all noun analyses revealed a consistent effect in the typical direction (similarly to DeLong et al., 2005 and Nieuwland et al., 2018), and noun cloze probability and noun surprisal were strongly negatively related (in line with theory; Pickering & Gambi, 2018). This may also suggest that the predictability of function words such as articles is more difficult to gauge, potentially because such words are not as semantically rich as content words (e.g., nouns). Whilst semantic information accumulates across a sentence to constrain subsequent word choices, early speech sounds do not strongly limit later word possibilities, which may render predictability measurements difficult (Huettig et al., 2022). Therefore, whilst the present N400 results at a superficial level appear to provide evidence against phonological prediction, the diversity in outcomes at the article underscores the substantial variability that may surround the processing of this word. This is further emphasised by the observation that the relationship between article surprisal and post-article N400 amplitude appears subject to individual and contextual variation.

2.4.3. Predictive processing depends on prior contextual information

While the above results may question the extent of prediction in language, the analyses including prior word surprisal suggest that predictive processing depends on prior context. When the surprisal of the two preceding words in the sentence was included in the statistical models, increases in article surprisal were associated with increases in N400 amplitude following the article (in line with DeLong et al., 2005). However, this effect was not present

when the surprisal of the two prior words was low, suggesting that the N400 is sensitive to prior contextual information. This notion is broadly compatible with past research, which manipulates the previous context experimentally, consequently changing the predictability of the critical words (Boudewyn et al., 2015; Fleur et al., 2020; Freunberger & Roehm, 2017; Maess et al., 2016; Ness & Meltzer-Asscher, 2018; Szewczyk & Wodniecka, 2020; Szewczyk et al., 2022). Often, cloze probability at the critical words is used to gauge contextual effects (e.g., Maess et al., 2016; Federmeier et al., 2007). In contrast, the current analysis directly quantified the prior context in a continuous fashion, highlighting the importance of prior predictability as it unfolds naturally and incrementally over the course of a sentence. Whilst this analysis may not directly inform the underlying mechanisms behind these contextual effects, establishing that prior predictability is relevant for this relationship has value for the literature as it may form the basis of future, more in-depth explanations. Therefore, the observation of an N400 effect following the article when accounting for prior predictability may thus suggest that participants were predicting the phonological characteristics of the following noun, although only under certain circumstances. Nevertheless, it offers stronger support for the N400 as reflecting prediction versus integration. The shared semantic meaning of 'a/an' in this context should not cause challenges in semantic integration and, consequently, should not result in an N400 effect akin to the one observed in the present study (DeLong et al., 2005). While this may thus support prediction perspectives of the N400, the absence of an article effect in cases of low prior word surprisal might be taken to suggest that participants were not predicting under such circumstances. At a first glance, this result appears somewhat counterintuitive: shouldn't predictions theoretically be strongest in this case, given that prior context provides converging support for the current predictive model?

An alternative explanation for this effect may stem from the notion that the N400 reflects a precision-weighted prediction error signal (Bornkessel-Schlesewsky & Schlesewsky, 2019), with precision reflecting the amount of certainty (or inverse of variance) in the data (Feldman & Friston, 2010; Friston, 2005). According to Bayesian frameworks, precision influences the relative weightings of the sensory input vis-à-vis the prior belief, which has consequences for predictive model updating (Adams et al., 2013). In the present study, low prior word surprisal may have fostered highly precise predictions, thereby concomitantly decreasing the precision attributed to the article such that it was deemed irrelevant for hypothesis testing. This may have consequently resulted in weaker N400 amplitudes as prediction errors at the article were 'ignored' in favour of predictions. The potential for articles to be overlooked is compatible with prior eye-tracking findings, where shorter words are typically skipped more frequently than longer words (Slattery & Yates, 2018). Two-letter words have been shown to be skipped by skilled readers at a rate of approximately 75% during reading (Rayner & McConkie, 1976 in Leinenger & Rayner, 2017). Further, whilst word skipping is also influenced by predictability, such that highly predictable words are more likely to be skipped (e.g., Balota et al., 1985; Ehrlich & Rayner, 1981; Slattery & Yates, 2018), these effects appear to differ for articles. For example, Angele and Rayner (2013) presented participants with a preview of the article 'the' in parafoveal vision, in a manner that rendered it syntactically anomalous given the prior sentence context. Participants tended to skip the preview despite its poor fit with the sentence, suggesting that the anomalous article was overlooked. Taken together, these findings

may suggest that articles are frequently skipped, even when unpredictable. Furthermore, readers with greater print exposure and spelling ability have been shown to skip words more frequently (Faber et al., 2020; Slattery & Yates, 2018), highlighting the role of individual variability in this relationship. Therefore, even though results from natural reading are, of course, not directly comparable to the word-by-word presentation employed in the present experiment, it appears possible that article-induced prediction errors were not considered here under conditions of high prior predictability, analogous to the article skipping findings. In addition to providing a potential explanation for the reduced N400 amplitudes that we observed, this notion is compatible with active inference theories, which propose that prediction error is not only reduced via changes to one's predictive model, but through active sampling of the sensory environment in accordance with one's hypothesis (Friston et al., 2016; Friston & Frith, 2015; Parr et al., 2022). As such, comprehenders may at times neglect unexpected articles in favour of a top-down expectation.

Ultimately, the present results, in addition to the mixed findings regarding cloze and surprisal described above, point towards a uniqueness within the article that gives rise to significant variability, and which may question the utility of this and similar paradigms. If information at the article is overlooked under certain circumstances, and if the relative weighting of the bottom-up versus top-down information influences the N400, interpretations from such paradigms may be more complicated than initially assumed. Interestingly, this could also suggest that the original appeal of Delong and colleagues' (2005) design – that the article does not contain rich lexical-semantic content of its own – may simultaneously be its greatest weakness. Further, the results of the present study align with the proposal that pre-nominal prediction effects may be small and difficult to detect (Kochari & Flecken, 2019; Nicenboim et al., 2020), as a pattern in the expected direction was only observed when prior predictability was considered. This suggests that the difficulty in observing the trend could arise from the inherent variability surrounding processing at the article (as well as at similar pre-nominal words). In further support of the variability surrounding the article is the observation that this relationship was influenced by IAF.

2.4.4. Individual alpha frequency (IAF) modulates predictive processing during language comprehension

In addition to effects of prior context, N400 amplitude following the article was influenced by IAF, emphasising the subject-specific nature of prediction. Whilst the post-article N400 amplitude increased (i.e., became more negative) with increasing article surprisal, this trend was strongest for high IAF individuals when article-2 surprisal was high. Therefore, it is possible to suggest that under conditions of uncertainty, high IAF individuals rely on prediction to a greater extent than low IAF individuals. Alternatively, and in line with our previous discussions concerning precision, this result may also imply that high IAF individuals were weighting the bottom-up information at the article more strongly (i.e., they were affording more precision to the article), resulting in stronger post-article N400 effects. As high prior surprisal likely renders it difficult to form a precise prediction, such individuals may have prioritised the sensory input for model updating. This is supported by prior research, where those with a high IAF demonstrate faster information processing speeds, suggesting that they may sample the

perceptual environment more rapidly (Samaha & Postle, 2015; Klimesch, Doppelmayr, Schimke, et al., 1996; Surwillo, 1961, 1963). Other research proposes that such individuals have a greater inclination towards predictive model updating (Kurthen et al., 2020), which may manifest in larger N400 amplitudes following surprising articles as observed here. Therefore, whilst N400 effects time-locked to the article are typically discussed as reflecting prediction for the upcoming noun, the components' ties to precision (Bornkessel-Schlesewsky & Schlesewsky, 2019) imply that high IAF individuals may adopt a more flexible model updating strategy during conditions of uncertainty. However, further research would be beneficial to determine whether IAF directly influences stimulus precision weightings, potentially by investigating correlates that index prediction errors for precision weightings themselves (e.g., the P300 ERP component, as suggested by Bornkessel-Schlesewsky, Alday, et al., 2022). Additionally, whilst IAF influenced N400 amplitudes, we did not detect any effects relating to the 1/*f* aperiodic slope. Although we investigated 1/*f* as a between-subjects (trait-like) measure, in line with prior research (e.g., Bornkessel-Schlesewsky, Sharrad, et al., 2022; Demuru & Fraschini, 2020; Dziego et al., 2023; McSweeney et al., 2021; Voytek & Knight, 2015), the 1/*f* slope also shows state-like changes and has been linked with norepinephrine activity and phasic changes in neural gain (Pertermann et al., 2019; Rosenblum et al., 2023). Consequently, future research may benefit from examining 1/*f* on a trial-by-trial basis to determine whether changes relating to prediction may be more transient. Nevertheless, the present findings emphasise the role of IAF in predictive processing and suggest that whilst prediction may be an inherent property of cognition (Friston, 2010), the extent to which information is used for predictive model updating is subject to inter-individual variability.

2.4.5. Conclusion

The present study sheds light on the adaptability of predictive processing, whilst emphasising the susceptibility of the N400 component to judgements concerning precision. Whilst we observed evidence for phonological linguistic prediction under certain circumstances, our results speak to the potential sources of variability that alter prediction tendencies at the article, implying that under conditions of high prior predictability, prediction errors at the article may be overlooked in favour of one's predictive model. This may explain how internal language models cope with change as an inherent property of language, as prior context may inform the extent to which subsequent information is used for predictive model updating. The role of IAF in this relationship also suggests that some individuals may be more likely to adjust their predictions than others, having implications for understandings of prediction as a fundamental cognitive mechanism.

Interim summary

Chapter 2 aimed to capture the neural correlates associated with prediction and to shed light on the sources of individual and contextual variability that may shape prediction during language comprehension. The analysis did not reveal a relationship between SPP amplitude and word predictability that would support the component's role as a prediction signal. Conversely, N400 amplitudes were related to changes in word predictability at nouns and, most notably, at articles (according to IAF and prior predictability), situating the N400 within the realm of predictive processing. The article effects observed may provide stronger evidence for the N400 as a prediction error signal as opposed to an index of semantic integration, highlighting the relevance of the N400 for understandings of prediction.

While there is much debate regarding the extent of prediction in language, this chapter makes a novel contribution to the literature by capturing sources of variability that have not previously been investigated in pre-nominal prediction contexts. This provides a potential explanation behind the mixed nature of the prior literature whilst also highlighting the limitations of the original DeLong and colleagues (2005) study design. Ultimately, this investigation provided useful preliminary evidence to suggest that prediction tendencies differ at the inter-individual and contextual level, which could have implications for general cognitive functioning.

Following on from the insights gained in Chapter 2, Chapter 3 describes an experimental study investigating the effect of prediction on memory encoding via an analysis of the N400 component. Capitalising on the sequential dependencies that underly predictive processing more generally, the study sought to extend beyond the linguistic domain and to examine the naturalistic development of predictions. Participants engaged in a study/test paradigm where they viewed predictable and unpredictable sequences of outdoor scene images, before taking part in a recognition test. Note that sequences containing four images were used (as opposed to prior research, which often examines pairs or triplet relationships), to capture predictive processing in a way that could more closely mirror linguistic sentence structure. N400 amplitudes during the study phase were compared with an aggregate measure of memory recognition performance, contributing insight into the neurophysiological activity related to prediction and memory formation.

Chapter 3

How predictability and individual alpha frequency shape memory: insights from an event-related potential investigation

ABSTRACT

Prediction and memory are strongly intertwined, with predictions relying on memory retrieval, whilst also influencing memory encoding. However, it is unclear how predictability influences explicit memory performance, and how individual neural factors may modulate this relationship. The current study sought to investigate the effect of predictability on memory processing with an analysis of the N400 event-related potential in a context extending beyond language. Participants (N = 48, females = 33) completed a study-test paradigm where they first viewed predictable and unpredictable four-item 'ABCD' sequences of outdoor scene images, whilst their brain activity was recorded using electroencephalography. Subsequently, their memory for the images was tested, and N400 patterns during learning were compared with memory outcomes. Behavioural results revealed better memory for images in predictable sequences in contrast to unpredictable sequences. Memory was also strongest for predictable images in the 'B' position, suggesting that when processing longer sequences, the brain may prioritise the data deemed most informative. Strikingly, greater N400 amplitudes during learning were associated with enhanced memory at test for individuals with low versus high individual alpha frequencies. In light of the relationship between the N400 and stimulus predictability, this finding may imply that predictive processing differs between individuals to influence the extent of memory encoding. Finally, exploratory analyses provided evidence for a later positivity that was predictive of subsequent memory performance. Ultimately, the results highlight the complex and interconnected relationship between predictive processing and memory, whilst shedding light on the accumulation of predictions across longer sequences.

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3.1. Introduction

Modern conceptualisations of memory highlight its importance for predicting the future as opposed to purely remembering the past (Bar, 2007; Exton-McGuinness et al., 2015). According to predictive coding, the brain generates predictions about future inputs from prior experience, which are refined in response to prediction errors (mismatches between the prediction and the incoming sensory input; Friston, 2010; Friston & Kiebel, 2009; Hohwy, 2013; Rao & Ballard, 1999). This refinement optimises predictions towards a maximisation of explanatory power, such that the causes of sensory inputs are more accurately inferred and error (or free energy) in the system is reduced (Friston, 2009, 2010). However, the consequences of prediction for learning and memory are not entirely evident, with the relationship between memory and predictive processing stemming from a reliance of predictions on past experiences (involving the retrieval of established memory representations; Chow et al., 2016; Rauss & Born, 2017), and from the effect of prediction on information uptake (concerning memory encoding; Kim et al., 2020; Sherman & Turk-Browne, 2020). Therefore, not only do predictions appear to rely on memory, but they may have implications for informational accuracy and biases. The present experiment sought to shed light on the effect of predictability on memory performance via an investigation into the neural underpinnings of predictive processing across sequences.

3.1.1. Predictions rely on memories of statistical relationships

The notion that predictions rely on memory representations is grounded in the brain's ability to extract environmental regularities – a process known as statistical learning (Turk-Browne, 2012; Siegelman & Frost, 2015). Regularities are abundant in the natural world, such that similar patterns are encountered across time and space (Turk-Browne, 2012, p. 118-119). There is strong evidence that the brain can learn and encode patterns of this nature into memory (i.e., that it can engage in statistical learning); for example, classic visual statistical learning tasks show successful learning of triplets of shapes (Fiser & Aslin, 2002) and syllables (Saffran et al., 1996), presented in a continuous sequence (for similar research in mice, see Gavornik & Bear, 2014). This learning also appears relatively implicit, with participants judging old triplets as more familiar than foil triplets despite being unaware of an underlying relationship and having low confidence in their decisions (Fiser & Aslin, 2002; Turk-Browne, 2012, p. 123). This proficiency for pattern learning has been shown to facilitate predictive processing, with research demonstrating enhanced prediction of upcoming visual orientations following structured versus random sequences (Baker et al., 2014). Additionally, studies employing Serial Reaction Time tasks have revealed faster reaction times for spatial locations that were preceded by predictable versus unpredictable sequences (Nissen & Bullemer, 1987, in Schwarb & Schumacher, 2012). As such, a statistical learning mechanism within memory has been proposed, where statistical relationships are encoded as generalized memory traces to enable the anticipation of future states (Bar, 2007; Turk-Browne, 2012; Sherman & Turk-Browne, 2020). Statistical learning may thus act as a precursor to the formation of a predictive model (Rauss & Born, 2017), such that regularities are learnt and stored as associative traces in memory, which are subsequently retrieved for future use (Bar, 2007). This highlights the reliance of prediction on memory, with both prediction and episodic recall proposed to share

hippocampal machinery (Barron et al., 2020). This common hippocampal dependence, coupled with the brain's ability to encode environmental regularities into memory, places statistical learning and the retrieval of statistical regularities from memory as likely prerequisites for predictive processing.

3.1.2. Predictive processing influences memory encoding

The dependence of both memory and prediction on the hippocampus may additionally explain the role of prediction in regulating memory encoding. Prior research has demonstrated poorer memory for stimuli that are predictive of upcoming items, suggesting that the brain may be unable to predict information and encode new memories simultaneously (Sherman & Turk-Browne, 2020). According to Sherman and Turk-Browne (2020), prediction may expend hippocampal memory retrieval resources that cannot be concurrently used to encode new traces. In the face of a prediction violation, the hippocampus is proposed to switch to an encoding state to incorporate the sensory information (Mack et al., 2018; Sinclair et al., 2021). This suggests that prediction errors may drive the formation of new memories; a proposal that is supported by behavioural research demonstrating enhanced memory for inconsistent (high prediction error-eliciting) items (Greve et al., 2017), reward prediction errors (Jang et al., 2019; Rouhani et al., 2018), surprising images (Michelon et al., 2003), bizarre sentences (Worthen & Roark, 2002), novel words (Habib et al., 2003), and unpredictable, implausible nouns (however, see Haeuser & Kray, 2022 for a discussion of this effect as being driven by the implausibility of the word, as opposed to the predictability itself). To further support the suggestion that the brain prioritises unpredictable information, Furutachi and colleagues (2023) observed amplified sensory representations in the visual cortex of mice for prediction error-eliciting stimuli. According to predictive coding perspectives, prediction errors represent sensory data (Feldman & Friston, 2010). Consequently, amplified sensory representations (observed in Furutachi et al., 2023) may imply stronger prediction errors corresponding to greater model revision and information uptake. As such, the prediction error signals resulting from expectation violations may disrupt predictive processing, such that the brain switches to an encoding state to prioritise updating of the incoming information into the predictive model. Naturally, such a mechanism would likely have important consequences for everyday functioning, as novel information could be prioritised during memory encoding.

Although prediction error-eliciting information may be preferentially encoded into memory, other research demonstrates better memory for both highly expected and unexpected stimuli, as opposed to moderately expected information (Quent et al., 2022). This latter result is congruent with the suggestion that the relationship between expectancy and memory follows a U-shaped, nonlinear pattern, such that schema-congruent and schema-incongruent information is prioritised in memory (with schemas proposed to form the basis of predictions; Quent et al., 2022; van Kesteren et al., 2012). On a similar note, Bein and colleagues (2023) propose that consistency with expectations promotes the integration of that information into existing memory representations. However, prediction errors can promote both integration and memory separation, depending on a number of factors (e.g., the type of prediction error and the strength of the memory reactivation associated with a prediction; Bein et al., 2023). In contrast, other research demonstrates enhanced memory for items eliciting low – as opposed to medium or high – levels of prediction error (Turan et al., 2023). Similarly, Gronau & Schachar (2015)

observed better memory for the perceptual details of objects presented in contextually related versus unrelated pairs, suggesting that contextually congruent (i.e., expected) information is better remembered (aligning with behavioural results from van Kesteren et al., 2013). Taken together, these findings emphasise the mixed nature of the current literature and the importance of further research into the effect of predictability on memory. If predictive processing regulates information uptake, the predictive model applied, and the predictability of the sensory information, may influence what is subsequently encoded into memory. Importantly, whilst most studies rely on changes in probability or consistency to inform the level of prediction error that is evoked (e.g., Greve et al., 2017; Ortiz-Tudela et al., 2023; Turan et al., 2023), an investigation into the neural correlates related to prediction may shed further light on the effect of predictability on memory.

3.1.3. Predictability and the N400 event-related potential (ERP)

A neural correlate frequently related to predictive processing is the N400 event-related potential (ERP), a negative-going component arising approximately 400ms post-stimulus onset (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019; Hodapp & Rabovsky, 2021; Kutas & Hillyard, 1980b). The N400 exhibits greater amplitudes following incongruent or unexpected words (e.g., Federmeier & Kutas, 1999; Kutas & Hillyard, 1980b, 1984), demonstrating a graded relationship with word predictability (e.g., DeLong et al., 2005; Federmeier et al., 2007; Wlotko & Federmeier, 2012). Consequently, current perspectives posit that the component reflects the degree of mismatch between a prediction and the sensory input (i.e., a prediction error; e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019; Hodapp & Rabovsky, 2021). This is broadly compatible with computational modelling work (Eddine et al., 2024; Fitz & Chang, 2019; Rabovsky et al., 2018; Rabovsky & McRae, 2014, for a review see Eddine et al., 2022), highlighting the relevance of the N400 for gauging predictive processing. Although the N400 has primarily been studied in linguistic contexts, N400 effects have also been observed in non-linguistic settings (e.g., relating to action and arithmetic), suggesting that the component may embody more general functions related to meaning processing (Amoruso et al., 2013; Kutas and Federmeier, 2011; Niedeggen et al., 1999; Reid & Striano, 2008; Sitnikova et al., 2008). For example, Urgen and colleagues (2018) observed an N400 effect when participants viewed a realistic robot moving mechanically, suggesting that movement violations of appearance-based predictions may play an important role in the uncanny valley effect. However, despite the component's applicability to non-linguistic contexts, most research relating the N400 to memory outcomes pertains to language, revealing enhanced implicit memory (as evidenced by faster reaction times) for words that evoked greater N400 amplitudes (Hodapp & Rabovsky, 2021). Meyer and colleagues (2007) also observed a correlation between N400 amplitudes to words during learning and ERP old/new effects reflecting familiarity at test, suggesting that the N400 may support familiarity-based recognition. Other research on repetition suppression provides indirect evidence supporting the role of the N400 in memory encoding, demonstrating N400 amplitude decreases following repeated exposure to incongruent sentence endings (Besson et al., 1992). This decrease in N400 activity has been interpreted to reflect adaptation of a predictive model to initially unexpected stimuli (Hodapp & Rabovsky, 2021, 2024); for similar research on the mismatch negativity (MMN) ERP, see Garrido and colleagues (2009). External to traditional language experiments, Abla and colleagues (2008) measured the N400 during a statistical learning task involving triplets of tones. Those who demonstrated stronger

familiarity with the tone triplets at test showed increased N400 amplitudes for the first tone in the sequence during learning. Abla and colleagues (2008) linked this to a novelty effect due to the first tone being the least predictable. Whilst this study measured memory in the form of statistical learning, further research is necessary to test the assumption that the N400 influences behavioural memory outcomes in contexts extending beyond language.

3.1.4. The role of individual neural variability

If memory encoding is influenced by predictability, it may also be susceptible to individual differences in predictive processing. The N400 response has been shown to differ between individuals according to intrinsic neural factors, namely the aperiodic slope of the 1/*f* distribution and individual alpha frequency (IAF), the peak frequency within the alpha rhythm (Bornkessel-Schlesewsky, Sharrad, et al., 2022; Dave et al., 2018; Jano, Cross, et al., 2024; Klimesch, 1999). This may suggest that IAF and the 1/*f* slope influence predictive processing and consequent memory performance. However, to our knowledge, N400 patterns during learning have not been related to explicit memory outcomes in non-linguistic settings, and with a consideration of intrinsic neural differences. Further, while many studies examine the effect of prediction on memory with pairs or triplet relationships (e.g., Long et al., 2016; Otsuka & Saiki, 2016; Rouhani et al., 2020; Sherman et al., 2022; Sherman & Turk-Browne, 2020; Turan et al., 2023), it is important to explore this connection across longer sequences of information. The temporal accuracy of ERPs may provide a means to track predictive processing in real-time and across longer associations, to understand how predictions adapt according to information accrual. Therefore, an investigation into the relationship between the N400 and memory across sequences may have important implications for learning in naturalistic settings, where information is received in a continuous stream (Parr et al., 2022). Such an investigation may aid in understanding the consequences of predictability for learning more generally, whilst providing insight into prediction as a probabilistic and adaptive process.

3.1.5. The present study

The present study aimed to determine the effect of predictability on memory and the role of individual neural variability in this relationship. Participants first engaged in a learning task where they were exposed to predictable and unpredictable sequences of outdoor scene images, after which their recognition of the images was tested. As prior research suggests that memory is impaired for stimuli that promote predictions (Sherman & Turk-Browne, 2020), it was hypothesised that memory performance would be better for images in the unpredictable sequences, in contrast to images in the predictable sequences. Based on research highlighting the relationship between the N400 component, stimulus predictability, and memory updating (described above), it was also hypothesized that greater N400 amplitudes during learning would be associated with enhanced memory performance at recognition.

3.2. Materials and methods

3.2.1. Participants

Fifty individuals took part in the experiment; a sample size based on similar research (Sherman & Turk-Browne, 2020) that aimed to increase statistical power whilst accounting for participant

drop-out rates or data corruption. Two participants were removed from the sample, one due to technical difficulties and the other due to misinterpretation of the task instructions. Consequently, the final sample size was 48 (mean age = 26.8 years old, SD = 6.6 years), consisting of 15 males and 33 females. All participants were right-handed adults between the ages of 18 and 39, with normal to corrected-to-normal vision. Participants were not taking regular medication that could impact the EEG and did not have any diagnosed psychiatric conditions (e.g., depression), diagnosed intellectual impairments, or a diagnosis of dyslexia. They also reported no recreational drug use in the past 6 months. Due to the within-groups nature of the study design, all participants were exposed to all experimental conditions (predictable and unpredictable sequences).

3.2.2. Stimuli and task

3.2.2.1. Outdoor scene task

Stimuli during the learning phase of the outdoor scene task consisted of 102 sequences containing four outdoor scene images each (408 images total). Images were primarily obtained from Sherman and Turk-Browne (2020), and belonged to one of twelve categories (beaches, bridges, deserts, forests, fields, lighthouses, mountains, parks, waterfalls, canyons, lakes, and reefs). In contrast to Sherman and Turk-Browne's (2020) experiment, we included the 'reefs' category to replace the category 'marshes,' as many of the images within the 'marshes' category were either of a low resolution or were highly similar to each other, and we believed that they may have been too difficult to distinguish from one another. Images belonging to the 'reefs' category were taken from Google image searches and were identical in size to the images from the other categories (800 x 600 pixels). Images were presented in the centre of the screen using the *Opensesame* program (Mathôt et al., 2012).

Of the 102 sequences in the learning phase, 68 were predictable, as they contained the same image categories in the same A→B→C→D order (either park, bridge, lighthouse, waterfall or desert, beach, forest, mountain). Although the categories and their order remained stable within the predictable sequences, the specific image belonging to that category always differed, such that no one image was repeated during learning. This is in line with Sherman and Turk-Browne's (2020) study, which probed item-specific memory whilst retaining predictable relationships in the form of categorical associations. The remaining 34 sequences always consisted of images from the categories canyons, reefs, fields, and lakes. Images in these sequences were presented in random order, and as such, multiple images belonging to the same category could be present in the same sequence. This rendered the sequences and the images completely unpredictable, and they were hence labelled 'Z' images. The initial assignment of categories to the two conditions (predictable ABCD sequences and unpredictable Z sequences) was random but did not differ between participants. Further, the order in which each sequence appeared was randomised across participants, although the specific images in each sequence remained consistent between individuals. As the images belonging to 6 of the 12 overall image categories contained a man-made object, it was ensured that this distribution was balanced between the two sequence conditions, such that the predictable (ABCD) sequences contained four (out of eight total) categories with man-made objects, and the unpredictable (Z) sequences

(of which there were half as many as the predictable sequences) contained two (out of four) categories with man-made objects.

During the recognition phase, stimuli consisted of the 408 'old' images shown during the learning phase, belonging to both the predictable (ABCD) and unpredictable (Z) sequences. Additionally, 72 'new' lure images that participants were not previously exposed to were included; 48 belonging to the predictable (ABCD) categories, and 24 belonging to the unpredictable (Z) categories. The differing number of lures between the two sequence conditions was proportional to the distribution of sequence types during learning, such that there were double the number of predictable images as compared to unpredictable images (note that this was considered when calculating memory performance). To maintain consistency regarding the distributions of the various image categories, six lures belonged to each of the 12 outdoor scene categories, resulting in 12 lure images per A, B, C, D position for the predictable ABCD sequences. For example, as A images belonged to the 'park' and 'desert' categories, six lures were images of parks, and six were images of deserts. As the Z condition consisted of four image categories (canyons, reefs, fields, and lakes), six lures from each category were presented. The number of lures per category is adapted from Sherman & Turk-Browne (2020), who presented participants with predictable AB pairings and included four lures per predictable (AB) category in their recognition phase. As our design was extended to include longer image sequences and unpredictable sequences, we chose six lures per category to account for this increase. All images during the recognition phase were presented sequentially and in a random order across participants. A schematic of the outdoor scene task is presented in *Figure 3.1*.

3.2.2.2. Pilot testing

Prior to the main study, a brief pilot test with five participants who did not take part in the main experiment was conducted to determine whether individuals were able to learn the predictable four-item ABCD sequences. The same predictable sequences as in the main experiment were used, and participants completed the learning phase as usual. However, instead of a following recognition test, participants engaged in a simple statistical learning test, similar to the pattern completion tests reported in Siegelman and colleagues (2017). Participants viewed the A, B, and C images in the original predictable sequences. However, for the final D image, they were required to choose between two images; the image that was present in the original sequence, and a foil image belonging to a different image category. Feedback was not provided throughout the task. Mean accuracy on this task was 74%, suggesting that the design facilitated sequence learning.

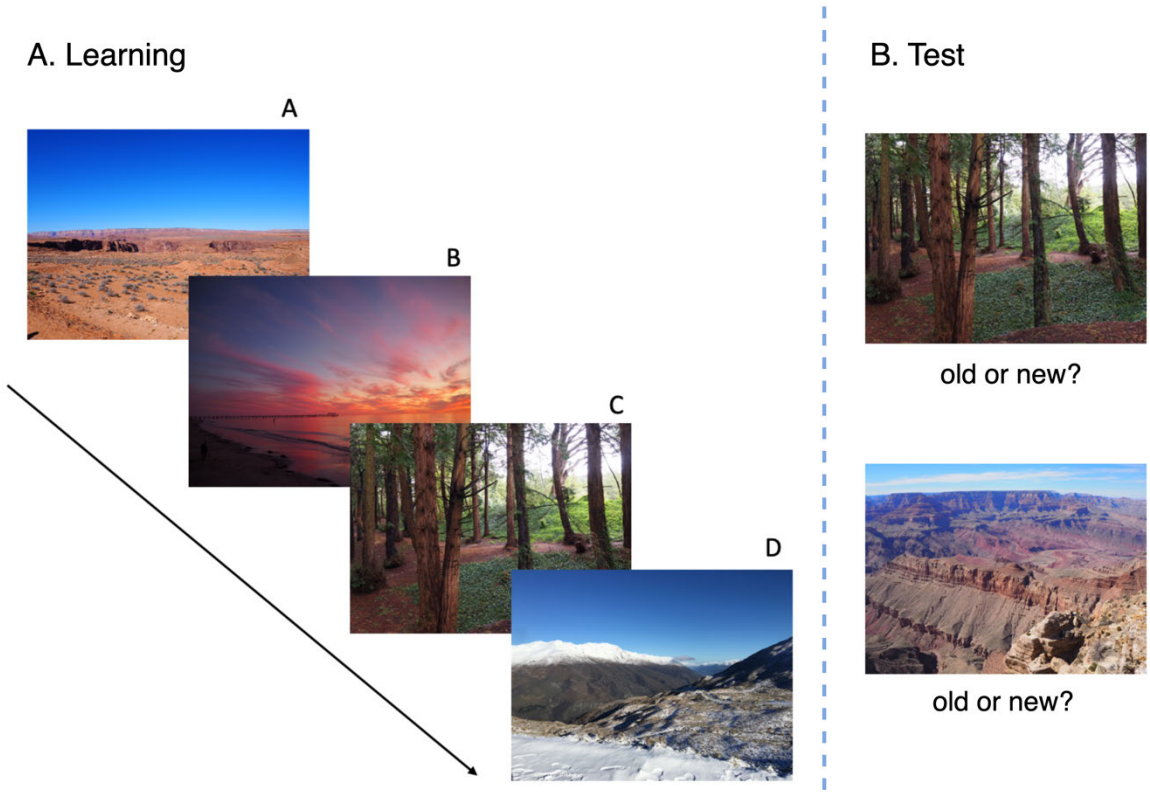


Figure 3.1. *Schematic of the outdoor scene task.* **(A)** *The learning phase of the outdoor scene task, where participants were presented with predictable and unpredictable four-item sequences of outdoor scene images. Each image was presented sequentially and was separated by a fixation dot. This example is of a predictable ABCD sequence (A: desert, B: beach, C: forest, D: mountain).* **(B)** *The recognition test phase of the outdoor scene task, where participants were presented with old images from the original learning phase, and new lure images, to which they made an 'old' or 'new' judgement.*

3.2.3. EEG measures

Electroencephalography (EEG) was recorded throughout the experimental tasks using a 32-channel Brainvision ActiCHamp system (Brain Products GmbH, Gilching, Germany). For the reference electrode, the T7 electrode in the Afz position was used. However, one participant had a faulty T7 electrode, and so the FT9 electrode was used as the reference instead. The ground electrode was placed in the Fpz position and dropdown electrodes from the Fp1 and Fp2 positions were used as the bipolar electrooculogram (EOG) channels, placed above and below the left eye. The data were sampled at a frequency of 500Hz (DC coupled), and the impedances of the channels were maintained below 10kΩ.

3.2.4. Experimental design and procedure

Ethical approval for the study was first sought from the University of South Australia Human Research Ethics committee. Eligible participants provided written informed consent to participate in the research, after which their EEG was set up by an experienced technician. They were seated at a computer in a quiet testing room, with their eyes closed for two minutes,

and then with their eyes open for two minutes, to obtain recordings of their resting state brain activity for the calculation of IAF and aperiodic activity. Following this, participants either engaged in the main outdoor scene task, or completed short control tasks. The order in which participants completed the main task and the control tasks was counterbalanced between participants to control for fatigue effects.

The procedure for the outdoor scene task is loosely based on Sherman & Turk-Browne (2020)'s protocol. For the learning phase of the outdoor scene task, participants viewed the four-item sequences whilst their EEG was recorded. They were not informed of the underlying patterns amongst the images but were simply told that each sequence would consist of four images, presented one after the other, to which they must pay attention. Here, we avoided specifically instructing participants to predict the upcoming items, as prior research suggests that predictive mechanisms are engaged in the presence of probabilistic regularities (Baker et al., 2014; Bar, 2007; Dale et al., 2012; Mumford, 1992). Additionally, while some studies encourage participants to actively predict (e.g., Ortiz-Tudela et al., 2023; Turan et al., 2023), if prediction is a general mechanism underlying cognition (Huang & Rao, 2011), doing so may engender a form of explicit anticipation that differs from naturalistic predictive processing. Each image was presented for 1000ms, followed by a fixation dot in the centre of the screen that was present for 500ms. The between-sequence intervals were 2000ms in duration, to create noticeable boundaries between sequences. As a secondary cover task, throughout the learning phase, a prompt would appear on the screen telling participants to press 'Enter,' as quickly as possible. This would occur at seven random between-sequence intervals during the experiment and would time-out only once the enter key had been pressed. Participants were informed that this was a secondary task to ensure that they were paying attention. The total duration of the learning phase was approximately 15 minutes.

After the learning phase, participants performed a digit span task to minimize recency effects. The task was presented via the OpenSesame program (Mathôt et al., 2012) and took approximately 15 minutes to complete. Following this, participants engaged in a surprise recognition test, where they were presented with old images and new lure images in a random order whilst their brain activity was recorded. For each image, participants were required to state whether the image was 'old' (they saw it in the original learning phase), or 'new' (they did not remember seeing it during the learning phase), using the 'z' and 'm' keys, respectively. Participants responded to the image whilst it was on the screen, with a keypress triggering a switch to a fixation dot with a duration of 500ms. Image presentations timed out after 6 seconds if no response was provided. The duration of the recognition phase was approximately 15 minutes.

The control tasks, completed either before or after the outdoor scene task, consisted of a visual statistical learning task (based on Siegelman et al., 2017) that took approximately 20 minutes to complete, and other short tasks. As the control tasks are not the focus of the current investigation, they will not be discussed further. Following completion of the experiment, the EEG cap was removed, and participants were provided with a $50 payment as compensation for their time. The total testing time for the experiment was approximately 2 hours.

3.3. Data analysis

3.3.1. d-prime (d') calculation

To quantify participants' recognition accuracy, d-prime (d'; McNicol, 2004) was calculated based on performance during the recognition testing phase of the outdoor scene task. Performance was grouped according to participants' old/new responses, where the number of hits (old images correctly identified as 'old') and false alarms (new images incorrectly judged as 'old') were calculated per image position/condition (predictable A, B, C, D, and unpredictable Z), across participants. Following this, d' scores for each image type (predictable 'A', 'B', 'C', 'D' and unpredictable 'Z' images) were computed using the *psycho* package in R version 4.3.1, which subtracts the z-score of the false alarm rate from the z-score of the hit rate (Makowski, 2018). Six subjects with false alarm rates equal to zero were identified, and as such, the d' function was run with adjust = 'TRUE' to adjust for extreme scores in line with Hautus (1995). Note that it was not possible to obtain d' scores for each image position for images in the unpredictable 'Z' condition. This is because lure images were based on categories, but the categories' positions in the unpredictable sequences differed each time (e.g., for one sequence, an image of a canyon might be in the 'A' position, but for the next sequence, a canyon image might be in the 'C' position). As such, d' for unpredictable 'Z' images was calculated across all image positions.

Unforeseen technical difficulties were experienced by five participants during the learning phase of the outdoor scene task, such that the task crashed at variable positions. For one participant, the task crashed towards the beginning (after the 32nd sequence), and they completed the learning phase again. The trials that they had seen twice were removed from their behavioural recognition results in case repeated exposure led to enhanced memory performance for those items. For the remaining four participants, the trials that they had not seen during learning were removed from their behavioural recognition results. We adjusted the d' calculations for all of these participants based on the number of lure and target images that were seen. However, one participant appeared to have made an abnormally large number of 'new' judgements, especially to 'old' images that were seen during learning. As this may have reflected a bias in performance, this participant was removed from subsequent analyses.

3.3.2. EEG data processing

To maintain EEG files in line with recommended standards, the EEG data from the learning phase were first transformed into the Brain Imaging Data Structure (BIDS; Appelhoff et al., 2019) using the *MNE-BIDS* package in MNE-Python (Gramfort et al., 2013; note that Python version 3.8.8 was used). Subsequent pre-processing occurred using MNE-Python, where the data were re-referenced to the mastoid channels (TP9 and TP10). Power spectral density (PSD) plots were then generated, and the data were visually inspected for bad channels, which were marked. EOG channels were set as Fp1 and Fp2 before an independent component analysis (ICA) was fit to a copy of the data that was band-pass filtered between 1 to 40Hz. The ICA was then applied to the raw data to identify and remove ocular noise, after which bad channels were interpolated using spherical splines. Next, the data was filtered with a bandpass filter ranging from 0.1 to 30Hz.

Following processing, the data were epoched around events of interest, between -0.3 seconds preceding the images to 1 second post-image (1.3 seconds total duration). The *Autoreject* function (Jas et al., 2017) was then applied to interpolate and/or remove bad epochs, resulting in an average of 246.9 epochs for predictable images and 123.2 epochs for unpredictable images across participants.

3.3.3. ERP generation

Event-related potentials (ERPs) were computed using MNE-Python (Gramfort et al., 2013) over an N400 window that ranged from 300ms to 500ms post-image onset, based on prior literature (Federmeier et al., 2007; Hodapp & Rabovsky, 2021; Hubbard et al., 2019; Van Berkum et al., 2003). The mean N400 amplitude within the window of interest, per channel, trial and participant was calculated. For a discussion of the chosen N400 topography, see *Results* section.

Rather than performing a traditional baseline correction, ERP activity was additionally computed over a pre-stimulus window ranging from -300 to 0ms prior to image presentation. Mean pre-stimulus ERP amplitudes were calculated for each channel and trial, and were used as a 'baseline' window, that was included as a covariate in statistical models. This approach is described by Alday (2019) and is proposed to enhance statistical power in contrast to traditional baseline correction methods. To generate ERP grand average plots, the data were resampled to 125Hz, and frequency and amplitude data at each time point was computed. Grand averages were plotted using the *ggplot2* package in R version 4.3.1 (Wickham, 2016).

3.3.4. Individual metrics

To obtain measures of individual alpha frequency (IAF) and the 1/*f* aperiodic slope, eyes closed data from resting state recordings was used. The data were re-referenced to TP9 and TP10 and filtered with a bandpass filter from 0.1 to 30Hz. IAF was calculated using the *Philistine* package in MNE-Python (Alday, 2018), over electrodes P3, P4, Pz, O1, O2 and Oz, as IAF is typically measured in parietal-occipital areas (e.g., Corcoran et al., 2018; Dziego et al., 2023; Grandy, Werkle-Bergner, Chicherio, Schmiedek, et al., 2013). The lower bound of the alpha frequency was set at 7Hz, and the upper limit was 13Hz. This method is based on Corcoran and colleagues (2018) and calculates both the peak alpha frequency (PAF; the most prominent peak in the alpha spectrum) and the centre of gravity (CoG; the weighted mean of power across the alpha frequency band; Corcoran et al., 2018).

To obtain estimates of the aperiodic 1/*f* slope, the power spectral density was first calculated across the raw data, for channels P3, P4, Pz, Oz, O1 and O2, to maintain consistency with the IAF metrics. The *Fitting Oscillations and One Over f (FOOOF)* package (version 1.0.0; Donoghue, Haller, et al., 2020) was then used to parameterize the power spectrum, which occurred across a 1 to 30Hz frequency range. The *FOOOF* model settings included a fixed aperiodic mode with a peak width limit of two to eight, a peak threshold of two, a minimum peak height of zero, and a maximum number of four peaks. Subsequently, the data were averaged across the three channels, resulting in a single 1/*f* aperiodic slope measure per participant.

3.3.5. Statistical analysis

Linear mixed-effects models (LMMs) were computed with the *lme4* package in R version 4.3.1 (Bates et al., 2015) to examine effects of interest, as such models allow for the specification of both fixed and random factors (see *Table 3.1* for statistical model structures). Whilst random intercepts were included in all models, the inclusion of by-subject and/or by-item random slopes led to convergence/singularity issues for some. As such, random slopes were omitted in some cases, as this may reflect overfitting (for a discussion of model overparameterization, see Bates et al., 2018). To calculate *p*-values, type II Wald tests from the *car* package were used (Fox & Weisberg, 2019), which were computed according to an alpha level of 0.05. The categorical variables of condition and position were sum contrast coded using the *contr.sum* function from the *car* package (Fox & Weisberg, 2019), and continuous predictors were scaled and centred. Model effects were visualised with 83% confidence intervals using *ggplot2* (Wickham, 2016). In some cases, IAF and the 1/*f* slope were included in the same model as separate interaction terms to reduce the number of models. Also note that for statistical models including IAF, CoG is specifically used as it may perform better when a discernible alpha peak is not present (e.g., in cases where a split peak is observed; Corcoran et al., 2018; Klimesch, 1997; Klimesch et al., 1993). Finally, as IAF could not be estimated for two participants, models with IAF were computed with a sample size of 46, whilst models that did not include the factor of IAF included the full sample size of 48 participants. Models were fitted using variables of interest. However, if a predictor did not interact to influence the outcome variable, and if it did not provide a grouping structure for the data, it was removed to reduce model complexity. Note that this resulted in the removal of a model predicting d' from 1/*f* slope, condition, position and N400 amplitude, as 1/*f* slope did not interact with the variables of interest to influence the outcome variable. As such, a reduced version of this model (without 1/*f* slope) could not contribute additional insights beyond those captured by Model 5 (see *Supplementary material 3A, Model 5.2* for model output).

Table 3.1. *Linear mixed-effects model structures including outcome variables, fixed effects, covariates, random intercepts, and random slopes.*

Behavioural models					
Model	**Outcome**	**Fixed effects**	**Separate interaction terms**	**Random intercepts**	**Random slopes**
1	d’	Condition (predictable/ unpredictable)	1/*f* slope IAF	+ Subject	
2	d’	Image type (predictable A/B/C/D, unpredictable Z)	1/*f* slope IAF	+ Subject	
ERP models					
Model	**Outcome**	**Covariates**	**Fixed effects**	**Random intercepts**	**Random slopes**
3	N400 amplitude (300-500ms)	Pre-stimulus ERP amplitude	Sagitallity (anterior/ central/posterior) Laterality (left/middle/right)	+ Subject + Item	
4	N400 amplitude (300-500ms; averaged over anterior channels)	Pre-stimulus ERP amplitude	Condition (predictable/ unpredictable) Position (A/B/C/D)	+ Subject + Item	
Combined ERP and behavioural models					
Model	**Outcome**	**Covariates**	**Fixed effects**	**Random intercepts**	**Random slopes**
5	d’	Pre-stimulus ERP amplitude	Condition (predictable/ unpredictable) Position (A/B/C/D) N400 amplitude (300-500ms; averaged over anterior channels) IAF	+ Subject	By-subject according to condition

3.4. Results

Statistical model outputs are presented in *Supplementary material 3A*, whilst the data and analysis scripts necessary for replication of the results are freely available at the following repository: https://osf.io/qvjer/.

3.4.1. Descriptive statistics

The mean reaction time in response to the 'enter' prompt during the cover task of the learning phase of the outdoor scene task was 0.770 seconds (*SD* = 0.399 seconds). Mean and standard deviation d' scores from the learning phase of the outdoor scene task are presented in *Table 3.2.*

Table 3.2. *Mean d' scores per image condition and position, with standard deviations in brackets. Note that d' was computed across all images in the unpredictable 'Z' sequences, regardless of their position, as category lures could not be made specific for each position.*

Condition	***Predictable***				***Unpredictable***
Position	**A images**	**B images**	**C images**	**D images**	**Z images**
Mean (*sd*)	0.50 (0.44)	0.69 (0.45)	0.22 (0.37)	0.23 (0.41)	0.31 (0.31)

3.4.2. Linear mixed model results of primary analyses

3.4.2.1. Behavioural results

To investigate the hypothesis that predictable images would be remembered more poorly than unpredictable images, Model 1 was fitted to the data including the variables of image condition (predictable/unpredictable), IAF and 1/*f* slope. The model detected a significant main effect of *condition* on d' ($\chi2(1) = 4.50$, $p = .034$; see *Figure 3.2A*). However, the interaction between *IAF* and *condition* was nonsignificant ($\chi2(1) = 1.54$, $p = .214$), in addition to the interaction between *condition* and *1/f slope* ($\chi2(1) = 3.00$, $p = .083$).

To investigate the effect of both image condition and image position, the 'image type' variable was used for the behavioural analyses, as the levels of this variable were divided into predictable 'A', 'B', 'C' and 'D' images, and unpredictable 'Z' images. To investigate the effect of image type, IAF and the 1/*f* slope on d' scores, Model 2 was computed. A significant main effect of *image type* on d' was detected ($\chi2(4) = 50.97$, $p < .001$), such that d' scores were greatest for predictable B images (see *Figure 3.2B*).

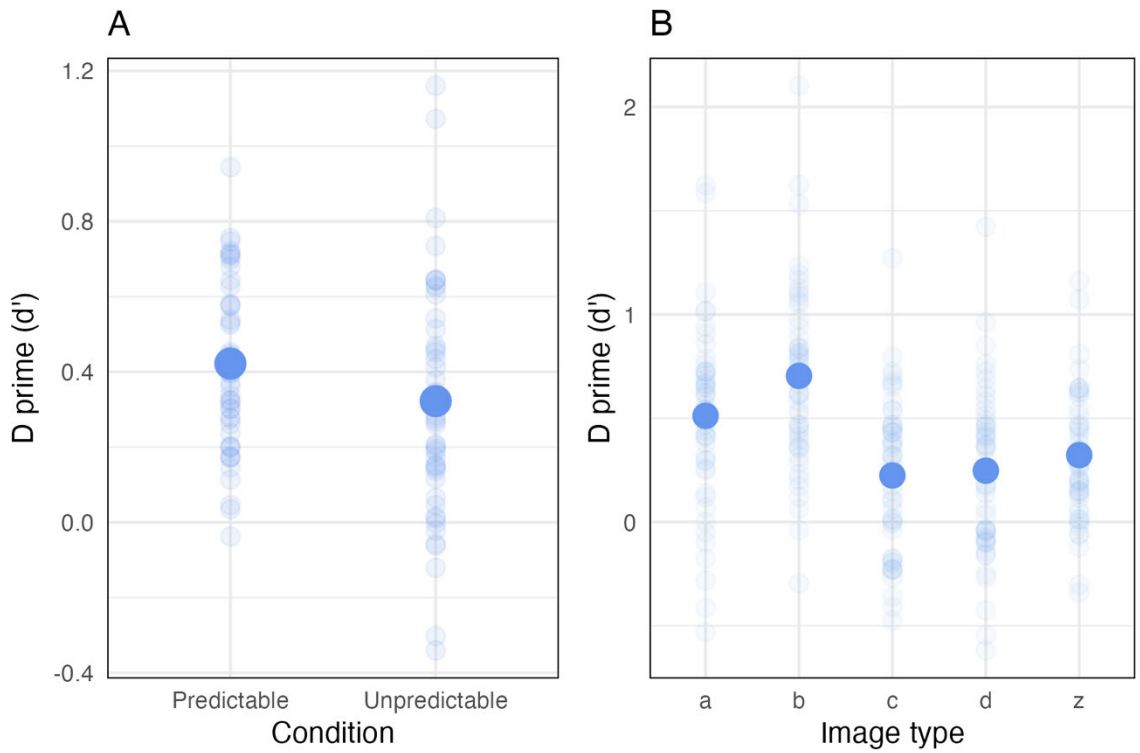


Figure 3.2. Behavioural data. **(A)** *d' score predicted by image condition (predictable versus unpredictable).* **(B)** *d' score predicted by image type (predictable A, B, C, D, and unpredictable Z images). Faded dots in both plots indicate raw data points, and filled dots reflect predicted model values.*

3.4.2.2. N400 results

To determine a region of interest for analyses of the N400, Model 3 predicted N400 amplitude from sagitallity and laterality. A significant interaction between *sagitallity* and *laterality* was observed ($\chi 2(4) = 175.24$, $p < .001$), whereby N400 amplitude was largest over anterior regions, particularly over the midline area (for topography map and grand average across all regions, see *Figure 3.3*). This is consistent with previous research, which suggests that the N400 in pictorial paradigms exhibits a frontal topography (Kutas & Federmeier, 2011; Urgen et al., 2018). As such, for subsequent models including N400 amplitude, the data were filtered to capture activity over anterior electrodes (Fz, F3, F7, FT9, FC5, FC1, FT10, FC6, FC2, F4, F8). This method was chosen as the inclusion of the variables 'sagitallity' and 'laterality' in other models (which consisted of additional predictors) would otherwise likely lead to overcomplexity that would not be supported by the number of observations. Additionally, whilst we detected an interaction between both sagitallity and laterality, we opted to include all anterior electrodes, as only a single electrode was classified as belonging to the anterior-mid region (Fz).

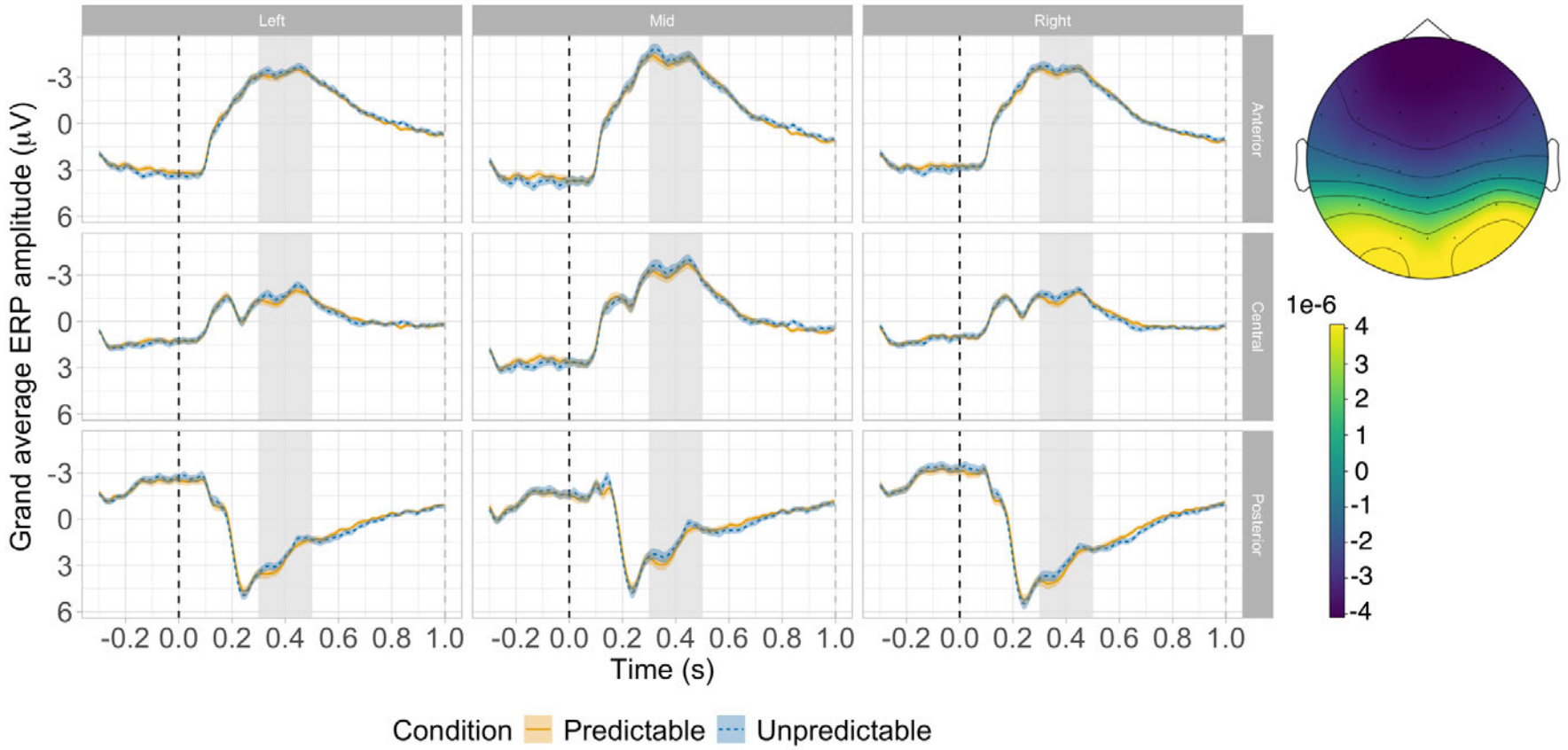


Figure 3.3. *Grand average plots depicting mean ERP activity according to image condition (predictable versus unpredictable), sagitallity (anterior, central, posterior) and laterality (left, mid, right). Black dotted lines represent image onset, grey dotted lines mark the end of image presentation, and grey shading depicts the N400 window used in statistical analyses. Orange lines reflect ERP activity in the predictable condition, whilst blue dotted lines represent the unpredictable condition. Orange and blue shading depicts the standard errors for each condition. A topography map in the bottom right-hand corner displays the mean ERP activity across the scalp in the N400 window (300 to 500ms post-stimulus onset), with the colour gradient (light to dark) representing ERP amplitude in volts. Note that whilst the N400 was initially examined over all electrodes to determine a region of interest (Model 3), models examining the effect of image condition were computed across anterior electrodes sites.*

Model 4 was fitted to examine the effects of image condition and position on the amplitude of the N400 component (averaged over anterior channels to reduce complexity). Note that as ERPs were computed at the single trial level (versus subject level for d' scores), the variables 'condition' and 'position' contained differing information and could thus be included in the same model, in contrast to the behavioural models, where 'image type' is used. While the interaction between image *condition* and *position* was non-significant ($\chi2(3) = 3.02$, $p = .388$), the main effect of *position* was significant ($\chi2(3) = 21.28$, $p < .001$). N400 amplitudes were greatest for images in the 'B' position (see *Figure 3.4 and Figure 3.5A*).

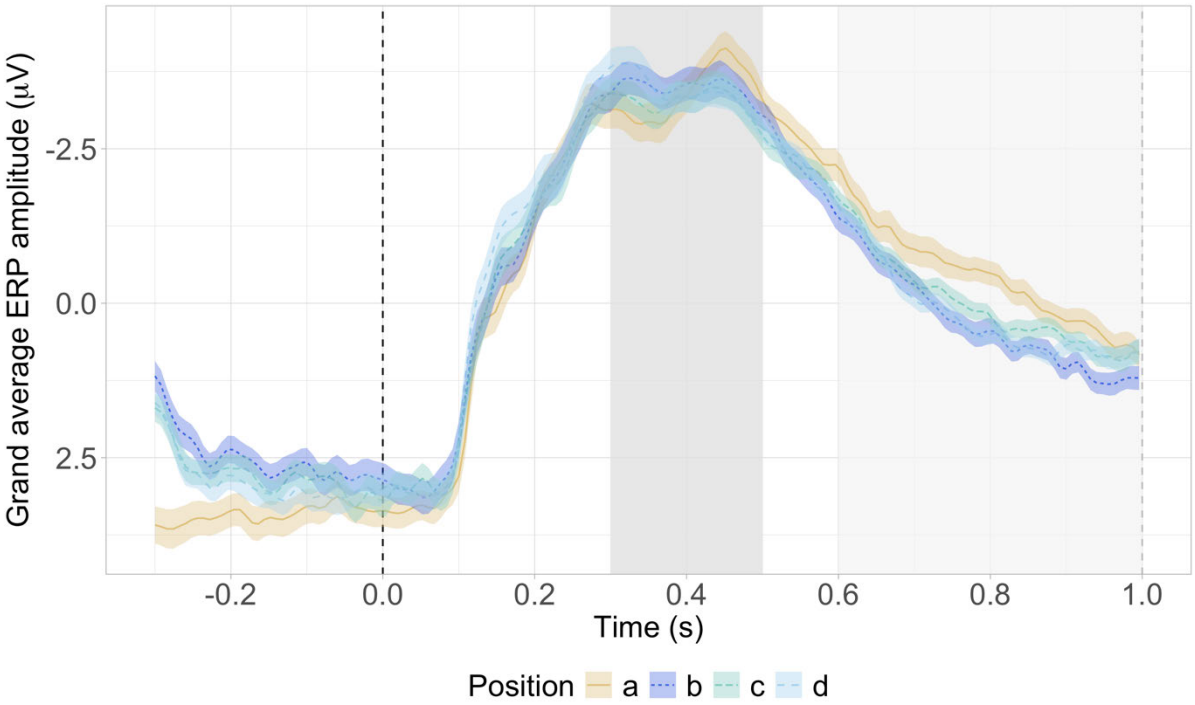


Figure 3.4. *Grand average plots depicting mean ERP activity according to image position across all anterior channels. Black dotted lines represent image onset, grey dotted lines mark the end of image presentation. The first, darker grey box depicts the N400 window used in statistical analyses, while the second, lighter grey box shows the time window used for exploratory statistical analyses (described in section 3.4.3).*

3.4.2.3. Combined N400 and behavioural results

It was predicted that images that evoked greater N400 amplitudes during learning would be better remembered. To investigate this hypothesis, we ran a combined LMM (Model 5) predicting d' from image condition (predictable/unpredictable), position (A, B, C, D), N400 amplitude, and IAF. Importantly, as d' is an aggregated variable, this analysis could not be completed at the single trial level. Instead, N400 amplitude was averaged such that a mean N400 amplitude score per image condition, position, and subject, was computed. A significant interaction between *N400 amplitude* and *IAF* was revealed ($\chi2(1) = 7.59$, $p = .006$), such that for low IAF individuals, d' scores increased as N400 amplitudes during learning increased. This pattern was not observed for those with a high IAF (see *Figure 3.5B*).

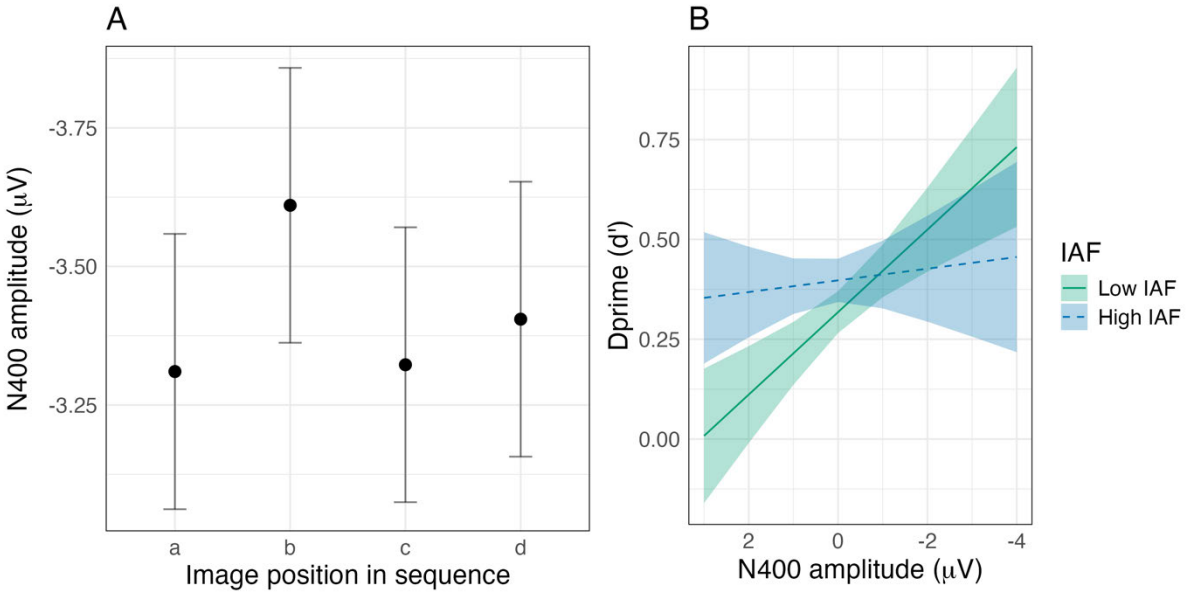


Figure 3.5. (A) *The modelled effect of image position (A, B, C, D) on N400 amplitude. Error bars reflect 83% confidence intervals.* **(B)** *Linear mixed model results depicting the interaction between N400 amplitude and IAF on d'. Green lines represent low IAFs, whilst blue dotted lines depict high IAFs, with this dichotomisation calculated according to the first and third quartiles for visualisation purposes only. Green and blue shading depicts the 83% confidence intervals.*

3.4.3. Exploratory late positivity models

ERP grand average plots (specifically *Figure 3.4* according to image position) revealed differences in a later component potentially resembling a late positive complex (LPC) ERP. As an additional exploratory analysis, we computed this component over a 600ms to 1000ms window post-image onset. Prior research generally examines the LPC over an approximate 500ms to 800ms window post stimulus onset (Stróżak et al., 2016; H. Yang et al., 2019), although it has been measured within a 500ms to 1000ms window before (Brezis et al., 2017). We extended the typical window to capture the prominent differences in the component (as identified via visual inspection), whilst avoiding overlap with the subsequent inter-stimulus interval. A data-driven approach was taken to determine the region of interest for this component, similarly to the N400 models, where sagitallity and laterality were first entered into a model. Following this, the region demonstrating the largest amplitude was used for subsequent models (for exploratory model structures see *Table 3.3*).

Table 3.3. *Linear mixed-effects model structures for exploratory models including outcome variables, fixed effects, covariates, random intercepts, and random slopes.*

ERP models					
Model	**Outcome**	**Covariates**	**Fixed effects**	**Random intercepts**	**Random slopes**
6	Amplitude of late positivity	Pre-stimulus ERP amplitude	Sagitallity (anterior/ central/posterior) Laterality (left/middle/right)	+ Subject + Item	
7	Amplitude of late positivity (averaged over anterior channels)	Pre-stimulus ERP amplitude	Condition (predictable/ unpredictable) Position (A/B/C/D)	+ Subject + Item	By-subject according to condition
Combined ERP and behavioural models					
Model	**Outcome**	**Covariates**	**Fixed effects**	**Random intercepts**	**Random slopes**
8	d’	Pre-stimulus ERP amplitude	Condition (predictable/ unpredictable) Position (A/B/C/D) amplitude of late positivity (averaged over anterior channels)	+ Subject	By-subject according to condition

3.4.3.1. Late positivity results

Model 6 tested the effect of sagitallity and laterality on the amplitude of the late positivity, revealing a significant interaction between *sagitallity* and *laterality* ($\chi2(4) = 156.53$, $p < .001$). Amplitude was greatest over anterior midline regions. However, similarly to the N400, all anterior channels were chosen for subsequent analyses as only a single electrode belonged to the anterior midline region (Fz).

Model 7 examined the effect of image condition and position on late positivity amplitude (averaged across anterior channels). The effect of *condition* and *position* on the amplitude of this later component was significant ($\chi2(3) = 8.32$, $p = .040$), such that amplitudes were greatest for unpredictable versus predictable images at the ‘A’ position, whilst at the ‘D’ position, this pattern reversed (see *Figure 3.6A*).

3.4.3.2. Combined behavioural and late positivity results

Finally, the effect of late positivity amplitude, condition and position on d' was investigated via Model 8. While the interaction of all three variables was non-significant ($\chi2(3) = 7.48$, $p = .058$), the main effect of *late positivity amplitude* on d' was significant ($\chi2(1) = 4.07$, $p = .044$), such that the two variables were positively correlated (see *Figure 3.6B*). As such, the amplitude of this later component differed according to image position and condition and was predictive of later memory performance.

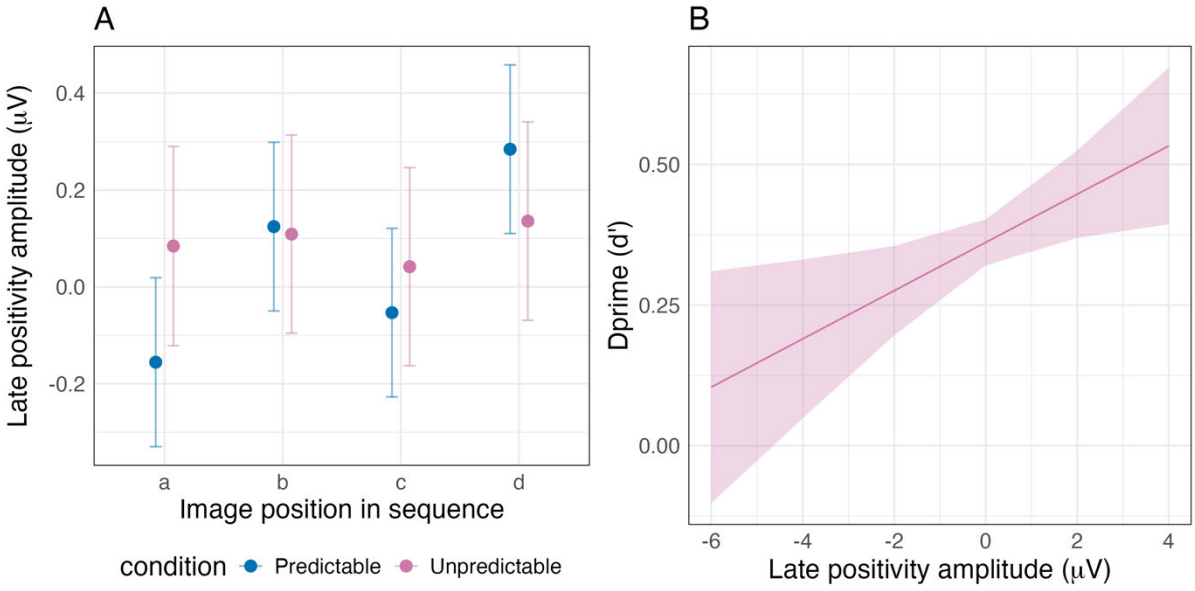


Figure 3.6. (A) *The modelled effect of image position (A, B, C, D) and condition (predictable, unpredictable) on the amplitude of the late positivity. Error bars reflect 83% confidence intervals.* **(B)** *Linear mixed model results depicting the effect of late positivity amplitude on d'. Pink shading depicts the 83% confidence interval.*

3.5. Discussion

The present experiment aimed to shed light on the relationship between predictability and memory, by relating ERP activity during exposure to predictable and unpredictable sequences to memory recognition outcomes. Contrary to hypothesised effects, the results revealed enhanced memory for images in predictable, as compared to unpredictable conditions. However, when taking image position into account, memory performance was best for predictable images in the 'B' sequence position. This finding will be subsequently discussed in relation to precision and attentional mechanisms. Strikingly, greater N400 amplitudes during learning were associated with better memory outcomes at test for low versus high IAF individuals. This may imply that intrinsic neural differences modulate the extent to which N400 activity influences memory processing. Note however, that the 1/*f* aperiodic slope did not affect this relationship, suggesting that IAF may be particularly relevant for the association between ERP activity and subsequent memory. Additionally, exploratory analyses revealed changes in a later positive component (potentially resembling the LPC) according to image position and

condition. This component was positively associated with later memory performance, emphasising the relevance of this activity for learning. Overall, the current findings shed new light on the interconnectedness between predictability and memory, whilst emphasising the importance of between-subject neural variability for memory encoding.

3.5.1. Changes in precision may influence the extent of memory encoding

Memory recognition was strongest for images in the predictable versus unpredictable condition, calling to question the potential trade-off between prediction and memory encoding (Hubbard et al., 2019; Sherman et al., 2022; Sherman & Turk-Browne, 2020). However, while at a surface level, this finding may suggest that increases in predictability promote memory recognition, the observation that predictable 'B' images were best remembered could highlight a role for attentional mechanisms in this relationship. Not only was the 'B' image predictable and predictive of the upcoming 'C' and 'D' items, but it was likely the first image that confirmed whether the sequence was unfolding in a predictable manner. As such, it is possible that predictable images in this position were attended to more strongly than other images, due to their relevance for evaluating the sequence. In predictive coding, attention is proposed to reflect judgements concerning the *precision* associated with a prediction error; that is, the amount of certainty or variance in the signal (Bastos et al., 2012; Feldman & Friston, 2010; Friston et al., 2011). Increases in attention may be associated with increases in the precision of sensory signals, enhancing the extent to which the stimulus prompts model updating (Hohwy, 2012). In the present study, attention might have been directed towards the predictable 'B' images once participants learnt their relevance for the broader sequence, leading to increased precision-weightings. Stronger precision-weightings could have consequently triggered a switch to memory encoding, thus explaining the enhanced memory for the 'B' image.

This explanation is further complemented by the observation that N400 amplitudes were generally greatest for images in the 'B' position, regardless of image condition (predictable/unpredictable). The N400 is proposed to not only reflect a prediction error, but to be indicative of a *precision-weighted* prediction error signal that is dependent on stimulus uncertainty (Bornkessel-Schlesewsky & Schlesewsky, 2019). As such, greater N400 amplitudes may reflect stronger precision-weightings, potentially due to enhanced attention toward the 'B' images. Although the degree to which the N400 reflects prediction error in the present study is uncertain (discussed further in section *3.5.3*), these results could suggest that in longer sequences, the brain may prioritise the items deemed most informative, and direct attention away from subsequent items if the prior information is sufficient for predictive processing. This is supported by Darriba & Waszak (2018), who investigated predictions across four-item sequences. Increases in the P2a and P3 ERP components (proposed to reflect evidence accumulation) were observed from the first to the third stimulus, but not at the final stimulus in the predictable sequences (Darriba & Waszak, 2018). Consequently, it was suggested that evidence accumulates until sufficient information for the prediction is acquired, potentially explaining the prioritisation of the 'B' image observed here. However, it is important to note that whilst we assume that the 'B' images received more attention, this was not explicitly measured, and future research may benefit from relating more direct measures of attention (e.g., eye-tracking; Carter & Luke, 2020) to prediction during sequence learning.

To explain why the above N400 effects occurred regardless of image condition, we also highlight a crucial aspect of our study design: whilst predictable sequences likely promoted predictions about upcoming image *categories*, it is unlikely that *item-specific* predictions could be precise enough to lead to N400 reductions, because each item was unique. This distinction between category and item-based predictability is congruent with hierarchical predictive coding views, where predictions at higher levels may code for more complex information (e.g., sequential categorical associations), whilst predictions at lower levels pertain to more basic (e.g., item-specific) attributes (Rao & Ballard, 1999; Summerfield & DeLange, 2014). As such, memory for images in predictable sequences might have been enhanced at the item-level, which importantly, is also the level at which memory recognition was tested. Therefore, whilst at a first glance, our behavioural findings suggest that predictable information is better remembered, an interpretation of findings at the 'B' image suggests that the relationship between stimulus predictability and memory encoding may be more nuanced and stimulus dependent.

3.5.2. The relationship between N400 amplitude and memory processing

Whilst our behavioural results highlight the importance of precision and attentional mechanisms in predictive processing, findings relating the N400 to memory performance shed light on the neurophysiological activity that contributes to memory encoding. Notably, we observed a positive relationship between N400 amplitude and memory performance for individuals with a low IAF, whilst this effect was absent for those with a high IAF. Given the well-established sensitivity of the N400 to stimulus expectancy (e.g., DeLong et al., 2005; Wlotko & Federmeier, 2012; for a review, see Kutas & Federmeier, 2011), and it's links to prediction error (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019; Fitz & Chang, 2019; Hodapp & Rabovsky, 2021; Rabovsky and McRae, 2014), this may suggest that the extent to which predictability predictability (and by extension, prediction error) drives memory encoding is subject to individual differences. Prediction error purportedly prompts memory updating via memory reconsolidation mechanisms (Exton-McGuinness et al., 2015; R. S. Fernández et al., 2016; Sinclair et al., 2021; Sinclair & Barense, 2019). Reconsolidation is the process by which an existing memory is reactivated, becoming unstable and prone to change, whether that be interference or memory strengthening (Sinclair & Barense, 2019). When a stimulus is encountered, a memory trace for a previously learnt association is reactivated (Kveraga et al., 2007; Sinclair & Barense, 2019). Prediction errors then weaken the associations between the originally learnt items, prompting reconsolidation and enabling the new information to be updated into the existing memory representation (Exton-McGuinness et al., 2015; Sinclair & Barense, 2019). This effect appears contingent on the magnitude of the prediction error, with minimal prediction errors seeming insufficient to prompt reconsolidation and updating of the new, error-inducing information into memory (Gura et al., 2020). In the present study, larger N400 amplitudes (potentially reflecting prediction error; a suggestion that will be discussed further in section *3.5.3*) may have prompted memory reconsolidation for low IAF individuals, where the unpredictable information was updated into the existing memory trace. However, it is important to explore in further detail why this relationship may differ according to between-subject neural variability.

3.5.3. The effect of N400 amplitude on memory is modulated by individual alpha frequency (IAF)

The present study is the first to our knowledge to demonstrate a role for IAF in modulating the effect of N400 amplitude on memory recognition. This result may imply that the extent to which stimulus predictability promotes learning is subject to between-participant variation. A high IAF has been linked to better general cognitive ability (Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013) and to faster information processing speeds, reflected by shorter reaction times (Surwillo, 1961, 1963) and more accurate responses to near-threshold stimuli (Samaha & Postle, 2015). In an emotional memory study by Cross and colleagues' (2020), high IAF individuals exhibited stronger memory for both neutral and positive items, in contrast to low IAF individuals. Here, negative information was argued to be of greatest importance, and from this it was suggested that high IAF individuals may possess a heightened ability to encode less relevant information into memory (Cross et al., 2020). With this in mind, the weak relationship between the N400 and memory performance in the present study for those with a high IAF may imply that memory encoding can occur independently of the level of predictability. Whilst it has been previously suggested that high IAF individuals are more likely to update their predictive models (Kurthen et al., 2020), it may also be the case that they adopt a more widespread memory encoding strategy. This potentially explains the positive associations between IAF and memory performance described in previous literature (e.g., Klimesch et al., 1990, 1993) and implies that the extent to which predictability (presumably captured via the N400) drives model updating depends on intrinsic neural differences.

However, it is important to note that the effect of IAF and N400 amplitude on memory performance occurred regardless of whether images belonged to predictable or unpredictable sequences. Although this renders it difficult to confidently conclude that the N400 reflects prediction error in the present study, it does not exclude the possibility that participants were predicting. The current design, capitalising on statistical regularities in a manner similar to Sherman and Turk-Browne (2020), included consistent categorical relationships that should give rise to predictions (Baker et al., 2014; Bar, 2007; Dale et al., 2012; Mumford, 1992). However, the uniqueness of the items, coupled with the enhanced memory performance and greater N400 amplitudes surrounding the ‘B’ images (as described above), may suggest that our predictability manipulation was less sensitive to subtle differences in item-specific expectancy. To further elucidate the relationship between the N400 and prediction (error) in future research, a more nuanced manipulation could be introduced. For example, participants could learn contingencies that are later violated (as in Ortiz-Tudela et al., 2023), promoting comparisons between the amplitude of the N400 component and the degree of violation. Additionally, we did not explicitly instruct participants to predict, as doing so would have shifted the focus to explicit forms of prediction, which was not our aim. However, more objective measures of prediction, such as Dale and colleagues’ (2012) analysis of computer mouse trajectories during a sequential learning task, could complement N400 findings by providing converging evidence for predictive processing in future investigations. This may facilitate more confident conclusions surrounding the extent to which participants predicted upcoming stimuli, extending upon the manipulation of stimulus predictability employed here.

Furthermore, while prediction-related processes could explain the current findings, it is also possible that other mechanisms may be at play here. For example, the N400 has also been

linked to the integration of information with existing meaning representations stored in long term memory (Brown & Hagoort; 1993; Meyer et al., 2007). For low IAF individuals in the current study, difficulty integrating an image with a prior semantic representation may have promoted the encoding of that information as a new memory trace. In contrast, for those with high IAFs, information uptake may have occurred independently of the ease of integration with the prior context. Ultimately, whilst the present study cannot speak explicitly to whether prediction or integration underlies the observed trends, it provides important preliminary evidence demonstrating a relationship between event-related activity, memory updating, and individual neural variability. This could explain inter-subject differences in behavioural memory performance, by suggesting that such variability might stem from disparities in IAF. Interestingly, while the effect of the N400 on memory was modulated by individual variability, the exploratory late positive component appears to drive learning regardless of IAF.

3.5.4. The significance of late ERP activity for memory encoding

Whilst the observed N400 effects could suggest that predictability influences memory formation for some individuals, differences in the later component (potentially resembling an LPC) may be explained by research on the P300 ERP. In the current research, at the position of the 'A' image, the amplitude of this later positivity was greater for unpredictable versus predictable images. In contrast, this effect reversed at the 'D' image position. Traditionally, increases in the LPC have been linked to episodic recollection (Curran, 2000; Curran & Cleary, 2003). However, as each image in the learning phase was unique, items seen during this phase could not be explicitly 'recollected,' rendering it difficult to explain the observed differences in this component from a purely recollection-based account. However, it is possible that effects here reflect recognition at the category level, as compared to specific episodic recollection, such that LPC amplitudes differed according to recollection of the various image categories.

As an alternative explanation, what we originally deemed a potential LPC might correspond to either a late P300 or a P600, with Finnigan and colleagues (2002) discussing how such late positivities are often labelled interchangeably. Moreover, there is evidence supporting the P600 as a P300 (Coulson et al., 1998a, Gunter et al., 1997; Sassenhagen et al., 2014; Sassenhagen & Bornkessel-Schlesewsky, 2015; Sassenhagen & Fiebach, 2019), and for a discussion see Coulson and colleagues (1998b). The P300 component is modulated by stimulus probability and relevance (Berlad & Pratt, 1995; Polich & Margala, 1997), and is commonly observed in oddball paradigms, in response to deviant target stimuli that are presented amongst standard stimuli (for a review see Picton, 1992). For this reason, classical conceptions of the component link it to context updating (i.e., a need to revise one's schema of the current context following a contextual change; Donchin, 1981). This notion of 'context updating' may bear similarities to predictive model updating, potentially explaining the differences in amplitude according to image position and condition observed here. However, it is important to note that the effect of this late component on memory occurred independently of image condition and position, suggesting that these position- and condition-specific amplitude changes do not directly translate to behavioural effects. This could arise because subtle amplitude differences are less pronounced when related to aggregate memory performance measures (such as d').

Nevertheless, this finding, coupled with the P300's link to context updating (Donchin, 1981), could, at a first glance, support the notion that prediction errors promote memory updating.

Building upon the link between the late positive ERP observed here and memory formation, recent research demonstrates a positive correlation between the amplitude of the P600 to semantic violations, and subsequent behavioural recognition memory performance (Contier et al., 2024). Contier and colleagues (2024) interpret these findings in light of the proposal that the N400 reflects implicit prediction error, which in turn may drive implicit learning (Hodapp & Rabovsky, 2021; Rabovsky & McRae, 2014). In contrast, the authors link the P600 to explicit memory and highlight the component's association with sustained attention and conscious awareness (Batterink & Neville, 2013; Contier et al., 2022, 2024). This interpretation also aligns with the P300's emergence primarily in response to task-relevant or attended-to stimuli (for a review see Picton, 1992), implying that such positivities are connected to explicit processes. Moreover, based on prior research suggesting that the P600 demonstrates similar response-locked properties to the P300 (e.g., Sassenhagen et al., 2014; Sassenhagen & Bornkessel-Schlesewsky, 2015), Bornkessel-Schlesewsky and Schlesewsky (2019) propose that positive language-related ERPs might be reflective of the behavioural outcomes of predictive coding rather than the process of predictive coding itself.

If the late positive component observed here belongs to the P300/P600 family, the effect of this later component on memory performance could stem from more explicit processes that can additionally drive memory formation. It may also explain why the later ERP exhibits a slightly different pattern to the N400. Therefore, the possible distinction between the N400 and later, P600-like components suggests that, in the present study, the N400 may better capture the effects arising from implicit predictions (the focus of the present investigation), as opposed to the late positivity. Interestingly, the N400 effect on explicit memory recognition (for some individuals) observed here could hint at an overlap between implicit and explicit processes, which would be an intriguing topic for future ERP research.

3.5.5. Conclusion

The present study investigated the effect of stimulus predictability on memory, with behavioural results providing evidence to suggest that predictable information is encoded into memory more readily than unpredictable information. At a first glance, this opposes the notion that predictions, due to their reliance on prior memory representations, inhibit the encoding of new information (Sherman et al., 2022; Sherman & Turk-Browne, 2020). However, the positive correlation between the magnitude of the N400 and subsequent memory for low IAF individuals may be supportive of a prediction error-based learning mechanism, highlighting the complexity of the relationship between prediction and memory. The enhanced memory for predictable 'B' images, and the increased N400 amplitudes following items in this position may also imply that memory encoding during prediction is sensitive to subtle differences that surpass basic categorical boundaries of predictability. Importantly, further research would be ideal to determine the extent to which the N400 and the late positivity relate to implicit/explicit prediction and learning. Nevertheless, this study highlights the functional relevance of the two

correlates for memory processing, whilst emphasising the importance of individual neural factors for learning.

Interim summary

Chapter 3 sought to extend upon the insights gained in Chapter 2 by capitalising on the N400's potential to reflect prediction error in a context beyond language. A visual sequence learning task was employed, where participants were exposed to predictable and unpredictable sequences. Importantly, the stimuli in both Chapter 2 (being language-based) and Chapter 3 (pertaining to visual scenes) have in common the reliance on statistical probabilities.

The EEG experiment revealed that greater N400 amplitudes during learning were associated with enhanced memory performance at test for those with low versus high IAFs. This implies that the amplitude of the N400 (and potentially the level of prediction error) in response to a stimulus has consequences for memory encoding. Furthermore, it also provides insight into the limited N400-subsequent memory literature by suggesting that individual neural variability modulates the effect of this component on memory. Chapter 3 also supports the results of Chapter 2, which revealed differential N400 patterns between a high and a low IAF that were attributed to varying model updating tendencies. Moreover, exploratory analyses demonstrated a role for a late ERP component in memory processing, which is associated more strongly with explicit learning than with implicit predictive processing. Given the strong links between the N400 and stimulus expectancy in other literature, the study described in Chapter 3 suggests that predictability influences learning, but only for low IAF individuals. These results raise the question: does memory encoding occur independently of the level of prediction error for those with a high IAF?

In attempt to answer this question, Chapter 4 examined the oscillatory activity in the same dataset, directly relating oscillatory dynamics and N400 amplitudes during learning to IAF and subsequent memory. Chapter 4 included a more fine-grained analysis of the relationship between electrophysiological activity and memory, as memory was measured at the item-level (focussing on subsequently remembered and forgotten stimuli). This facilitated a more direct investigation into how brain activity in real-time influences encoding on an item-by-item basis.

Chapter 4

Predictive influences on memory encoding: investigating oscillations and the N400 event-related potential component

ABSTRACT

To effectively function in an ever-changing environment, the brain is proposed to make predictions about upcoming information. However, the association between prediction and memory formation and the role of between-subject neural variability in this relationship is unclear. To shed light on the relationship between prediction and memory, the present study reanalysed data from Jano, Chatburn, and colleagues (2024). In the original experiment, participants were exposed to naturalistic images in predictable and unpredictable four-item sequences, after which their memory was tested using an old/new paradigm. In the present analysis (N = 46), N400 amplitude and oscillatory power during learning was measured to gauge processes related to prediction error and memory encoding, respectively. This activity was compared with subsequent memory outcomes and individual alpha frequency (IAF) calculated at rest. Linear mixed-effects regressions revealed an alpha power subsequent memory effect that was not related to the amplitude of the N400, suggesting that memory encoding may occur independently of the level of prediction error. Notably, IAF influenced the relationship between theta power, N400 amplitude and subsequent memory, implying that the electrophysiological conditions for successful memory formation differ between individuals. Consequently, the degree to which prediction errors (presumably gauged via the N400) drive memory encoding could depend on inter-individual variability in intrinsic neural activity. These findings emphasise the flexible nature of memory, whilst having potential implications for prediction error-driven accounts of learning.

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4.1. Introduction

Perception and cognition may be supported by the brain's attempts to predict the future (A. Clark, 2013; Friston, 2005). While predictions could enhance perceptual processing efficiency (Huang & Rao., 2011), they may also incur costs in informational accuracy (as illustrated by their proposed association with false memories; Hubbard et al., 2019; Hubbard & Federmeier, 2024; Jano et al., 2021; Rauss & Born, 2017), although the intricacies of this relationship are currently unclear. According to the predictive coding theory, the degree of departure between what the brain predicts and what it encounters (encoded as prediction error) informs the need for predictive model updating, allowing for more accurate predictions and a consequent reduction of future error (A. Clark, 2013; den Ouden et al., 2012; Friston, 2005; Rao & Ballard, 1999). As such, prediction errors may prompt memory updating, where the information is encoded into a memory trace (Exton-McGuinness et al., 2015; R. S. Fernández et al., 2016; Mack et al., 2018; Sinclair et al., 2021). On the other hand, predictions are proposed to activate an existing associative memory representation (Bar, 2007, 2009), which may interfere with memory encoding (Sherman & Turk-Browne, 2020). As such, a trade-off between prediction and encoding has been proposed (Hubbard et al., 2019), such that the reliance of predictions on memory retrieval may interfere with the encoding of new information (Sherman et al., 2022; Sherman & Turk-Browne, 2020). This could manifest in a tendency for shallower processing of predictable stimuli, where the brain verifies congruence with predictions rather than meticulously processing each instance of the sensory information (Hubbard et al., 2019; Van Berkum, 2010). Consequently, information that is surprising or incongruent with expectations should be better remembered than predictable information; a suggestion that is supported by prior research (e.g., Federmeier et al., 2007; Greve et al., 2017; Rouhani et al., 2018; Worthen & Roark, 2002). However, other literature demonstrates enhanced memory for predictable information (e.g., Gronau & Shachar, 2015; Turan et al., 2023), and for high frequency stimuli (G. Fernández et al., 1998). This highlights the potential complexity surrounding the relationship between prediction and memory, which may be difficult to capture with behavioural analyses alone. As such, an investigation into the effect of prediction on memory at the neurophysiological level may extend upon existing behavioural research (e.g., Gronau & Shachar, 2015; Ortiz-Tudela et al., 2023), as processes relating to prediction and memory may be gauged more explicitly.

4.1.1. The relationship between oscillations, memory, and prediction

Oscillatory activity can inform the nature of neuronal communication and information representation within the brain (Buzsáki & Draguhn, 2004; Schnitzler & Gross, 2005). Particularly relevant are theta oscillations in the approximate 4–7Hz range, which have strong ties to memory (e.g., Hasselmo, 2005; Hasselmo & Stern, 2014), prediction error processing (e.g., Cavanagh et al., 2010), and to broader functions such as spatial navigation (Buzsáki, 2005). Increases in theta power during learning have been associated with enhanced subsequent memory at test, highlighting the relevance of this activity for understandings of memory encoding (Hanslmayr et al., 2009; Klimesch, Doppelmayr, Russegger, et al., 1996, Klimesch, Doppelmayr, Schimke, et al., 1997; White et al., 2013). Theta power is typically prominent over frontal regions (Hanslmayr et al., 2009; Klimesch, Doppelmayr, Schimke, et al., 1997; White et al., 2013), prompting the suggestion that scalp-recorded frontal midline theta (FMT)

is especially relevant for successful episodic memory encoding (for a review see Hsieh & Ranganath, 2014). Mechanistically, the relationship between theta oscillations and memory functioning could be supported by theta's ties to long-term potentiation (LTP; a type of synaptic plasticity involving an enduring strengthening of synaptic potentials; Collingridge et al., 2010; Leung & Law, 2020; Martin et al., 2000). LTP is proposed to underly memory formation (Martin et al., 2000), and to be elicited during phases of hippocampal theta that reflect depolarization (for a review, see Leung & Law, 2020). Consequently, theta rhythms may be integral for the synaptic changes that give rise to memory encoding (Leung & Law, 2020), suggesting that such activity can provide insight into the extent to which predictions facilitate or impair memory.

Not only are theta rhythms relevant for memory processing, but they have also been heavily studied in the prediction error literature. Prior research linking theta oscillations to prediction demonstrates greater theta power (i.e., increased synchrony; Klimesch, 1999) in response to incongruent information (Dini et al., 2022), semantic violations (Pu et al., 2020), prediction errors during reinforcement learning (Cavanagh et al., 2010; Mas-Herrero & Marco-Pallarés, 2014), and behavioural errors (Cohen, 2011). As prediction errors result from a discrepancy between predicted and actual events (Friston, 2005; Hohwy, 2020), a behavioural error would likely also induce a prediction error, highlighting the functional relevance of theta power for predictive processing. The link between theta and error processing is also supported by its relationship to the error-related negativity (ERN); an event-related potential (ERP) component that peaks after an erroneous response (Holroyd & Coles, 2002; Luu et al., 2004; Trujillo & Allen, 2007). Moreover, theta power increases following negative feedback have been shown to predict subsequent behavioural adjustments (Van de Vijver et al., 2011), suggesting that theta oscillations play an important role in the memory encoding processes related to prediction error correction and learning. From this perspective, if predictions impair memory encoding, theta power should theoretically be weaker when individuals are predicting, and stronger in the face of a prediction error, indicating enhanced encoding.

While memory formation may be fostered by increased power in the theta frequency range, it may also be supported by changes in power in the alpha oscillatory band (~8–12 Hz; Hanslmayr et al., 2009, 2012). Desynchronisation in the alpha rhythm during learning has been linked to enhanced memory at test (Hanslmayr et al., 2009; Klimesch, Schimke, et al., 1996; Klimesch, Doppelmayr, Schimke, et al., 1997; Sederberg et al., 2003, for a review see Hanslmayr et al., 2012), suggesting that alpha power is functionally relevant for memory processing. Klimesch and colleagues (2007) postulate that alpha is linked to inhibition, such that greater alpha synchronisation (giving rise to stronger alpha power; Klimesch, 1999) reflects increased inhibition, while alpha desynchronisation reflects a discharge of this inhibitory mechanism. The relationship between alpha power, prediction and memory was explored and interpreted in the context of inhibition by Ergo and colleagues (2019), who manipulated the degree of reward prediction error (RPE) and found enhanced recognition for large, positive RPEs (where the reward is better than expected). Supplementing these behavioural findings was the observation that alpha power decreased following positive RPEs and increased following negatively valanced RPEs (when the reward is worse than expected). This increase in response to negative

RPEs was proposed to reflect the inhibition of task-irrelevant stimulus representations (Ergo et al., 2019). In contrast, positive RPEs could have facilitated memory encoding (evidenced by alpha power decreases) as individuals learnt the contingencies that led to positive outcomes. This interpretation implies that prediction errors can at times impair memory, somewhat challenging traditional predictive coding schemes where prediction errors drive model correction (Rao & Ballard, 1999).

Although the literature described above suggests that memory encoding is supported by decreases in alpha power, Klimesch and colleagues (2007) conversely propose that increases in alpha power prompt the suppression of memory retrieval mechanisms, facilitating memory encoding. Consequently, alpha desynchronisation may be linked to memory retrieval (Klimesch et al., 2007), suggesting that alpha power could be weakest during prediction (when a prior memory representation is likely retrieved; Bar, 2007, 2009; Schacter et al., 2008), and strongest during processing of unpredictable stimuli. While this highlights the complex relationship between alpha power, inhibition, and memory performance, it also emphasises the importance of alpha oscillations for understanding the influence of prediction on memory uptake. This may be further supplemented by an analysis of ERP activity, which can provide a fine-grained, real-time measure of the processes associated with prediction (Luck, 2014).

4.1.2. The importance of the N400 event-related potential (ERP) for understanding the effect of predictive processing on memory

Unlike oscillations, which fluctuate across longer time periods, ERPs reflect transient activity that can be captured with precise temporal accuracy (Luck, 2014). As such, ERPs are important for measuring nuanced changes in cognition as expectations unfold. Specifically, an analysis of the N400 ERP could allow for learning to be tracked as predictions naturally develop in the absence of explicit behavioural responses or feedback. The N400 peaks approximately 400ms post-stimulus onset and is sensitive to the degree of stimulus expectancy, exhibiting larger (more negative) amplitudes to unexpected items (for a review, see Kutas & Federmeier, 2011). Whilst this pattern has primarily been observed in language paradigms (e.g., Federmeier & Kutas, 1999; Kutas & Hillyard, 1980b, 1984), N400 effects are also observable in non-linguistic contexts, linking the component to meaning processing more broadly (Amoruso et al., 2013; Federmeier & Kutas, 2011; Sitnikova et al., 2008; Urgen et al., 2018). The correlation between the N400 and stimulus predictability in turn supports its proposed relationship with prediction error, where the magnitude of the N400 reflects the extent of prediction violation (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019; Eddine et al., 2024; Hodapp & Rabovsky, 2021; Rabovsky & McRae, 2014). According to the predictive coding theory, the brain reduces redundancy by representing unexplained sensory data in the form of a prediction error (Feldman & Friston, 2010; Huang & Rao, 2011; Rao & Ballard, 1999). Consequently, when sensory information is explained, it may not be represented (Rao & Ballard, 1999). This may render a prediction error-related component (such as the N400) a useful measure of predictive processing in the brain. As such, an analysis of the N400, due to its ties to prediction error (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019), could be effective in capturing prediction more directly than, for example, pre-stimulus neural activity at the time of prediction (as we observed in a previous study; Jano, Cross, et al., 2024).

Moreover, the question remains as to whether oscillatory patterns and ERPs reflect the same or differing processes in the context of prediction. For example, whilst theta activity has been considered an error processing signal in the past, being proposed to underlie ERPs such as the ERN and the feedback-related negativity (FRN; Cavanagh et al., 2010; Cavanagh & Frank, 2014; Trujillo & Allen, 2007), its general relationship to memory (described above) could also suggest that it reflects the updating that accompanies an error signal, as opposed to the error itself. This is supported by Munneke and colleagues' (2015) study, which suggests that theta/delta power (in the approximate 2–8Hz range) and the ERN reflect both disparate but complementary processes. Prior research has also observed increased N400 amplitudes to incongruent stimuli alongside oscillatory theta increases (Dini et al., 2022), highlighting the strong connection between these neurophysiological measures. However, few studies directly compare the relationship between oscillations and N400 patterns during learning with behavioural subsequent memory outcomes at test. While a previous study by Klimesch, Schimke, and colleagues (1996) examined the N400 and the oscillatory rhythms that contribute to later remembering, the direct relationship between these combined factors was not explicitly tested. Additionally, most studies, if engaging in a combined oscillatory and ERP investigation, measure the N400 (and related components, such as the FN400) at test to gauge the level of memory recognition (e.g., Chen & Caplan, 2017; Ordin et al., 2020). Consequently, a comparison of N400 patterns with oscillatory activity during learning may provide insight into the extent to which predictability (measured via the N400) influences memory encoding (potentially gauged via oscillatory rhythms). Relating this to memory recognition could in turn shed light on how these neurophysiological components influence later memory outcomes, potentially capturing variability that extends beyond the behavioural domain.

4.1.3. Individual alpha frequency (IAF)

While a combined investigation of oscillatory patterns, N400 activity and subsequent memory may be useful for understanding the relationship between prediction and memory, supplementing this with an analysis of individual neural variability could provide insight into the individual variability associated with prediction. In a previous study (Jano, Chatburn, et al., 2024), we observed a positive relationship between the magnitude of the N400 during a prediction task and later memory recognition (for similar effects relating to implicit memory see Hodapp & Rabovsky, 2021). However, this trend was only observed for individuals with a low individual alpha frequency (IAF; the dominant frequency within the range of the alpha band; Corcoran et al., 2018; Klimesch, 1999; Jano, Chatburn, et al., 2024). This raises the question of whether prediction errors prompt memory updating for individuals with a high IAF, or whether memory encoding occurs independently to a prediction error signal for these individuals. Furthermore, the relationship between IAF and prediction is currently unclear, with some research suggesting that individuals with a high IAF have a stronger propensity for model updating (Kurthen et al., 2020; particularly under conditions of high prior stimulus surprisal; Jano, Cross, et al., 2024), and other research observing greater model updating for low versus high IAF individuals (Bornkessel-Schlesewsky, Sharrad, et al., 2022). Given also that IAF is positively correlated with general intelligence (Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013) and with memory outcomes (Klimesch et al., 1990, 1993), it is important to explore its relationship to prediction and memory formation in more detail.

4.1.4. The present study

The current study sought to further examine the effect of prediction on memory via a reanalysis of Jano, Chatburn, and colleagues (2024), with a focus on oscillations, the N400, and individual neural variability (as measured via IAF). In our original experiment, participants took part in a sequence learning task, where they were presented with predictable and unpredictable sequences of naturalistic outdoor scene images, and their memory for the images was subsequently tested (Jano, Chatburn, et al., 2024). Importantly, memory performance was not quantified on an item-by-item level but was instead measured at the aggregate level via the sensitivity measure d' (McNicol, 2004). However, a subsequent memory analysis measuring hits and misses at test, coupled with an investigation into oscillatory patterns during learning, may provide a more granular and nuanced understanding of how neural patterns during prediction influence the encoding of a particular stimulus into memory.

Based on the relationship between theta oscillatory activity and subsequent memory described in previous literature, it was hypothesised that: a) theta power would be stronger for images in unpredictable versus predictable sequences. As the research linking alpha rhythms to inhibition and subsequent memory is mixed, we also formulated a non-directional hypothesis stating that b) alpha power would differ during the processing of predictable versus unpredictable images. It was further predicted that: c) theta power during learning would be greatest for subsequently remembered items (memory hits) as compared to subsequently forgotten items (memory misses), while d) alpha power during learning would be associated with memory recognition performance at test. Importantly, while the previous study included a categorical manipulation of stimulus predictability, changes in the N400 were proposed to reflect more subtle, item-specific differences in predictability and potentially, the level of prediction error elicited by a stimulus (Jano, Chatburn, et al., 2024). As such, we also aimed to consolidate the distinct perspectives that separately link prediction to the N400 ERP, to oscillations, and to memory outcomes, hypothesising that e) N400 patterns would relate to oscillatory activity during learning, and that this would be associated with later remembering (quantified as hits and misses). Finally, we also aimed to capture the inherently individual nature of prediction via the inclusion of resting state individual alpha frequency (IAF) in the above analyses.

4.2. Methods

4.2.1. Original study

The present reanalysis used data from our previous study (Jano, Chatburn, et al., 2024; https://osf.io/qvjer/), which included 48 healthy individuals in the final sample (mean age = 26.8 years old, SD = 6.6 years). Participants completed a task adapted from Sherman and Turk-Browne (2020). They first underwent a learning phase where they viewed 102 four-item ABCD sequences of outdoor scene images, belonging to 12 categories of scenes. Sixty-eight of these sequences were predictable, such that images from the same categories in the same order were presented. The remaining 34 sequences contained images from other categories in a random order, such that multiple images from the same category could be present in the sequence, rendering it impossible to predict the upcoming image category. Each item was unique and was only viewed once. Images were presented for 1000ms and were separated by a 500ms inter-

stimulus interval displaying a fixation dot in the middle of the screen. Each sequence was followed by a 2000ms interval where participants viewed the same fixation dot as in the interstimulus interval. To ensure that participants were attending to the task, a prompt would randomly appear in the between-sequence intervals, instructing participants to press the 'Enter' key. This occurred on seven occasions, and participants were required to press the key as quickly as possible. Participants were told that this was a secondary task, and that their primary objective was to pay attention to the images in the sequences. Individuals were not informed of the relationships between the images and were not asked to actively predict. This is because we sought to probe naturalistic predictive processing, which should be engaged in scenarios where statistical regularities are present (Baker et al., 2014; Bar, 2007; Mumford, 1992). Participants' electroencephalography (EEG) was recorded during the task using a 32-channel Brainvision ActiCHamp system (Brain Products GmbH, Gilching, Germany).

To avoid recency effects, participants then engaged in a 15-minute digit span task, after which they underwent a surprise memory recognition test. Old images that were seen during the learning phase, along with categorically related lures that had not been viewed during learning were presented in a random order, external to any sequential relationships. Participants were instructed to make an old/new judgement to each image ('old' being that they remembered seeing the image during learning, and 'new' meaning that they did not remember the image). A keypress was used to indicate their response (z = old, m = new), allowing for the measurement of participants' memory recognition performance. For a full description of the study materials, protocol, and EEG recording procedure, see Jano, Chatburn, and colleagues (2024), and for a schematic of the task, see *Figure 4.1*.

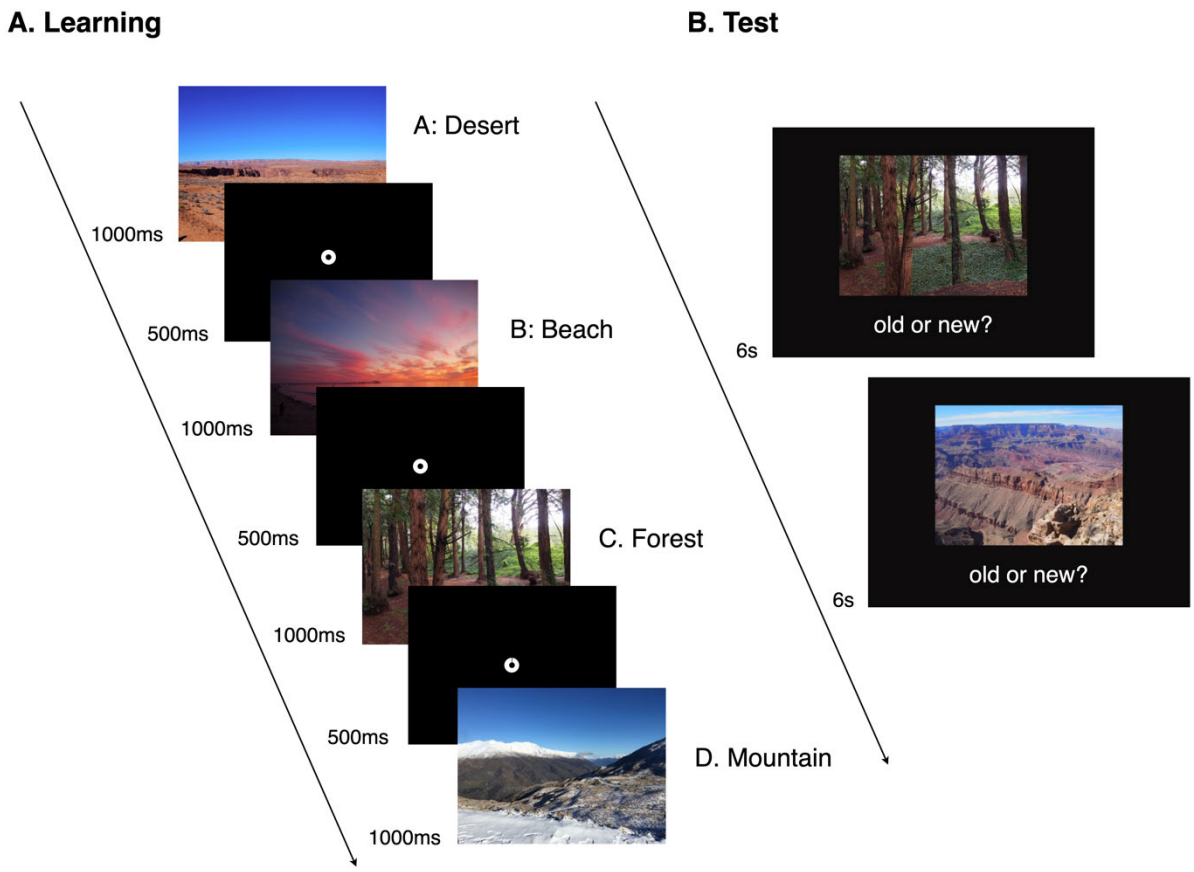


Figure 4.1. *Adapted from Jano, Chatburn, and colleagues (2024) showing the outdoor scene task.* **(A)** *Learning phase: Participants were instructed to attend to four-item sequences of outdoor scene images in predictable and unpredictable relationships.* **(B)** *Recognition test: Participants were presented with old images seen during learning, and lure images that were not encountered during the learning phase. Participants were tasked with making an old/new judgement for each image.*

4.2.2. Participants

The sample for the present reanalysis included a total of 46 participants (mean age = 26.5, SD = 6.5, 15 males, 31 females). The sample size was slightly reduced from the previous experiment (which included 48 participants) as IAF metrics for two individuals could not be estimated. As time frequency measures were obtained by adjusting frequency bands according to each individual's IAF, oscillatory bandwidths could not be defined for these participants, and they were hence removed. Participants' ages ranged from 18-39, and all individuals were right-handed with corrected-to-normal vision. They also did not have any diagnosed psychiatric conditions, intellectual impairments, or a diagnosis of dyslexia. Finally, they were not taking medication that could affect the EEG and had not taken recreational drugs in the previous six months.

4.3. Data analysis

4.3.1. Electroencephalography (EEG) data processing

The data from Jano, Chatburn, and colleagues (2024) was used for the current analysis. Raw EEG data were re-referenced to mastoid channels (TP9 and TP10) and Fp1 and Fp2 were set as electrooculogram (EOG) channels. An independent component analysis (ICA) was fit to a 1 to 40Hz band-pass filtered copy of the data, before subsequently being applied to the raw data to detect and remove ocular artefacts. Following this, bad channels were interpolated, and the data were band-pass filtered from 0.1 to 30Hz. Next, 5 second epochs were generated from the pre-processed EEG data around each image in the sequences using MNE-Python version 1.6.1 (Gramfort et al., 2013). Epochs ranged from -1 to 4 seconds surrounding each image to avoid edge artifacts and to capture a sufficient number of oscillatory samples. Finally, the *Autoreject* function (Jas et al., 2017) was run, which interpolated or excluded bad epochs. This resulted in an average of 249.8 epochs remaining in the predictable condition and 124.5 remaining in the unpredictable condition (total images in the predictable condition = 272, total images in the unpredictable condition = 136).

4.3.2. Metrics from the original study

The IAF data and the N400 ERP data from the original study were used in the present experiment. For a full description of how these metrics were calculated in the original analysis, see Jano, Chatburn, and colleagues (2024). To briefly summarise, IAF was computed across channels P3, P4, Pz, Oz, O1 and O2 from eyes-closed resting state recordings that were captured at the start of the experiment. The *Philistine* package (Alday, 2018) was used to calculate participants' IAF within 7–13 Hz. Centre of gravity (CoG) was specifically used as a measure of IAF, which reflects the mean power within the alpha frequency band (Corcoran et al., 2018). These procedures consequently resulted in single-subject IAF values that were used for the current reanalysis.

Mean N400 ERP activity across all channels was computed over 1.3 second epochs, across a 300-500ms window following stimulus onset (in line with prior research; Federmeier et al., 2007; Hodapp & Rabovsky, 2021; Hubbard et al., 2019; Van Berkum et al., 2003). Activity in a pre-stimulus window (-300 to 0ms) was also generated, to obtain an ERP baseline estimate for analyses in which N400 activity was included as a predictor. Following ERP generation, the data were averaged over frontal channels (Fz, F3, F7, FT9, FC5, FC1, FT10, FC6, FC2, F4, F8), in line with previous research (Kutas & Federmeier, 2011; Urgen et al., 2018), and to maintain consistency with the original study (Jano, Chatburn, et al., 2024). This resulted in mean ERP amplitude data per subject and item, for both the N400 and the prestimulus window. For grand average plotting, downsampled data (at 125Hz) spanning the full epochs were used and plots were generated using the *ggplot2* (Wickham, 2016) package in R version 4.3.1.

4.3.3. Time frequency analysis

A time frequency analysis was performed using MNE-Python version 1.6.1 (Gramfort et al., 2013). To measure the oscillatory activity associated with each image during the learning phase, frequency bands were first individually adjusted according to each participant's IAF

(specifically, their CoG values). This procedure is recommended by Klimesch (1999) and Klimesch, Doppelmayr, Schimke, and colleagues (1997). Once the upper and lower bounds of the alpha and theta frequencies were defined for each participant, a time frequency analysis was performed on the 5 second epochs, on a trial-by-trial basis using the Morlet wavelet transformation from the *tfr_morlet* function. To define the length of the Morlet wavelet, the data within each frequency band was divided into five points, and the number of cycles was calculated as each frequency value divided by four. A fast Fourier transform (FFT) was applied using the *use_fft = True* argument. Following this, the data were initially extracted over five 200ms long windows across the duration of image presentation (0-1000ms), to capture transient alterations in oscillatory activity that may occur within each segment. However, the inclusion of such windows in statistical models led to multicollinearity, suggesting that the windows explained similar variance in the data. As such, we opted to instead collapse the data over one window of interest (200ms to 1000ms post-image onset). This window was chosen to avoid activity relating to early sensory processing (Pratt, 2011). It was also based on similar research, where alpha and theta oscillations associated with error processing and/or subsequent memory appeared maximal within an approximate 200ms to 700ms window (e.g., Hald et al., 2006; Klimesch, Schimke, et al., 1996; Van de Vijver et al., 2011). For the present study, the upper limit was extended to 1000ms to account for the complexity of the naturalistic outdoor scene images, and to capture the whole duration of image presentation. Additionally, a baseline window ranging from -350ms to -150ms prior to image onset was defined, to capture the time-frequency activity in the inter-stimulus window whilst avoiding overlap with the previous stimulus and the upcoming stimulus. Activity within each window was then averaged across time points, resulting in a mean amplitude measure per window and frequency band of interest, for each item and channel. To perform a power normalization, a decibel conversion was then applied to the time frequency data using the below formula:

$$X_{dB} = 10log_{10}(\frac{X_{activity}}{X_{baseline}})$$

4.3.4. In-task 1/f aperiodic activity

Oscillations reflect brain activity in the periodic domain, presenting as peaks in amplitude at distinguishable temporal frequencies (He, 2014). Such patterns are purportedly confounded with the aperiodic (scale-free) component, which is independent of specific frequency bands, and which follows the 1/*f* power law (Donoghue, Dominguez, et al., 2020; Donoghue, Haller, et al., 2020; He, 2014; He et al., 2010). Consequently, recent accounts emphasise the importance of measuring both periodic and aperiodic activity during neurophysiological investigations, to estimate effects relating to oscillatory components more directly (Donoghue, Dominguez, et al., 2020). The present analysis employed the Irregular Resampling Auto-Spectral Analysis (*IRASA;* version 0.6.4) function (Wen & Liu, 2016) implemented through the YASA toolbox (Vallat & Walker, 2021) to separate the aperiodic component from the periodic component. The function was applied to the same 5-second epochs used in the time frequency analysis (described above), across a frequency range of 1 to 30Hz, with a sliding window length of 2 seconds. This returned the fractal aperiodic values for each channel and event of interest. Importantly, whilst this method also produced measures of the aperiodic-

independent oscillatory activity, this data could not be segmented into windows of interest as it did not return information at the temporal level that could be subsequently sliced. An alternative may have been to compute the function over shorter windows. However, we sought to estimate the spectrum over longer epochs to avoid edge artifacts, and to ensure that a sufficient number of samples was obtained. As such, only the aperiodic 1/*f* slope values from this analysis were used for subsequent investigation. This data was included as a *covariate* in statistical models with oscillatory power calculated from the *TFR_morlet* function (described above). This allowed for the aperiodic patterns related to the events of interest to be accounted for.

4.3.5. Subsequent memory

Behavioural performance on the memory recognition test was quantified on an item-by-item basis via a subsequent memory analysis, based on participants' 'old' and 'new' responses to stimuli. 'Old' responses to old images seen during the learning phase were labelled as subsequently remembered 'hits,' whilst 'new' responses to old images were defined as subsequently forgotten 'misses.' As we were primarily interested in how activity during learning predicted encoding and subsequent remembering, the analysis did not focus on behavioural responses to new lure items.

4.3.6. Statistical analysis of hypothesized effects

Statistical analysis of the data was performed using linear mixed-effects models (LMMs) computed using the *lme4* package (Bates et al., 2014) in R version 4.3.2. These models allowed for estimation of the effects of interest, whilst accounting for random variation. For models predicting theta power, data were summarised across electrodes F3, Fz and F4, as prior research suggests that mid-frontal theta activity is relevant for memory processing (Hsieh & Ranganath, 2014). For analyses predicting alpha power, a more exploratory, data-driven approach was first taken, such that electrodes were grouped according to sagitallity (anterior, central, posterior) and averaged, resulting in a mean value per level. Sagitallity was then entered as a predictor into the models.

All continuous predictors in the LMMs were scaled and mean-centred, whilst categorical predictors (image condition [predictable, unpredictable], image position [A, B, C, D], recognition [hit, miss] and sagitallity [anterior, central, frontal]) were sum contrast coded with the *contr.sum* function from the *car* package (Fox & Weisberg, 2019). All models included random effects on the intercept of subject and item, whilst random slopes of predictors were included when this did not impact model convergence or lead to singular fits (for further discussion of the implications of model overcomplexity, see Bates et al., 2018). To account for task-related aperiodic patterns, on-task 1/*f* slopes were included in all models as a covariate with an additive term. Additionally, whilst image position was not a primary factor of interest, it was included in models 1 and 4 to account for the structure of the underlying data. However, as this structure was accounted for by the variable 'recognition' in the other models, position was omitted as a predictor to reduce unnecessary complexity (for a full specification of final statistical model structures, see *Table 4.1*). P-values were obtained via type II Wald tests from

the *car* package (Fox & Weisberg, 2019). Model effects were estimated using *ggeffect* (Lüdecke, 2018), and were visualised using *ggplot2* (Wickham, 2016).

Table 4.1. *Linear mixed-effects model structures, including fixed and random effects. The levels of each variable include* ***condition*** *(predictable/unpredictable),* ***position*** *(A/B/C/D),* ***recognition*** *(hit/miss), and* ***sagitallity*** *(anterior/central/posterior).*

Model number	Outcome variable	Fixed effects	Covariates	Random intercept terms	Random slope terms
1	Theta power (dB)	Condition Position IAF	In-task 1/*f* aperiodic slope	Subject Item	By-subject according to condition
2	Theta power (dB)	Recognition Condition IAF	In-task 1/*f* aperiodic slope	Subject Item	By-subject according to recognition
3	Theta power (dB)	Recognition Condition N400 amplitude IAF	In-task 1/*f* aperiodic slope Pre-stimulus ERP activity	Subject Item	By-subject according to condition
4	Alpha power (dB)	Condition Position Sagitallity IAF	In-task 1/*f* aperiodic slope	Subject Item	By-subject according to condition
5	Alpha power (dB)	Recognition Sagitallity Condition IAF	In-task 1/*f* aperiodic slope	Subject Item	By-subject according to condition
6	Alpha power (dB) over posterior regions	Recognition Condition N400 amplitude Sagitallity IAF	In-task 1/*f* aperiodic slope Pre-stimulus ERP activity	Subject Item	By-subject according to condition

4.4. Results

Outputs from the statistical models are presented in *Supplementary material 4.A*, and the data analysis scripts for the present reanalysis can be freely accessed here https://osf.io/zvpku/.

4.4.1. Behavioural results from the memory recognition test

The number of hits ('old' responses to old images seen during the learning phase) and the number of misses ('new' responses to old images) were counted for each subject, condition, and position. Hit and miss rates were also calculated per participant and condition by dividing the number of hits and misses by the number of old items in each condition for each subject,

to account for item imbalances between conditions (see *Figure 4.2*). Note that while hit rates alone are at or below chance, average d' scores across image types (which are computed based on both old and new stimuli) were above chance in the prior study (greater than 0; Jano, Chatburn, et al., 2024). This may suggest that participants specifically experienced difficulty recognising old items, but not at rejecting new items.

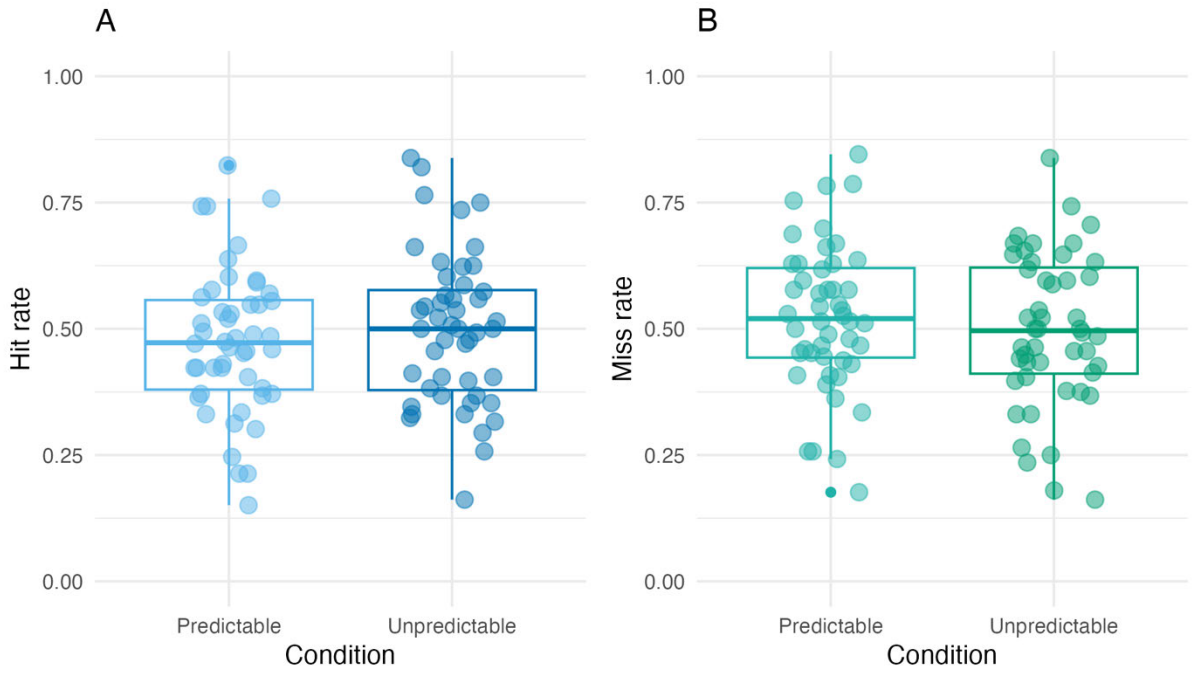


Figure 4.2. *Boxplots depicting* **(A)** *hit rates and* **(B)** *miss rates between predictable and unpredictable image conditions. Data was extracted from performance during the recognition test. Dots reflect individual participants, centre lines within the boxes depict median values, with lines below and above reflecting the first and third quartiles, respectively.*

4.4.2. Visualizing Oscillatory Activity and ERP Patterns

Time frequency plots demonstrating raw data visualisations of oscillatory activity are presented in *Figure 4.3* and *Figure 4.4*, along with the topography plots for theta and alpha power. Broadly, these plots demonstrate immediate power increases in both the theta and alpha oscillatory bands, followed by a reduction in power at the approximate 200ms to 250ms mark. While visual inspection of the heat maps shows differences between the conditions (predictable/unpredictable) and between the memory outcomes (hit/miss) in the alpha and theta bands, the most prominent differences appear in the beta frequency range (displayed in the difference plots). Grand average ERP plots according to subsequent memory performance do not reveal discernible differences in N400 amplitude to subsequently remembered versus forgotten images (see *Figure 4.5*). Note that this interaction alone was not a focus of the present study and was thus not examined in statistical analyses. For grand average ERP plots of the N400 across image conditions, the reader is directed to the original manuscript (Jano, Chatburn, et al., 2024).

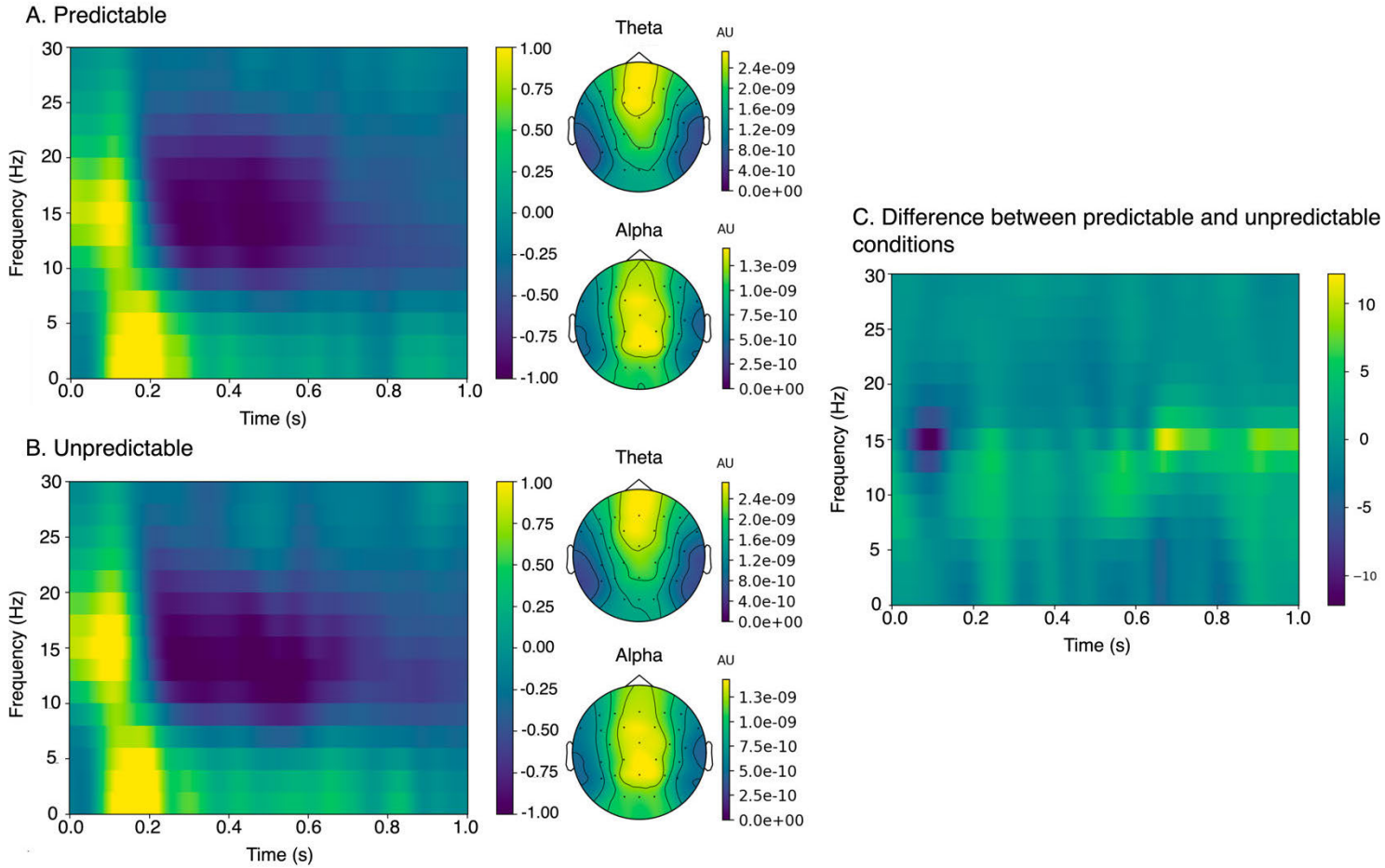


Figure 4.3. *Time-frequency heat maps (displaying data averaged over all channels across the duration of image presentation; 0-1000ms) and topography plots according to* **(A)** *predictable* and **(B)** *unpredictable conditions. For heat maps, data across the whole epoch was divided by the data in the baseline window (-350 to -150ms pre-stimulus onset) and a decibel conversion was applied. Note that for statistical models, data in the 200-1000ms window post-image onset was used. For topography plots showing theta and alpha power, no baseline correction was applied.* **(C)** *Difference plot (predictable – unpredictable), showing z-scored, baseline corrected data (according to a -350 to -150ms pre-stimulus onset window).*

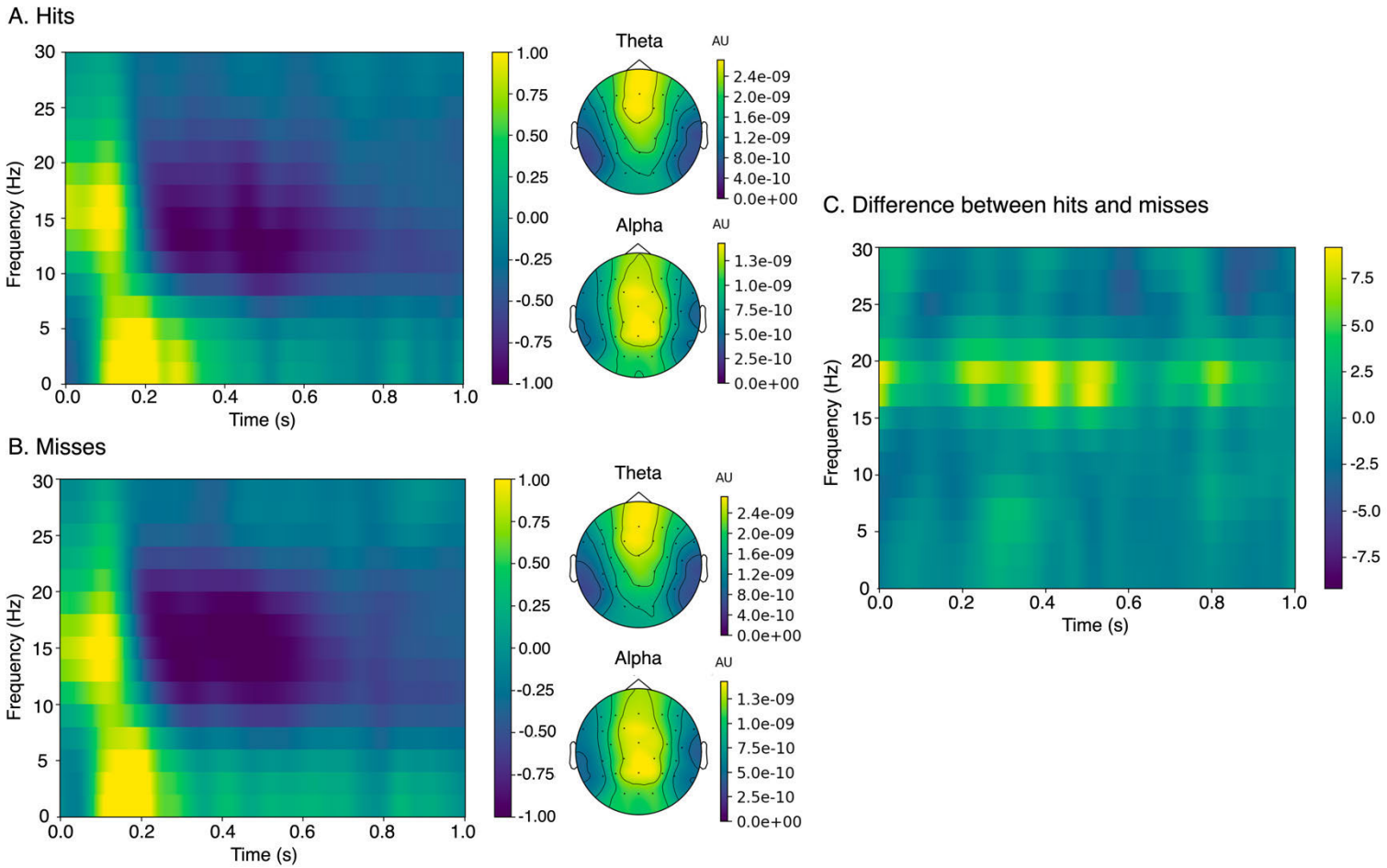


Figure 4.4. *Time-frequency heat maps (displaying data averaged over all channels across the duration of image presentation; 0-1000ms) and topography plots according to* **(A)** *memory hits* and **(B)** *memory misses. For heat maps, data across the whole epoch was divided by the data in the baseline window (-350 to -150ms pre-stimulus onset) and a decibel conversion was applied. Note that for statistical models, data in the 200-1000ms window post-image onset was used. For topography plots showing theta and alpha power, no baseline correction was applied* **(C)** *Difference plot (hits – misses), showing z-scored, baseline corrected data (according to a -350 to -150ms pre-stimulus onset window).*

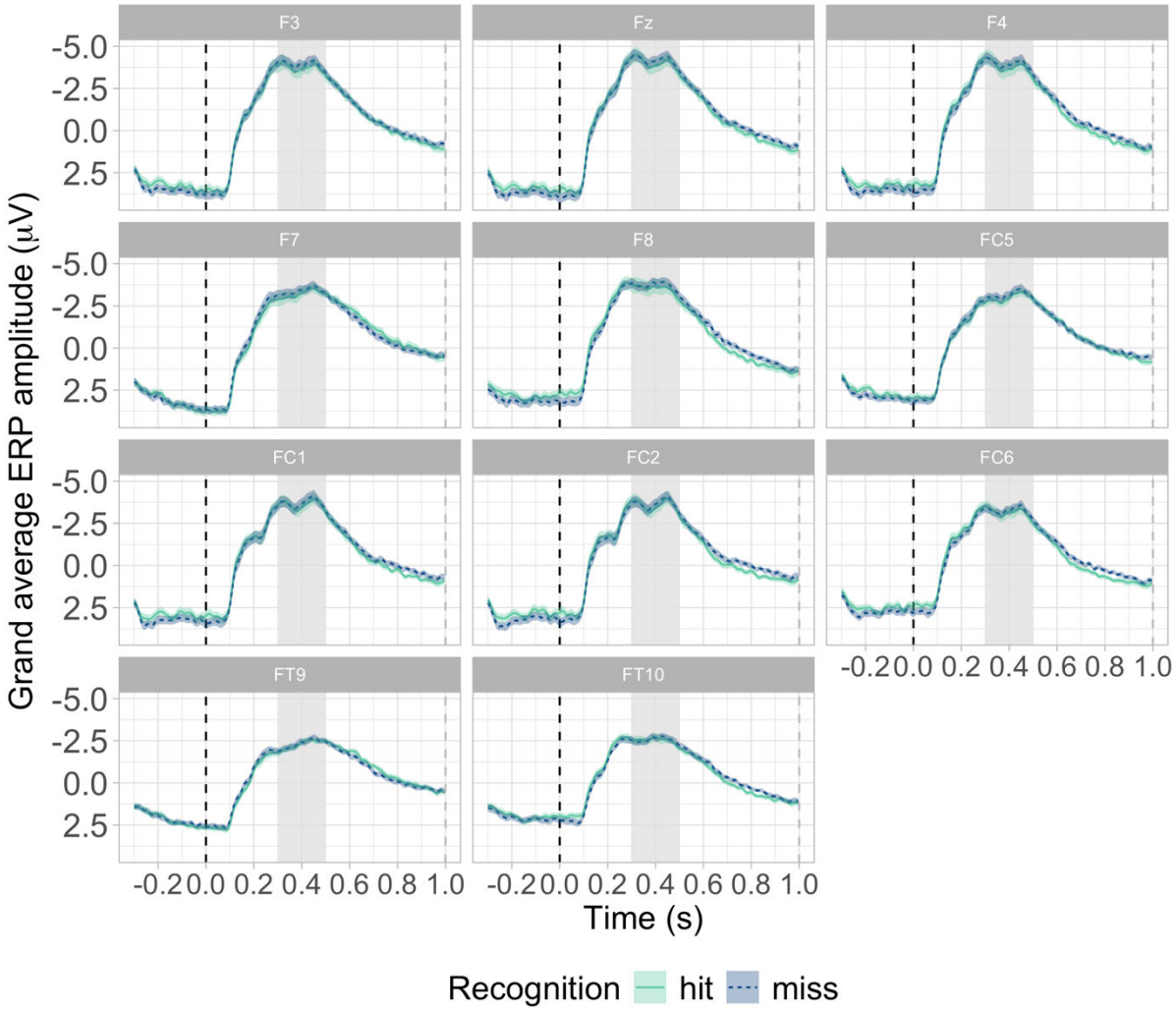


Figure 4.5. *Grand average ERP amplitude at frontal channels according to time and subsequent memory performance. The black dotted line depicts image onset, while grey shading shows the N400 window. Solid turquoise lines reflect memory hits while dotted dark blue lines depict memory misses. Turquoise and dark blue shading represents the standard errors for the recognition types.*

4.4.3. Linear mixed model results of primary analyses

It was hypothesised that theta power during learning would be greatest for images in the unpredictable condition, as compared to images in the predictable condition (Hypothesis a). This was addressed via Model 1, which did not detect a significant main effect of *image condition* on theta power ($\chi^2(1) = 0.98$, $p = .322$). The interaction between *image condition, position* and *IAF* was also non-significant ($\chi^2(3) = 5.09$, $p = .166$), and as such, the hypothesis was unsupported.

The second hypothesis (Hypothesis b) predicted that alpha power during learning would differ between images in the predictable and unpredictable sequences (investigated via Model 4). While the main effect of *condition* on alpha power across all sagittal regions was non-significant ($\chi^2(1) = 0.01$, $p = .925$), the interaction between *condition, position* and *IAF* on alpha power was significant ($\chi^2(3) = 8.42$, $p = .038$). At 'A' images, higher IAFs were associated

with greater alpha power across the predictable and unpredictable conditions. However, in the predictable condition, this relationship reversed at the 'D' image, with high IAFs being associated with decreases in alpha power (see *Figure 6*). As such, the hypothesis was partially supported, with the effect of image condition on alpha power depending on IAF and image position.

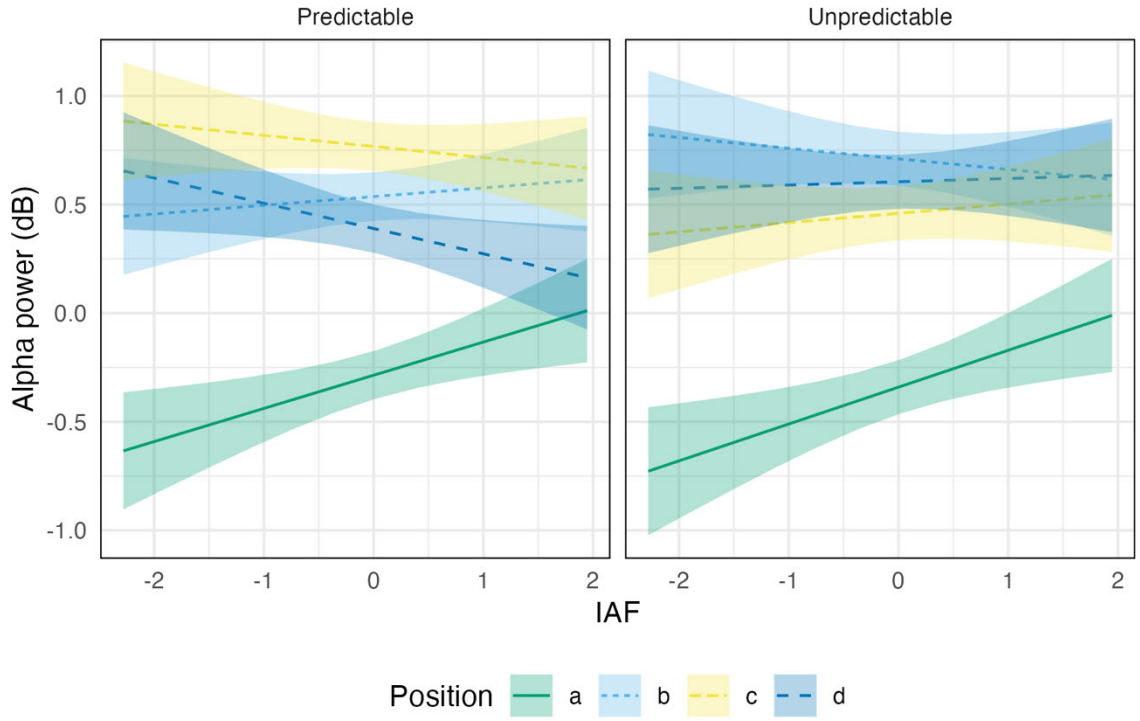


Figure 4.6. *Linear mixed-effects model results of the relationship between alpha oscillatory power (across all sagittal regions), image position, image condition, and individual alpha frequency (IAF). Plots are faceted according to condition, whilst green, light blue, yellow and dark blue colours correspond to each image position (A, B, C, D, respectively). Shading represents 83% confidence intervals.*

It was predicted that theta power during learning would be greatest for subsequently remembered items (memory hits) than subsequently forgotten items (memory misses; Hypothesis c). This was analysed via Model 2, which, in contrast to hypothesised effects, failed to detect a significant main effect of *memory recognition* on theta power ($\chi^2(1) = 1.92$, $p = .166$). The interaction between *recognition, IAF* and *condition* was also non-significant ($\chi^2(1) = 0.04$, $p = .835$), suggesting that theta power was not related to subsequent memory.

It was additionally predicted that alpha power during learning would be associated with memory recognition outcomes (Hypothesis d). This prediction was tested via model 5, which, in support of the hypothesis, revealed a significant main effect of *memory recognition* on alpha power across all sagittal regions ($\chi^2(1) = 4.43$, $p = .035$). Alpha desynchronisation was strongest for subsequently forgotten images (memory misses) as compared to subsequently remembered images (memory hits). However, the interaction between *recognition, sagitallity, condition* and

IAF was non-significant ($\chi^2(2) = 0.11$, $p = .948$). Consequently, the relationship between alpha power and memory encoding may not depend on IAF or N400 amplitudes.

It was also hypothesised that the relationship between the N400 and oscillatory activity during learning would be linked to subsequent memory outcomes at test (Hypothesis e). Model 3 was computed to test this hypothesis in relation to theta power, and, in support of the hypothesis, revealed a significant interaction between *memory recognition, IAF* and *N400 amplitude* on theta power ($\chi^2(1) = 4.24$, $p = .039$). For low IAF individuals, subsequently forgotten items (memory misses) were associated with increases in theta power as the N400 amplitude became larger (more negative). For subsequently remembered items (memory hits), this relationship was present albeit weaker. In contrast, for high IAF individuals, subsequently forgotten items (memory misses) were associated with decreased theta power as the N400 amplitude increased. Subsequently remembered items (memory hits) were associated with a weak relationship between theta and the N400 amplitude (see *Figure 4.7*). However, the main effect of N400 amplitude on theta power was nonsignificant ($\chi^2(1) = 2.07$, $p = .150$). Therefore, while N400 amplitudes alone were unrelated to changes in theta power, the N400, theta power and IAF interacted to influence later remembering.

Finally, Model 6 tested the hypothesis concerning oscillatory and N400 subsequent memory effects (Hypothesis e) in relation to alpha power. Contrary to hypothesised effects, the model did not detect a significant interaction between *memory recognition, N400 amplitude, IAF, condition* and *sagitallity* on alpha power ($\chi^2(2) = 1.04$, $p = .594$). The main effect of N400 amplitude on alpha power was also nonsignificant ($\chi^2(1) = 0.13$, $p = .720$). As such, alpha power did not interact with N400 amplitude to influence subsequent memory, and N400 amplitude alone was not associated with changes in alpha power.

4.4.3. Exploratory correlation analysis

As primary models revealed that memory hits and misses were supported by differential patterns of neural activity between high and low IAF individuals, we sought to determine whether such patterns might be related to increased or decreased hit rates. As such, a Pearson correlation was conducted to explore the relationship between IAF and hit rate, after Shapiro-Wilk tests revealed that the variables were normally distributed. The Pearson correlation revealed a significant but weak relationship between the two variables ($r(44) = 0.36$, $p = .014$), such that increases in IAF were associated with increasing hit rates (see *Figure 4.8*).

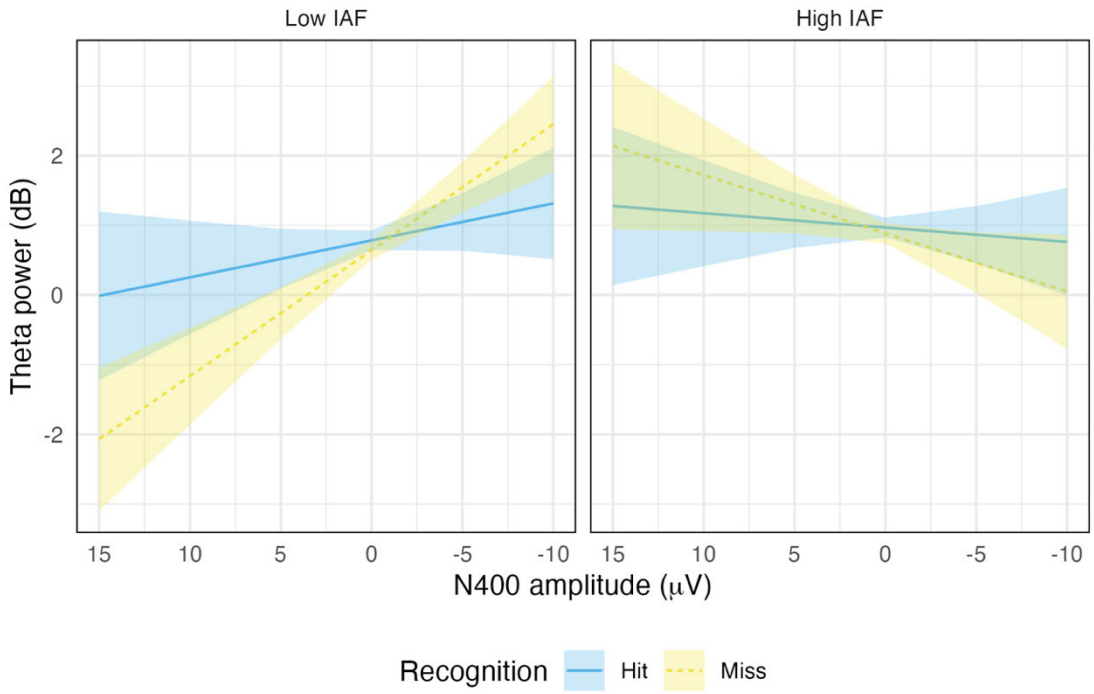


Figure 4.7. *Linear mixed-effects model results depicting the relationship between theta power, N400 amplitude, memory recognition, and individual alpha frequency (IAF). Blue lines reflect subsequently remembered items (memory hits) whilst yellow dotted lines represent subsequently forgotten items (memory misses). The plot is faceted into low and high IAF, with this dichotomisation for visualisation purposes only.*

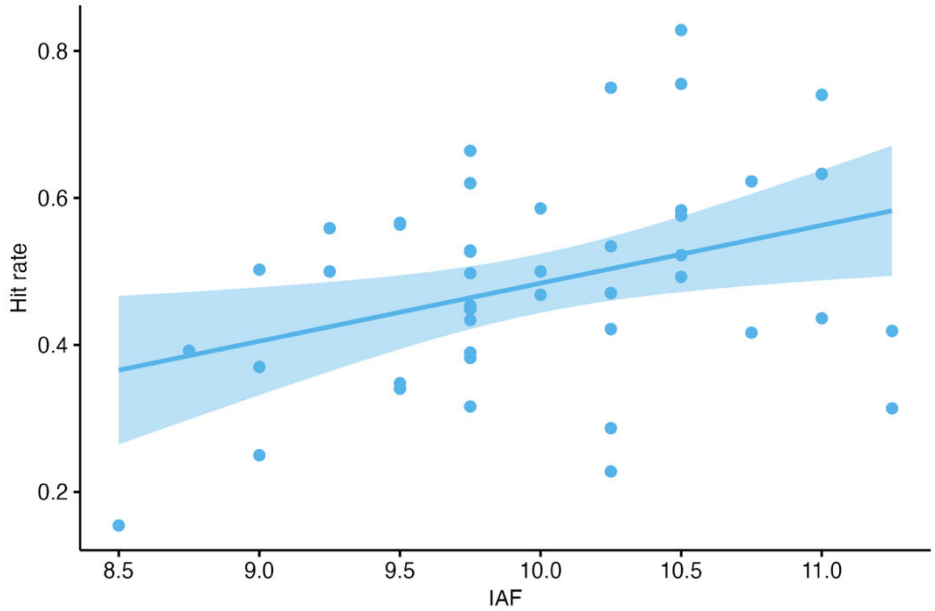


Figure 4.8. *The correlation between individual alpha frequency (IAF) and hit rate (across all image positions and conditions). Dots represent individual data points (N = 46).*

4.5. Discussion

The present investigation reanalysed data from a previous study (Jano, Chatburn, et al., 2024) to further elucidate the relationship between prediction and memory. Participants' brain activity was recorded using EEG whilst they viewed predictable and unpredictable sequences of outdoor scene images. Electrophysiological activity during learning was then compared for images subsequently recognised and forgotten. Contrary to expectations, theta power did not differ between images in unpredictable and predictable conditions. However, theta power interacted with IAF and the N400 component to influence later remembering. Based on the strong relationship between the N400 and item expectancy (DeLong et al., 2005; for a review see Kutas & Federmeier, 2011), the present findings could imply that intrinsic neural variability modulates the degree to which prediction errors drive memory encoding. Additionally, alpha desynchronisation was strongest for items later forgotten versus remembered. This reiterates the functional relevance of alpha power for learning and information uptake. Ultimately, the results emphasise the importance of ERPs and oscillatory rhythms for memory formation, whilst suggesting that the effect of prediction on memory differs at the inter-individual level.

4.5.1. Theta power alone does not relate to subsequent memory

Oscillatory theta power has previously been linked to successful memory (Klimesch, 1999; Klimesch, Doppelmayr, Schimke, et al., 1997; Sederberg et al., 2003) and to prediction error processing (Cavanagh et al., 2010, 2012), suggesting that theta is useful in gauging the memory updating processes related to prediction. Given also that prediction and encoding may be inversely related (Sherman et al., 2022; Sherman & Turk-Browne, 2020), it was hypothesised that theta power would be stronger for images in the unpredictable sequences as compared to the predictable sequences, reflecting heightened memory encoding in the absence of a strong prediction. While the expected trend was somewhat evident in the present time-frequency plots, this between-condition difference in theta synchronisation did not reach significance. At a first glance, this suggests that predictions do not influence theta synchronisation (and by extension, memory encoding). However, as discussed in Jano, Chatburn, and colleagues (2024), it is also likely that the categorical manipulation of predictability in the present experiment was too superficial to capture the nuanced changes in stimulus expectancy present in the dataset. Given also that each image was unique (despite belonging to either a predictable or unpredictable categorical sequence), predictability at the item level may not have been measured. This may explain the failure of the present study to detect a condition-specific effect relating to theta power, as memory encoding might have occurred in both conditions. However, the relationship between theta, prediction, and memory is more clearly illuminated via the effects relating to subsequent memory.

It was predicted that increases in theta power during learning would be associated with successful remembering at test. However, in contrast to previous literature linking theta synchronisation to enhanced subsequent memory (e.g. Klimesch, Doppelmayr, Russegger, et al., 1996; Long et al., 2014; Sederberg et al., 2003), the present analysis did not reveal a relationship between theta power and memory performance. Whilst theta power during learning did not influence later remembering, this finding may relate to the level of processing

required by the present task. Subsequent memory effects of oscillatory patterns are largely variable and task-dependent, as the type of paradigm employed may give rise to varying depths of processing, consequently influencing the extent of memory encoding (Hanslmayr et al., 2009; Hanslmayr & Staudigl, 2014). The present study employed an incidental memory encoding paradigm with realistic, complex outdoor scene images, as we sought to examine the consequences of prediction for memory as predictions naturally develop. This is in contrast to prior research reporting theta subsequent memory effects, which often uses more simplistic stimuli (e.g., word lists or pictures of objects), informs participants that their memory will later be tested, instructs participants to remember the content, or requires that they answer a question about each item during learning (e.g., Klimesch, Doppelmayr, Russegger, et al., 1996; Long et al., 2014; White et al., 2013). Such procedures may encourage memory encoding to a greater extent than the present paradigm (although may be limited in their ability to gauge more naturalistic forms of learning and prediction).

This is furthered by the low hit rates observed in the behavioural data (at approximately 0.50), suggesting that overall encoding in the current study may have been weak. However, it is important to note that the original study by Sherman & Turk-Browne (2020), upon which the present design was based, obtained similar average hit rate values (ranging from 0.38 to 0.61). Furthermore, while lower hit rates might be problematic for research primarily interested in behavioural memory performance, the focus of the present investigation was on the electrophysiological patterns that relate to later remembering and forgetting. As such, we do not view the lower hit rates as a limitation of the paradigm per se, but instead as a novel contribution to the existing literature, highlighting the limits of memory formation under more complex and dynamic circumstances. Additionally, as d' scores in the previous study were above chance (Jano, Chatburn, et al., 2024), the lower hit rate implies a specific encoding decrement as opposed to overall impaired memory performance. Consequently, future research could vary the level of stimulus complexity to determine the bounds of memory formation in more naturalistic scenarios. Moreover, since the learning in the current study resembles learning in an everyday context, where individuals are not explicitly told to remember or predict information, day-to-day memory performance may be weaker compared to that observed in experimental settings. Importantly, these results alone do not speak directly to effects relating to prediction, particularly given the potential for varied stimulus predictability levels within both the predictable and unpredictable image conditions. This further underscores the importance of considering the N400, which may capture the extent of predictive processing more directly due to its ties to prediction error.

4.5.2. IAF may modulate the relationship between prediction and memory encoding

The current study is the first to our awareness to directly compare the relationship between oscillatory and N400 patterns during a prediction task with subsequent memory performance and intrinsic neural factors. Interestingly, when the N400 component was incorporated into models of theta power, IAF and subsequent memory, a relationship between the variables was observed. For individuals with a low IAF, increases in N400 amplitude (becoming more negative) were associated with increases in theta power, with this relationship being strongest for subsequently forgotten items (memory misses) versus subsequently remembered items

(memory hits). Prior research links the N400 to prediction error (e.g., Bornkessel-Schlesewsky & Schlesewsky, 2019; Eddine et al., 2024; Rabovsky & McRae, 2014). Therefore, the present results could indicate that for low IAF individuals, optimal remembering is supported by a weak positive relationship between the magnitude of prediction error and theta power during learning. This implies that for such individuals, 'too much' encoding in response to a prediction error, or 'too little' encoding in the absence of a prediction error is maladaptive for later remembering. Conversely, for high IAF individuals, successful remembering was supported by the absence of a relationship between theta power and the N400 during learning. Moreover, subsequently forgotten stimuli were associated with a stronger *negative* relationship between theta power and the magnitude of the N400, suggesting that 'too little' encoding in the face of a prediction error and 'too much' encoding in response to predictable information is detrimental. This could point more generally to an 'optimal' level of prediction error-related memory uptake, which appears to differ between individuals. Here, over-encoding might lead to interference in memory, while under-encoding might prevent the information from entering memory. However, the underlying reason for these differential effects across varying levels of predictability and IAF remains uncertain, rendering it challenging to draw confident conclusions. Nevertheless, the effects associated with successful memory might be illuminated by a consideration of how those with high and low IAFs differ with regard to cognitive processing.

Higher IAFs are associated with better general intelligence (Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013), enhanced memory (Klimesch, 1997; Klimesch et al., 1990, 1993), and faster perceptual processing windows (Samaha & Postle, 2015). Although IAF has particularly been linked to the speed of memory retrieval, it has also exhibited differences during memory encoding between good and bad performers, suggesting that those with a high IAF might have a heightened memory encoding ability (Klimesch, 1997; Klimesch et al., 1993). Consequently, the observation that successful memory was not supported by the relationship between theta and the N400 for those with a high IAF may imply that such individuals rely less on prediction error signals to inform memory updating than their low IAF counterparts. This is compatible with our previous findings, where N400 amplitudes did not relate to memory for those with a high IAF, prompting the suggestion that such individuals adopt a more widespread encoding strategy (Jano, Chatburn, et al., 2024). Moreover, the present results suggest that this more widespread "strategy" can have benefits for memory performance, as IAF and hit rate were (allbeit weakly) positively correlated. To build upon this suggestion, if high IAF individuals are better at encoding information more generally, prediction errors may not contribute over and above to the memory encoding that is already occurring (hence the weak relationship between theta and the N400 amplitude observed for memory hits). While the current analysis cannot speak directly to how these disparate memory strategies may manifest, it may be a useful first step in explaining why at times, memory is enhanced in cases of low prediction error (i.e., for predictable stimuli; e.g., Gronau & Shachar, 2015; Turan et al., 2023), but also for unexpected (i.e., prediction error-eliciting) information (Federmeier et al., 2007; Rouhani et al., 2018).

Although the relationship between prediction and memory appears to be modulated by IAF, it is important to emphasise that the present study could not explicitly relate the amplitude of the N400 to fluctuations in image predictability due to the limits of the categorical predictability manipulation. As such, the extent to which the N400 reflects a prediction error signal in this context is unclear, although the generalisability of this component to non-linguistic settings is highly promising (for discussion see Eddine et al., 2024; Kutas & Federmeier, 2011). Similarly, as theta power alone did not relate to subsequent memory, it is possible that such activity was not reflective of memory encoding in the present study. As visual inspection of the time frequency heat maps reveals strong beta power differences between subsequently remembered and forgotten images, activity in this frequency band might have related more strongly to memory encoding. Consequently, an analysis of the beta frequency band, and it's relationship to prediction and memory, may be an interesting endeavour for future research. However, returning to a discussion of the theta rhythm, it is likely that theta subsequent memory effects were generally smaller than in previous studies and as such, only detectable once other sources of variability (such as N400 amplitude) were considered. Similarly, grand average ERP plots did not show discernible differences in N400 amplitude according to subsequently remembered and forgotten stimuli. This could suggest that the effect of the N400 on memory is also dependent on other factors; a proposal that is supported by the variable relationship observed here according to theta power and IAF. Nevertheless, these findings imply that the association between theta power and the N400 is functionally significant for later remembering, although future research may benefit from more fine-grained predictability measurements. Ultimately, the current results emphasise the more intricate relationship between prediction and memory; while prediction errors could promote memory formation, the mixed findings according to IAF also cannot rule out the potential for encoding to occur independently of, or over and above, the level of prediction error. This suggestion is further reiterated by the results pertaining to alpha power.

4.5.3. The effect of alpha power on memory encoding does not relate to the N400

To provide further insight into oscillatory changes during predictive processing, alpha activity during the learning phase was measured. The present results revealed that IAF and alpha power were positively related at the 'A' images (regardless of image condition), and negatively related at predictable 'D' images. It is possible that this pattern arises from differences in memory encoding during naturalistic sequence processing, potentially stemming from changes in predictability. At the beginning of the sequence, it was likely difficult to determine whether the sequence would be predictable or unpredictable. However, this would be clear by the end of the sequence, where the observed items either matched or mismatched previously learnt regularities. The decreased alpha power observed following predictable 'D' images for high IAF individuals may suggest that alpha activity adapted according to changes in stimulus relevance and predictability. Alpha desynchronisation has been linked to successful memory formation (Hanslmayr et al., 2009; Klimesch, Schimke, et al., 1996; Sederberg et al., 2003), and as such, high IAF individuals may have been more likely to encode predictable 'D' images into memory than low IAF individuals. This is compatible with the above suggestion that such individuals have a more widespread propensity for memory encoding. Alternatively, *increased* alpha synchronisation could promote memory encoding because it inhibits the retrieval of task-

irrelevant memory representations (Klimesch et al., 2007). With this in mind, those with a high IAF, upon encountering a predictable stimulus, may have directed their encoding resources away from the redundant information. However, while this result points toward a potential optimisation of processing according to stimulus predictability and intrinsic neural differences, the effects relating to alpha and subsequent memory can permit more direct conclusions regarding alpha's relevance for memory encoding.

Greater alpha desynchronisation (i.e., reduced alpha power) during learning was associated more strongly with forgetting versus successful remembering. This is in line with previous research (Meeuwissen et al., 2011), and with alpha's proposed relation to inhibitory processing (Klimesch et al., 2007), suggesting that increases in alpha power during learning positively influence memory formation. However, alpha subsequent memory effects in the present study were not related to image condition or to the amplitude of the N400 component, providing further support for the notion that prediction error may not be a necessary prerequisite for memory formation. Given also that N400 amplitudes were not correlated with alpha power, the two components appear to reflect differing mechanisms. Taken together, these findings have implications for predictive processing theories, which conceptualise prediction as a general coding strategy (Huang & Rao, 2011). Prediction errors are proposed to signal a need for model updating and may be minimized through changes in neuronal connections (i.e., synaptic plasticity; Barron et al., 2020; den Ouden et al., 2012; Friston, 2005). These neuronal alterations purportedly underlie memory encoding, suggesting that prediction errors drive learning (Friston, 2005; for a review of synaptic plasticity and memory see Martin et al., 2000). However, while prediction may be a general cognitive mechanism, the present results question the role of prediction errors as the primary learning signals in the brain. As it is difficult to determine the extent to which the present categorical predictability manipulation captures subtle changes in predictability, a design that adjusts stimulus probabilities at a more fine-grained level could provide stronger insights into how changes in oscillatory and ERP activity relate to prediction and subsequent memory.

4.5.4. Conclusion

The current study emphasises the dynamic and inter-individual nature of the relationship between prediction and memory. Although likely interconnected, memory encoding may not depend completely on the magnitude of prediction error, adding a layer of complexity to the potential trade-off between prediction and memory uptake (Hubbard et al., 2019; Sherman et al., 2022; Sherman & Turk-Browne, 2020). Most notably, whilst low IAF individuals appear more inclined to update their predictive memory representations according to prediction errors, individuals with a high IAF could rely on a more general memory updating strategy that is independent of prediction error, or that contributes to memory encoding over and above the model updating resulting from prediction errors. Although this may have significant implications for predictive coding schemes, it also presents intriguing opportunities for future research, which should further examine individual neural variability in the context of prediction and memory. Finally, the present reanalysis provides evidence for an inherent link between oscillatory activity, IAF, N400 amplitude, and subsequent memory, whilst also suggesting that oscillations in the alpha and theta bands reflect somewhat distinct processes to the N400 ERP.

Interim summary

Chapter 4 related oscillatory activity and N400 amplitudes during exposure to predictable and unpredictable sequences with IAF and subsequent memory, to better characterise the relationship between prediction, memory and individual differences. Most notably, the study described in this chapter reiterates what has come to be a running theme of the present thesis, namely that IAF is critical in modulating prediction-related brain activity and its association with memory.

As with Chapter 3, Chapter 4 demonstrated a relationship between the neurophysiological activity recorded during learning and subsequent memory that differed between high and low IAF individuals. Specifically, subsequently recognised images were associated with a weak positive relationship between theta power and N400 amplitude, for low versus high IAF individuals. This may provide further support for the notion that prediction errors drive memory encoding for individuals with low IAFs. However, a strong relationship between theta and the N400 was related to poorer memory outcomes, potentially suggesting that 'too much' or 'too little' updating in the face of a prediction error is detrimental for memory, for low and high IAF individuals, respectively.

Additionally, while theta power interacted with N400 amplitudes, IAF and subsequent memory, alpha power subsequent memory effects occurred independently of N400 amplitude and image condition, further supporting the suggestion that memory encoding may not always depend on stimulus predictability or the level of prediction error. Importantly, the item-based subsequent memory approach in Chapter 4 facilitated a comparison of neural activity to specific items with later memory for that item, capturing subtle distinctions underlying the relationship between predictive processing and memory.

Taken together, the findings of all three chapters paint a complex picture of prediction and memory that may have implications for perspectives that view prediction error as integral for learning. In Chapter 5, the results of these three studies will be further discussed and framed in relation to prior literature and existing theoretical accounts, providing a synthesis of ideas and lending novel insights to understandings of prediction and memory.

Chapter 5

General Discussion & Conclusion

As far as the brain is concerned, the past, present and future are tightly intertwined, and their unification often comes naturally during daily functioning. At any given moment, we appear well equipped to draw on the past to interpret the present and envisage the future; a seemingly intuitive process that has been formally conceptualised via the predictive coding framework (e.g., Friston & Kiebel, 2009; Rao & Ballard, 1999). Notions of predictive processing shape the present thesis, and broadly propose that the brain uses prior experience to anticipate future states (Friston, 2005; Hohwy, 2013). This neural propensity for anticipation, while traditionally investigated in the context of the visual system (e.g., Huang & Rao, 2011; Kveraga et al., 2007; Rao & Ballard, 1999), can unite perception, cognition and action (A. Clark, 2013; Hohwy, 2020). The potential for prediction to underly general brain functioning (Huang & Rao, 2011; Friston, 2010) renders an understanding of it a crucial pursuit for neuroscientific research. Furthermore, the precise nature of the relationship between prediction and memory is unclear, although some research suggests that prediction and memory encoding compete (Hubbard et al., 2019; Sherman et al., 2022; Sherman & Turk-Browne, 2020). This relationship could have potential consequences for learning, whilst informing understandings of the brain's adaptability. This doctoral thesis aimed to explore 1) the association between prediction and memory, 2) the neural foundations of this relationship, and 3) how these processes vary according to individual neural factors.

The existing body of research on prediction and memory often focusses on the behavioural domain, linking differences in stimulus probability and consistency to memory recognition performance (e.g. Greve et al., 2017; Ortiz-Tudela et al., 2023; Turan et al., 2023). However, while behavioural approaches are extremely useful in shedding light on the performance-related outcomes of prediction, they are limited in the extent to which they can draw conclusions regarding the underlying brain-based mechanisms. In light of this limitation, the present thesis focussed on identifying the neural substrates underpinning prediction and memory functioning. This investigation was framed with particular emphasis on ERP activity and oscillatory rhythms, which can provide insight into the event-related fluctuations in the brain spanning both short and longer timescales, respectively (Luck, 2014). This research also sought to inform the transferability of prediction across cognitive domains, and consequently employed investigations of both linguistic and non-linguistic stimuli. Moreover, while few studies consider the role of between-subject neural variability in such investigations, the experience-dependent nature of prediction (Friston, 2005) suggests that this mechanism could function not only as a broad computational strategy (Huang & Rao, 2011) but also as a uniquely individual process, shaping perceptions and worldviews. Therefore, the current research sought to explore the inter-individual contribution to prediction and its ability to constrain what is

predicted and used for model correction. This discussion chapter begins with a summary of the findings of the present body of work. Following this, the significance of the results in light of prior literature and theory will be discussed, with a consideration of implications and suggestions for future research.

5.1. Summary of findings and contributions of the research

This doctoral thesis commenced with an investigation into the electrophysiological correlates underpinning prediction in language, via a reanalysis of a large-scale replication study by Nieuwland and colleagues (2018). This analysis took an innovative approach by measuring pre- and post-stimulus ERP correlates, in conjunction with alternative sources of variability, including IAF and word-by-word changes in prior context. Following this, the research transitioned toward the application of this knowledge to understand the consequences of prediction for memory processing in a subsequent memory experiment. These investigations measured ERP and oscillatory activity during exposure to predictable and unpredictable sequences of outdoor scene images. Such analyses allowed for an extension beyond behavioural work, shedding light on the neural fluctuations underpinning the brain's ability to anticipate and learn. Broadly, the findings paint an emerging picture of a complex and individually variable connection between the two processes.

This research presents several key findings that contribute to existing understandings of prediction and memory. Firstly, it demonstrates the importance of the N400 for tracking predictive processing and learning in real-time. Expanding upon the suggestion that the brain predicts upcoming linguistic stimuli to a highly detailed level (DeLong et al., 2005), this work shows that that there are certain individual and contextual constraints surrounding this effect. These findings contribute to the ongoing debate surrounding prediction in language (for discussion see Kuperberg & Jaeger, 2016; Van Petten & Luka, 2012), by suggesting that the brain's pre-activation of upcoming linguistic units is subject to variability. Moreover, the results demonstrate the N400's broader applicability as a learning signal beyond language processing. Additionally, the relationship between N400 patterns and subsequent memory performance, while modulated by individual neural differences, reiterates the component's promise as a domain-general prediction error correlate (for discussion see Eddine et al., 2024). This sheds light on the pervasiveness of prediction errors in the brain (den Ouden et al., 2012) and provides an important foundation for future work on the neurophysiological patterns that index prediction and learning across a range of contexts.

Furthermore, this work offers a unique perspective on the association between prediction and memory, by showing that prediction-related neural activity influences memory processing, based on individual differences measurable in the EEG. This supports a prediction error-driven account of learning, whilst also implying that memory encoding can occur independently of stimulus predictability. Extending beyond previous literature which primarily focusses on group-level effects, but which sometimes controls for the variance associated with participants (e.g., Bein et al., 2015; Ortiz-Tudela et al., 2023; Turan et al., 2023), this research provides empirical evidence suggesting that predictive processing may operate within the constraints of

the individual. Consequently, it highlights the importance of directly considering (as opposed to controlling for) individual differences when examining the impact of prediction on memory. This discussion of individual variability leads naturally into the significance of IAF for prediction and memory. The present body of work demonstrated a crucial role for IAF in prediction during language processing, and in modulating the relationship between brain activity and memory performance. While much of the literature on IAF focusses on its relationship to cognition (e.g., Grandy, Werkle-Bergner, Chicherio, Lövdén et al., 2013; C.R. Clark et al., 2004; Zhang et al., 2021), few explicitly relate this component to the domain of predictive processing (however see Bornkessel-Schlesewsky, Sharrad, et al., 2022). In contrast, the current research provides a novel contribution to the existing literature, by demonstrating the relevance of IAF for prediction during language comprehension. The findings also build upon the association between IAF and memory ability observed in previous literature (Klimesch et al., 1990, 1993), suggesting that this relationship could be underpinned by differences in predictive processing. Consequently, the present results support IAF's role as a trait-like correlate (Grandy, Werkle-Bergner, Chicherio, Schmiedek et al., 2013).

Overall, the current body of work addresses gaps in the existing literature via the use of novel methodological, analytical and theoretical approaches. Notably, it demonstrates a role for prior context in shaping predictions about the future and subsequent memories of the past (i.e., model updating). However, the mixed findings according to IAF also provide evidence for memory encoding that occurs independently of prediction error, bringing to light the dynamic and complex relationship between prediction and memory processing. These findings, and their broader meaning for understandings of brain functioning and behaviour, will now be explored in the context of previous literature and theory.

5.2. Implications of the present results for understanding the relationship between prediction and memory processing

A common theme throughout the present doctoral thesis is the lack of a straightforward relationship between predictive processing and memory encoding. In Chapter 3, stronger prediction error signals (presumably captured via greater N400 amplitudes) were associated with enhanced memory for those with low versus high IAFs. In Chapter 4, a weak positive relationship between theta power and N400 amplitude during learning was associated with successful memory recognition for low, but not high IAF individuals. Taken together, these findings indicate that encoding may not always be dependent on the level of prediction error and can occur under conditions of high predictability. Such results contrast with the suggestion that predictions (due to their connection to memory retrieval; Chow et al., 2016; Schoknecht et al., 2022), disrupt the encoding of new information into memory (Hubbard et al., 2019; Sherman et al., 2022; Sherman & Turk-Browne, 2020), while prediction errors trigger memory updating (Sinclair et al., 2021). Although Sherman and Turk-Browne (2020) propose that prediction and encoding compete for limited hippocampal resources, other research suggests that predictable stimuli may be processed more shallowly (Hubbard et al., 2019; Van Berkum, 2010). Both proposals, while approaching the question from slightly different angles, touch upon an optimisation mechanism whereby the brain prioritises information for processing that

can contribute new insights to its worldview (Hubbard et al., 2019; Sherman & Turk-Browne, 2020; Van Berkum, 2010). This is highly compatible with predictive coding accounts, wherein the brain reduces redundancy by explaining away predictable content, and only representing *unpredicted* information in the sensory system (Friston, 2005; Huang & Rao, 2011; Rao & Ballard, 1999). However, the results of the present thesis add a layer of complexity to this relationship by suggesting that encoding can be both dependent and independent of stimulus predictability. To interpret this effect, a discussion of how predictions might drive memory more generally will first occur, followed by a consideration of theories of prediction and memory processing that can account for the more mixed nature of the observed effects.

5.2.1. Understanding how predictability drives memory encoding

The current body of work provides evidence to suggest that prediction errors drive memory formation for certain individuals (namely those with a low IAF, although the importance of IAF will be discussed further in section *5.2.5*). Of relevance for understanding the mechanism behind this effect is the increased neural activity associated with a prediction error, which is purportedly representational in nature, reflecting information at each level of the prediction hierarchy (den Ouden et al., 2012). Supporting this proposal, Murray and colleagues (2002) observed stronger blood-oxygen-level-dependent (BOLD) activity in primary visual cortex (V1) to random lines that did not form a coherent shape, than to coherent shapes. Interestingly, this activity in V1 showed an inverse pattern to the activity in higher-order object-processing regions, potentially suggesting that, when lines formed discernible shapes, prediction errors in lower sensory regions were reduced while high-level predictions could effectively cascade (Murray et al., 2002; Summerfield & de Lange, 2014). Furthermore, as prediction error signals are presumably accompanied by precision-weightings that encode synaptic gain (i.e., neuronal sensitivity; Feldman & Friston, 2010; Friston, 2009; Nour & Dolan, 2022; Pertermann et al., 2019), such signals likely have representational properties, providing an important first step in understanding their translation to memory.

From here, the relationship between prediction and associative plasticity becomes relevant (Friston, 2003, 2005). Prediction errors are proposed to drive plasticity and predictive model updating (Barron et al., 2020). According to the *synaptic plasticity and memory hypothesis* (SPM), alterations in synaptic plasticity support the formation of a memory trace (for a review see Martin et al., 2000). These changes are *activity-dependent* and may be realised via the mechanism of long-term potentiation (LTP; introduced in Chapter 4 of this thesis; Martin et al., 2000). If prediction errors increase the activity of sensory neurons responsible for representing that information (den Ouden et al., 2012), this activity may promote synaptic changes that translate to the encoding of the sensory content (Martin et al., 2000). This provides a mechanistic explanation behind the potential connection between prediction error and memory formation which may stem from the representational nature of prediction error (den Ouden et al., 2012). However, this effect was not observed for all individuals, suggesting that encoding can occur in the face of both predictable and unpredictable information. To explain this result, it is helpful to discuss a model that is compatible with memory encoding at both ends of the predictability spectrum.

5.2.2. A potential U-shaped relationship between prediction and memory

The present results, showing evidence for memory encoding that is not dependent on the level of stimulus predictability for some individuals, imply that prediction and encoding are not mutually exclusive. Encoding can occur in response to predictable information and following a prediction error. This may be compatible with research suggesting that memory and prediction are related via a U-shaped distribution, such that memory is best for both highly predictable (schema-congruent) and highly unpredictable (schema-incongruent) content (Greve et al., 2019; Quent et al., 2022; however for results demonstrating an inverted U-shaped relationship, see Ortiz-Tudela et al., 2023). This relationship is formally articulated via the *schema-linked interactions between medial prefrontal and medial temporal lobe* (SLIMM) model (see *Figure 5.1*), which proposes two pathways for memory encoding (van Kesteren et al., 2012). According to the SLIMM model, incongruence between sensory input and stored schemata elicit a prediction error that prompts the binding of information into a new, unique trace, via a hippocampal network in the medial temporal lobe (MTL). On the other hand, schema-congruence increases activity in the medial prefrontal cortex (mPFC), activating existing neocortical representations while fostering new connections to stimulate rapid memory consolidation (van Kesteren et al., 2012). Under conditions of high congruence, the mPFC inhibits activity in the MTL, so as to prevent the formation of an alternative, distinct trace (van Kesteren et al., 2012). This implies that the MTL circuit is bypassed under conditions of high congruity, while the mPFC is avoided in incongruent situations as the sensory information cannot be integrated into an existing schema (van Kesteren et al., 2012).

The SLIMM model draws parallels with theories on pattern separation and pattern completion in its relation to predictive processing (Barron et al., 2020; van Kesteren et al., 2012). Schema-congruent information appears to 'pattern complete' existing memory representations via the mPFC pathway, potentially leading to generalised, gist-like traces (Barron et al., 2020; Libby et al., 2019; van Kesteren et al., 2012). In contrast, schema-incongruent information (encoded in the MTL) may elicit prediction error, promoting pattern separation (van Kesteren et al., 2012) and the formation of a rich episodic trace (Barron et al., 2020; Mack et al., 2018; Ngo et al., 2021). The pattern separation and completion accounts of memory and prediction were presented in Chapter 1 of the present thesis to explain why unpredictable information may be better remembered than predictable information. However, relating this to the SLIMM model may instead imply that pattern completion does not necessarily lead to impaired memory for predictable content, but rather that the two processes give rise to different forms of memory that can be recalled with somewhat similar ease (Quent et al., 2022; van Kesteren et al., 2012). In line with this proposal, Quent and colleagues (2022) further predicted that schema-congruent (predictable) information would be associated with memory familiarity, while schema-incongruent (unpredictable) content would be related to recollection. However, the authors found evidence for recollection at both ends of the U-shape, suggesting that the memory pathways supporting processing at the extreme ends of the spectrum may not necessarily lead to distinct memory types (Quent et al., 2022). Nevertheless, the SLIMM model accounts for scenarios in which memory encoding occurs in response to predictable information, providing a potential explanation for some of the findings observed within this thesis. As such, increases in the N400 may recruit the MTL pathway, while reduced N400 amplitudes could be associated

with activity in the mPFC pathway. Although the current body of work cannot draw precise conclusions concerning the neuroanatomical locus of the observed effects, the connection between the N400 and the MTL is supported by prior research on the anterior medial temporal lobe (AMTL)-N400 ERP; an intracranial component that exhibits similar patterns to the scalp-recorded N400 (Nobre & McCarthy, 1995). Nobre and McCarthy (1995) propose that the AMTL-N400 is involved in the generation of the scalp-recorded N400, and as such, the present findings may be highly congruent with the engagement of the MTL by prediction error described in the SLIMM model (van Kesteren et al., 2012).

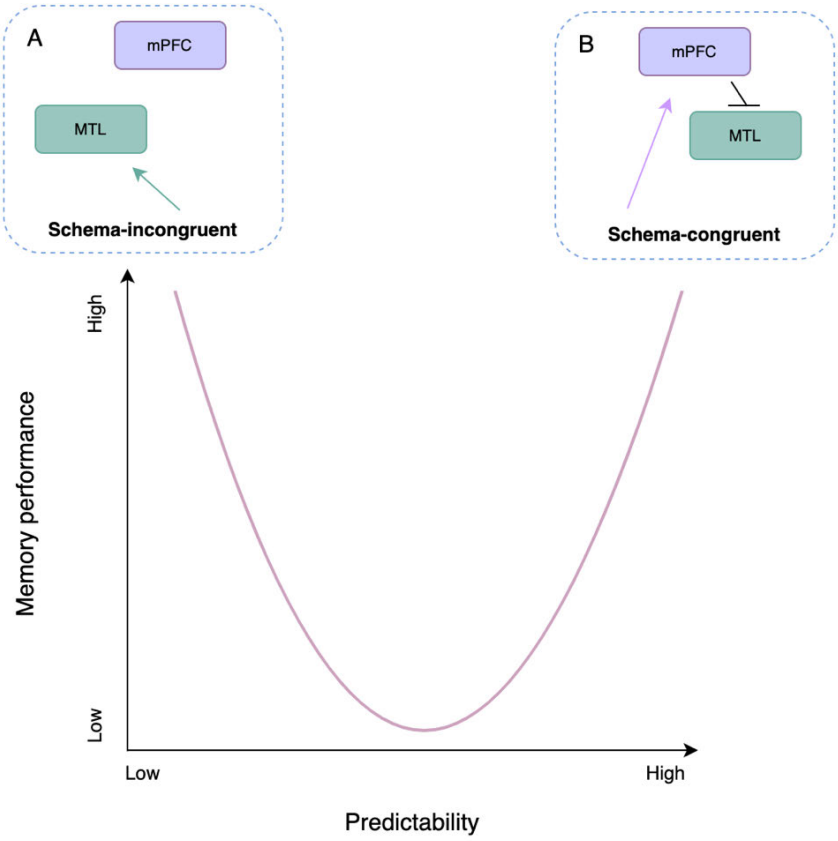


Figure 5.1. *Schematic of the schema-linked interactions between medial prefrontal and medial temporal lobe (SLIMM) model (based on Van Kesteren et al., 2012).* **(A) Schema-incongruence:** *When predictability is low, the information is encoded via the MTL pathway.* **(B) Schema-congruence:** *When predictability is high, memory encoding occurs via the mPFC pathway, which inhibits activity in the MTL. Note that Van Kesteren and colleagues' (2012) model primarily describes the relationship between memory and schema-congruence/prediction error. The term 'predictability' has been used here to encompass this information, as predictions are purportedly based on schemas (Van Kesteren et al., 2012).*

Although the SLIMM model can explain memory effects at either ends of the predictability spectrum, the framework still implies a dependency of memory formation on stimulus predictability and prediction error (van Kesteren et al., 2012). In contrast, the current results, whereby memory performance for some individuals was unrelated to N400 amplitude, provide evidence for memory encoding that occurs *independently* of predictability. This may not necessarily exclude explanations that rely on the SLIMM account, because an encoding effect

that occurs regardless of stimulus congruency implies that both predictable and unpredictable information is encoded. However, it is somewhat inconsistent with the U-shaped pattern that characterises the model, where moderately expected information should be poorly encoded (van Kesteren et al., 2012). Rather, the present findings provide evidence for a lack of a relationship between predictability and encoding for certain individuals. This work has implications for the SLIMM model (van Kesteren et al., 2012), which in future could consider individual neural differences and cases in which encoding is not purely constrained to changes in schema-congruence and predictability.

The independence of memory encoding from predictability is in line with results from Pupillo and colleagues (2023), who employed a context-object study/test paradigm and did not observe an effect of model-computed prediction error alone on memory recognition. During the experiment, participants were presented with a context and instructed to predict the corresponding object category (Pupillo et al., 2023). They received feedback throughout, allowing them to learn the context-object contingencies (Pupillo et al., 2023). In a second phase, they completed a similar task without explicit feedback, before their memory of the objects was tested (Pupillo et al., 2023). While the degree of prediction error alone was not related to subsequent memory, the outcome of the prediction modulated the relationship between prediction error and memory recognition (Pupillo et al., 2023). Specifically, when participants correctly predicted the upcoming object *category*, but model-computed prediction error relating to the *object* itself was high, memory was enhanced, while incorrect category predictions and high prediction error were associated with memory decrements (Pupillo et al., 2023). Although the present thesis did not explicitly instruct participants to predict (and therefore could not measure whether their predictions were correct or incorrect), the findings are similar in that an effect of prediction error on memory was modulated by alternative factors. Taken together, these results suggest that not all prediction errors are created equal, as some prompt memory updating to a greater extent than others. Furthermore, while Pupillo and colleagues (2023) measured explicit predictions, an important contribution to the mixed literature on prediction and memory may stem from the engagement of either implicit or explicit mechanisms, which will now be considered in light of the present results.

5.2.3. The N400 as an implicit learning signal

In the current research, N400 amplitudes were related to subsequent memory only for certain individuals; an effect that may be further elucidated by a consideration of the N400's relationship to implicit processing (a topic that was touched upon in Chapter 3; Rabovsky & McRae, 2014). While the N400 has strong ties to prediction error (Bornkessel-Schlesewsky & Schlesewsky, 2019; Eddine et al., 2024; Fitz & Chang, 2019), research by Rabovsky and colleagues (2018) and Rabovsky and McRae (2014) relates the component to *implicit* prediction error more specifically. This form of error supposedly results from implicit predictions, which are constantly occurring (Rabovsky & McRae, 2014). In contrast, more conscious forms of prediction should arise when participants deliberately anticipate upcoming information (Brod et al., 2022). Extending upon the N400's relationship to implicit prediction error, the component has also been associated with implicit *learning* (Hodapp & Rabovsky, 2021, 2024; Rabovsky et al., 2018; Rabovsky & McRae, 2014). For example, Hodapp and

Rabovsky (2021) showed that increased N400 amplitudes during learning were related to enhanced implicit memory at test. Importantly, the studies described throughout the body of this thesis should have led to the generation of implicit predictions, as participants were not instructed to consciously predict. However, the memory recognition task that was employed in Chapters 3 and 4 probed explicit memory, as participants were required to make an old or new recognition judgement for each image. Consequently, the variability surrounding the relationship between the N400 and memory recognition observed here may arise from the discrepancy between an *implicit* measure of prediction error (N400), and an *explicit* measure of memory performance (old/new judgement).

Implicit and explicit processing appear closely linked to traditional notions of implicit and explicit *memory* (sometimes related to declarative and non-declarative memory, respectively; for a summary, see Reber, 2013). The traditional distinction between the two forms of memory primarily stems from research employing varying tests of memory retrieval, showing that individuals can convey learnt information without being consciously aware of that content (e.g., via a performance-based test; Parkin et al., 1990; for a summary see Reber, 2013). This more implicit form of memory recall contrasts with the explicit ability to consciously retrieve a memory, which is typically probed via tests of free recall, cued recall, and recognition (Parkin et al., 1990). Research demonstrating impaired explicit memory recall but intact implicit memory recall in patients with amnesia (Gabrieli et al., 1997) and Alzheimer's disease (Golby et al., 2005) has prompted the suggestion that two separate systems exist in memory, which can be characterised according to the level of conscious awareness involved (Parkin et al., 1990; for discussion see Henke, 2010; Reber, 2013). *Table 5.1.* shows the traditionally proposed distinctions between the two types of memory, characterising implicit memory as unconscious, abstract and automatic, and explicit memory as conscious, voluntary and concrete (Rovee-Collier, 1997). The distinction between these two systems will subsequently be used to interpret the present findings. However, it is important to note that the boundary between the two proposed memory types may not be as concrete as initially proposed; a notion that will be discussed further in section *5.2.3.3.* Nevertheless, the purported dual memory systems are a useful first step in explaining why memory formation in the present study occurs in a manner that is both dependent and independent of implicit prediction error.

Table 5.1. *Frequently cited distinctions between implicit and explicit memory from Rovee-Collier (1997, Table 1), included with permission from the American Psychological Association. While traditional perspectives viewed the two systems as discrete, more recent work emphasises their interconnectedness.*

Implicit memory	Explicit memory
Without conscious awareness	With conscious awareness
Nonepisodic, general	Episodic, particular time or place
Abstract	Concrete
Automatic (incidental)	Deliberate (controlled)
Involuntary	Voluntary
All-or-none retrieval	Partial retrieval (decay effects)
No capacity demand	Limited capacity
Weighted for object form	Weighted for object function

5.2.4. A dual mechanism for memory processing

The conditional link between memory encoding and the N400 observed throughout the current body of work could stem from the involvement of two memory mechanisms – one that operates according to predictive coding principles at an implicit level and another, potentially more explicit process. This broad proposal rests upon the suggestion that 1) prediction errors captured via the N400 are implicit and may thus drive implicit memory formation (Hodapp & Rabovsky, 2021; Rabovsky & McRae, 2014), and that 2) explicit memory formation might be fostered by a (potentially explicit) mechanism that is independent of implicit prediction error (discussed further in section *5.2.4.2*). Here, it is crucial to note that according to this proposal, each mechanism could be directly tied to its respective memory system and may be associated with certain neural correlates and strategies at encoding. While this assumption facilitates ease of interpretation at this stage, the distinction between the two systems will be considered in more detail in section *5.2.4.3.* Nevertheless, to explore this initial proposal further, the implicit prediction mechanism will first be introduced, followed by a discussion of the potential explicit mechanism.

5.2.4.1. An implicit mechanism

Predictions, when viewed from a predictive coding perspective, should be constant and unconscious (for a review see A. Clark, 2013), rendering them implicit in nature (Rabovsky & McRae, 2014). As such, the implicit prediction mechanism proposed here may subscribe to the principles underlying predictive coding, such that prediction errors represent sensory information and prompt model updating (den Ouden et al., 2012; Rao & Ballard, 1999). The present findings – showing that greater N400 amplitudes were associated with increased explicit memory recognition performance for some individuals – supports the general idea that implicit prediction errors can drive adaptation. However, the conditional nature of this effect might arise because implicit prediction errors influence implicit memory (Hodapp & Rabovsky, 2021; Rabovsky & McRae, 2014), which could suggest a reduced role for such errors in explicit memory. Intuitively, it appears sensible that if an individual is unaware of their brain's

predictions, they will be unaware of the prediction error resulting from these predictions. As such, they may experience difficulty explicitly recalling the event because their conscious awareness was never drawn directly to the error-eliciting stimulus. Consequently, implicit prediction errors might primarily shape the memories that contribute to the development of unconscious knowledge and associations. However, the present results, which show a dependence of explicit memory on implicit prediction error, provide evidence for implicit learning that cascades into explicit awareness. While this relationship will be discussed further in section *5.2.4.3,* it is important to address the other aspect of this effect – specifically, that memory formation appears to occur independently of the level of implicit prediction error.

5.2.4.2. An explicit mechanism

The current body of work showed that explicit memory performance was not consistently dependent on the level of implicit prediction error, suggesting the involvement of an additional mechanism that drives memory formation independently of predictive processing. If implicit prediction errors drive implicit learning (Hodapp & Rabovsky, 2021; Rabovsky & McRae, 2014), explicit encoding mechanisms might support the development of an explicit memory. While the current work can cannot confidently speak to what these explicit mechanisms may be, prior research suggests that physically enacting the activity in question (e.g., 'lift the pen'), during learning benefits explicit memory more strongly than implicit memory (Nyberg & Nilsson, 1995). Although participants could not enact the stimuli in the present experiment, they may have used other intentional strategies during encoding that contributed to the development of an explicit memory. Furthermore, it follows that explicitly instructing participants to predict could influence memory at an explicit level. Brod and colleagues (2022) found that explicit predictions improved memory recall for highly unexpected and highly expected content. In contrast, in a condition without deliberate prediction, memory was only enhanced for highly expected information (Brod et al., 2022). Consequently, the authors proposed that "Explicit predictions might increase the subjective value of the outcome, resulting in a stronger surprise response in case of expectancy violations, which in turn triggers increased attention to the outcome" (Brod et al., 2022, p. 2200). This implies that actively predicting upcoming content may engender a memory encoding process that can contribute over and above to implicit predictions (Brod et al., 2022).

While Brod and colleagues (2022) link conscious predictions to attention, Rabovsky & McRae (2014) highlight the possibility that explicit prediction error signals are represented by later positive ERPs that are associated with updates to *working memory*. In contrast, the N400 – presumably representing implicit prediction error – might correspond to changes in long-term semantic memory (Rabovsky & McRae, 2014). In Chapter 3, the amplitude of the late positive component showed a positive correlation with memory recognition regardless of IAF. This late positive ERP was proposed as a potential P600, which was related to the explicit system due to its ties to explicit memory recognition (Contier et al., 2024), attention (Contier et al., 2022) and awareness (Batterink & Neville, 2013). In further support of the association between late positivities and explicit memory, other research proposes that the N400 reflects an automatic response, while the P600 relates to processes involving cognitive/executive control and

attention (Kolk & Chwilla, 2007; Rabovsky & McClelland, 2019). This P600-related process supposedly arises when revision of the original automatic interpretation is necessary, for example, in a garden path sentence such as '*the horse raced past the barn fell*' (Fodor & Inoue, 1994; Rabovsky & McClelland, 2019). The connection between the P600 and revision therefore provides further support for the suggestion that explicit processes might occur as an addition to implicit, automatic predictions.

Furthermore, if the P600 is an explicit correlate, its association with attention, working memory, and executive control could imply that explicit processing during encoding involves the activation of these mechanisms. This is compatible with the role of working memory in the *active* maintenance of information (at least in initial stages; for a summary see Ranganath et al., 2005). Moreover, Cowan (1999) proposes an embedded-process model of working memory, viewing working memory not as a separate system to long-term memory, but as consisting of long-term memory, an activated portion of long-term memory, and a focus of attention (for the original information processing model, see Cowan, 1988). The focus of attention is directed by a central executive system relating to voluntary processes (Cowan, 1988, 1999), and as such, this perspective unites many of the cognitive functions associated with explicit processing in the literature described so far. Returning to a discussion of ERPs, the differences between the N400 and the P600 described by Rabovsky and McClelland (2019) could explain why the effect of the late positivity on explicit memory recognition did not vary with IAF – processes relating to the P600 likely enhance memory in the explicit system. This does not exclude the possibility that high and low IAF individuals differ in their reliance on the explicit system (as discussed further in section *5.2.5*), but implies that once they engage these explicit processes, the impact on memory could be somewhat pervasive across individuals. However, to further understand this system, it is crucial to delve deeper into the observed effects concerning alpha power.

In the current research, alpha power was associated with subsequent memory outcomes (hit/miss), although this relationship was not influenced by N400 amplitude. Accordingly, it was suggested in Chapter 4 that alpha power reflects a memory encoding process that occurs independently of prediction. This can be extended by considering previous research that links the alpha rhythm to working memory, with alpha power proposed to gate the maintenance and updating of task-relevant information in the working memory system (Manza et al., 2014). If explicit memory is supported to a greater extent by working memory-related mechanisms, changes in alpha power might be more strongly associated with the engagement of the explicit system. However, in Chapter 1, alpha's links to attention and inhibition (Janssens et al., 2018; Sauseng et al., 2005) were proposed to render this activity relevant for precision, and consequently, predictive processing (Feldman & Friston, 2010). In the predictive coding field, increases in attention enhance *precision* (i.e., the inverse of variance; Feldman & Friston, 2010) and the degree of model updating (Friston, 2010; Hohwy, 2012). In light of the N400's proposed role as a precision-weighted prediction error correlate (Bornkessel-Schlesewsky & Schlesewsky 2019), it was suggested that alpha power and the N400 could be related.

Although this proposal was not supported by the present results, more recent work by Klimesch (2012), suggests that rather than directly indexing specific cognitive functions, alpha activity reflects underlying processes associated with inhibition and timing. Consequently, alpha oscillations may not correspond directly to changes in attention, and by extension, precision (Feldman & Friston, 2010; Hohwy, 2012). Alternatively, attention's optimisation of precision (Feldman & Friston, 2010) might not necessarily limit it to the implicit domain, especially given its links to the later positivities implicated in explicit learning (Contier et al., 2022; 2024). Ultimately, the independence of alpha subsequent memory effects from prediction-related correlates, and the role of later positivities in explicit prediction and learning, could suggest that this explicit system is characterised more strongly by the involvement of attention and working memory. However, it is important to note that whilst this research links neural substrates and cognitive functions to implicit and explicit memory, compartmentalizing these correlates may have certain limitations. This is particularly relevant as the current findings show an effect of the N400 on explicit memory for certain individuals, highlighting the potential challenges associated with categorizing memory into distinct systems.

5.2.3.3. On the distinction between the implicit and explicit systems

So far, predictions have been characterised as implicit and automatic, contributing to memory at a similar level. A distinction has also been drawn with more explicit forms of memory that may arise from conscious, voluntary processes occurring during learning. Although the dichotomisation of memory into implicit and explicit systems can serve to streamline research and has allowed for a unifying and accessible interpretation of the results of the present thesis up to this point, the observation that N400 amplitudes enhance explicit recognition for some individuals provides evidence for a crossover between the two systems. Indeed, given the links between attention, precision and prediction error in the literature (Feldman and Friston, 2010), it is not surprising that implicit predictions might have consequences for the explicit domain, adding complexity to the fairly simple dichotomisation that has been described thus far. Hohwy (2012) highlights how stimuli that attract attention tend to also enter conscious awareness. He suggests that "what gets selected for conscious perception is the hypothesis or model that, given the widest context, is currently most closely guided by the current (precise) prediction errors" (Hohwy, 2012, p. 5), implying that predictions (and their associated precision-weightings) can give rise to conscious perception. Moreover, Dale and colleagues (2012) examined prediction during a sequential learning task via an analysis of computer mouse movements and obtained evidence for both implicit and explicit statistical learning. The authors proposed that when patterns are detected automatically, upcoming stimuli can be anticipated, evoking error signals that prompt explicit awareness (Dale et al., 2012). With this information in mind, the effect of the N400 on explicit memory observed for some individuals could imply that implicit prediction errors entered conscious awareness, contributing to the formation of an explicit memory.

In further support of the interconnectedness between the two systems, a recent meta-analysis suggests that implicit and explicit memory *encoding* involve overlapping brain regions, whilst implicit and explicit memory *retrieval* recruit mostly separate areas (Kim, 2019). This provides

potential evidence for the involvement of shared encoding mechanisms, offering an alternative perspective to the earlier idea that implicit and explicit encoding strategies primarily foster memory within their respective systems (Kim, 2019). Moreover, based on the difficulties distinguishing and defining implicit and explicit memory, Reber (2013, p. 2027) proposes that implicit memory reflects an "emergent property of general plasticity," being universally related to all forms of behavioural adaptation, and interestingly, to statistical learning. This is highly compatible with the proposed generalisability of prediction (Huang & Rao, 2011; Kveraga et al., 2007), and with the close relationship between prediction and statistical learning (Sherman & Turk-Browne, 2020). Based on this relationship, predictions could be pervasive, extending beyond the boundaries of the traditional implicit/explicit memory divide. Furthermore, if working memory and attention are associated with activation and conscious awareness (due to the reasons described above), implicit and explicit memory may not reflect separate *systems* but may be associated with a greater or lesser degree of engagement of these mechanisms. Although traditional perspectives viewed implicit memory as being non-episodic and general (see *Table 5.1* from Rovee-Collier, 1997), prediction as an implicit process (in the traditional implicit sense) appears to contradict the proposal that prediction errors prompt pattern separation (Barron et al., 2020) and the development of an episodically detailed trace (Ngo et al., 2021). Therefore, prediction should not be reduced entirely to the implicit system, highlighting the need for further research on the relationship between prediction and this purported dichotomy.

The association between implicit and explicit memory is also reiterated by the current results pertaining to theta power. Theta rhythms have been linked to the broader memory literature (related to both working memory and episodic memory; for a review see Hsieh & Ranganath, 2014) and to research on prediction error (Cavanagh et al., 2010; Mas-Herrero & Marco-Pallarés, 2014). This places theta activity firmly at the intersection of prediction and memory processing, hence its measurement in Chapter 4 to gauge the model updating associated with prediction. In the current research, theta power alone was unrelated to subsequent memory recognition. However, a relationship was revealed when IAF and N400 amplitude were included in statistical models, supporting a less concrete boundary between implicit and explicit memory. Unlike alpha power, which did not interact with the N400 to influence memory, theta power's association with the N400 and subsequent memory in the present work may render it more relevant for the memory updating that extends beyond the implicit domain. Interestingly, a stronger relationship between theta power and the N400 during learning appeared mostly predictive of subsequent forgetting (i.e., memory misses). This potentially implies that, depending on the individual, 'too much' or 'too little' memory encoding in the face of an implicit prediction error can impair explicit memory recognition, pointing towards an optimal level of updating (as discussed in Chapter 4). Here, it is possible that explicit awareness of a violation, or of highly predictable content, becomes distracting in some way, although this proposal is merely speculative. Nevertheless, this research highlights the functional relevance of the relationship between these neural correlates for memory processing. While some studies investigate both theta and N400 activity side-by-side (e.g., Dini et al., 2022; Klimesch, Schimke, et al., 1996), this thesis provides an important first step in demonstrating a direct connection between these variables in a subsequent memory context.

In summary, the current body of work shows that explicit memory performance is both dependent on, and independent of, the level of implicit prediction error. This independence could stem from the engagement of additional explicit mechanisms that contribute over and above to the model updating resulting from implicit prediction error. Speculatively, such mechanisms might involve general attentional and/or working memory-based functions that are independent of implicit prediction. Conversely, the dependence of explicit memory on implicit prediction could arise because implicit prediction error signals reach conscious awareness. Ultimately, such a proposal emphasises the interconnectedness between implicit predictions and explicit memory, whilst suggesting that the ability to consciously recollect a memory is not entirely dependent on predictive processing. Finally, while the discussion of this dual memory mechanism has not yet directly addressed the role of individual variability, a consideration of IAF can shed further light on why these effects might differ according to individual differences that are measurable in the EEG.

5.2.5. A role for individual neural variability as measured via IAF

The current body of work revealed an important role for IAF in modulating predictive processing (Chapter 2), the relationship between the N400 and subsequent memory (Chapter 3), and the association between N400 amplitude, theta power and subsequent memory (Chapter 4). Chapters 3 and 4 in particular demonstrated a connection between the neural activity during learning and memory encoding for individuals with low IAFs, whilst for those with a high IAF, successful memory did not appear dependent on this activity. Such effects were attributed to differences in predictive processing styles, suggesting that high IAF individuals adopt a more general memory encoding strategy. However, a consideration of implicit and explicit processing may greatly extend upon, and provide a theoretical basis for, this broad notion. If the N400 is an implicit signal (Rabovsky et al., 2018; Rabovsky & McRae, 2014), the effect of the N400 on explicit memory for low IAF individuals hints at a stronger interconnectedness between the two systems. In contrast, high IAF individuals may rely more strongly on additional (and potentially explicit) prediction-independent mechanisms. This broad proposal is somewhat similar to work in the linguistic domain purporting a declarative/procedural model of language processing (Ullman, 2004). Ullman (2004) suggests that declarative memory supports lexical representations of word-specific knowledge, while procedural memory is proposed as a form of implicit memory that underpins learning of the rule-based patterns within language. Within this model, individuals purportedly vary in the extent to which they rely on either system, according to factors such as sex or age (Ullman, 2016). This brings attention to the significance of between-subject variability in influencing the dependence on each system. But why might IAF influence the connection between implicit prediction and explicit memory in the current research?

5.2.5.1. Explaining the effect of IAF from the perspective of a dual mechanism

A consideration of IAF's association with working memory (C.R. Clark et al., 2004) and attention (Zhang et al., 2021) may provide insight into the variable connections between the implicit and explicit systems observed here. Returning to an earlier discussion, explicit processes likely recruit working memory and attention. Interestingly, IAF has been positively

related to working memory ability (C.R. Clark et al., 2004) and to attention (Zhang et al., 2021). Consequently, those with a high IAF could employ a stronger working memory- or attention-based strategy during learning that gives rise to the development of an explicit memory. This may explain the associations between high IAF and better memory performance that have been observed in studies employing tests of explicit memory (e.g., Klimesch et al., 1990, 1993). It is also congruent with the present findings, where IAF and hit rate exhibited a weak but significant positive correlation, suggesting that high IAF individuals demonstrate enhanced explicit memory performance as compared to their low IAF counterparts. On the other hand, if low IAF individuals' working memory and attentional abilities are reduced (C.R. Clark et al., 2004; Zhang et al., 2021), their engagement of additional explicit processes may be impaired, leading them to rely more heavily on implicit prediction errors for memory formation. This is compatible with research showing that low IAF individuals' N400 amplitudes attune more strongly to surprisal (Bornkessel-Schlesewsky, Sharrad, et al., 2022) and exhibit greater reductions across a language learning task (Nalaye et al., 2022). With regard to how the present effects translate to the explicit domain, it is possible that a greater reliance on implicit prediction error promotes enhanced conscious awareness of what is being predicted. Such a proposal could be empirically tested in future research by contrasting IAF with the level of self-reported prediction in an implicit prediction task. However, to understand the potential origins of these trends in more detail, it is important to delve beyond IAF's connection to working memory and attention.

Research by Samaha & Postle (2015) suggests that high IAF individuals have shorter windows of temporal perception, as they are better able to discriminate between two flashes of light shown in rapid succession, in contrast to those with a low IAF. As such, resting state-based differences in the speed of alpha oscillations were proposed to shape the way that individuals perceive information (Samaha & Postle, 2015). While the slower processing windows that accompany a low IAF could result in the merging of two temporally proximal stimuli into a single percept, one stimulus could also be processed more poorly than the other for these individuals (Samaha & Postle, 2015). Consequently, low IAF individuals may miss or merge certain information, while those with a high IAF process the external environment more thoroughly (Samaha & Postle, 2015). Based in part on this information, Bornkessel-Schlesewsky, Sharrad, and colleagues (2022) proposed that IAF reflects the resolution or quality of a sensory signal, reasoning that high IAF individuals would attribute greater precision to, and thus rely more on, bottom-up sensory signals for predictive model updating. Contrary to the authors' expectations, low IAF individuals in their study showed evidence potentially indicative of enhanced model updating (Bornkessel-Schlesewsky, Sharrad, et al., 2022). As an alternative explanation, high IAF individuals' perceptual systems might receive more content in general (especially if low IAF individuals miss or merge information; Samaha & Postle, 2015). As such, they may require mechanisms that can more readily manipulate and sort through this volume of information. This is potentially where working memory and attention come into play (especially considering attention's role in selecting the information that enters memory; Chun & Turk-Browne, 2007). On the other hand, low IAF individuals' perceptual systems might receive less information, and as such, these individuals can "fall back" on the implicit system without activating additional explicit processes (for a schematic

of this relationship see *Figure 5.2*). Ultimately, the variability surrounding the relationship between prediction error and memory encoding observed in the present work might arise from trait-like discrepancies in the quality of sensory sampling.

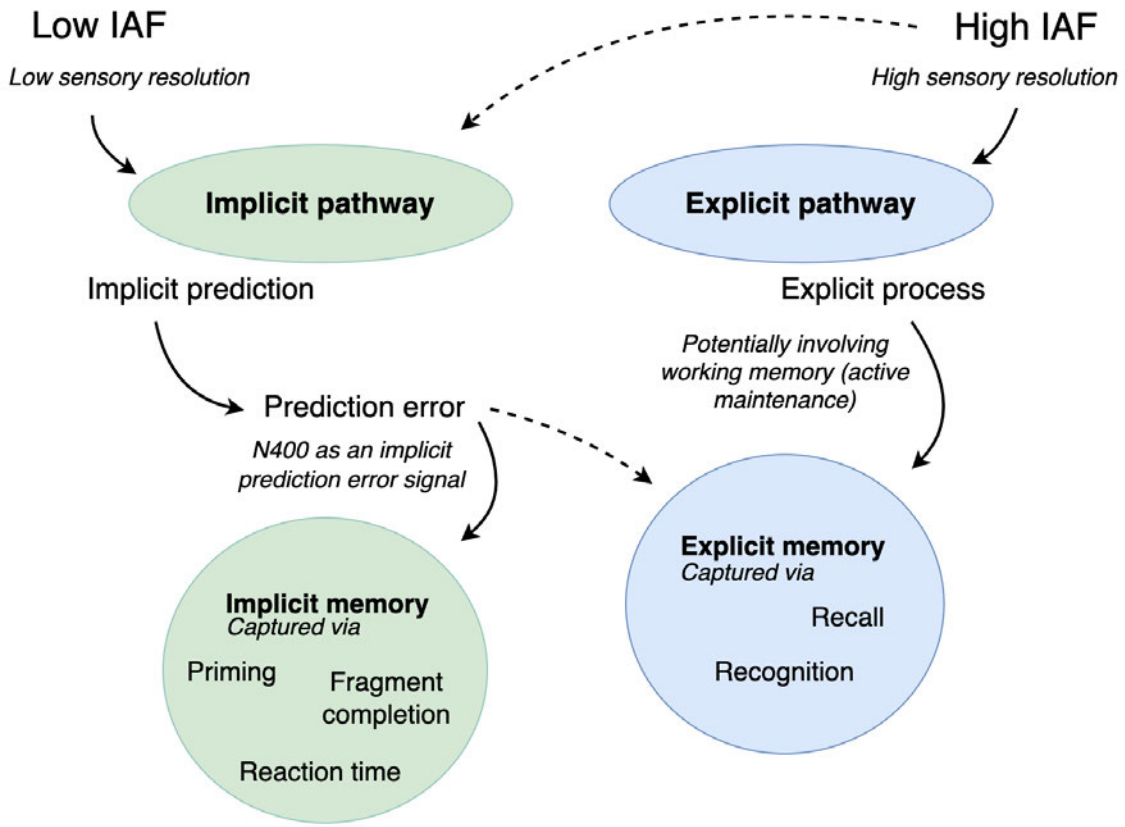


Figure 5.2. *Schematic of the proposed relationship between prediction, individual alpha frequency (IAF) and memory. Low IAF individuals may favour an implicit learning pathway that comprises the process of prediction. These predictions, when violated, result in implicit prediction error signals that drive learning primarily in the implicit domain. However, this learning also has indirect consequences for explicit memory, indicated via the dashed line from 'prediction error.' On the other hand, individuals with a high IAF, due to their enhanced working memory capacity, may engage prediction-independent explicit memory mechanisms more frequently, resulting in memory encoding at a more explicit level that contributes over and above to the learning associated with implicit predictions (with the potential engagement of this implicit system indicated via the dashed line stemming from 'high IAF'). Additionally, while their engagement of an additional explicit mechanism could influence implicit memory, the present thesis could not probe this directly and as such, the current model does not make assumptions about this relationship.*

To further build upon the notion of the implicit system as a fallback mechanism, traditional research has regarded the implicit system as the developmentally older system (for a summary see Parkin in Lewandowsky et al., 1989; though see Rovee-Collier, 1997, for an alternative perspective). Moreover, Vöhringer and colleagues (2018) conducted a longitudinal study of young children and found no increases in implicit memory performance with age, suggesting that implicit memory remains relatively stable. This stability is also supported by research

which demonstrates greater performance declines on explicit versus implicit memory tasks with older age (Davis et al., 2001; Fleischman et al., 2004). Similarly, IAF increases from childhood to young adulthood and subsequently decreases into old age (for a review, see Klimesch, 1999). This somewhat mirrors the change in explicit memory performance described above, further reiterating the connection between a low IAF and reduced engagement of the explicit system. Such a proposal would require empirical testing, for example, with a longitudinal study that contrasts changes in IAF with performance on implicit and explicit memory tasks across the lifespan. Based on the current proposal, intraindividual shifts in IAF across the lifespan should correlate with changes in explicit memory performance. Therefore, despite the need for further testing, it may be more appropriate to describe the present effects relating to IAF less in terms of a reliance on one system over the other, but more so with regard to the degree of reliance on prediction-independent *explicit* processes.

To summarise, implicit prediction errors may promote explicit memory formation for low IAF individuals. Conversely, whilst high IAF individuals might still rely on implicit prediction error signals for updating to an extent, exposure to a greater deal of sensory information could prompt stronger working memory- and attention-based processes that contribute to memory uptake in a manner that is less dependent on unconscious predictive processing (the broader implications of which will be discussed further in section 5.4). Moreover, although the present discussion rests heavily on a dual mechanism, the above interpretations assume that this prediction-independent mechanism arises from more explicit mechanisms during encoding. However, future investigations may benefit from testing this suggestion more directly in a prediction context, especially given the overlap in brain regions involved in both implicit and explicit memory encoding (Kim, 2019). Here, it is possible that high IAF individuals' stronger explicit memory recognition arises from a consolidation- or retrieval-based mechanism, as opposed to being encoding-specific. Therefore, future analyses could be supplemented with measures such as eye-tracking during both encoding and retrieval, to gauge attentional processes (Carter & Luke, 2020) and the potential involvement of the explicit system. Additionally, the present research did not probe implicit memory, although low IAF individuals might perform better in this domain than their high IAF counterparts. As such, it may be possible that neither a high nor a low IAF is inherently 'better' than the other. Rather, the advantage could depend on how memory performance is assessed. This emphasises the functional relevance of IAF as a trait-like contributor to prediction and memory processing and serves as an important foundation for further investigations into the complexity underlying this relationship. This research thus has crucial implications for understandings of prediction and beyond to real-world contexts, which will now be discussed.

5.3. Implications for the predictive coding theory

Predictive coding proposes a general strategy for brain functioning, relying on the notion that the brain applies predictions to incoming sensory information to minimise its free energy (Friston, 2010; Huang & Rao, 2011; Rao & Ballard, 1999). Prediction error is integral to this account, representing the difference between predicted and actual input (Friston, 2005). According to den Ouden and colleagues (2012), prediction errors correspond to a fundamental

computational mechanism, with the specific information that they communicate arising as a product of the neural circuitry involved in their computation. The present body of work provides support for the generalisability of prediction error, by successfully demonstrating a role for the N400 in both a linguistic and non-linguistic setting. Notably, the reanalysis of Nieuwland and colleagues' (2018) data described in Chapter 2 provided novel insight into the role of prediction in language processing, as N400 effects dependent on prior context and IAF were observed. These article-related effects imply that prediction violations concerning upcoming nouns occurred, providing stronger support for the N400 as reflecting a prediction violation as opposed to indexing meaning integration (DeLong et al., 2005). This aligns with prior studies that link the N400 to prediction error (Bornkessel-Schlesewsky & Schlesewsky, 2019; Eddine et al., 2024; Hodapp & Rabovsky, 2021; Rabovsky & McRae, 2014), emphasizing the component's relevance to the present research. Furthermore, the N400's potential relationship with meaning processing, as highlighted in previous literature (Amoruso et al., 2013; Kutas & Federmeier, 2011), reinforces the importance of its measurement in both linguistic and non-linguistic contexts. Although the current research could not confidently determine that the N400 reflects prediction error in a domain external to language, its relationship to memory encoding observed here may be compatible with prediction error as a common mechanism underlying brain functioning and learning (den Ouden et al., 2012). Moreover, it could render the N400 a marker of this general coding scheme, suggesting that future research on the N400 as a learning signal can provide fruitful insights into brain functioning and prediction more broadly. Ultimately, the trends observed throughout the current thesis support the component's proposed role as a domain-general correlate, paving the way for future N400 research that explores its association with prediction and memory in other areas.

One of the main questions arising from this research is whether the present results provide support for prediction as a generalisable mechanism (Huang & Rao, 2011; Kveraga et al., 2007). At a first glance, the dependency of linguistic prediction on individual and contextual factors (exhibited in Chapter 2) implies constraints on prediction during language processing. This suggests that the brain does not consistently predict upcoming stimuli to the level of phonological details. However, a lack of evidence for phonological prediction under certain circumstances does not necessarily exclude the potential for expectations that operate at other levels. It does however, become difficult to consolidate with hierarchical predictive processing, where the brain should generate predictions at each level of the stimulus hierarchy (Rao & Ballard, 1999). Evidence for and against phonological prediction in language was obtained via an analysis of the N400 in the present research. However, if the component does represent a precision-weighted prediction error (Bornkessel-Schlesewsky & Schlesewsky, 2019), a lack of an N400 effect could also stem from a decreased precision weighting, not the absence of a prediction; a perspective that is raised in Chapter 2. Therefore, one of the major limitations to using a prediction error signal to gauge prediction is that such effects may be confounded with the perceived relevance of the sensory signal for model updating (for a suggestion on how to overcome this, see section *5.6*). Moreover, in Chapter 2, an N400 effect at the article was not observed when the surprisal of the prior words in the sentence was low. Here, it was proposed that prior predictability confirms the prediction, resulting in greater precision being attributed

to the predictive model over the sensory information. This interpretation assumes that model precision and sensory precision have a give-or-take relationship, such that increases in model precision reduce the precision attributed to the external information. This may be probable given the opposite effect (that sensory imprecision is proposed to lead to increased weighting of the top-down model for perception; Hesselmann et al., 2010; Hohwy, 2012). However, it may be important to test this assumption more directly in the future. N400 analyses that manipulate the precision of predictive models (e.g., via feedback), but which keep the noise-level of the sensory input constant, could more directly gauge whether increases in model precision reduce the weighting of the external information for perceptual processing. Despite this need for further testing, the present thesis shows that the N400 is functionally significant for understandings of prediction in language.

Turning now to the relationship between prediction and memory, the current body of work observed an effect of the N400 on memory encoding for some individuals and not others. This could, at a first glance, imply that these individuals do not engage in prediction, questioning predictive coding as a unifying principle (Huang & Rao, 2011). However, when considering prediction as an implicit process (for discussion see Rabovsky & McRae, 2014), the present results, particularly relating to a high IAF, may not necessarily exclude the potential for predictions to be occurring. While those with a high IAF could engage more explicit working memory and attention-based mechanisms, the observed N400 effects for these individuals in Chapter 2 demonstrates a predictive capability. Therefore, the present body of work implies that high IAF individuals do at times engage in predictive processing, at least during linguistic comprehension. This points more strongly toward explicit memory as a supplementary mechanism, as detailed above. Ultimately, this thesis builds upon the universality of prediction by situating it within the framework of implicit and explicit memory processing; a proposal that relies on prior research (e.g., Contier et al., 2024; Hodapp & Rabovsky, 2024; Rabovsky et al., 2018; Rabovsky & McRae, 2014) and which has been more deeply developed here in the context of individual neural differences.

5.4. Implications for real-world functioning

The present body of work suggests that individuals may vary in their memory encoding strategies, which could result in diverse perceptions and memory representations. If high IAF individuals engage prediction-independent explicit mechanisms to manage larger amounts of sensory information, their systems may be geared more towards information uptake as opposed to energy conservation (which might be a stronger focus for those with low IAFs). Importantly, whilst the enhanced explicit memory performance observed for high IAF individuals could suggest that higher IAFs are optimal, an argument could be made wherein moderate or lower IAF values are ideal. Certainly, a running theme throughout the present thesis is that the brain cares less about accuracy, and more about redundancy reduction and free energy minimisation (Friston, 2010; Rao & Ballard, 1999). As such, whilst enhanced memory performance in an experimental context is often viewed favourably, in the real world, a balance between prediction error-driven memory updating and explicit encoding may be optimal for coping with complexity. Additionally, having a high or low IAF may offer advantages depending on the

specific context. This is supported by research by Cross, Chatburn, and colleagues (2022), who investigated dyadic team performance in the context of military-based simulation training tasks. Dyads were comprised of a commander and a gunner, with the former being the more directive role (Cross, Chatburn, et al., 2022). The authors successfully used machine learning techniques to classify participants' roles (commander or gunner) according to IAF, showing that the gunner role was associated with a higher IAF than the commander role (Cross, Chatburn, et al., 2022). It was suggested that a high IAF might be beneficial for gunners, as this may facilitate more accurate sensorimotor performance, while lower IAFs might be advantageous for commanders, allowing for the integration of content over longer temporal periods (Cross, Chatburn, et al., 2022). This supports the notion that IAF may differentially impact performance depending on the task demands (Cross, Chatburn, et al., 2022).

While the current research potentially provides evidence for differential information uptake strategies according to intrinsic neural activity, it could also serve as a potential foundation for educational research more generally. The present body of work advocates for techniques and tests that might be better tailored to account for the individual variation in implicit and explicit processing that could be occurring here. For example, low IAF individuals may enhance their explicit learning by engaging in techniques such as enactment (Nyberg & Nilsson, 1995) or conscious prediction (Brod et al., 2022) during learning. Moreover, this research has consequences for exposure to misinformation and the development of bias, particularly in today's technological climate. If individuals with a low IAF are more inclined to learn from implicit predictions, while high IAF individuals recruit a supplementary explicit mechanism, learning for those with a low IAF may primarily be tailored towards efficiency as opposed to informational accuracy. As a result, such individuals might exhibit a reduced tendency to encode information that is congruent with their predictions. While this could be adaptive, over time it could lead to gaps in knowledge or generalisations. More generally, if low IAF individuals rely more strongly on implicit memory, while high IAF individuals perform better with regard to explicit memory, tests could be tailored to better capture this learning. However, this is merely speculative, and it would be interesting for future research to investigate IAF's connection to prediction and memory in a more naturalistic learning setting, for example, in a classroom. Importantly, there are many behaviours in everyday life that can be successfully performed without conscious awareness of that knowledge (e.g., driving a manual car). As such, a reduced engagement of the explicit system may not necessarily disadvantage learning or performance, as implicit strategies can be relied upon instead.

In summary, the current work has important implications for the predictive coding theory and for real-world functioning, unifying perspectives on prediction across the domains of linguistic and visual processing, and shedding light on the factors that modulate the effect of prediction on memory formation. This PhD thesis presents several exciting possibilities for upcoming research that can enhance understandings of the interconnectedness between the past, present and future.

5.5. Challenges and future directions

The current body of work offers unique insights into the relationship between prediction and memory, fostering interesting opportunities for future exploration within this developing field. From here, a promising direction for upcoming research arises from the association between prediction, electrophysiological activity and the implicit and explicit memory systems. If memory encoding is supported by a dual mechanism – one subscribing more strongly to predictive coding principles at an unconscious level, and another operating on a more conscious level – it will be crucial for future research to conduct more targeted analyses of these purported systems (and of how they overlap) in the context of prediction. Prior research has manipulated implicit (incidental) and explicit (intentional) learning by either withholding information about an underlying sequential relationship from participants, or by informing participants of these relationships during learning, respectively (Tagarelli et al., 2011; van Abswoude et al., 2020; J. Yang & Li, 2012). However, such designs cannot speak directly to the differences between implicit and explicit *predictions*. Therefore, research that contrasts both implicit and explicit forms of prediction and memory recall, with analyses of the N400, the P600, and oscillatory activity, could be highly beneficial in verifying the claims made here concerning the two forms of learning, their relationship to prediction, and the neural correlates underpinning this association. If this distinction is relevant for prediction and memory, it will also be imperative for future research to carefully control the form of prediction engendered to ensure compatibility with research aims. Furthermore, incorporating measurements of IAF and other sources of individual variability (e.g., age or prior knowledge) into such a design could further capture the variability associated with prediction, paving the way for more applied research that acknowledges the inherent uniqueness of human experience.

Additionally, the present research highlights the utility of the N400 in gauging the neuronal fluctuations associated with prediction, with the reanalysis described in Chapter 2 providing conditional evidence for prediction during linguistic processing. However, the connection between the N400 and precision-weighted prediction error (Bornkessel-Schlesewsky & Schlesewsky, 2019) renders it difficult to confirm whether phonological predictions occurred at all times. Although this study did not provide evidence to suggest that the semantic prediction potential (SPP) reflects prediction during natural language processing, future investigations that focus on other pre-stimulus correlates (e.g., oscillatory activity; Cao et al., 2017; Mayer et al., 2016) may be beneficial in more directly capturing anticipatory processing and its effects on memory. Interestingly, this language study highlighted the iterative and developmental nature of research more generally, yielding slightly different results to the original analysis by Nieuwland and colleagues (2018) with regard to the effect of cloze probability and N400 amplitude time-locked to articles. This shows how varying EEG preprocessing and analysis techniques can produce differential outcomes, providing a crucial contribution to open science.

Regarding the studies described in Chapters 3 and 4, the subsequent memory paradigm allowed for the probing of memory for specific items, providing important insight into how predictions across longer sequences influence memory recognition. For this experiment, the number of items in the sequence was extended to more closely mirror typical sentence structure.

Therefore, continuing investigations that seek to draw parallels between prediction in language and prediction in other domains should similarly employ longer sequences. Additionally, it is important to note that whilst images in the sequences were trial-unique, the assignment of categories to predictable and unpredictable conditions, and to each position in the sequence, was not counterbalanced between participants. Therefore, observations relating to image position and condition could arise from category-specific effects, and as such, counterbalancing is recommended in the future. Future versions of this paradigm could also reduce the complexity associated with the stimuli (e.g., by using images of objects instead of natural scenes), to increase the ease at which participants can extract the information. Further, such studies may benefit from capturing confidence judgements surrounding each 'old' or 'new' response (in line with prior research e.g., Ortiz-Tudela et al., 2023; Turan et al., 2023), to mitigate the risk of guesses interfering with the results. Moreover, Brady and colleagues (2023) highlight the limitations of old/new subsequent memory paradigms more broadly, where performance is typically quantified using signal detection measures (e.g., d'; McNicol, 2004). Such measures rely on theoretical assumptions about the underlying memory distribution, which, when applied to old/new data, yield variable results (Brady et al., 2023). As such, the authors advocate for the use of forced-choice paradigms instead, involving the presentation of an old and a new stimulus side-by-side, to which participants must choose the old stimulus (Brady et al., 2023). These methods yield more consistency between memory performance measures (Brady et al., 2023), and as such, future iterations of this research (if interested in memory at the aggregate level), could benefit from the use of forced-choice tasks. However, the trial-by-trial approach in Chapter 4, where neural activity in response to a specific item was compared with later memory for that item, also circumvents limitations surrounding the use of aggregate memory performance measures. Additionally, this item-based approach increased the number of data samples, likely boosting statistical power. Although aggregate measures are heavily relied upon in the existing memory literature more generally (for a summary see *Table* 1 of Brady et al., 2023) and were used in the analyses described in Chapter 3, the subsequent item-based approach is a major strength of the present research as it served to capture subtle fluctuations in performance. Going forth, future studies could examine memory performance at both the aggregate and item-based level.

Finally, despite fluctuations in oscillatory power being informative for the present research, future investigations may benefit from examining other characteristics of the oscillatory signal. For example, other research segregates the alpha rhythm into the lower alpha band/s (~6 to 8Hz and ~8 to 10Hz) and the upper alpha band (~10 to 12Hz; Klimesch, Doppelmayer, Pachinger et al., 1997). Klimesch, Doppelmayer, Pachinger et al. (1997) employed a semantic processing task, where participants were presented with word pairs of varying semantic congruity (e.g., eagle – claws, pea – huge). The authors observed stronger upper alpha desynchronisation during the semantic task (as compared to other tasks), concluding that upper alpha is reflective of semantic processing (Klimesch, Doppelmayer, Pachinger et al., 1997). In contrast, desynchronisation in the lower alpha bands increased with task difficulty, suggesting that lower alpha relates more strongly to general attentional and task demands (Klimesch, Doppelmayer, Pachinger et al., 1997). Given that the semantic task draws on existing contextual knowledge (Klimesch, Doppelmayer, Pachinger et al., 1997), which should form the basis of predictions

(Friston, 2005), it is possible that upper alpha is more strongly related to predictive processing in the implicit system, than the lower alpha band/s.

Additionally, while increases in theta power are associated with later remembering (Klimesch, Doppelmayr, Russegger, et al., 1996; Long et al., 2014; Sederberg et al., 2003), Hasselmo and colleagues (2002) propose a *separate phases of encoding and retrieval* (SPEAR) model in which the *phase* of the theta rhythm regulates periods of memory processing. According to this model, peaks and troughs within the theta rhythm correspond to changes in the synaptic current that influence LTP (Hasselmo et al., 2002, for a review see Hasselmo & Stern, 2014). During the peak of the theta rhythm, LTP is purportedly stronger, facilitating memory encoding, while LTP is weaker during the trough, promoting memory retrieval (Hasselmo et al., 2002). Consequently, an analysis of phasic fluctuations in theta activity in future research may further elucidate theta's seemingly dynamic relationship with predictive processing and memory encoding. Furthermore, theta oscillations have proved relevant for functions external to the memory domain, for example, spatial navigation (Buzsáki, 2005) and sensoriotor integration (for a review see Bland & Oddie, 2001). Therefore, the practical relevance of such activity may extend beyond memory processing, as the continuous and dynamic nature of behaviour may require the ongoing integration of motor function with memory retrieval processes (Hasselmo, 2005). Consequently, future research may benefit from a more widespread analysis of the features that comprise oscillatory activity as a whole.

5.6. Conclusion

The present doctoral thesis sought to investigate the connection between prediction and memory processing and the neural substrates underlying this relationship. With a strong theoretical and electrophysiological foundation, this research makes an important contribution to understandings of prediction and memory by considering the uniqueness surrounding this relationship, a uniqueness that may stem from between-subject differences in intrinsic neural activity. Importantly, this research does not exclude prediction as a general coding strategy (Huang & Rao, 2011), but rather emphasises a complexity and a flexibility to this process that has not been directly tested and demonstrated in this manner before. The present thesis suggests that those with a low IAF rely on implicit prediction error signals for explicit memory encoding. On the other hand, high IAF individuals may engage additional (potentially explicit) strategies to cope with increased volumes of information, rendering the effects of prediction error on memory formation less pronounced. This is a crucial contribution to the existing literature, as it implies that individual neural factors could influence whether the memory system is oriented towards information accrual, or whether it adopts a more conservative information uptake strategy. Moreover, much of the predictive coding literature focusses on prediction's applicability to other contexts, seeking to unify cognition, perception and action within a common computational scheme (A. Clark, 2013). The current work was successful in situating prediction-related neural activity within the context of familiar (albeit somewhat controversial) dual memory systems, emphasising prediction's broader applicability to other domains and theories of brain function. In summary, the relationship between prediction and memory is complex and individually variable, but integral for understanding how humans

adapt to change and function effectively in a dynamic world. The current field is new and there remain a multitude of avenues to further explore the association between prediction and learning. However, the present doctoral thesis serves as an integral first step towards understanding how the neural substrates associated with prediction relate to learning more broadly.

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Supplementary material

Chapter 2: Supplementary material A (2A)
Model comparison tables

2A.1. *Akaike criterion (AIC) values for combined IAF and 1/f slope models, compared to separate IAF and 1/f slope models. P values reflect the comparison of the combined models' AIC and the IAF and 1/f slope models' AIC values, respectively.*

Model number	**Model outcome**	**Model type**	**AIC**	***P* value**
1	**Pre-article** SPP amplitude (-300 to 0ms)	Combined	136137	
		IAF	136133	0.92
		1/*f* slope	136136	0.16
2	**Pre-noun** SPP amplitude (-300 to 0ms)	Combined	131412	
		IAF	131409	0.75
		1/*f* slope	131410	0.45
3	**Post-article** N400 amplitude (200 to 500ms)	Combined	134668	
		IAF	134664	0.81
		1/*f* slope	134664	0.84
4	**Post-noun** N400 amplitude (200 to 500ms)	Combined	135498	
		IAF	135514	<.001
		1/*f* slope	135516	<.001

2A.2. *Results of likelihood ratio tests comparing basic model versus complex model including random slopes.*

Model number	Model type		P-value
	Basic	**Complex (with random slopes)**	
2	-65719	-65707	<.001
3	-67340	-67339	0.62
4	-67834	-67749	<.001
5	-67346	-67336	<.001
6a	-65695	-65688	<.01
6b	-65696	-65688	<.01
7	-59292	-59244	<.001

Chapter 2: Supplementary material B (2B)
Statistical model outputs

2B.1. *Model 1: SPP_amp_mean ~ cloze_scale * iaf_scale + cloze_scale * slope_scale + baseline_amp_scale + (1|subjnr) + (1|item_no), data= art_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.00	0.12	-0.23 – 0.23	0.993
cloze scale	0.06	0.13	-0.18 – 0.31	0.620
iaf scale	0.12	0.08	-0.04 – 0.28	0.157
slope scale	0.03	0.08	-0.13 – 0.19	0.696
baseline amp scale	-1.20	0.04	-1.27 – -1.12	**<0.001**
cloze scale × iaf scale	-0.03	0.08	-0.19 – 0.13	0.748
cloze scale × slope scale	-0.03	0.08	-0.19 – 0.13	0.715
Random Effects				
σ^2	28.78			
$\tau_{00\ subjnr}$	0.33			
$\tau_{00\ item_no}$	0.16			
ICC	0.02			
$N_{\ subjnr}$	312			
$N_{\ item_no}$	80			
Observations	21922			
Marginal R^2 / Conditional R^2	0.046 / 0.062			

2B.2. *Model 2: SPP_amp_mean ~ cloze_scale * iaf_scale + cloze_scale * slope_scale + baseline_amp_scale + (1+cloze_scale|subjnr) + (1+cloze_scale|item_no), data= noun_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-1.04	0.07	-1.18 – -0.90	**<0.001**
cloze scale	0.11	0.05	0.01 – 0.21	**0.038**
iaf scale	-0.01	0.05	-0.11 – 0.10	0.882
slope scale	0.04	0.05	-0.06 – 0.14	0.449
baseline amp scale	-0.54	0.04	-0.61 – -0.46	**<0.001**
cloze scale × iaf scale	-0.05	0.04	-0.12 – 0.03	0.220
cloze scale × slope scale	-0.00	0.04	-0.08 – 0.07	0.919
Random Effects				
σ^2	27.58			
$\tau_{00\ subjnr}$	0.43			
$\tau_{00\ item_no}$	0.17			
$\tau_{11\ subjnr.cloze_scale}$	0.07			
$\tau_{11\ item_no.cloze_scale}$	0.08			
$\rho_{01\ subjnr}$	-0.20			
$\rho_{01\ item_no}$	-0.16			
ICC	0.03			
N_{subjnr}	312			
N_{item_no}	80			
Observations	21282			
Marginal R^2 / Conditional R^2	0.011 / 0.037			

2B.3. *Model 3: N400_amp_mean ~ cloze_scale * iaf_scale + cloze_scale * slope_scale + prestim_scale + (1|subjnr) + (1|item_no), data= combo_art_sum*

	N400_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.33	0.07	-0.47 – -0.19	**<0.001**
cloze scale	-0.14	0.03	-0.20 – -0.07	**<0.001**
iaf scale	0.03	0.04	-0.06 – 0.11	0.561
slope scale	-0.00	0.04	-0.08 – 0.08	0.985
prestim scale	-1.71	0.03	-1.77 – -1.65	**<0.001**
cloze scale × iaf scale	0.00	0.03	-0.06 – 0.07	0.937
cloze scale × slope scale	-0.02	0.03	-0.09 – 0.04	0.512
Random Effects				
σ^2	21.95			
$\tau_{00\ subjnr}$	0.24			
$\tau_{00\ item_no}$	0.27			
ICC	0.02			
N_{subjnr}	312			
N_{item_no}	80			
Observations	22669			
Marginal R^2 / Conditional R^2	0.115 / 0.135			

2B.4. *Model 4: N400_amp_mean ~ cloze_scale * iaf_scale + cloze_scale * slope_scale + prestim_scale + (1+cloze_scale|subjnr) + (1+cloze_scale|item_no), data= combo_noun_sum*

	N400_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	1.11	0.10	0.92 – 1.31	**<0.001**
cloze scale	0.71	0.07	0.56 – 0.85	**<0.001**
iaf scale	0.15	0.07	0.01 – 0.29	**0.039**
slope scale	-0.02	0.07	-0.16 – 0.12	0.790
prestim scale	-1.97	0.03	-2.03 – -1.90	**<0.001**
cloze scale × iaf scale	-0.03	0.04	-0.11 – 0.04	0.395
cloze scale × slope scale	0.06	0.04	-0.02 – 0.13	0.127
Random Effects				
σ^2	23.47			
$\tau_{00\ subjnr}$	1.20			
$\tau_{00\ item_no}$	0.38			
$\tau_{11\ subjnr.cloze_scale}$	0.13			
$\tau_{11\ item_no.cloze_scale}$	0.30			
$\rho_{01\ subjnr}$	0.00			
$\rho_{01\ item_no}$	0.04			
ICC	0.08			
N_{subjnr}	312			
N_{item_no}	80			
Observations	22463			
Marginal R^2 / Conditional R^2	0.148 / 0.217			

2B.5. *Model 5: N400_amp_mean ~ art_s_scale * iaf_scale + art_s_scale * slope_scale + prestim_scale + (1+art_s_scale|subjnr) + (1+art_s_scale|item_no), data=combo_art_sum*

	N400_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.33	0.07	-0.47 – -0.19	**<0.001**
art s scale	-0.08	0.05	-0.18 – 0.02	0.124
iaf scale	0.02	0.04	-0.06 – 0.11	0.564
slope scale	0.00	0.04	-0.08 – 0.08	0.995
prestim scale	-1.71	0.03	-1.77 – -1.65	**<0.001**
art s scale × iaf scale	-0.02	0.04	-0.09 – 0.05	0.557
art s scale × slope scale	-0.02	0.04	-0.09 – 0.06	0.671
Random Effects				
σ^2	21.84			
$\tau_{00\ subjnr}$	0.25			
$\tau_{00\ item_no}$	0.25			
$\tau_{11\ subjnr.art_s_scale}$	0.10			
$\tau_{11\ item_no.art_s_scale}$	0.05			
$\rho_{01\ subjnr}$	-0.13			
$\rho_{01\ item_no}$	0.27			
ICC	0.03			
N_{subjnr}	312			
N_{item_no}	80			
Observations	22669			
Marginal R^2 / Conditional R^2	0.114 / 0.140			

2B.6. *Model 6a: N400_amp_mean ~ art_s_scale * a1_s_scale * a2_s_scale * slope_scale + prestim_scale + (1+art_s_scale|subjnr) + (1+art_s_scale|item_no), data=combo_art_sum*

	N400_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.34	0.07	-0.48 – -0.20	**<0.001**
art s scale	-0.07	0.05	-0.17 – 0.03	0.177
a1 s scale	0.26	0.07	0.13 – 0.39	**<0.001**
a2 s scale	0.02	0.07	-0.11 – 0.16	0.738
slope scale	0.01	0.05	-0.08 – 0.11	0.768
prestim scale	-1.72	0.03	-1.78 – -1.66	**<0.001**
art s scale × a1 s scale	0.01	0.05	-0.08 – 0.10	0.778
art s scale × a2 s scale	-0.04	0.05	-0.13 – 0.06	0.429
a1 s scale × a2 s scale	-0.04	0.08	-0.19 – 0.11	0.600
art s scale × slope scale	0.01	0.04	-0.08 – 0.09	0.881
a1 s scale × slope scale	0.01	0.04	-0.07 – 0.08	0.856
a2 s scale × slope scale	0.00	0.04	-0.08 – 0.08	0.963
(art s scale × a1 s scale) × a2 s scale	0.11	0.05	0.01 – 0.22	**0.035**
(art s scale × a1 s scale) × slope scale	-0.06	0.04	-0.13 – 0.01	0.082
(art s scale × a2 s scale) × slope scale	-0.01	0.04	-0.08 – 0.06	0.747
(a1 s scale × a2 s scale) × slope scale	0.04	0.04	-0.05 – 0.13	0.396
(art s scale × a1 s scale × a2 s scale) × slope scale	0.05	0.04	-0.03 – 0.13	0.224
Random Effects				
σ^2	21.87			

$\tau_{00\ subjnr}$	0.24
$\tau_{00\ item_no}$	0.18
$\tau_{11\ subjnr.art_s_scale}$	0.10
$\tau_{11\ item_no.art_s_scale}$	0.02
$\rho_{01\ subjnr}$	-0.14
$\rho_{01\ item_no}$	0.11
ICC	0.02
N_{subjnr}	312
N_{item_no}	78
Observations	22108
Marginal R^2 / Conditional R^2	0.120 / 0.141

2B.7. *Model 6b: N400_amp_mean ~ art_s_scale * a1_s_scale * a2_s_scale * iaf_scale + prestim_scale+ (1+art_s_scale|subjnr) + (1+art_s_scale|item_no), data=combo_art_sum*

	N400_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.34	0.07	-0.49 – -0.20	**<0.001**
art s scale	-0.07	0.05	-0.17 – 0.03	0.172
a1 s scale	0.26	0.07	0.13 – 0.39	**<0.001**
a2 s scale	0.02	0.07	-0.11 – 0.16	0.742
iaf scale	0.04	0.05	-0.06 – 0.13	0.430
prestim scale	-1.72	0.03	-1.78 – -1.66	**<0.001**
art s scale × a1 s scale	0.01	0.05	-0.08 – 0.10	0.765
art s scale × a2 s scale	-0.04	0.05	-0.13 – 0.06	0.428
a1 s scale × a2 s scale	-0.04	0.08	-0.19 – 0.11	0.592
art s scale × iaf scale	-0.04	0.04	-0.13 – 0.04	0.312
a1 s scale × iaf scale	0.04	0.04	-0.04 – 0.11	0.367
a2 s scale × iaf scale	0.03	0.04	-0.04 – 0.11	0.396
(art s scale × a1 s scale) × a2 s scale	0.11	0.05	0.01 – 0.22	**0.035**
(art s scale × a1 s scale) × iaf scale	-0.04	0.04	-0.11 – 0.03	0.292
(art s scale × a2 s scale) × iaf scale	-0.07	0.04	-0.15 – -0.00	**0.045**
(a1 s scale × a2 s scale) × iaf scale	-0.01	0.05	-0.10 – 0.08	0.839
(art s scale × a1 s scale × a2 s scale) × iaf scale	-0.04	0.04	-0.12 – 0.03	0.273
Random Effects				
σ^2	21.87			

$\tau_{00\ subjnr}$	0.24
$\tau_{00\ item_no}$	0.18
$\tau_{11\ subjnr.art_s_scale}$	0.10
$\tau_{11\ item_no.art_s_scale}$	0.02
$\rho_{01\ subjnr}$	-0.13
$\rho_{01\ item_no}$	0.10
ICC	0.02
N_{subjnr}	312
N_{item_no}	78
Observations	22108
Marginal R^2 / Conditional R^2	0.120 / 0.141

2B.8. *Model 7: N400_amp_mean ~ noun_s_scale * iaf_scale + noun_s_scale * slope_scale + prestim_scale + (1+noun_s_scale|subjnr) + (1+noun_s_scale|item_no), data= combo_noun_sum*

	N400_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	1.13	0.12	0.91 – 1.36	**<0.001**
noun s scale	-0.79	0.12	-1.03 – -0.55	**<0.001**
iaf scale	0.13	0.07	-0.01 – 0.27	0.070
slope scale	-0.04	0.07	-0.18 – 0.10	0.563
prestim scale	-1.99	0.04	-2.06 – -1.92	**<0.001**
noun s scale × iaf scale	0.03	0.04	-0.05 – 0.10	0.473
noun s scale × slope scale	-0.01	0.04	-0.08 – 0.07	0.832
Random Effects				
σ^2	23.54			
$\tau_{00\ subjnr}$	1.19			
$\tau_{00\ item_no}$	0.49			
$\tau_{11\ subjnr.noun_s_scale}$	0.06			
$\tau_{11\ item_no.noun_s_scale}$	0.71			
$\rho_{01\ subjnr}$	0.01			
$\rho_{01\ item_no}$	0.33			
ICC	0.09			
N_{subjnr}	312			
N_{item_no}	78			
Observations	19635			
Marginal R^2 / Conditional R^2	0.149 / 0.229			

Chapter 2: Supplementary material C (2C)
Statistical outputs of SPP models with surprisal

2C.1. *Model 1b: SPP_amp_mean ~ cloze_scale * iaf_scale + cloze_scale * slope_scale + a1_s_scale + baseline_amp_scale + (1|subjnr) + (1|item_no), data= art_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.00	0.12	-0.24 – 0.23	0.987
cloze scale	0.06	0.13	-0.19 – 0.31	0.619
iaf scale	0.12	0.08	-0.04 – 0.28	0.157
slope scale	0.03	0.08	-0.13 – 0.19	0.696
a1 s scale	0.00	0.06	-0.11 – 0.12	0.942
baseline amp scale	-1.20	0.04	-1.27 – -1.12	**<0.001**
cloze scale × iaf scale	-0.03	0.08	-0.19 – 0.13	0.748
cloze scale × slope scale	-0.03	0.08	-0.19 – 0.13	0.715
Random Effects				
σ^2	28.78			
$\tau_{00\ subjnr}$	0.33			
$\tau_{00\ item_no}$	0.16			
ICC	0.02			
$N_{\ subjnr}$	312			
$N_{\ item_no}$	80			
Observations	21922			
Marginal R^2 / Conditional R^2	0.046 / 0.062			

2C.2. *Model 1a_surp: SPP_amp_mean ~ art_s_scale * iaf_scale + art_s_scale * slope_scale + baseline_amp_scale + (1|subjnr) + (1|item_no), data= art_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	0.05	0.07	-0.08 – 0.18	0.494
art s scale	-0.03	0.06	-0.16 – 0.09	0.590
iaf scale	0.10	0.05	-0.00 – 0.20	0.054
slope scale	0.01	0.05	-0.09 – 0.11	0.875
baseline amp scale	-1.20	0.04	-1.27 – -1.12	**<0.001**
art s scale × iaf scale	0.03	0.04	-0.05 – 0.12	0.404
art s scale × slope scale	-0.01	0.04	-0.09 – 0.07	0.843
Random Effects				
σ^2	28.78			
$\tau_{00\ subjnr}$	0.33			
$\tau_{00\ item_no}$	0.16			
ICC	0.02			
N_{subjnr}	312			
N_{item_no}	80			
Observations	21922			
Marginal R^2 / Conditional R^2	0.046 / 0.062			

2C.3. *Model 1c_slope: SPP_amp_mean ~ art_s_scale * a1_s_scale * a2_s_scale * slope_scale + baseline_amp_scale + (1+art_s_scale|subjnr) + (1|item_no), data= art_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.01	0.08	-0.17 – 0.15	0.897
art s scale	-0.04	0.08	-0.19 – 0.11	0.576
a1 s scale	0.00	0.07	-0.14 – 0.15	0.975
a2 s scale	-0.04	0.07	-0.18 – 0.11	0.614
slope scale	0.01	0.06	-0.10 – 0.12	0.880
baseline amp scale	-1.19	0.04	-1.26 – -1.12	**<0.001**
art s scale × a1 s scale	-0.02	0.07	-0.17 – 0.12	0.768
art s scale × a2 s scale	-0.04	0.08	-0.21 – 0.12	0.600
a1 s scale × a2 s scale	-0.17	0.09	-0.34 – 0.00	0.051
art s scale × slope scale	-0.03	0.05	-0.13 – 0.06	0.488
a1 s scale × slope scale	0.03	0.05	-0.07 – 0.12	0.580
a2 s scale × slope scale	0.01	0.05	-0.08 – 0.10	0.786
(art s scale × a1 s scale) × a2 s scale	-0.00	0.10	-0.19 – 0.18	0.963
(art s scale × a1 s scale) × slope scale	-0.04	0.05	-0.13 – 0.05	0.419
(art s scale × a2 s scale) × slope scale	-0.01	0.05	-0.11 – 0.09	0.843
(a1 s scale × a2 s scale) × slope scale	0.02	0.05	-0.08 – 0.13	0.690
(art s scale × a1 s scale × a2 s scale) × slope scale	-0.04	0.06	-0.15 – 0.08	0.544

Random Effects

σ^2	28.57
$\tau_{00\ subjnr}$	0.36
$\tau_{00\ item_no}$	0.16
$\tau_{11\ subjnr.art_s_scale}$	0.04
$\rho_{01\ subjnr}$	0.27
ICC	0.02
N_{subjnr}	312
N_{item_no}	78
Observations	21379
Marginal R^2 / Conditional R^2	0.047 / 0.065

2C.4. *Model 1c_iaf: SPP_amp_mean ~ art_s_scale * a1_s_scale * a2_s_scale * slope_scale + baseline_amp_scale + (1+art_s_scale|subjnr) + (1|item_no), data= art_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.01	0.08	-0.17 – 0.14	0.871
art s scale	-0.04	0.08	-0.19 – 0.11	0.590
a1 s scale	-0.00	0.07	-0.15 – 0.14	0.996
a2 s scale	-0.04	0.07	-0.18 – 0.11	0.603
iaf scale	0.14	0.06	0.03 – 0.25	**0.014**
baseline amp scale	-1.19	0.04	-1.26 – -1.12	**<0.001**
art s scale × a1 s scale	-0.02	0.07	-0.16 – 0.13	0.799
art s scale × a2 s scale	-0.04	0.08	-0.21 – 0.12	0.623
a1 s scale × a2 s scale	-0.17	0.09	-0.34 – -0.00	**0.048**
art s scale × iaf scale	0.03	0.05	-0.07 – 0.12	0.585
a1 s scale × iaf scale	0.10	0.05	0.01 – 0.19	**0.031**
a2 s scale × iaf scale	0.01	0.05	-0.09 – 0.10	0.891
(art s scale × a1 s scale) × a2 s scale	-0.00	0.10	-0.19 – 0.19	0.988
(art s scale × a1 s scale) × iaf scale	-0.07	0.05	-0.17 – 0.02	0.118
(art s scale × a2 s scale) × iaf scale	-0.08	0.05	-0.18 – 0.03	0.152
(a1 s scale × a2 s scale) × iaf scale	0.06	0.05	-0.05 – 0.17	0.269
(art s scale × a1 s scale × a2 s scale) × iaf scale	0.03	0.06	-0.08 – 0.15	0.571
Random Effects				
σ^2	28.56			

$\tau_{00\ subjnr}$	0.35
$\tau_{00\ item_no}$	0.16
$\tau_{11\ subjnr.art_s_scale}$	0.04
$\rho_{01\ subjnr}$	0.24
ICC	0.02
N_{subjnr}	312
N_{item_no}	78
Observations	21379
Marginal R^2 / Conditional R^2	0.047 / 0.065

2C.5. *Model 2b: SPP_amp_mean ~ cloze_scale * iaf_scale + cloze_scale * slope_scale + baseline_amp_scale + art_s_scale + (1|subjnr) + (1+cloze_scale|item_no), data= noun_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-1.04	0.07	-1.18 – -0.90	**<0.001**
cloze scale	0.11	0.05	0.01 – 0.20	**0.030**
iaf scale	-0.01	0.05	-0.11 – 0.10	0.872
slope scale	0.04	0.05	-0.06 – 0.14	0.450
baseline amp scale	-0.54	0.04	-0.61 – -0.46	**<0.001**
art s scale	0.03	0.05	-0.07 – 0.14	0.558
cloze scale × iaf scale	-0.05	0.04	-0.12 – 0.02	0.199
cloze scale × slope scale	-0.00	0.04	-0.07 – 0.07	0.974
Random Effects				
σ^2	27.66			
$\tau_{00\ subjnr}$	0.43			
$\tau_{00\ item_no}$	0.17			
$\tau_{11\ item_no.cloze_scale}$	0.08			
$\rho_{01\ item_no}$	-0.18			
ICC	0.02			
N_{subjnr}	312			
N_{item_no}	80			
Observations	21282			
Marginal R^2 / Conditional R^2	0.011 / 0.035			

2C.6. *Model 2a_surp: SPP_amp_mean ~ noun_s_scale * iaf_scale + noun_s_scale * slope_scale + baseline_amp_scale + (1|subjnr) + (1+noun_s_scale|item_no), data= noun_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-0.98	0.07	-1.13 – -0.84	**<0.001**
noun s scale	-0.16	0.06	-0.28 – -0.04	**0.009**
iaf scale	-0.00	0.05	-0.11 – 0.10	0.956
slope scale	0.07	0.05	-0.03 – 0.18	0.174
baseline amp scale	-0.54	0.04	-0.61 – -0.46	**<0.001**
noun s scale × iaf scale	-0.01	0.04	-0.08 – 0.07	0.891
noun s scale × slope scale	0.05	0.04	-0.03 – 0.13	0.220
Random Effects				
σ^2	27.61			
$\tau_{00\ subjnr}$	0.42			
$\tau_{00\ item_no}$	0.17			
$\tau_{11\ item_no.noun_s_scale}$	0.07			
$\rho_{01\ item_no}$	0.09			
ICC	0.02			
N_{subjnr}	312			
N_{item_no}	78			
Observations	18622			
Marginal R^2 / Conditional R^2	0.011 / 0.034			

2C.7. *Model 2c_slope: SPP_amp_mean ~ noun_s_scale * art_s_scale * a1_s_scale * slope_scale + baseline_amp_scale + (1|subjnr) + (1+noun_s_scale|item_no), data= noun_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-1.01	0.07	-1.15 – -0.87	**<0.001**
noun s scale	-0.18	0.06	-0.30 – -0.05	**0.005**
art s scale	0.00	0.06	-0.11 – 0.11	0.996
a1 s scale	0.08	0.07	-0.06 – 0.21	0.262
slope scale	0.07	0.05	-0.03 – 0.18	0.181
baseline amp scale	-0.53	0.04	-0.61 – -0.46	**<0.001**
noun s scale × art s scale	-0.08	0.07	-0.21 – 0.05	0.229
noun s scale × a1 s scale	-0.06	0.07	-0.19 – 0.08	0.414
art s scale × a1 s scale	0.10	0.06	-0.01 – 0.21	0.063
noun s scale × slope scale	0.04	0.04	-0.04 – 0.12	0.350
art s scale × slope scale	-0.02	0.04	-0.10 – 0.06	0.697
a1 s scale × slope scale	0.05	0.04	-0.04 – 0.13	0.253
(noun s scale × art s scale) × a1 s scale	-0.04	0.07	-0.18 – 0.11	0.598
(noun s scale × art s scale) × slope scale	-0.01	0.04	-0.10 – 0.07	0.803
(noun s scale × a1 s scale) × slope scale	-0.05	0.05	-0.14 – 0.03	0.231
(art s scale × a1 s scale) × slope scale	-0.01	0.04	-0.10 – 0.07	0.727
(noun s scale × art s scale × a1 s scale) × slope scale	0.03	0.05	-0.07 – 0.13	0.505

Random Effects

σ^2	27.62
$\tau_{00\ subjnr}$	0.41
$\tau_{00\ item_no}$	0.15
$\tau_{11\ item_no.noun_s_scale}$	0.08
$\rho_{01\ item_no}$	0.17
ICC	0.02
$N_{\ subjnr}$	312
$N_{\ item_no}$	78
Observations	18622
Marginal R^2 / Conditional R^2	0.012 / 0.035

2C.8. *Model 2c_iaf: SPP_amp_mean ~ noun_s_scale * art_s_scale * a1_s_scale * iaf_scale + baseline_amp_scale + (1|subjnr) + (1+noun_s_scale|item_no), data= noun_locs_sum*

	SPP_amp_mean			
Predictors	*Estimates*	*std. Error*	*CI (95%)*	*p*
(Intercept)	-1.01	0.07	-1.16 – -0.87	**<0.001**
noun s scale	-0.18	0.06	-0.30 – -0.05	**0.005**
art s scale	0.00	0.06	-0.11 – 0.11	0.976
a1 s scale	0.08	0.07	-0.06 – 0.21	0.270
iaf scale	-0.01	0.05	-0.12 – 0.09	0.799
baseline amp scale	-0.54	0.04	-0.61 – -0.46	**<0.001**
noun s scale × art s scale	-0.08	0.07	-0.21 – 0.05	0.229
noun s scale × a1 s scale	-0.06	0.07	-0.19 – 0.08	0.418
art s scale × a1 s scale	0.10	0.06	-0.01 – 0.21	0.063
noun s scale × iaf scale	0.00	0.04	-0.08 – 0.08	0.981
art s scale × iaf scale	-0.01	0.04	-0.09 – 0.08	0.880
a1 s scale × iaf scale	-0.05	0.04	-0.13 – 0.04	0.294
(noun s scale × art s scale) × a1 s scale	-0.04	0.07	-0.19 – 0.11	0.596
(noun s scale × art s scale) × iaf scale	0.04	0.04	-0.05 – 0.13	0.362
(noun s scale × a1 s scale) × iaf scale	0.06	0.05	-0.03 – 0.15	0.209
(art s scale × a1 s scale) × iaf scale	0.02	0.04	-0.06 – 0.10	0.603
(noun s scale × art s scale × a1 s scale) × iaf scale	-0.04	0.05	-0.14 – 0.06	0.467

Random Effects

σ^2	27.62
$\tau_{00\ subjnr}$	0.42
$\tau_{00\ item_no}$	0.15
$\tau_{11\ item_no.noun_s_scale}$	0.08
$\rho_{01\ item_no}$	0.16
ICC	0.02
N_{subjnr}	312
N_{item_no}	78
Observations	18622
Marginal R^2 / Conditional R^2	0.012 / 0.035

Chapter 2: Supplementary material D (2D)

Exploratory Bayesian sensitivity analyses

2D. To further quantify the magnitude of the effect of cloze probability on SPP amplitude, two Bayesian sensitivity analyses were conducted using the *brms* package in *R*, which is based on the Stan programming language (Bürkner, 2017). The first model tested the effect of article cloze on pre-article SPP amplitude, while the second model tested the effect of noun cloze on pre-noun SPP amplitude. The basic model structure of the models of interest (M_1) is presented below:

```
SPP_amp_mean ~ c_cloze + baseline_amp_scale + (c_cloze|subjnr) +
(c_cloze|item_no)
```

These models were compared against corresponding null models (M_0), which took the following form:

```
SPP_amp_mean ~ 1 + baseline_amp_scale + (c_cloze|subjnr) +
(c_cloze|item_no)
```

We adopted a similar strategy as detailed in Nicenboim et al. (2024; Chapter 15). Cloze probability was mean-centered, and priors for predictors (β) were assigned to a normal distribution with a mean of zero and with a range of standard deviations (from 0.5 to 10). This allowed for the manipulation of the amount of expected variance around an effect, facilitating the computation of multiple Bayes factors. The settings for the remaining priors were based on Nicenboim et al.'s (2020) uninformative priors. This decision was based on the limited availability of information from existing SPP studies, which predominantly employ t-tests or ANOVAs. The specifications for priors not relating to predictors (β) in *brms* for all models were as follows:

```
other_priors <- c(
  prior(normal(0, 10), class = Intercept),
  prior(normal(0, 10), class = sigma),
  prior(normal(0, 10), class = sd),
  prior(lkj(2), class = cor))
```

Sensitivity analyses yield Bayes factors indicating the amount of evidence for or against the effects, with a Bayes factor below one ($BF_{10} < 1$) representing evidence in favour of M_0, and a Bayes factor above one ($BF_{10} > 1$) reflecting evidence for M_1 (Nicenboim et al., 2024; Chapter 15).

Results

Article results

The analysis at the article yielded divergent transitions, which may be reflective of poor model fit. To combat this, the priors were adjusted based on Nicenboim et al. (2024; see below).

However, these priors also led to divergent transitions. Therefore, whilst we present the results of the sensitivity analysis with the uninformative priors here, it is recommended that such results be interpreted with caution (see *Figure 1*).

```
priors1 <- c(
  prior(normal(2, 5), class = Intercept),
  prior(normal(10, 5), class = sigma),
  prior(normal(0, 2), class = sd),
  prior(lkj(4), class = cor)
)
```

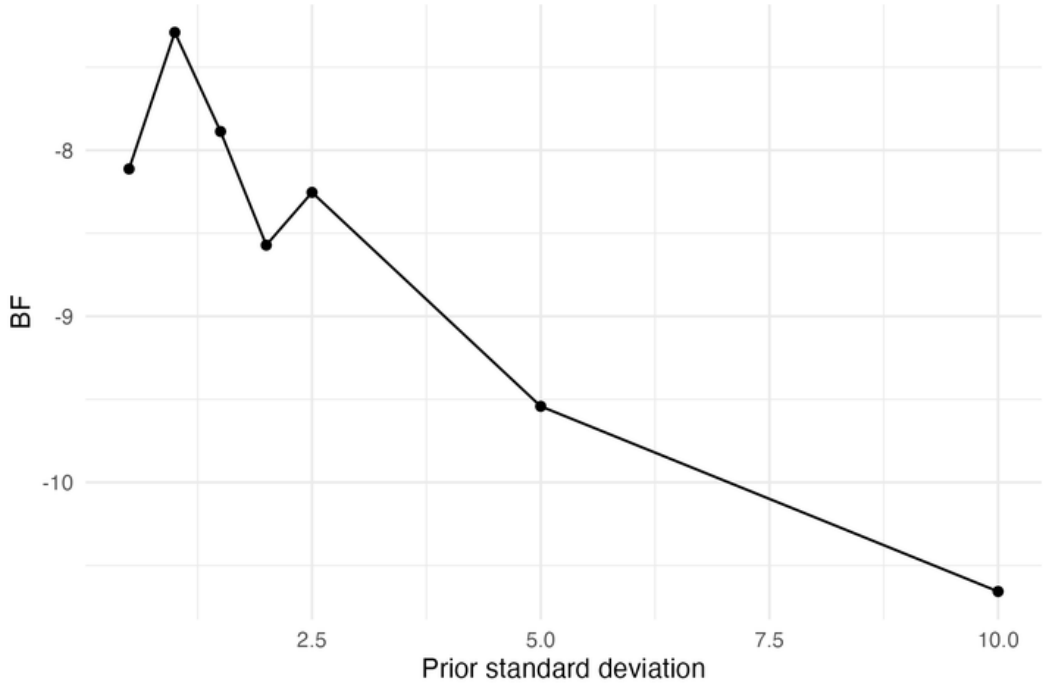


Figure 1.
Bayesian sensitivity analysis of the effect of article cloze probability on SPP amplitude preceding the articles. Bayes factors (log transformed) are presented on the Y axis, which are plotted according to each prior standard deviation for the predictor (β; cloze probability).

Noun results
In contrast to the article results, the sensitivity analysis at the noun with the uninformative priors ran successfully, revealing Bayes factors below 1 for all prior standard deviations (see *Figure 1* below). This suggests stronger evidence for the null model (M_0) over M_1, providing evidence against an effect of noun cloze on pre-noun SPP amplitude.

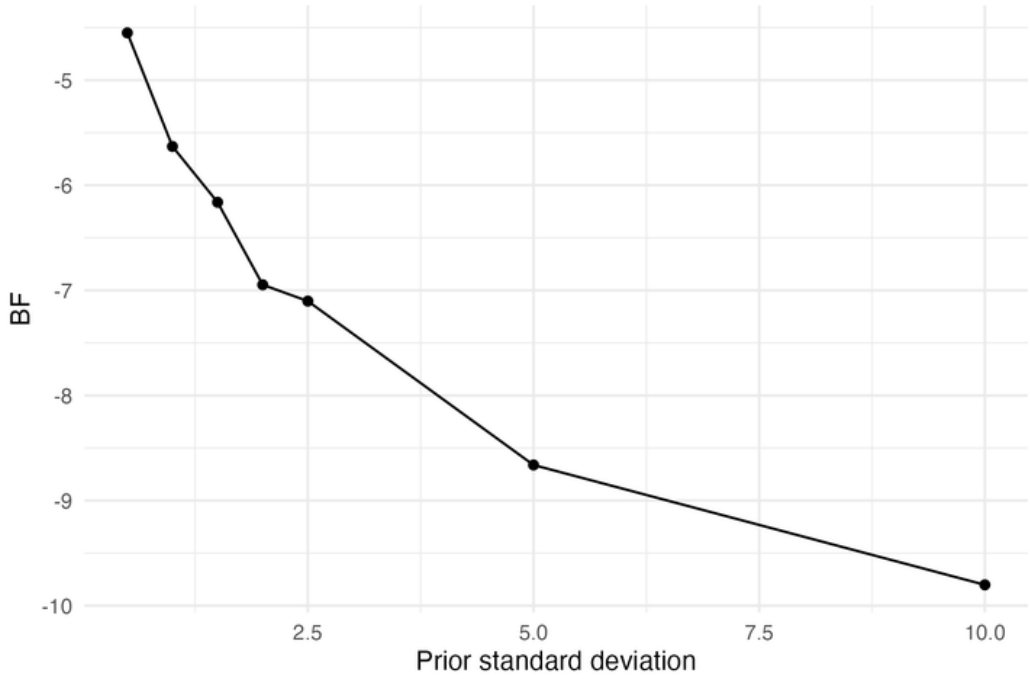


Figure 2.
Bayesian sensitivity analysis of the effect of noun cloze probability on SPP amplitude preceding the nouns. Bayes factors (log transformed) are presented on the Y axis, which are plotted according to each prior standard deviation for the predictor (β; cloze probability).

Chapter 3: Supplementary material A (3A)

Statistical model outputs

*3A.1. Model 1: dprime ~ condition * cog_scale + condition * slope_scale + (1|subjnr), data= behav_indiv*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: dprime
                      Chisq Df Pr(>Chisq)
condition             4.4970  1    0.03395 *
cog_scale             0.6893  1    0.40641
slope_scale           1.1125  1    0.29154
condition:cog_scale   1.5425  1    0.21425
condition:slope_scale 2.9956  1    0.08349 .
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC    |   AICc |    BIC | R2 (cond.) | R2 (marg.) |   ICC |  RMSE |
Sigma
-------------------------------------------------------------------------
---
55.397 | 57.132 | 75.571 |      0.351 |      0.095 | 0.282 | 0.192 |
0.225
```

*3A.2. Model 2: dprime ~ imagetype * cog_scale + imagetype * slope_scale + (1|subjnr), data= behav_indiv*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: dprime
                        Chisq Df Pr(>Chisq)
imagetype             50.9653  4   2.27e-10 ***
cog_scale              2.1886  1     0.1390
slope_scale            0.0878  1     0.7670
imagetype:cog_scale    3.7278  4     0.4441
imagetype:slope_scale  4.1881  4     0.3811
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC     |    AICc |     BIC | R2 (cond.) | R2 (marg.) |   ICC |  RMSE |
Sigma
-------------------------------------------------------------------------
------
313.484 | 316.371 | 371.931 |      0.250 |      0.199 | 0.063 | 0.364 |
0.386
```

*3A.3. Model 3: N400amp_mean ~ sag. * lat. + prestim_amp_scale + (1|subjnr) + (1|item_no), data= N4_small*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: N400amp_mean
                     Chisq Df Pr(>Chisq)
sag.              12210.07  2  < 2.2e-16 ***
lat.                800.35  2  < 2.2e-16 ***
prestim_amp_scale  9897.59  1  < 2.2e-16 ***
sag.:lat.           175.24  4  < 2.2e-16 ***

---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
2.035e+05 | 2.035e+05 | 2.036e+05 |      0.585 |      0.533 | 0.113 |
2.569 | 2.574
```

*3A.4. Model 4: N400amp_mean ~ condition * position + prestim_amp_scale + (1|subjnr) + (1|item_no), data= N4_region_sum*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: N400amp_mean
                      Chisq Df Pr(>Chisq)
condition             1.7119  1     0.1907
position             21.2828  3  9.196e-05 ***
prestim_amp_scale  3039.1971  1  < 2.2e-16 ***
condition:position    3.0227  3     0.3881
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
95701.969 | 95701.986 | 95795.389 |      0.229 |      0.141 | 0.103 |
3.538 | 3.548
```

*3A.5. Model 5: dprime ~ condition * position * N400amp_scale * cog_scale + prestim_amp_scale + (1+condition|subjnr), data= N4_region_small*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: dprime
                                              Chisq Df Pr(>Chisq)
condition                                    4.5271  1   0.033361 *
position                                    36.5846  3  5.633e-08 ***
N400amp_scale                                5.9736  1   0.014522 *
cog_scale                                    5.5366  1   0.018622 *
prestim_amp_scale                            1.4208  1   0.233264
condition:position                          41.0432  3  6.403e-09 ***
condition:N400amp_scale                      0.0159  1   0.899565
position:N400amp_scale                       1.9143  3   0.590392
condition:cog_scale                          0.2071  1   0.649035
position:cog_scale                           2.8871  3   0.409360
N400amp_scale:cog_scale                      7.5882  1   0.005875 **
condition:position:N400amp_scale             1.6228  3   0.654224
condition:position:cog_scale                 2.6895  3   0.442015
condition:N400amp_scale:cog_scale            2.5164  1   0.112671
position:N400amp_scale:cog_scale             0.2516  3   0.968850
condition:position:N400amp_scale:cog_scale   0.2615  3   0.967096
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC     |    AICc |     BIC | R2 (cond.) | R2 (marg.) |   ICC |  RMSE |
Sigma
-------------------------------------------------------------------------
------
459.242 | 467.763 | 603.841 |      0.466 |      0.198 | 0.334 | 0.263 |
0.297
```

*3A.6. Model 5.2: dprime~ condition * position * N400amp_scale * slope_scale + prestim_amp_scale + (1+condition|subjnr), data= N4_region_small*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: dprime
                                                Chisq Df Pr(>Chisq)
condition                                      5.1646  1    0.02305 *
position                                      38.5385  3  2.174e-08 ***
N400amp_scale                                  5.0417  1    0.02474 *
slope_scale                                    1.3963  1    0.23734
prestim_amp_scale                              1.5373  1    0.21501
condition:position                            43.7228  3  1.728e-09 ***
condition:N400amp_scale                        0.2257  1    0.63477
position:N400amp_scale                         1.7015  3    0.63661
condition:slope_scale                          2.2678  1    0.13209
position:slope_scale                           0.9144  3    0.82195
N400amp_scale:slope_scale                      0.1615  1    0.68776
condition:position:N400amp_scale               1.2515  3    0.74067
condition:position:slope_scale                 1.2471  3    0.74174
condition:N400amp_scale:slope_scale            0.0172  1    0.89564
position:N400amp_scale:slope_scale             1.1464  3    0.76587
condition:position:N400amp_scale:slope_scale   1.3827  3    0.70960
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC     |    AICc |     BIC | R2 (cond.) | R2 (marg.) |   ICC |  RMSE |
Sigma
-------------------------------------------------------------------------
------
478.487 | 486.614 | 624.661 |      0.473 |      0.178 | 0.358 | 0.258 |
0.294
```

*3A.7. Model 6: LPCamp_mean ~ sag. * lat. + prestim_amp_scale + (1|subjnr) + (1|item_no), data= LPC_small*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: LPCamp_mean
                     Chisq Df Pr(>Chisq)
sag.              10633.66  2  < 2.2e-16 ***
lat.                515.13  2  < 2.2e-16 ***
prestim_amp_scale 25087.56  1  < 2.2e-16 ***
sag.:lat.           156.53  4  < 2.2e-16 ***
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
1.889e+05 | 1.889e+05 | 1.890e+05 |      0.423 |      0.377 | 0.073 |
2.171 | 2.174
```

*3A.8. Model 7: LPCamp_mean ~ condition * position + prestim_amp_scale + (1+condition|subjnr) + (1|item_no), data= LPC_region_sum*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: LPCamp_mean
                        Chisq Df Pr(>Chisq)
condition              0.5444  1    0.46063
position              27.3080  3  5.074e-06 ***
prestim_amp_scale  14056.6948  1  < 2.2e-16 ***
condition:position     8.3177  3    0.03988 *
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
90797.889 | 90797.912 | 90906.878 |      0.479 |      0.442 | 0.065 |
3.089 | 3.095
```

*3A.9. Model 8: dprime ~ condition * position * LPCamp_scale + prestim_amp_scale + (1+condition|subjnr), data= LPC_region_small*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: dprime
                                 Chisq Df Pr(>Chisq)
condition                       5.2725  1    0.02166 *
position                       45.4632  3  7.376e-10 ***
LPCamp_scale                    4.0667  1    0.04374 *
prestim_amp_scale               2.6205  1    0.10549
condition:position             40.4966  3  8.361e-09 ***
condition:LPCamp_scale          1.6588  1    0.19777
position:LPCamp_scale           4.4041  3    0.22100
condition:position:LPCamp_scale 7.4791  3    0.05810 .
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.


# Indices of model performance

AIC     |    AICc |     BIC | R2 (cond.) | R2 (marg.) |   ICC |  RMSE |
Sigma
-------------------------------------------------------------------------
------
356.237 | 358.790 | 439.201 |      0.469 |      0.175 | 0.356 | 0.259 |
0.288
```

Chapter 4: Supplementary material A (4A)

Statistical model outputs

*4A.1 Model 1: theta_db_mean ~ condition * position * cog_scale + intask_slope_scale + (1+condition|subjnr) + (1|item_no), data= theta_sum*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: theta_db_mean
                              Chisq Df Pr(>Chisq)
condition                    0.9827  1  0.3215231
position                    18.4255  3  0.0003593 ***
cog_scale                    3.5053  1  0.0611737 .
intask_slope_scale          76.3551  1  < 2.2e-16 ***
condition:position           4.3868  3  0.2226124
condition:cog_scale          0.0092  1  0.9237765
position:cog_scale           6.2000  3  0.1022769
condition:position:cog_scale 5.0871  3  0.1655301
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.

# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
94194.456 | 94194.515 | 94365.038 |      0.032 |      0.013 | 0.020 |
3.698 | 3.706
```

*4A.2. Model 2: theta_db_mean ~ recognition * cog_scale * condition + intask_slope_scale + (1+recognition|subjnr) + (1|item_no), data= theta_sum*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: theta_db_mean
                                 Chisq Df Pr(>Chisq)
recognition                     1.9161  1    0.16629
cog_scale                       4.0538  1    0.04407 *
condition                       0.5320  1    0.46579
intask_slope_scale             81.6596  1    < 2e-16 ***
recognition:cog_scale           0.0719  1    0.78864
recognition:condition           0.1046  1    0.74640
cog_scale:condition             0.0274  1    0.86851
recognition:cog_scale:condition 0.0432  1    0.83535
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.

# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
93182.985 | 93183.010 | 93291.391 |      0.030 |      0.011 | 0.019 |
3.701 | 3.708
```

*4A.3. Model 3: theta_db_mean ~ recognition * N400_scale * cog_scale * condition + intask_slope_scale + prestim_scale + (1+condition|subjnr) + (1|item_no), data= theta_sum*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: theta_db_mean
                                            Chisq Df Pr(>Chisq)
recognition                                2.8058  1  0.0939219 .
N400_scale                                 2.0718  1  0.1500449
cog_scale                                  3.6717  1  0.0553436 .
condition                                  0.0583  1  0.8091591
intask_slope_scale                        80.9985  1  < 2.2e-16 ***
prestim_scale                             50.3693  1  1.274e-12 ***
recognition:N400_scale                     0.4787  1  0.4890038
recognition:cog_scale                      0.3663  1  0.5450136
N400_scale:cog_scale                      15.0427  1  0.0001051 ***
recognition:condition                      0.8215  1  0.3647433
N400_scale:condition                       0.7831  1  0.3761924
cog_scale:condition                        0.0237  1  0.8777489
recognition:N400_scale:cog_scale           4.2423  1  0.0394291 *
recognition:N400_scale:condition           0.0019  1  0.9654653
recognition:cog_scale:condition            0.0265  1  0.8706525
N400_scale:cog_scale:condition             1.2085  1  0.2716230
recognition:N400_scale:cog_scale:condition  0.9222  1  0.3368851
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.

# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
87842.391 | 87842.459 | 88019.293 |      0.033 |      0.015 | 0.018 |
3.622 | 3.630
```

*4A.4. Model 4: alpha_db_mean ~ position * condition * cog_scale * sag. + intask_slope_scale + (1+condition|subjnr) + (1|item_no), data= region_sum*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: alpha_db_mean
                                    Chisq Df Pr(>Chisq)
position                         818.8705  3  < 2.2e-16 ***
condition                          0.0088  1    0.92513
cog_scale                          0.1158  1    0.73366
sag.                              22.5502  2  1.269e-05 ***
intask_slope_scale                 3.3245  1    0.06825 .
position:condition                52.9300  3  1.897e-11 ***
position:cog_scale                38.7955  3  1.918e-08 ***
condition:cog_scale                0.5697  1    0.45039
position:sag.                    150.0279  6  < 2.2e-16 ***
condition:sag.                     0.2828  2    0.86816
cog_scale:sag.                    26.3612  2  1.887e-06 ***
position:condition:cog_scale       8.4154  3    0.03816 *
position:condition:sag.            8.7738  6    0.18670
position:cog_scale:sag.           15.2049  6    0.01872 *
condition:cog_scale:sag.           0.9283  2    0.62866
position:condition:cog_scale:sag.  1.1034  6    0.98139
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.

# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
2.635e+05 | 2.635e+05 | 2.640e+05 |      0.047 |      0.021 | 0.027 |
3.077 | 3.083
```

*4A.5. Model 5: alpha_db_mean ~ recognition * sag. * condition * cog_scale + intask_slope_scale + (1+condition|subjnr) + (1|item_no), data= region_sum*

```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: alpha_db_mean
                                      Chisq Df Pr(>Chisq)
recognition                          4.4307  1    0.03530 *
sag.                                22.5520  2  1.267e-05 ***
condition                            0.0021  1    0.96311
cog_scale                            0.0576  1    0.81041
intask_slope_scale                   0.0573  1    0.81078
recognition:sag.                     0.5904  2    0.74438
recognition:condition                3.7274  1    0.05353 .
sag.:condition                       0.2374  2    0.88806
recognition:cog_scale                0.5962  1    0.44005
sag.:cog_scale                      24.0406  2  6.021e-06 ***
condition:cog_scale                  0.6759  1    0.41100
recognition:sag.:condition           1.0570  2    0.58949
recognition:sag.:cog_scale           0.3053  2    0.85843
recognition:condition:cog_scale      0.1331  1    0.71523
sag.:condition:cog_scale             0.7338  2    0.69288
recognition:sag.:condition:cog_scale 0.1077  2    0.94756
---
Signif. codes:  0***, 0.001**, 0.01*, 0.05.

# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
2.618e+05 | 2.618e+05 | 2.620e+05 |      0.027 |      0.001 | 0.026 |
3.112 | 3.117
```

*4A.6. Model 6: alpha_db_mean ~ recognition * N400_scale * sag. * cog_scale * condition + prestim_scale + intask_slope_scale + (1+condition|subjnr) + (1|item_no), data= region_sum*

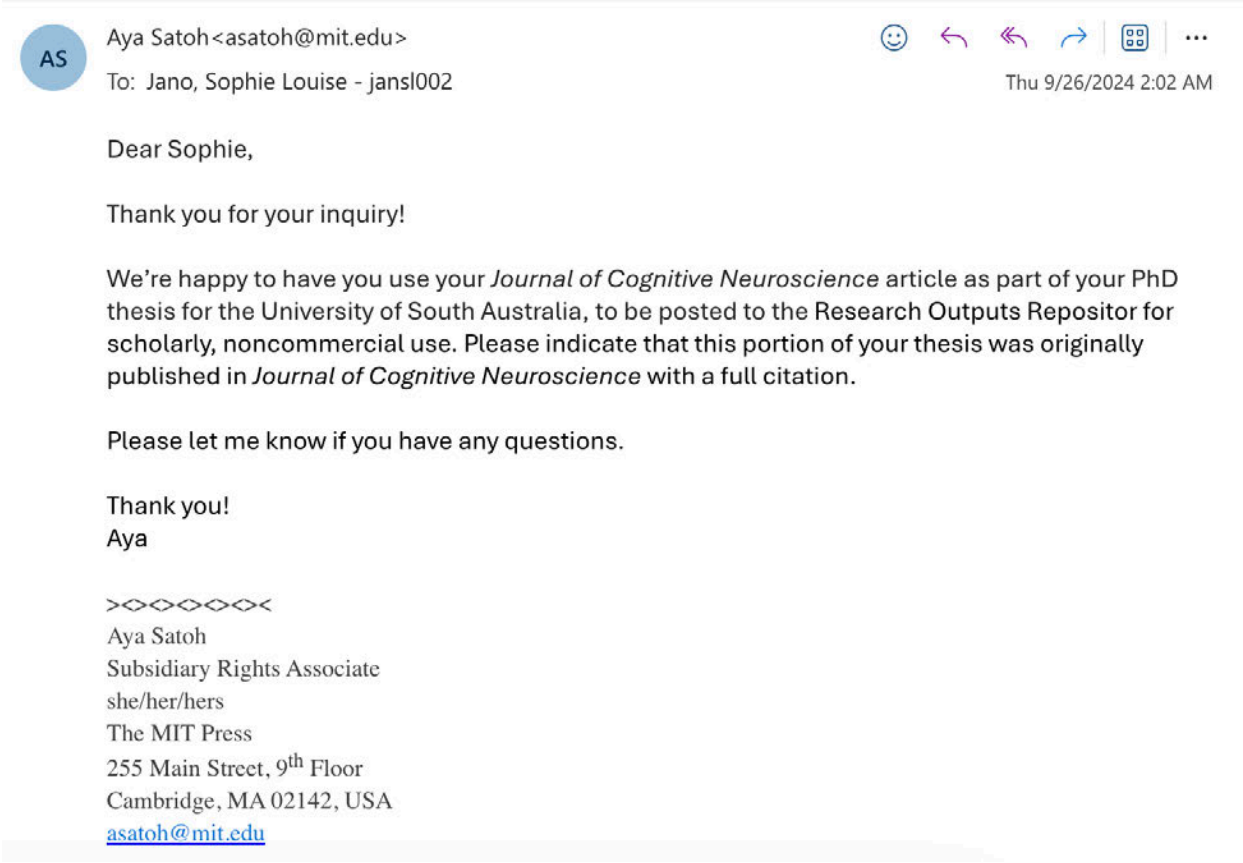
```
Analysis of Deviance Table (Type II Wald chisquare tests)

Response: alpha_db_mean
                                                  Chisq Df Pr(>Chisq)
recognition                                      6.2839  1    0.01218 *
N400_scale                                       0.1288  1    0.71966
sag.                                            20.7551 2  3.112e-05***
cog_scale                                        0.0161  1    0.89899
condition                                        0.0738  1    0.78589
prestim_scale                                   15.8839 1  6.735e-05***
intask_slope_scale                               1.2628  1    0.26112
recognition:N400_scale                           0.4087  1    0.52262
recognition:sag.                                 0.4092  2    0.81498
N400_scale:sag.                                  0.2021  2    0.90390
recognition:cog_scale                            1.0000  1    0.31730
N400_scale:cog_scale                            16.0917 1  6.035e-05***
sag.:cog_scale                                  20.7931 2  3.054e-05***
recognition:condition                            0.7711  1    0.37988
N400_scale:condition                             1.4623  1    0.22656
sag.:condition                                   0.2449  2    0.88474
cog_scale:condition                              0.6889  1    0.40654
recognition:N400_scale:sag.                      0.2311  2    0.89086
recognition:N400_scale:cog_scale                 3.7515  1    0.05276 .
recognition:sag.:cog_scale                       0.3747  2    0.82916
N400_scale:sag.:cog_scale                        3.1968  2    0.20222
recognition:N400_scale:condition                 0.4468  1    0.50384
recognition:sag.:condition                       1.1473  2    0.56346
N400_scale:sag.:condition                        1.0961  2    0.57809
recognition:cog_scale:condition                  0.0317  1    0.85879
N400_scale:cog_scale:condition                   0.0734  1    0.78650
sag.:cog_scale:condition                         0.3274  2    0.84902
recognition:N400_scale:sag.:cog_scale            1.5689  2    0.45637
recognition:N400_scale:sag.:condition            0.1864  2    0.91103
recognition:N400_scale:cog_scale:condition       0.6700  1    0.41305
recognition:sag.:cog_scale:condition             0.0277  2    0.98625
N400_scale:sag.:cog_scale:condition              1.1490  2    0.56297
recognition:N400_scale:sag.:cog_scale:condition  1.0418  2    0.59399
---
# Indices of model performance

AIC       |      AICc |       BIC | R2 (cond.) | R2 (marg.) |   ICC |
RMSE | Sigma
-------------------------------------------------------------------------
------------
2.467e+05 | 2.467e+05 | 2.471e+05 |      0.027 |      0.002 | 0.024 |
3.045 | 3.051
```

Appendices

Appendix A: Permissions



AS

Aya Satoh<asatoh@mit.edu>

To: Jano, Sophie Louise - jansl002

Thu 9/26/2024 2:02 AM

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