WESTFÄLISCHE
WILHELMS-UNIVERSITÄT
MÜNSTER

Marlen A. Roehe

Measures and Content of Anticipation in the Brain

- 2023 -

Measures and Content of Anticipation in the Brain

Inaugural-Dissertation

zur Erlangung des Doktorgrades

im Fachbereich Psychologie und Sportwissenschaft

der Westfälischen Wilhelms-Universität in Münster

Vorgelegt von

Marlen A. Roehe

Geboren in Guelph, Ontario, Canada

- 2023 -

Dekan: Prof. Dr. Gerald Echterhoff

Erste Gutachterin: Prof. Dr. Ricarda Schubotz

Zweite Gutachterin: Prof. Dr. Pienie Zwitserlood

Tag der mündlichen Prüfung: 10. März 2023

Tag der Promotion: ……………………………

Table of Contents

Acknowledgements

My profound gratitude goes out to Prof. Ricarda Schubotz for giving me the opportunity to pursue a PhD in biological psychology. I have deeply appreciated her guidance and supervision throughout this time, as well as her stimulating ideas and constructive feedback: I have truly learned a lot, thank you! Furthermore, I am sincerely grateful for Prof. Pienie Zwitserlood's co-supervision and her insightful advice and speedy response to any EEG-related questions.

I will be eternally grateful to Daniel Kluger for taking me under his wings. His unceasing enthusiasm for research was infectious and enriched each day spent in our music-filled office. A special thanks goes to Nina Heins, Lena Leeners, Svea Schröder and Nico Broers for all their uplifting support, insightful discussions, and their cheerful dispositions. On the same note, I would like to thank Ima Trempler, Nadiya El-Sourani, Jennifer Pomp, Laura Quante, Klara Hagelweide, Amelie Hübner, Benjamin Jainta, Sophie Siestrup, Falko Mecklenbrauck, and Rosari Naveena Selvan for their company and all their constructive feedback and input, especially during the early stages of conceptualising new experiments. Monika Mertens' help throughout experimental procedures and Jutta Linke's assistance in administration related motives made them both irreplaceable. A very warm thank you also goes to Axel Kohler, Jens Bölte, Thomas Jacobsen, and Anoushiravan Zahedi for sharing their expertise in EEG analyses.

As always, I am indebted to my family for their undying support, love, and encouragement regardless of the time of day. All in all, I am exceedingly lucky to have been surrounded by a vast group of people who have each contributed to this thesis in their own special way: thank you!

Summary

In predictive processing accounts of the brain, visual perception is believed to be a dynamic interplay between two competing sources of information: bottom-up driven information based on external influences, and top-down projected predictions generated from prior knowledge. These two sources of information are continuously matched to compute discrepancies which, in form of prediction errors, are drawn upon to update internal representations. Within this framework, the brain is seen as a hierarchical generative model of the environments we inhabit.

The present thesis comprises three studies which collectively aimed to shine light on the generation, maintenance, and development of cued predictions. By exploiting the temporal advantages of electroencephalography, *Study I* examined the temporal aspects underlying the formation and development of cued face-related expectations. Neural signatures of expectation-facilitation marked the early onset of a neural state optimal for top-down processes which prevailed until the expected event occurred. *Study II* built upon these findings by investigating to what extent different contextually relevant interferences might impact the maintenance and development of such cued expectations. Whilst temporal delays appeared to have little effect on the active maintenance of anticipatory processes, visual interferences appeared to overwrite the internal representation of the expected event. *Study III* extended these assumptions by examining whether visual interferences were merely processed to a certain extent along the visual processing hierarchy to ensure expectation-facilitated behavioural responses. Indeed, the brain seemed to compensate for processing contextually relevant interferences by restricting how far these sensory signals were processed within higher cognitive levels.

Overall, the present thesis emphasises how the brain fluctuates between neural states facilitating either top-down or bottom-up processes to efficiently prioritise the source of information relevant to the present environmental context.

List of Original Publications

The present thesis is based on the following research articles:

Study I: Roehe, M. A., Kluger, D. S., Schroeder, S. C. Y., Schliephake, L. M., Boelte, J., Jacobsen, T., & Schubotz, R. I. (2021). Early alpha/beta oscillations reflect the formation of face- related expectations in the brain. *PLOS ONE*, *16*(7), e0255116.

Study II: Roehe, M. A., Kluger, D. S., & Schubotz, R. I. (*under review: revisions*). Fluctuations in alpha and beta power provide neural states favourable for contextually relevant anticipatory processes. *Manuscript under review*.

Study III: Roehe, M. A., Kluger, D. S., & Schubotz, R. I. (*to be submitted*). The brain downregulates higher cognitive processes to compensate for processing contextually relevant interferences. *Manuscript to be submitted for peer-review*.

1. Theoretical and Empirical Background

The notion that the brain takes on the role of merely a passive orchestrator in how we experience the external world has, over the past decades, been increasingly challenged by a more pro-active view of the brain (Helmholtz, 1948). Through interlacing compelling bodies of work from cognitive science, psychology, philosophy of mind and psychophysics, a picture emerges that presents the brain as an ever-active 'prediction engine' that strives to predict ensuing incoming sensory information (Clark, 2013, 2015). This active prediction process, coined *predictive processing*, uses prior knowledge stored in the brain to generate relevant predictions of the external world (Clark, 2013; Hohwy, 2013). These predictions are compared with incoming sensory information to yield a percept that best reflects the state of the present context. When the brain gets a prediction wrong, a prediction error is generated upon which the internal model is revised (Clark, 2013; Friston, 2009). By trying to minimize and obviate prediction errors as one attempts to predict the incoming stream of sensory evidence, a structured world is gradually brought into view (Clark, 2015; Friston, 2009). On these grounds, how we experience the world depends on the extent to which we can predict the present flow of sensory information. In the following sections, I will explore the fundamental underpinnings of the predictive brain whilst also accentuating the lucrative benefits that a predictive processing picture of visual perception upholds. Towards the end, a number of abiding research questions will be raised and upon which the main objectives of the thesis will be addressed and elucidated.

1.1 The brain as a 'prediction engine'

Envision a scenario in which you hear a dog bark just as you are about to walk around a corner. If your eyes fall upon a dog sitting in the middle of the pavement, you will think nothing

special of it. If, however, you see a cat in place of the dog, you would undoubtedly be a little bewildered by the incompatibility between what was initially heard and what was then observed. The traditional passive account of perception would dictate that the brain passively awaits these streams of sensory information, which it then processes by propagating the signals up from lower to higher cortical regions along bottom-up pathways. As such, the brain takes in information from the senses to assemble coherent percepts which are build-up in a stepwise motion, starting with simple and finishing with complex features (Egner et al., 2010). More precisely, whilst neurons in the primary visual cortex (V1) respond to simple lines and edges, regions higher up in the visual processing hierarchy (V2 and V4) appear to respond to more complex features, i.e., whole shapes and contours (Huang & Rao, 2011; Hubel & Wiesel, 1968). The predictive processing approach builds on this passive account by adding so-called 'generative internal models' to the framework (Clark, 2013; Friston, 2005; Hohwy, 2013). These generative models are acquired in a bottom-up fashion similar to the process mentioned above. What sets predictive processing apart from the traditional passive approach, however, is a *Bayesian* spin on how sensory processing is conducted. Following the predictive processing approach, generative models are assembled in order to predict afferent sensory signals before or whilst they occur. In other words, instead of passively awaiting sensory stimuli, the brain actively tries to predict incoming sensory occurrences via a cascade of *top-down* propagated predictions (Friston, 2005; Lee & Mumford, 2003; Rao & Ballard, 1999). Essentially, these predictions reflect what the brain already 'knows' about the statistical regularities of the external environment (Bar et al., 2006). The focal aim of the predictive brain is thus to match the multi-layered incoming sensory data with predictions at each level. That is, each level within this hierarchy tries to predict the signal of the level below. The discrepancies between the internal prediction and the sensory signal at each level are computed using Bayesian inference (Friston, 2003). The resulting mismatch is returned in the form of a *prediction error*

signal that is drawn upon to revise the internal model (Den Ouden et al., 2012; Huang & Rao, 2011; Rao & Ballard, 1999). Depending on the magnitude of the residual mismatch, individual levels can either be updated independently or in a way that cascades up several levels of the multi-level hierarchical model. To gain better insight, let us return to the fictional scenario mentioned above. In general, predictive processing would dictate that the pro-active brain attempts to predict external information on the basis of prior knowledge. In this case, predictions most probable with regard to the dog's bark would be generated. If a dog was indeed observed after rounding the corner, only little adjustments would be made to the internal generative model, e.g., regarding the dog's colour, size, and breed, etc. If, on the contrary, a cat was observed, the dog-related predictions would be compared with contradicting sensory data, leading to a cascade of prediction errors upon which the internal model would be revised. The role of these prediction error signals is therefore to inform the internal model of sensory information which, to this point in time, was not hypothesised (Huang & Rao, 2011). In turn, the model is revised and newly sharpened predictions are generated which are closer matches of the incoming sensory information. This continuous circular process is referred to as *prediction error minimisation* (Feldman & Friston, 2010) and enables the predictive brain to establish probabilistic models that best explain the external world.

Ideally, the predictive brain strives towards accommodating the most up-to-date model of our natural surroundings. Taking into account that our environments comprise a myriad of different sensory data which are prone to shift incessantly, this idealistic approach is highly improbable. Thus, these generative internal models are subject to concurrent and continuous re-evaluation and revision. On a similar note, not every sensory signal that our natural environment hosts is of relevance at any given point in time. The notion that the brain can select relevant whilst filtering out irrelevant sensory data is well established in empirical literature (Ligeza et al., 2017; van Moorselaar et al., 2020). This begs the question: on what grounds does

the predictive brain deal with the sensory overload of our surroundings and compartmentalises which information is relevant, and which can be considered environmental 'noise'?

1.2 Efficiency in the face of environmental 'noise'

As mentioned previously, our environments are laced with a plethora of sensory stimuli. Naturally, it would seem inefficient for the predictive brain to predict and process every sensory signal that one is brought in contact with equally. To overcome this, informative or even crucial sensory signals are isolated from redundant sensory 'noise'. In terms of perception, the present state of our natural surroundings can heavily influence which incoming sensory information is processed along the hierarchy of the generative models (Clark, 2015, 2017a; Limanowski et al., 2020). The dog's bark, for instance, provides an indication of what to expect when rounding the corner. Thus, to cope with the noisy and dynamic nature of our surroundings, the predictive brain makes use of the current context to hypothesise what up- and/or incoming visual data would be most probable. Consider the visual example depicted below from Lupyan & Clark (2015). When reading from top to bottom, the numeric context would lead one to read 12, 13,

Figure 1.1 Visual example of how the current context impacts perception. Image taken from Lupyan & Clark (2015).

and 14. In contrast, reading from left to right, the letter A prompts one to read the central character as the letter B. Even though the character in the centre is the same in both cases, the

context influences whether a number or letter is perceived. As such, top-down predictions pinpoint which visual input (13 versus B) is most probable based on the present context. According to predictive processing, this is brought about by flexibly varying the impact top-down and bottom-up signals can have at different levels of processing, given the current context (Clark, 2015, 2022). In the above case, the balance of influence between top-down and bottom-up signals is swayed towards the former. In other words, the influence of the top-down predictions overrides, at least to some extent, that of the incoming sensory input. Hence, less 'weight' is given to bottom-up driven signals. This well-calibrated process is a vital feature of predictive processing and is referred to as *precision-weighting* (Clark, 2017b; Friston, 2005, 2009; Lupyan & Clark, 2015). By estimating the uncertainty of our predictions, the predictive brain can determine to what extent predictions based on the past should guide current perceptual inferences (O'Reilly, 2013). The underlying mechanisms believed to be involved recruit certain neuromodulators, such as dopamine (Diederen et al., 2017; Haarsma et al., 2021) or noradrenaline (Lawson et al., 2021; Yu & Dayan, 2005), to adjust the synaptic gain given to either top-down or bottom-up signals depending on how precise they are estimated to be, given the current context (Yon, 2021). Take, for instance, sensory signals generated when scanning a landscape during a foggy day. These bottom-up signals tend to be more noisy and less reliable than those generated on a clear sunny day. By efficiently altering the weight given to prediction errors of varying degrees of reliability subsequently impacts to what extent they influence the revision of the internal model (Clark, 2017b). Thus, low-precision-weighted prediction errors subsequently tend to have minimal to no impact on influencing the revision of the generative model, whereas highly weighted prediction errors have a greater influence on ongoing processes (Den Ouden et al., 2012). In general, this systematic, yet flexible, process modulates how influential top-down versus bottom-up information is at a given point in time (Clark, 2013, 2017b; Lupyan & Clark, 2015). This grants us, for instance, to: (a) rely more strongly on top-

down predictions to guide one through the house in the darkness of night, or (b) let incoming sensory information play a more substantial role when walking along unfamiliar terrain. Hence, in ideal circumstances, the predictive brain seems to efficiently select different contextually driven patterns of weightings to ensure that one's perceptual hypotheses are updated based on relevant sensory signals, and 'noise' is disregarded somewhere along the hierarchy of the internal model.

With this in mind, let us revisit the '13 versus B' example shown above. Considering that over the years we have established a rich representation and understanding of both numbers and the alphabet, the subsequent contexts allow us to predominantly rely on top-down predictions. Hence, we can interchangeably read either from top to bottom or from left to right and allow the weight given to these top-down predictions to give rise to the most probable visual data with respect to the current context. In summary, by integrating precision-weighting as a tool to variably 'sharpen' and 'mute' incoming sensory or top-down signals, the predictive brain can efficiently guide visual perception by drawing on the most reliable source of information.

1.3 Neural and behavioural signatures of anticipatory processes

In theory, a central signature of predictive processing is the suppression of signal by 'explaining away' prediction error by means of precisely predicting incoming sensory information (Rao & Ballard, 1999). Indeed, previous functional neuroimaging research has demonstrated such expectation-based signal suppressions. For instance, fMRI studies have shown that expected (versus unexpected) visual stimuli induced a diminished response in early visual cortex (Alink et al., 2010; Kok et al., 2012). Other neurophysiological studies conveyed that high frequency gamma-band activity, commonly associated with mediating bottom-up

signals (Bastos et al., 2015; Bauer et al., 2014; Brodski et al., 2015; van Pelt et al., 2016), was suppressed when processing expected (versus unexpected) events (Todorovic et al., 2011). Relatedly, prior expectations regarding upcoming events also appear to speed up behavioural responses (Ran et al., 2014; Schliephake et al., 2021; Turk-Browne et al., 2010).

In term of experimental design, a cuing paradigm is most commonly used to examine anticipatory processes. For low level visual processing, grayscale luminance-defined sinusoidal grating stimuli are most often used (Kok et al., 2012), whereas for more complex visual perception, face and house stimuli tend to be implemented (Schliephake et al., 2021; Summerfield et al., 2008; Turk-Browne et al., 2010). As such, the face-sensitive event-related potential N170, a negative deflection at approximately 170 – 200ms after stimulus onset (Luck, 2014), has been examined and shown to index expectation-related reductions in amplitude, i.e., a reduced negative deflection (Johnston et al., 2016; Ran et al., 2014).

Notably, and somewhat contradictory to the 'suppression feature' posed by predictive processing, enhancements in neural activity have also been associated with anticipatory processes. As such, recent studies have shown that the early activation of top-down processes is reflected by increases in alpha/beta oscillatory activity (Brodski-Guerniero et al., 2017; Cao et al., 2017; van Pelt et al., 2016). In early years of studying alpha oscillations, this low frequency band was considered to represent an 'idling' state of the brain. In occipital areas, alpha oscillations appeared to increase when participants had their eyes closed, and decreased upon opening their eyes (Berger, 1930; for a review, see Kropotov, 2009). As a result, alpha oscillations received considerably less empirical attention than other frequency bands. Only more recently have alpha waves gained more empirical interest particularly in the fields of attention and sensory inhibition (Klimesch, 2012; Klimesch et al., 2007). In the three upcoming studies, alpha oscillations, combined with beta oscillations, will be examined in terms of how these frequency bands may facilitate top-down processes by inhibiting bottom-up processes.

16

Overall, it becomes clear that not only expectation-based signal suppression underlies anticipatory processes. The focal premise of the present thesis draws on these neural and behavioural signatures of expectation to further advance our understanding of the fundamental signatures framing predictive processing. Given that face perception is intrinsic to daily life, we used neutral face images to construct a visual cuing paradigm to generate statistical regularities. The electrophysiological and behavioural signatures of expectation mentioned above will thus be discussed in more detail in the three studies comprising this thesis.

1.4 Research questions and objectives

The previous sections have outlined the notion that the brain can be viewed as a prediction engine that is constantly trying to acquire probabilistic situational models that best represent and predict the external world. To acquire such internal models, either internal or incoming signals are weighted to ensure that primarily reliable bottom-up signals are drawn upon during the revision of these models. Notably, the current context plays a substantial role in regulating which sensory signals can be compartmentalised as relevant or noise. By subsequently reducing the weight on the noisy signals, top-down processes can take on a larger influential role. All these underlying systematic features constituting predictive processing are not only restricted to visual perception but also provide a plausible framework for auditory perception (Cao et al., 2017), language (Kutas & Hillyard, 1980) and action (Bestmann et al., 2008; Clark, 2015; Schubotz, 2007). Thus, although the empirical and philosophical research in this field is beyond its infancy, many abiding questions still remain.

Foremost, previous research regarding visual predictions has conveyed little about the temporal aspects of how cued predictions are generated. Hence, it remains ambiguous whether

neural signatures reflecting the formation of cued expectations are instantly activated upon seeing a predictive cue and then subside, or whether this is a gradual process which prevails until the expected event occurs. In *Study I*, we thus exploited the temporal advantages of electroencephalography to examine the temporal constrains that mark the generation of cued face-related predictions.

Study II builds upon these findings by integrating the observation that cued expectations do not always immediately ensue their predictive cues in a realistic 'everyday' setting. Additionally, given that our natural environments host vast numbers of sensory stimuli, the predictive brain is likely to process other sensory data in the meantime if a cued expectation does not immediately follow its respective cue. The aim of this study was, thus, to examined whether the neural signatures reflecting the generation process of face-related expectations are affected by (i) a temporal delay in the onset of the expected image, or (ii) a visual interference (depiction of a randomly selected image) prior to the onset of the expected image. We hypothesised that a delay in the onset of the expected image would have little influence on the neural signatures reflecting top-down processes. In contrast, processing another visual stimulus whilst awaiting the expected stimulus may interfere with early anticipatory processes.

Based on the findings of *Study II*, *Study III* investigated how the present context influences how visual interferences are processed. Given that not every incoming sensory information can be exclusively compartmentalised as being either relevant or sensory noise, the following question arose: how are sensory stimuli processed which are contextually relevant but only to a certain extent? In this final study we hypothesised that contextually relevant interferences are merely processed to the extent (within the generative internal model) that is necessary for the present context.

Overall, these three studies draw on previously established knowledge regarding the underpinnings of the predictive brain to further elucidate: (a) the generation and development

of cued expectations, (b) the influences of temporal and visual disruptions on the aforementioned process, and (c) how the brain compensates for processing contextually relevant visual disruptions.

2. Research Articles

2.1 Study I: Early alpha/beta oscillations reflect the formation of face-related expectations in the brain

Marlen A. Roehe[1,2*], Daniel S. Kluger[2,3], Svea C. Y. Schroeder[1,2], Lena M. Schliephake[1], Jens Boelte[1,2], Thomas Jacobsen[4] and Ricarda I. Schubotz[1,2]

[1]Department of Psychology, University of Münster, Münster, Germany

[2]Otto-Creutzfeldt-Centre for Cognitive and Behavioural Neuroscience, University of Münster, Münster, Germany

[3]Institute for Biomagnetism and Biosignal Analysis, University of Münster, Münster, Germany

[4]Experimental Psychology Unit, Helmut-Schmidt-University/University of the Federal Armed Forces Hamburg, Hamburg, Germany

Abstract

Although statistical regularities in the environment often go explicitly unnoticed, traces of implicit learning are evident in our neural activity. Recent perspectives have offered evidence that both pre-stimulus oscillations and peri-stimulus event-related potentials are reliable biomarkers of implicit expectations arising from statistical learning. What remains ambiguous, however, is the origination and development of these implicit expectations. To address this lack of knowledge and determine the temporal constraints of expectation formation, pre-stimulus increases in alpha/beta power were investigated alongside a reduction in the N170 and a suppression in peri-/post-stimulus gamma power.

Electroencephalography was acquired from naive participants who engaged in a gender classification task. Participants were uninformed, that eight face images were sorted into four reoccurring pairs which were pseudorandomly hidden amongst randomly occurring face images. We found a reduced N170 for statistically expected images at left parietal and temporo-parietal electrodes. Furthermore, enhanced gamma power following the presentation of random images emphasized the bottom-up processing of these arbitrary occurrences. In contrast, enhanced alpha/beta power was evident pre-stimulus for expected relative to random faces. A particularly interesting finding was the early onset of alpha/beta power enhancement which peaked immediately after the depiction of the predictive face. Hence, our findings propose an approximate timeframe throughout which consistent traces of enhanced alpha/beta power illustrate the early prioritisation of top-down processes to facilitate the development of implicitly cued face-related expectations.

Introduction

Our environment is of a highly dynamic nature, veiling a cascade of statistical regularities. Explicitly, such regularities often go unnoticed, although traces of implicit learning are evident in the brain's neural activity. These regularities are extracted as sensory input and projected 'bottom-up' over multiple cortical levels in order to establish associative neural representations reflecting external influences [1]. These internal representations are henceforth frequently updated and revised to optimise their reliability. This accumulation of knowledge regarding statistically predictable external recurrences can then be drawn upon when the external input is less informative or lacks certainty [2]. To reduce this ambiguity, predictions based on prior knowledge regarding an external stimulus are sent 'top-down' along the cortical hierarchy and are compared with equivocal sensory-driven input to draw relevant inferences. According to predictive processing frameworks, if, for instance, the top-down prediction and bottom-up input carry dissimilar information, a mismatch in the form of a prediction error is propagated upwards to update a subsequent higher level. On the contrary, no revision of any given level would be necessary if the bottom-up signal is congruent with the top-down prediction. In the context of predictive processing, this bidirectional interplay between incoming sensory signals and top-down projected predictions is the underlying mechanism assisting perception [3,4].

Emerging principles within this field of research have highlighted several biomarkers which support this bidirectional predictive framework. For instance, the face-sensitive event-related potential (ERP), N170, is a reliable temporal marker which, amongst other factors, reflects the level of predictability of a face-related sensory input. Specifically, selected studies investigating face perception conveyed that the amplitude of the N170 component was significantly diminished for expected compared to unexpected faces [5–7]. In line with predictive processing, this suggests that the sensory-driven information of an expected face is

met by fairly accurate top-down prediction. To establish such predictions, the brain draws upon prior information of expected events in preparation for their actual occurrence [8]. Recent studies have shown that pre-activation of sensory information, and subsequent sensory priors, are mediated by low frequency oscillations encompassing alpha and beta frequency ranges [8-12]. These oscillations, primarily alpha, are believed to enhance the signal-to-noise ratio in task-related networks by carefully selecting relevant and simultaneously silencing irrelevant populations of neurons to establish a more focused access to representations of expected stimuli [13]. Due to the early access to relatively precise prior information, less cognitive resources are required to process anticipated perceptual input and in turn visual event-related potentials are modulated [7,9,13]. Additionally, updating and optimising this given neural representation would be unnecessary, hence, the forward projection of prediction errors is downregulated. Bottom-up processing as well as the projection of prediction errors functionally relate to high gamma frequency (60 – 100Hz) synchronisation, which requires a greater energetic cost than lower frequencies [14,15]. Based on these findings, a reduction in gamma power would be presumed to proceed the onset of expected events. In contrast, due to the limited access to pre-activated prior information, more cognitive resources would be allocated to processing unexpected occurrences [10,15,16]. Unexpected events could, therefore, be distinguishable from expected occurrences by enhanced post-stimulus gamma-band activity (GBA), whereas expected images are preceded by an enhancement in pre-stimulus alpha/beta power and a suppression in GBA post-stimulus onset [11]. In turn, whilst less cognitive resources are devoted to processing sensory information of expected targets, subsequently evoking a diminished ERP response, the opposite would be expected for novel or surprising occurrences [7,9].

Although the fundamental principles of adaptive perception have been well established, various aspects relating to the genesis and development of top-down driven expectations

remain underexplored. Several studies have investigated the presence of pre-stimulus alpha/beta power as an indicator of expectation [9,12,17], as well as examined the pre-activation, maintenance, and transfer of prior face-related knowledge [8]. Yet, these studies primarily focus on a small fragment of the pre-stimulus timeframe immediately prior to the onset of expected events. Therefore, it remains unclear at which point facilitatory processes aiding the development of cued face-related expectations commence and how this development evolves over time. The main aim of the present study was, therefore, to locate the point within the pre-stimulus period at which the enhancement in alpha/beta power is initiated for expected relative to random images. Moreover, we meant to investigate whether this enhancement in alpha/beta power either (i) fluctuates, (ii) shows a gradual and steady increase until the expected event occurs, or (iii) shows an accelerated increase just prior to stimulus onset. To our knowledge, the current study, therefore, provides new insight into the evolution of implicitly cued face-related expectations.

Through employing a statistical learning paradigm during a short training session, participants acquired implicit knowledge of the statistical relationships and, hence, predictable nature of certain stimuli. More specifically, the participants completed an explicit gender classification task whilst implicitly learning and predicting the statistically predictable occurrences of certain face images. Participants consequently relied on a previously establish representation of the interrelationships between certain images to form subsequent perceptual expectations. As such, the formation of these expectations was dependent on memory. Foremost, we aimed to replicate findings verifying the presence of implicit expectations. In line with previous studies, we expected a faster and more accurate behavioural response for expected faces alongside an attenuation of the N170 amplitude [1,7]. Furthermore, we assumed that whilst an enhancement in GBA should succeed the depiction of randomly occurring faces [11], the statistically expected images should be met with a prior elevation of alpha/beta activity

[8,11,12,17]. A systematic relationship between this increase in alpha/beta activity and the amplitude reduction of the N170 in response to the stimulus would subsequently support the suggestion that the increase in alpha/beta activity reflects predictive processes. Thus, our primary motivation was to examine pre-stimulus alpha/beta power, indicating the development of face-related expectations, in order to determine the initial onset and offset confining the formation process of implicitly cued expectations.

Materials and methods

Participants

A total of 33 individuals participated in this study (23 women; 23.1 ± 3.51 years of age [mean $\pm$ SD]) after having signed informed consent based on the principles expressed in the declaration of Helsinki. All participants were right-handed as assessed by the Edinburgh Handedness Inventory [18], reported (corrected-to-) normal visual acuity and had no history of neurological and psychiatric disorders. For compensation, participants were either accredited with class credits or reimbursed for their participation (25 Euros). Four additional participants, whose EEG data contained excessive sweat artefact contamination (severe drifts in the signal), were excluded from further analyses. The study was approved by the Ethics Committee of the University of Münster (Department of Psychology).

Stimulus material

Participants were presented with 25 neutral face images (12 women) chosen from the Radboud Faces Database (RaFD) [19]. Since visual information to process faces is extracted using sequences of eye fixations over mainly eye regions (the mouth region being second), all

images were scaled so that those facial features (especially eyes) aligned [20]. This was done to reduce the amount of eye movements.

To generate statistical regularities, eight of these images were sorted into four reoccurring pairs under the following sequential guidelines: i) a male face invariably preceded a female face, ii) a male face invariably preceded another male face, iii) a female face invariably preceded a male face, and iv) a female face invariably preceded another female face. Each individual participant was assigned a unique set of four pairs which were pseudorandomly embedded amongst reoccurring arbitrary face images. The face images (W = 9.5cm, H = 14cm) were depicted individually in the centre of a black background for 500ms (subtending visual angles of approx. 9° vertically and 6° horizontally). These were immediately followed by a 17ms white noise mask and a fixation period of 2483ms. Each of these trials was, therefore, a total length of 3000ms (Figure 1).
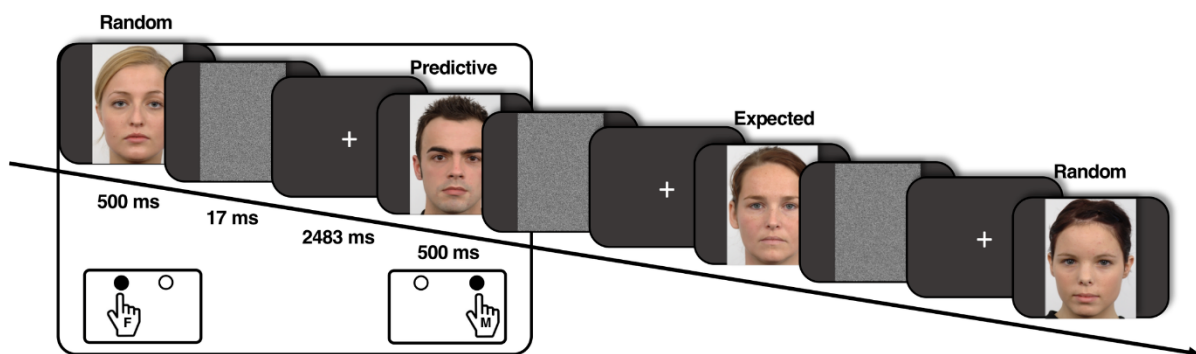

Figure 1 Schematic illustration of the experimental task. Each image was depicted for 500ms followed by a white noise mask (17ms) and a darkened fixation screen (2483ms). The participants were instructed to press either the left (right index finger) or right (right middle finger) button on a response box to discriminate between female (F) and male (M) images, respectively.

Task

The participants engaged in a gender classification task without having prior knowledge of the presence of the embedded pairs. They were given a response box and were instructed to respond as fast and accurately as possible – via a right-hand button press – respective to the gender of the face presented on screen. Here a left button press (right index finger) classified the presented image as a female face, whilst a right button press (right middle finger) classified the depicted face image as male (Figure 1).

Experimental procedure

Participants were tested on two consecutive days. The first day consisted of a short, 18-minute behavioural training session, providing a chance for the participants to gain implicit knowledge regarding the presence of the paired images and to familiarise themselves with the classification task at hand. Four image pairs were pseudorandomly hidden amongst 17 arbitrary face images, with each image depicted five times to form sequences (blocks) of approximately six to seven minutes (125 images within each block). The first image within each pair served as a predictive event for the second image and subsequently enhanced its predictability. Focusing on this predictability regarding the occurrence of a certain image, all images could be sorted into two image categories – *expected* and *random*. Given the confounding informative nature of a predictive image, these images were removed from analyses determining the predictability of a shown image (behavioural, ERP and gamma-band analyses). The timeframe following the onset of predictive images was, however, examined in the alpha/beta analysis, since it also served as the pre-stimulus timeframe for the expected images.

The EEG session on the following day comprised of an elongated replica of the training session. All images were equally distributed throughout eight blocks with self-determined breaks separating them (yielding a total of 1000 trials). Whilst the four image pairs remained

consistent throughout the training and EEG sessions for each individual participant, the combinations of paired images differed and were counterbalanced across participants. The participants were seated comfortably in a dimly lit EEG booth and advised to keep general movement to a minimum. Overall, the EEG session took approximately 50 – 60 minutes to complete depending on the length of the breaks.

A questionnaire following immediately after the EEG session tested the participants' explicit awareness of the predictive nature underlying the classification task. The participants were asked to state whether they had noticed face images which invariably ensued certain predictive images and asked to identify them seriatim.

The experiment was programmed and performed using Presentation 18.1 (Neurobehavioral Systems, San Francisco, CA, USA).

Behavioural data analysis

The statistical analysis of the behavioural response time (RT) and accuracy (percentage of correct responses) was performed in R (version 3.6.0; R Foundation for Statistical Computing, Vienna, Austria; Rstudio Team, 2015). Premature and prolonged responses (occurring 3 SDs faster/slower than the aggregated group mean), in addition to incorrect answers, were excluded from the behavioural analysis. Random images were arbitrarily selected to create a sample size equal to the number of expected images (~160 of expected and ~170 of random image trials per participant). Since we hypothesised that the responses for the expected faces would display an increase in accuracy aligned with a decrease in RT, these two aspects of performance were subjected to individual dependent, one-tailed t-tests for the two image categories (expected versus random).

EEG data analyses

EEG data acquisition. Scalp EEG was acquired using 62 Ag/AgCl-electrodes mounted to the actiCAP snap electrode cap in combination with the BrainVision Recorder software (Brain Products, Gilching, Germany). The electrodes were placed according to the 10-20 system and additional electrooculogram (EOG) electrodes were attached below and next to the right eye to account for vertical and horizontal eye movement, respectively. An online bandpass filter (0.1 – 1000Hz) was applied to the EEG data recorded at a sampling rate of 1kHz. Electrodes FCz and FPz served as online reference and ground, respectively, and were disregarded from all analyses. Electrode impedance was maintained below 10 kΩ.

EEG signal processing. EEG data was pre-processed offline using the EEGLAB toolbox (version 14.1.1b) [21] in MATLAB (R2017b). The raw data was down-sampled to 500Hz and bandpass filtered by applying a 0.1Hz high-pass and 30Hz low-pass Butterworth filter (12 db/octave) for the ERP analysis, whereas a 0.5Hz high-pass and 100Hz low-pass Butterworth filter was implemented for the time-frequency analysis (TFA) [22]. Line noise was suppressed at the source through a carefully designed set-up (as recommended by [23]). Continuous data was segmented into epochs extending from -200ms pre- to 600ms post-stimulus onset for ERPs. The 200ms prior to stimulus onset served as a baseline. For the TFA, data was epoched from -2000 to approximately 1500ms, time-locked to stimulus onset. These time segments of 3500ms framing image onset were used with the intention to allow edge artefacts to subside before and after our points of interest [22]. Consecutive epochs overlapped by approximately 500ms to minimise loss of data during convolution. Ocular correction was applied using the Gratton plug-in for EEGLAB [24]. Noisy channels (kurtosis criterion: z > 6) were manually inspected and replenished by an interpolation of neighbouring electrodes (ERPs: 1.14% and TFA: 0.66% of electrodes were interpolated). For the ERP analysis, semiautomatic artefact inspection discarded epochs contaminated by artefacts exceeding an

amplitude threshold of $\pm 75\ \mu V$ or voltage fluctuations greater than 50 μV with regard to the previous sample point (3.9% of trials removed). For the TFA, epochs with artefacts exceeding an amplitude threshold of $\pm 200\ \mu V$ and voltage fluctuations greater than 50 μV were rejected (6.2% of trials removed). A dataset was disregarded when more than 2 SDs of trials were removed during the semiautomatic rejection (ERP mean: 943 trials; TFA mean: 941 trials). Henceforth, four out of the 37 participants were dismissed from all further processing. During the final pre-processing step, datasets were re-referenced to a common average. For all EEG analyses, the number of expected and random trials was equalised across participants (expected: ~160 per participant; random: ~170 per participant).

Event-related potentials. The epochs framing the event of interest were averaged across each image category (expected and random) for each individual participant. The N170 was quantified by measuring the mean amplitude within the timeframe of 150 – 200ms in relation to a pre-stimulus baseline of 200ms. Based on former literature, we restricted the attributing electrode sites to exclusively P7/P8 and TP7/TP8 for our analysis [25-29]. In line with our directional hypothesis, the mean amplitudes for expected and random images were subjected to dependent, one-tailed *t*-tests for each set of electrodes (left hemisphere: TP7/P7; right hemisphere: TP8/P8; see S1 File for an alternative repeated measures cluster permutation test approach).

Time-frequency. The spectral analysis was performed using the MATLAB toolbox FieldTrip [30]. Spectral power was estimated by applying FFT to a sliding window passing through averaged trials (for both low and high frequencies). A Hanning taper was used for low frequencies (2 – 30Hz) by centring a 500ms fixed sliding window that moved in time steps of 50ms and 1Hz increments. This process subsequently constructed trial windows extending from -1750 to 1200ms (stimulus locked), as 250ms on either side of the original epoch frames (-2000 – approx. 1500ms stimulus locked) were discarded due to convolution. For high

frequencies (40 – 100Hz), an adaptive DPSS (discrete prolate spheroidal sequences) multitaper approach was applied [31]. Estimates were acquired using a 500ms fixed sliding window maintaining identical stepwise motion over time and frequency axes as previously stated (± 4Hz smoothing).

Cluster-based permutation tests were computed in three dimensions (frequency, channel, and time) to correct for multiple comparisons. Hence, voxels of the two image categories were subjected to Monte Carlo randomisation tests with 1000 iterations and a significance level of $\alpha = .05$. With reference to our hypotheses regarding the enhancement of alpha/beta power pre-stimulus and the diminution of gamma power post-stimulus onset for expected versus random faces, dependent, one-tailed t-tests were computed for these permutation tests. Statistical tests were performed on the normalised difference in raw power estimates between expected and random images (difference $_{\text{expected vs. random}} = (X-Y)/(X+Y)$). This normalisation was also applied to all spectral data used for time-frequency representations.

Lastly, data-driven analyses were carried out to assess the relationship between the observed effect in pre-stimulus alpha/beta power and the modulation of the N170. For each participant, the difference in normalised alpha/beta power between expected and random images was calculated and averaged over channels, frequency, and time. In this case, power was only averaged across those channels that contributed to the positive cluster. The difference in mean amplitude for the N170 was computed and averaged over time and left electrodes for each participant. The modulation of alpha/beta power within the immediate pre-stimulus timeframe (1250 – 3000ms) was z-standardised and correlated with the z-standardised magnitude of the difference in mean amplitude for the N170. To examine the functionality of the last two peaks more closely, their underlying alpha/beta power was segregated and correlated individually with the modulation of the N170. The timeframe proceeding the onset

of the predictive images was not included in these analyses because of the images' informative and 'cue-like' nature.

Results

Behavioural results

Throughout the EEG session, participants engaged in a classification task with the instructions to identify the gender of the depicted faces as fast and as accurately as possible. The performance for both image categories conveyed the participants' close engagement with the task at hand (expected: 96% accuracy; random: 96% accuracy; one-tailed: $t(32) = 0.51$, $p = .305$). The RT for the two observed image categories showed a mean of 478ms ($SD = 49$ms) for expected faces and 479ms ($SD = 46$ms) for random faces. The dependent, one-tailed t-test showed no significant difference between the two categories ($t(32) = 0.38$, $p = .352$).

Notably, the answers of the questionnaires revealed that only a single participant became explicitly aware and was capable of correctly identifying merely one out of the four confronted pairs.

Event-related potential results

The modulation of the N170 played a fundamental role in identifying whether the participants had gained implicit knowledge regarding the predictability of the paired images. Our approach examined four relevant channels – TP7 and P7 in addition to their right lateral counterparts –for a substantial reduction in mean amplitude (150 – 200ms) for expected faces. Supporting our hypothesis, a significant reduction in mean amplitude was observed for expected (-1.31 ± 2.40 μV) versus random images (-1.51 ± 2.25 μV) at left parietal and temporal-parietal channels (Bonferroni-corrected: $p = .039$; Figure 2). In contrast, no

significantly reduced amplitude for expected faces was evident at right-lateralised channels (expected: -1.80 ± 3.02 µV; random: -1.86 ± 3.05 µV; Bonferroni-corrected: p = .569).
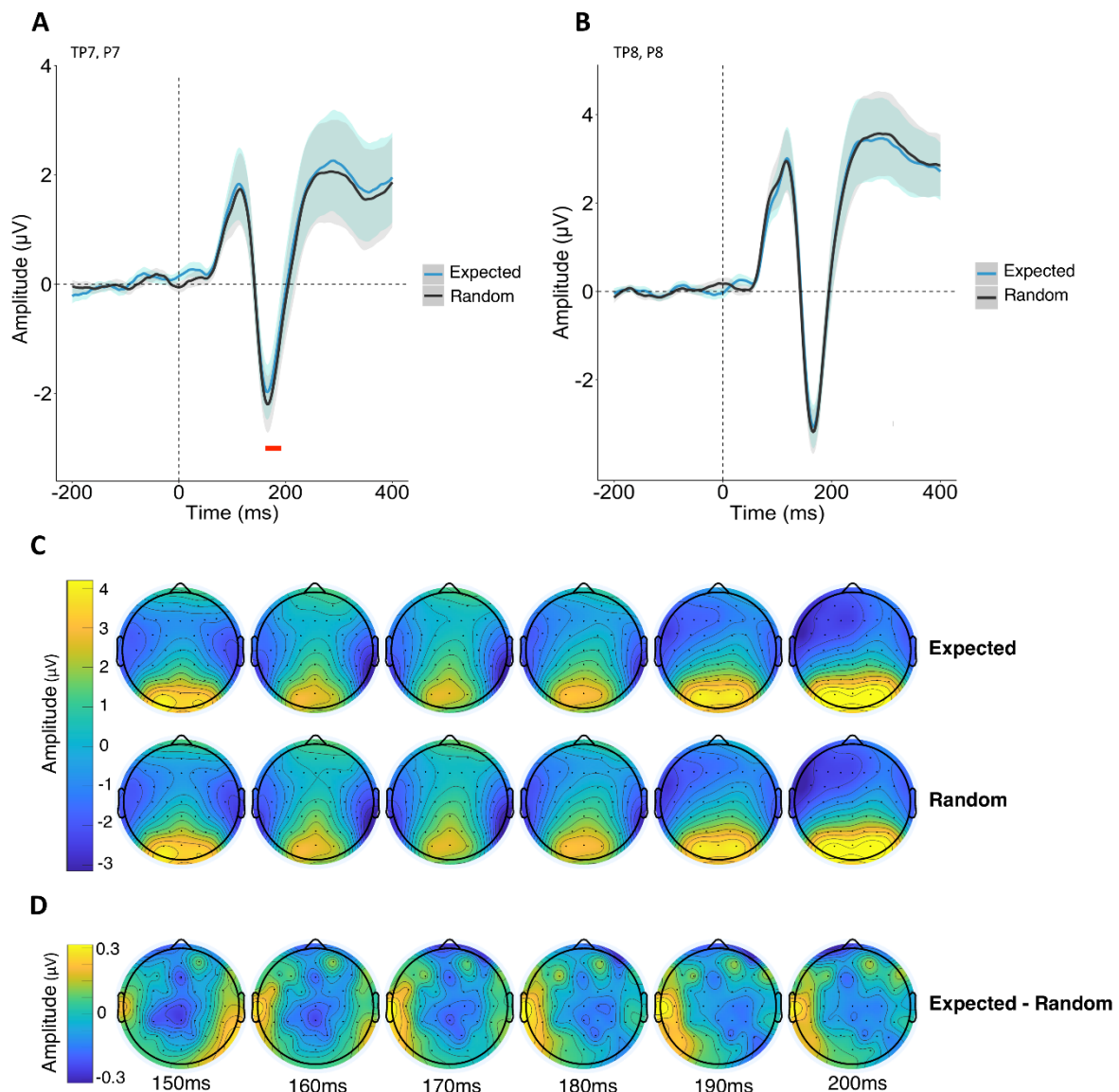

Figure 2 (A) A significant reduction in the N170 amplitude for expected (blue line) in comparison to random (black line) faces was found across the averaged electrodes TP7 and P7 (left hemisphere). The timeframe of the significant mean amplitude difference is marked by a red dash. The shaded area illustrates within-participants confidence intervals for the expected (blue) and random (grey) faces. **(B)** No vast differences in the N170 were evident across electrodes TP8 and P8 (right hemisphere). **(C)** Voltage topographies (µV) for expected and random images show activity in a timeframe from 150 – 200ms following stimulus onset. **(D)** Topographies show voltage differences between expected and random face images.

Time-frequency results: gamma oscillations

An underlying implication of predictive processing is the notion that the feeding forward of sensory information is upregulated for novel or unexpected as compared to expected occurrences [14]. In accordance with this conception, our time-frequency analysis showed a significant reduction in gamma power for expected versus random images within the first 1000ms upon stimulus onset ($p = .04$, cluster corrected; Figure 3). In other words, a significant enhancement in GBA was found in response to random compared to expected images. No particular frequencies within the broad gamma-band were singled out a priori, meaning, gamma power (40 – 100Hz) was treated as a singular entity. Interestingly, we observed that the gamma-related spectral difference between random and expected images appeared to reside in an early and late enhancement (Figure 3A). Visual inspection of the cluster revealed that the channels contributing to these elevations in GBA were predominantly located over posterior scalp regions (Figure 3B).
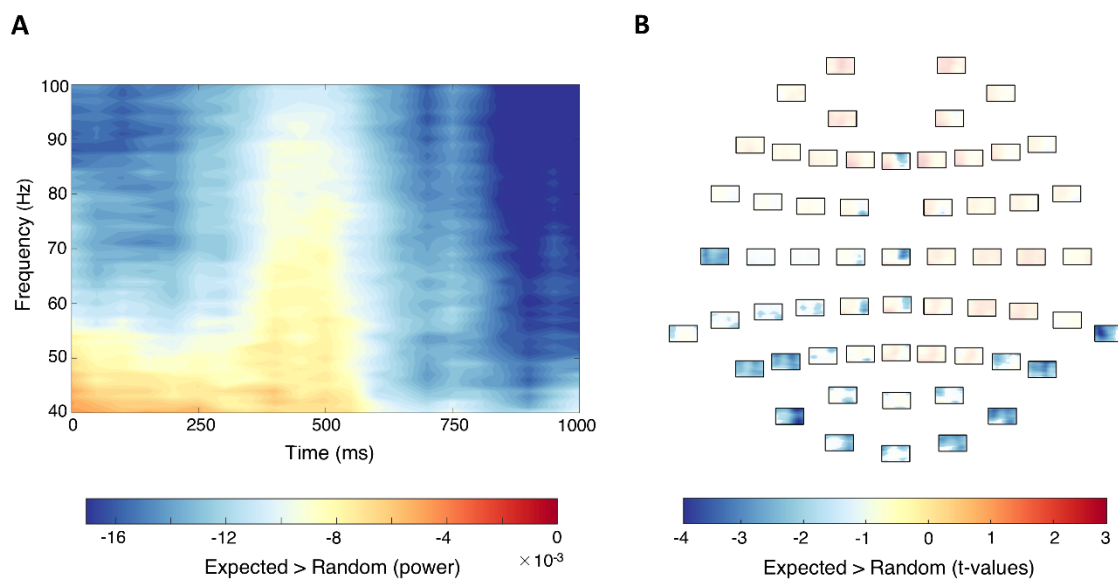

Figure 3 (A) Time-frequency representation (TFR) showing the normalised difference in gamma-band activity (GBA) between expected and random images peri- and post-stimulus onset (40 – 100Hz; 0 – 1000ms). Power was averaged across electrodes contributing to the negative cluster ($p = .04$, cluster corrected). **(B)** TFRs for each individual channel illustrate the topographical distribution of the negative cluster. The significant time and frequency points composing the negative cluster stand out as opaque; insignificant differences are transparent.

Time-frequency results: alpha and beta oscillations

The above analyses determined several neural traces which suggest that the predictive nature underlying the classification task was learned implicitly. Building upon this finding, we examined alpha and beta frequencies to determine a confined time-window preceding an expected event, in which the development of an expectation was reflected by its power distribution pattern. Hence, this analysis focused on the presence and distribution of low frequencies, primarily associated with top-down processes, in the short timeframe preceding the expected stimuli [12,17,32]. In line with our hypothesis, we found a significant enhancement in alpha and beta power for expected images (in comparison to random images) ranging from approximately 1250ms after the presentation of the predictive image to onset of the expected stimulus ($p = .017$, cluster corrected; Figure 4B). However, as displayed in Figure 4A, the positive cluster seems to commence prior to this enclosed timeframe. Thus, we additionally contrasted the time course extending from stimulus onset until 1200ms post-stimulus onset between predictive and random images. Interestingly, a further positive cluster enclosing alpha/beta frequency bands was observed in this timeframe ($p = .044$, cluster corrected). Visual inspection of the cluster suggested that the channels corresponding to the largest power differences between predictive and random images were predominantly located over central electrodes within occipital, parietal, and frontal regions (Figures 4Ai and 4Aii). These topographical distributions then spread to primarily occipital and frontal regions for the largest difference in alpha/beta power between expected and random images (Figure 4Bi). In contrast to the previous scalp maps, the final enhancement in alpha/beta power was mostly lateralised bilaterally over parietal regions (Figure 4Bii). Collectively, these findings suggest that the facilitation of the development of a cued expectation is initiated by the onset of the predictive image and ends shortly prior to depiction of the expected image.
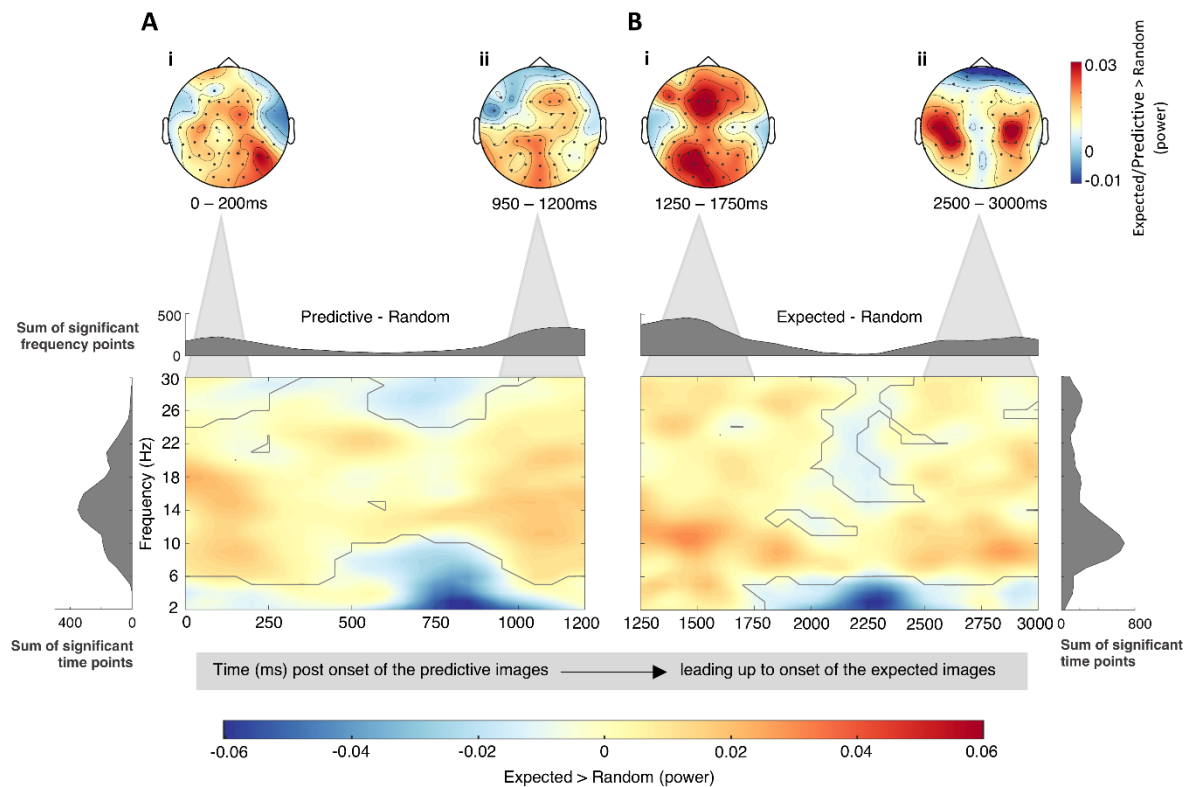
Figure 4 TFRs of the normalised differences in low frequency power (2 – 30Hz) averaged across channels contributing to the positive clusters (outlined in grey). The timeframe shown extends from stimulus onset (predictive/random) to stimulus onset (expected/random). The histograms along the x-axes show the sum of significant frequency points per time point across cluster contributing channels. The reversal is shown in the histograms along the y-axes (sum of significant time points for each frequency across cluster contributing channels). **(A)** Significant cluster for the alpha/beta power differences between predictive minus random images. Scalp maps illustrate the topographical distribution of the greatest power differences (predictive - random) within **(i)** 0 – 200ms (14 – 19Hz), and **(ii)** 950 – 1200ms (10 – 18Hz). **(B)** Significant cluster for the alpha/beta power differences between expected minus random images. The scalp maps illustrate the topographical distribution of power differences (expected - random) within **(i)**1250 – 1750ms (10 – 14Hz) and **(ii)** 2500 – 3000ms (6 – 11Hz). A 50ms rift disjoins the 3000ms interstimulus timeframe as a result of the chosen epoch size and Fourier transform parameters (see *Materials and methods*). Both **4A** and **4B**, however, provide supportive indications to assume that in place of the 50ms rift, a steady increase in significant frequency points (histograms along the x-axes) would link the gradual increase in **4A** with the peak seen in **4B**.

Post hoc correlations demonstrated that the modulations of alpha/beta power (8-30Hz) within neither the entire pre-stimulus timeframe immediately prior to stimulus onset (1250 – 3000ms) nor the middle peak (1250 – 1750ms) significantly correlated with the magnitude of

the reduction of the N170 (Spearman's rho = .19, *p* = .838, 95% CI [-0.16 0.50]; Spearman's

rho = .04, *p* = 1, 95% CI [-0.31 0.38], respectively). A significant positive relationship was,

however, observed between the modulation of alpha/beta power underlying the final peak (8-

30Hz; 2500 – 3000ms) and the modulation of the N170 (Spearman's rho = .46, *p* = .021, 95%

CI [0.14 0.69]; Figure 5). All above *p*-values were Bonferroni-adjusted to correct for multiple

comparisons. Collectively, these findings suggest that the final peak could reflect a relatively

precise expectation of the upcoming stimulus. The continuous enhancement of alpha/beta

power extending throughout the entire interstimulus interval may, on the other hand, provide

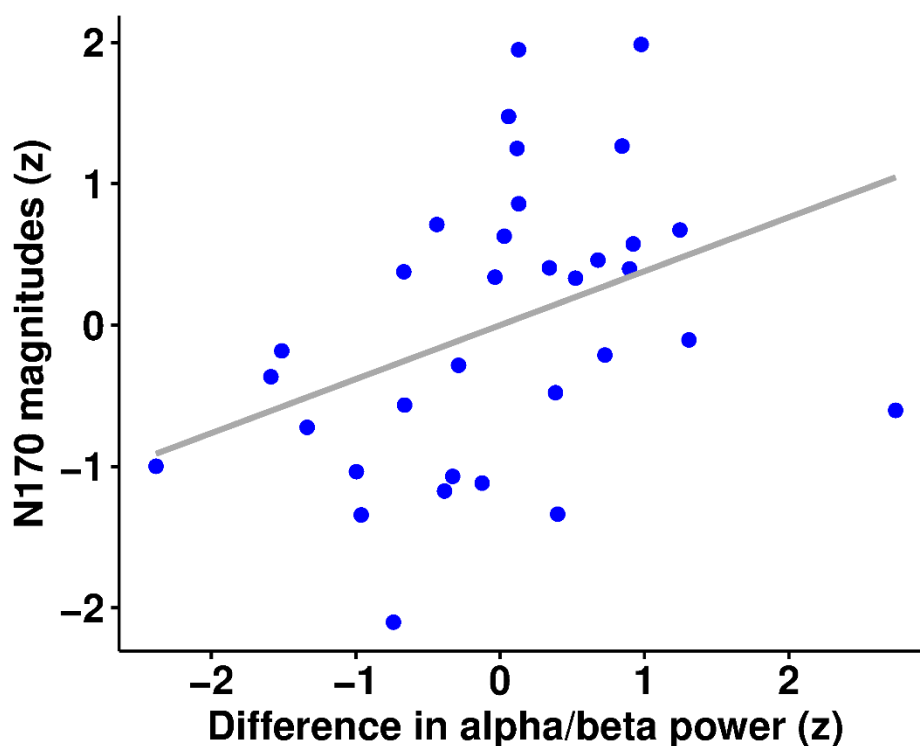an elongated favourable state optimal for expectation formation.

Figure 5 Correlation between the z-standardised modulations of pre-stimulus alpha/beta power (8-30 Hz; 2500 – 3000ms) and of the left-lateralised N170 (N = 33).

Discussion

The present study provides findings which suggest that the development of implicitly cued expectations is optimised by the early prioritisation of top-down processes. In turn, predictable visual events are met by relatively accurate implicit expectations to allow the brain to reserve cognitive resources. These processes were reflected by enhancements in pre-stimulus alpha/beta power for expected relative to randomly occurring faces. Intriguingly, this enhancement commenced as early as the onset of the predictive image and prevailed until the expected stimulus occurred. A correlation between the final elevation in alpha/beta power and the reduction of the N170 revealed a positive relationship between these two modulations. Ultimately, a reduction in bottom-up processing for expected relative to random images appeared to be reflected by a suppression in post-stimulus gamma power (Figure 6).

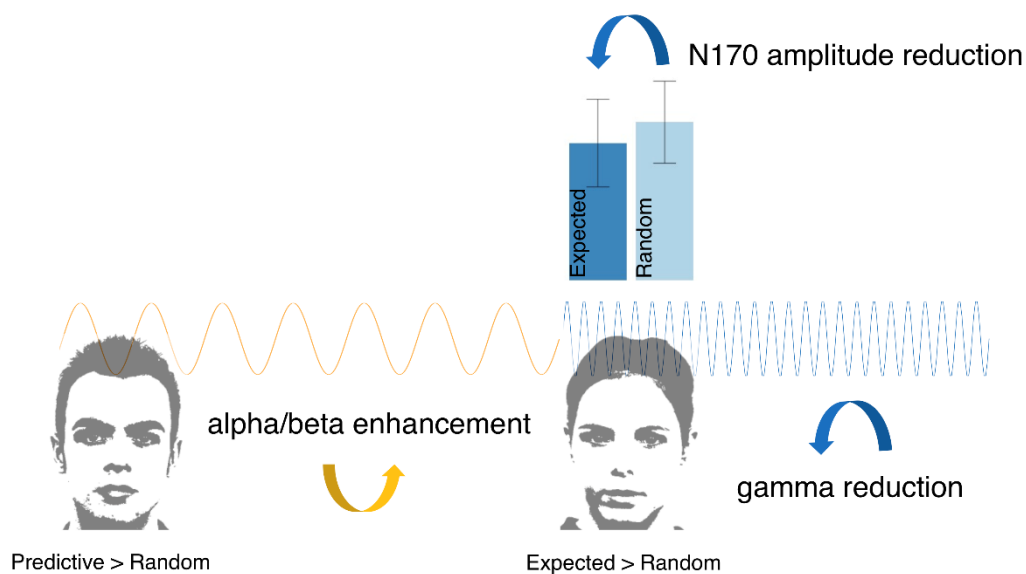**Figure 6** Schematic overview of observed electrophysiological modulations in response to predictive/expected relative to random images.

Through employing a short statistical learning test (training) prior to the EEG session, participants were given the chance to acquire implicit knowledge regarding the predictive relationship between paired face images. At first glance, the gain of neither a significant

decrease in response time nor a significant increase in accuracy for statistically expected images seems at odds with previous studies [1,7]. Considering the simplicity and repetitiveness of our task, however, the lack of behavioural effects could be caused by a ceiling effect. Turk-Browne and colleges [1], for instance, took into account that signs of statistical learning become evident after merely 2 to 3 repetitions. In their experiment, novel images and paired image combinations were introduced in each new block to eliminate the likelihood of reaching a plateau in response time and accuracy across expected and unexpected images. Noting that our focal point of interest lay with the origination of implicit expectations and not the statistical learning process as such, our task (the 25 images and paired-up faces remained the same throughout the experiment) may have permitted participants to quickly reach optimal proficiency. A further point to consider is that the images were presented for an entirety of 500ms which may have buffered a speeded reaction. A reduced presentation period could, thus, help encourage participants to give a more speeded response.

Whilst this study does not allow us to draw a strong conclusion regarding the lateralisation of the N170 effect, the observed modulation of the N170 does, however, appear to support the notion that participants implicitly differentiated between statistically expected and random images (Figure 2). This observation is in line with the established premise that a smaller fraction of cognitive resources is devoted to expected in comparison to somewhat unexpected or surprising events [5,7]. This in turn results in an attenuated electrophysiological response. An assumption as to why this attenuation was solely observed over left-lateralised electrodes is based on the principles that the right-lateralised N170 seems to be more sensitive to familiarity than the left-lateralised N170. That is, studies regarding the role of the N170 during face identity processing have shown that consecutive presentation of identical face images leads to a reduction in the N170 [33,34]. On the contrary, Jemel, Schuller & Goffaux [35] observed an enhanced N170 amplitude for familiar (famous) in comparison to unfamiliar

faces during overt face recognition. These habituation effects or memory-driven modulations were found to be predominantly right-lateralised, irrespective of gender [33-35]. Although consecutive depictions of the same face were not permitted within our pseudorandomisation parameters, each individual image was presented 55 times (regardless of its assigned category) throughout the two experimental sessions (training and EEG). Thus, it seems plausible that the N170 components for expected and random images may have, to some extent, been influenced by habituation. This right-lateralised habituation effect may, therefore, have dampened a considerable right-lateralised, expectation-related modulation.

On a different note, past studies have shown sex-related differences in face processing and the lateralisation of the N170. These findings suggest a dominating right lateralisation of the N170 in men and a more bilateral tendency in women [36,37]. Intriguingly, Proverbio and colleagues (2012) showed that sex-coding studies revealed a slightly different pattern in hemispheric lateralisation [38]. Here, women showed a more dominating left-lateralised response whilst men showed bilateral functioning; thus, suggesting that the involvement of the left hemisphere is essential during gender classification in both gender groups. Given that in the present study participants performed a gender classification task, the observed left-lateralised modulation of the N170 may have been influenced by the underlying nature of the task at hand and the fact that women outnumbered men (10 men and 23 women). However, this unbalanced sample makes it difficult to draw firm conclusions regarding any sex-related differences impacting hemispheric lateralisation. Ultimately, this question would be interesting to pursue in future, with an adequately designed study that specifically investigates how sex-related difference may impact the origination of face-related expectations.

On a final note, the current study used faces as stimuli because the N170 component is a well-established signature of face processing. We would, however, like to emphasize that the N170 has also been reported for non-face stimuli [5,39]. Whether the reduction of the N170

along with the modulations in alpha/beta power observed here for expected faces generalises across other stimulus categories remains to be investigated.

Acknowledging that the occurrence of the face images without a preceding predictive image lacked the predictability of the paired images, random images were deemed to require more cognitive resources and elicit an enhanced gamma-band response. In other words, since all images were task relevant and required a specific behavioural response, it seems likely that more cognitive resources were necessary for processing randomly occurring images, for which the gender was not foretold by a predictive image. In line with previous findings, we observed enhancements in GBA for the somewhat unexpected random images within peri- and post-stimulus periods (Figure 3A; for a review see [40]). Drawing on previous studies, gamma synchronisation has been shown to play a facilitatory role during specific neural functions such as feature binding of incoming visual information [16], the projection of prediction errors [10,14], and influencing synaptic strength during memory encoding and retention [15,41]. When linking these previous findings to our observations, the early peri-stimulus enhancement in GBA ($\sim 0 - 500$ms) could reflect the feeding forward of salient visual information which unifies each individual random image. This notion is supported by the observation that this early gamma-band enhancement is predominantly distributed over occipital electrodes (Figure 3B). Namely, regions which are associated with low-level perceptual processing. Initial processing of incoming visual information, therefore, seems to be augmented for the somewhat unexpected in comparison to expected stimuli.

Given that fast gamma frequencies ($\sim 60 - 100$Hz) are deemed optimal for strengthening synapses during the encoding and updating of short-term memories [14], the later post-stimulus enhancement in broadband gamma power ($\sim 500 - 1000$ms) could indicate that neural representations of the random images are encoded, retained, and revised [16]. Since the random images were recurrently presented over the duration of the experiment, it seems

plausible that associated representations could be kept "active" whilst being progressively updated by bottom-up sensory input upon depiction. Consistent with previous findings by Arnal, Wyart & Giraud [10] and Bauer and colleagues [11], the late enhancement in broadband GBA could, thus, reflect the augmented projection of prediction errors from early visual areas via low GBA and the revision of higher cortical levels via high GBA for random images (Figure 3B).

Complementary to previous studies, we found that the depiction of expected targets (in comparison to random faces) was met by an enhanced pre-stimulus alpha- and beta-band activity [11,12,17]. Extending previous findings, we observed that this enhanced alpha/beta activity persisted throughout the entire interstimulus interval. Interestingly, this elongated enhancement in alpha/beta power was governed by three peaks that marked the largest differences in power between expected and random images (Figure 4). The first peak, cresting shortly after stimulus onset (~ 0 – 200ms), suggests an elevation in alpha/beta activity for predictive relative to random images (Figure 4A). It appears that the initial activation of underlying processes facilitating expectation formation is subsequently triggered by the informative attribute of these cue-like images. Namely, the predictive image itself marks a pivotal juncture and foretells the approach of a certain expected face. The largest power difference between predictive/expected and random images appears to be primarily located across central electrodes within occipital, parietal, and frontal regions (Figures 4Aii and 4Bi). Even though the corresponding scalp map does not provide the same spatial resolution as magnetoencephalography results, this topographical distribution seems to show the engagement of predominantly dorsal regions, frequently associated with the propagation of top-down processes [10,11]. This continuous modulation in alpha/beta power, thus, seems to suggest that the prioritisation of top-down processes commences much earlier than just immediately prior to the occurrence of the expected target. Several past accounts have provided

evidence to suggest that alpha/beta power is an electrophysiological marker for the inhibition of forward feeding networks [13,42]. Arguably, it seems very plausible that a similar neural state is elicited upon the presentation of the predictive image. As such, the predictive image seems to give rise to a favourable condition in which increases in alpha/beta power reflect prioritisation of top-down processes whilst competing forward-feeding representations are suppressed. Especially since each predictive image only cued a single specific face, alternative neural representations were unnecessary to be processed or maintained during this interval. The reverse has been demonstrated recently in a study by Griffith et al., (2019), which showed that a decrease in alpha/beta power (disinhibition of relevant networks) facilitates information processing [42]. Thus, the continuous maintenance of a favourable condition within the timeframe confined by the onsets of the predictive and expected images could appear to aid the development of precise perceptual expectations.

In the context of predictive processing, alpha oscillations are leading modulators of attention and expectation. Yet, the process of how these two means modulate information processing remains controversial. Recent studies have suggested that whilst attention boosts the precision of prediction error by synaptic gain, expectation regulates the precision of top-down predictions [43,44]. In the latter case, a highly predictable event would, thus, yield fewer prediction errors which would be distinguishable by a subsequent attenuation in high frequency neural responses. Given that our predictive images invariably prompted certain face images, the expectation generated should ideally have been fairly accurate. Upon stimulus depiction, less iterative optimisations between hierarchical levels should, therefore, have been necessary to establish a relatively precise representation of the expected stimulus. The observed positive relationship between the final enhancement in alpha/beta activity (2500-3000ms; Figure 4B) and the left-lateralised reduction of the N170 appears to be coherent with this modulation framework. Namely, data-driven observation suggests that there is a systematic relationship

between the modulation in alpha/beta power occurring immediately prior to stimulus onset and the modulation of the peri-stimulus N170. This electrophysiological pattern is also in line with the notion that preactivated prior knowledge and subsequent predictions regarding an approaching target must be maintained until this predictable event is encountered [8]. Hence, this *post hoc* observation supports the hypothesis that processes of expectation are reflected in increased alpha/beta activity, which makes processing of expected stimuli more efficient and consequently reduces the amplitude of the N170. In this case, the prioritising of top-down predictions could, therefore, be elucidated in terms of prediction accuracy [11,43].

To summarise, we extended findings substantiating the presence of perceptual expectations. Of particular interest was the observation that the predictive images seemed to be essential for the initiation of the evolution of cued expectations. This was rendered by the enhanced alpha/beta activity cresting shortly after the depiction of the predictive faces. Even though the early peaks did not correlate with the modulation of the N170, the onset of the predictive image seems to initiate an early optimisation of a favourable neural state to boost the development of relatively precise perceptual expectations. The perception of predictable faces is subsequently facilitated through the implementation of these expectations, leading to a suppression in bottom-up information processing reflected by a reduction of the N170 and GBA. The facilitation of the development of implicitly cued face-related expectations, thus, appeared to prevail over the entire interstimulus period with fluctuations in alpha and beta power varying throughout the three second timeframe. One could question why this pre-stimulus enhancement in alpha/beta power fluctuates instead of being a stable and continual increase in power leading right up to the presentation of expected targets. An explanation could be that the spectral distribution pattern within this timeframe is biased by the temporal aspects of the experimental parameters. Given that three seconds are a relatively long interstimulus interval for this particular perceptual task, the gradual decrease in alpha/beta power (approx.

1500 – 2250ms; Figure 4B) could illustrate a progressive conservation of top-down processes before the final power enhancement which marks the imminent approach of the expected target. This would also explain why only the last peak in alpha/beta power positively correlated with the modulation of the N170. Averaging over the entire immediate pre-stimulus timeframe may have concealed a systematic relationship between the aggregated pre-stimulus alpha/beta power and the modulation of the ERP. The precise functional purpose of the second and most prominent peak would, however, benefit from further investigation, which we intend to do in a currently orchestrated study. In addition, although phase analysis is beyond the scope of the present study, it would be an intriguing research question for future studies to investigate alpha/beta phase coherence at the timepoints of each of the observed peaks.

In conclusion, the current study provides new insight into the temporal dynamics and development of face-related expectations. Notably, our findings raise the notion that the formation of cued expectations does not occur at random within the period preceding a statistically expected target. Instead, the facilitation of this developmental process appears to be instigated by the predictive image and proceeds, with fluctuations in growth, until shortly before the depiction of the target. In turn, expected stimuli are met by a relatively precise expectation to allow the brain to reserve cognitive resources. The evolution of implicit face-related expectations, thus, seems to prevail over the entire interstimulus period. From these results we could draw a timeframe confining the genesis and reflecting the developmental nature of cued face-related expectations. As such, these results open up opportunities for future studies to investigate and pinpoint more specific aspects underlying the anticipation of faces. It would, for instance, be of interest to narrow down the precise functional roles – as well as the neural networks – of the observed pre-stimulus peaks in alpha/beta power. Collectively, this would further advance our understanding of how the development of perceptual expectations is shaped in preparation for upcoming expected targets.

Acknowledgements

Supporting information

S1 File. Alternative ERP analysis. Repeated measures cluster permutation test approach.

References

1. Turk-Browne NB, Scholl BJ, Johnson MK, Chun MM. Implicit Perceptual

    Anticipation Triggered by Statistical Learning. J Neurosci. 2010;30(33): 11177–87.

    doi: 10.1523/JNEUROSCI.0858-10.2010.

2. Kluger DS, Quante L, Kohler A, Schubotz RI. Being right matters: Model-compliant

    events in predictive processing. PLoS One. 2019;14(6): e0218311.

    doi: 10.1371/journal.pone.0218311.

3. Clark A. Whatever next? Predictive brains, situated agents, and the future of cognitive

    science. Behav Brain Sci. 2013;36(3): 181–204.

    doi: 10.1017/S0140525X12000477.

4. Friston K. A theory of cortical responses. Philos Trans R Soc B Biol Sci.

    2005;360(1456): 815–36.

    doi: 10.1098/rstb.2005.1622.

5. Johnston P, Robinson J, Kokkinakis A, Ridgeway S, Simpson M, Johnson S, et al.

    Temporal and spatial localization of prediction-error signals in the visual brain. Biol

    Psychol. 2017;125: 45–57.

    doi: 10.1016/j.biopsycho.2017.02.004.

6. Johnston P, Overell A, Kaufman J, Robinson J, Young AW. Expectations about person

    identity modulate the face-sensitive N170. Cortex. 2016;85: 54-64.

    doi: 10.1016/j.cortex.2016.10.002.

7. Ran G, Zhang Q, Chen X, Pan Y. The effects of prediction on the perception for own-

    race and other-race faces. PLoS One. 2014;9(11): e114011.

    doi: 10.1371/journal.pone.0114011.

8. Brodski-Guerniero A, Paasch GF, Wollstadt P, Özdemir I, Lizier JT, Wibral M.

    Information-Theoretic Evidence for Predictive Coding in the Face-Processing System.

J Neurosci. 2017;37(34): 8273-8283.

doi: 10.1523/JNEUROSCI.0614-17.2017.

9.   Mayer A, Schwiedrzik CM, Wibral M, Singer W, Melloni L. Expecting to see a letter: Alpha oscillations as carriers of top-down sensory predictions. Cereb Cortex. 2016;26: 3146-3160.

doi: 10.1093/cercor/bhv146.

10.   Arnal LH, Wyart V, Giraud AL. Transitions in neural oscillations reflect prediction errors generated in audiovisual speech. Nat Neurosci. 2011;14(6): 797–801.

doi: 10.1038/nn.2810.

11.   Bauer M, Stenner MP, Friston KJ, Dolan RJ. Attentional Modulation of Alpha/Beta and Gamma Oscillations Reflect Functionally Distinct Processes. J Neurosci. 2014;34(48): 16117–25.

doi: 10.1523/JNEUROSCI.3474- 13.2014.

12.   Cao L, Thut G, Gross J. The role of brain oscillations in predicting self-generated sounds. Neuroimag. 2017;147: 895–903.

doi: 10.1016/j.neuroimage.2016.11.001.

13.   Klimesch W. Evoked alpha and early access to the knowledge system: The P1 inhibition timing hypothesis. Brain Res. 2011;1408: 52-71.

doi: 10.1016/j.brainres.2011.06.003.

14.   Bastos AM, Vezoli J, Bosman CA, Schoffelen J M, Oostenveld R, Dowdall JR, et al. Visual Areas Exert Feedforward and Feedback Influences through Distinct Frequency Channels. Neuron. 2015;85(2): 390–401.

doi: 10.1016/j.neuron.2014.12.018.

15.   Kaiser J, Lutzenberger W. Human gamma-band activity: A window to cognitive processing. Neuroreport. 2005;16(3): 207–11.

doi: 10.1097/00001756-200502280-00001.

16. Buschman TJ, Miller EK. Top-Down Versus Bottom-Up Control of Attention in the Prefrontal and Posterior Parietal Cortices. Science. 2007;315(5820): 1860–2. doi: 10.1126/science.1138071.

17. Spaak E, Fonken Y, Jensen O, de Lange FP. The Neural Mechanisms of Prediction in Visual Search. Cereb Cortex. 2016;26(11): 4327–36. doi: 10.1093/cercor/bhv210.

18. Oldfield RC. The assessment and analysis of handedness: The Edinburgh inventory. Neuropsychologia. 1971;9(1): 97–113. doi: 10.1016/0028-3932(71)90067-4.

19. Langner O, Dotsch R, Bijlstra G, Wigboldus DHJJ, Hawk ST, van Knippenberg A. Presentation and validation of the radboud faces database. Cogn Emot. 2010;24(8): 1377–88. doi: 10.1080/02699930903485076.

20. Blais C, Jack RE, Scheepers C, Fiset D, Caldara R. Culture shapes how we look at faces. PLoS One. 2008;3(8): e3022. doi: 10.1371/journal.pone.0003022.

21. Delorme A, Makeig S. EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. J Neurosci Methods. 2004;134(1): 9–21. doi: 10.1016/j.jneumeth.2003.10.009.

22. Cohen MX. Preprocessing Steps Necessary and Useful for Advanced Data Analysis. In: Analyzing Neural Time Series Data. Massachusetts: The MIT Press; 2014. pp. 73-85.

23. de Cheveigné A, Nelken I. Filters: When, Why, and How (Not) to Use Them. Neuron.

2019;102(2): 280–93.

doi: 10.1016/j.neuron.2019.02.039.

24. Gratton G, Coles MGH, Donchin E. A new method for off-line removal of ocular artifact. Electroencephalogr Clin Neurophysiol. 1983;55(4): 468–84.

doi: 10.1016/0013-4694(83)90135-9.

25. Gao C, Conte S, Richards JE, Xie W, Hanayik T. The neural sources of N170: Understanding timing of activation in face-selective areas. Psychophysiology. 2019;56(6): e13336.

doi: 10.1111/psyp.13336.

26. Kropotov JD. Sensory Systems and Attention Modulation. In: Functional Neuromarkers for Psychiatry. Elsevier; 2016. pp. 137–69.

27. Rossion B, Jacques C. The N170: Understanding the Time Course of Face Perception in the Human Brain. In: Kappenman ES, Luck SJ, editors. The Oxford Handbook of Event-Related Potential Components. New York: Oxford University Press; 2012. pp.115-142.

28. Shen C, Stasch J, Velenosi L, Madipakkam AR, Edemann-Callesen H, Neuhaus AH. Face identity is encoded in the duration of N170 adaptation. Cortex. 2017;86: 55–63.

doi: 10.1016/j.cortex.2016.10.010.

29. Taylor J, Shehzad Z, McCarthy G. Electrophysiological correlates of face-evoked person knowledge. Biol Psychol. 2016;118: 136–46.

doi: 10.1016/j.biopsycho.2016.05.011.

30. Oostenveld R, Fries P, Maris E, Schoffelen JM. FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. Comput Intell Neurosci. 2011;2011: 1–9.

doi: 10.1155/2011/156869.

31.   Cohen MX. Multitapers. In: Analyzing Neural Time Series Data. Massachusetts: The MIT Press; 2014. pp.203-9.

32.   van Pelt S, Heil L, Kwisthout J, Ondobaka S, van Rooij I, Bekkering H. Beta- and gamma-band activity reflect predictive coding in the processing of causal events. Soc Cogn Affect Neurosci. 2016;11(6): 973–80.

doi: 10.1093/scan/nsw017.

33.   Caharel S, D'Arripe O, Ramon M, Jacques C, Rossion B. Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: Evidence from the N170 ERP component. Neuropsychologia. 2009;47(3): 639–43.

doi: 10.1016/j.neuropsychologia.2008.11.016.

34.   Campanella S, Hanoteau C, Dépy D, Rossion B, Bruyer R, Crommelinck M, et al. Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. Psychophysiology. 2000;37(6): 796-806.

doi: 10.1017/S0048577200991728.

35.   Jemel B, Schuller AM, Goffaux V. Characterizing the Spatio-temporal Dynamics of the Neural Events Occurring prior to and up to Overt Recognition of Famous Faces. J Cogn Neurosci. 2010;22(10): 2289–305.

doi: 10.1162/jocn.2009.21320.

36.   Godard O, Leleu A, Rebaï M, Fiori N. Sex differences in interhemispheric communication during face identity encoding: Evidence from ERPs. Neurosci Res. 2013;76(1–2): 58–66.

doi: 10.1016/j.neures.2013.03.005.

37.   Proverbio AM, Riva F, Martin E, Zani A. Face coding is bilateral in the female brain. PLoS One. 2010;5(6): e11242.

doi: 10.1371/journal.pone.0011242.

38. Proverbio AM, Mazzara R, Riva F, Manfredi M. Sex differences in callosal transfer and hemispheric specialization for face coding. Neuropsychologia. 2012;50(9): 2325–32. doi: 10.1016/j.neuropsychologia.2012.05.036.

39. Thierry G, Martin CD, Downing P, Pegna AJ. Controlling for interstimulus perceptual variance abolishes N170 face selectivity. Nat Neurosci. 2007;10(4): 505–511. doi: 10.1038/nn1864.

40. Martinovic J, Busch NA. High frequency oscillations as a correlate of visual perception. Int J Psychophysiol. 2011;79(1): 32-38. doi: 10.1016/j.ijpsycho.2010.07.004.

41. Zheng C, Colgin LL. Beta and gamma rhythms go with the flow. Neuron. 2015;85(2): 236–7. doi: 10.1016/j.neuron.2014.12.067.

42. Griffiths BJ, Mayhew SD, Mullinger KJ, Jorge J, Charest I, Wimber M, et al. Alpha/beta power decreases track the fidelity of stimulus specific information. Elife. 2019;8: e49562. doi: 10.7554/eLife.49562.

43. Gordon N, Tsuchiya N, Koenig-Robert R, Hohwy J. Expectation and attention increase the integration of top-down and bottom-up signals in perception through different pathways. PLoS Biol. 2019;17(4): e300023. doi: 10.1371/journal.pbio.3000233.

44. Smout CA, Tang MF, Garrido MI, Mattingley JB. Attention promotes the neural encoding of prediction errors. PLoS Biol. 2019;17(2): e2006812. doi: 10.1371/journal.pbio.2006812.

S1 File

Alternative ERP analysis

The N170 amplitude was quantified by measuring the mean amplitude within the timeframe of 150 – 200ms in relation to a pre-stimulus baseline of 200ms. For this computation, the Mass Univariate ERP Toolbox for MATLAB [1] was employed to analyse the mean amplitude across selected channels (TP7/TP8, P7/P8) and within the respective timeframe. The ERPs for expected and random images were subjected to repeated measures cluster permutation tests with 5000 random iterations to correct for multiple comparisons. In line with our hypothesis that expected faces elicit a modulation in the N170 amplitude in comparison to random faces, a dependent, one-tailed t-test was computed for each electrode and timepoint (a total of 100 comparisons). Clusters arose when the one-tailed t-tests resulted in a p-value of or less than .05. The sum of the t-values within each cluster were compared and the maximum values extracted throughout each permutation to derive the null hypothesis distribution. Our test statistic of interest was thus deemed significant, if it grounded outwith the 95% tail of the derived distribution.

A significant reduction in amplitude was observed for expected in comparison to random images ($p = .039$) at left parietal and temporal-parietal channels (Fig 2A). The cluster permutation test also conveyed that this positive, left-lateralised cluster extends from approximately 158 – 188ms peri-stimulus (Fig 2A). In contrast, no significantly altered amplitude for expected faces ($p = .172$) was evident across the equivalent right-lateralised channels (Fig 2B).

References

1.   Groppe DM, Urbach TP, Kutas M. Mass univariate analysis of event-related brain

      potentials/fields I: A critical tutorial review. Psychophysiology. 2011;48(12): 1711–25.

      doi: 10.1111/j.1469-8986.2011.01273.x

References

2.2 Study II: Fluctuations in alpha and beta power provide neural states favourable for contextually relevant anticipatory processes

Marlen A. Roehe[a,b*], Daniel S. Kluger[b,c], and Ricarda I. Schubotz[a,b,d]

[a]Department of Psychology, University of Munster, Germany

[b]Otto-Creutzfeldt-Centre for Cognitive and Behavioural Neuroscience, University of Munster, Germany

[c]Institute for Biomagnetism and Biosignal Analysis, University of Munster, Germany

[d]Department of Neurology, University Hospital Cologne, Germany

under review

Abstract

Cued sensory input occasionally fails to immediately ensue its respective trigger. Given that our environments are rich in sensory cues, we often end up processing other contextually relevant information in the meantime. The experimental design of the present study allowed us to investigate how such temporal delays and visual interferences may impact anticipatory processes. Thirty-four participants were trained to remember an individualised set of eight paired-up faces. These paired-up faces were presented pseudorandomly in sequences of unpaired face images. To keep participants engaged throughout the electroencephalography study, they were instructed to classify each face image, according to its sex, as fast as possible without compromising accuracy. We observed dissimilar modulations in alpha and beta power between the 6-second timeframe encompassing the onsets of predictive and expected images (Temporal Delay block) and the 6-second timeframe encompassing the predictive, interference and expected images (Visual Interference block). Furthermore, an expectation-facilitated reduction of the face-sensitive N170 component was observed if an anticipated face image directly followed its corresponding predictive counterpart. This effect was no longer evident when the expected face was preceded by a distracting face image. Regardless of the block type, behavioural measures confirmed that anticipated faces were classified significantly faster and with fewer erroneous responses than faces not foretold by a predictive face. Collectively, these results demonstrate that whilst the brain continuously adjusts internal hierarchical generative models to account for temporal delays in stimulus onset and visual interference, the higher levels, and subsequent predictions, fundamental for expectation-facilitated behaviours remain intact.

Introduction

The sensory triggers constituting our natural surroundings are exceedingly fluid and common to rapidly change and develop. Our brains deal with this continual transmission of sensory material by means of filtering out relevant and dismissing irrelevant information (Ligeza et al., 2017; van Moorselaar et al., 2020). To achieve this, the current context plays a crucial role in assisting the brain to compartmentalise which sensory data to attend to (Limanowski et al., 2020). The contextual setting is therefore pivotal for narrowing down and selecting the most 'newsworthy' cues to focus on in order to adapt internal predictive models and behave accordingly. For instance, the sound of an ambulance siren informs us to vigilantly take in our surroundings in case we must make way for the onrushing vehicle. The notion that cues such as the latter evoke an array of internal predictions to optimise respective behaviours is well established (Clark, 2013; Friston, 2005). Within this *predictive processing* framework, predictions regarding upcoming events derive from prior knowledge and are propagated top-down within sensory hierarchies. Incoming sensory information, on the other hand, is mediated in a bottom-up motion. These complementary pathways are distinguishable by distinct neural signatures, whereby top-down processes are facilitated by alpha/beta frequency ranges (Arnal & Giraud, 2012; Bastos et al., 2015) and bottom-up processes by gamma frequencies (Bastos et al., 2015; also see Kaiser & Lutzenberger, 2005).

Apart from benefiting behavioural performance, having access to prior knowledge downregulates the amount of cognitive resources necessary to process a given stimulus (Blom et al., 2020; Klimesch, 2011). More precisely, the brain can draw information from these pre-activated stimulus-specific neural representations ahead of their respective afferent sensory input. Upon stimulus onset, fewer cognitive resources are required to process this already expected sensory input. In turn, neural activity such as gamma facilitated bottom-up processes can be minimised, leading to a subsequent reduction in neural expenses (Bauer et al., 2014;

also see Gordon et al., 2019). Diminished neural activity in response to a given target can, thus, be seen as a marker reflecting predictiveness. For instance, a reduction in the face-sensitive event-related potential, N170, can indicate if a face was expected and/or familiar (Johnston et al., 2016; Ran et al., 2014). A growing body of evidence has revealed that this pre-activation of already existing knowledge is associated with pre-stimulus enhancements in alpha/beta power (Brodski-Guerniero et al., 2017; Mayer et al., 2016). In a previous study, we even observed that this enhancement in low frequency power stretched throughout the entire interstimulus interval (ISI) between a cue and its implicitly expected target (Roehe et al., 2021). In a natural setting, however, it is relatively unlikely that a cue is immediately pursued by a single, specific anticipated event. More commonly, we are left to process various sensory input before the anticipated event occurs. Revisiting the ambulance scenario mentioned previously, sometimes a few seconds go by after first hearing the siren in which we are hastily scanning our surroundings for flashing blue lights. In these cases, we end up processing several afferent sensory input before glimpsing the anticipated event. To the best of our knowledge, the notion of how and to what extent contextually relevant interferences impact pre-activated expectations remains underexplored.

The central aim of the present electroencephalography (EEG) study was, therefore, to investigate how different 'interruptions', such as a delay in stimulus onset and distracting visual information, would impact the availability of cued prior knowledge and subsequent sensory predictions. Prior to the EEG study, participants were extensively trained to learn the identity of eight face images that were sorted into four customised pairs and were pseudorandomly embedded in sequences of unpaired faces. To remain engaged throughout the EEG experiment, participants were instructed to classify all occurring images as either female or male faces. To incorporate both a delay condition and an interference condition, we adapted our previous experimental design (Roehe et al., 2021) by (i) elongating the ISI between two paired-up face

images to generate a delayed temporal onset of the expected image, and (ii) inserting a contextually relevant face image in between the paired-up images to act as a visual interference. These *Temporal Delay* (TD) and *Visual Interference* (VI) blocks were presented in alternate succession.

Foremost, we expected to replicate findings indicating that expectations boost behavioural responses (Ran et al., 2014; Turk-Browne et al., 2010). In line with previous findings, we hypothesised that early access to a neural template of the anticipated face would permit bottom-up processes to be downregulated and hence, result in a diminished N170 response for expected images (Johnston et al., 2016; Ran et al., 2014; Roehe et al., 2021). On the contrary, since the interference images were contextually relevant, i.e., required a specific behavioural response and invariably occurred amidst the cue and anticipated images, we did not expect neural signatures of distractor suppression for these images. This foregoing assumption was based on previous research reporting that distractor interference was greatly reduced when their presentation was highly predictable in terms of spatial and temporal occurrences (van Moorselaar et al., 2020). Ultimately, we used time-frequency analyses to investigate to what extent a temporal delay in stimulus onset and visual interferences would influence the augmentation in pre-stimulus alpha/beta power and the predictive impact of the cueing stimulus. Succinctly, we observed that the brain shifts between prioritising neural states favourable for either top-down or bottom-up processes. These fluctuations in alpha/beta power conveyed different spectral patterns depending on whether a temporal delay in stimulus onset occurred or an interfering face image was presented in between the *predictive* and e*xpected* images. Thus, the brain seems to adapt internal predictive models to account for temporal delays in sensory input and visual interferences. Intriguingly, different levels within this hierarchical model seem to be fine-tuned to varying degrees so that contextually relevant predictions can continue to aid expectation-facilitated behavioural responses.

Materials and methods

Participants

A total of 37 participants took part in the study (31 females; 21.57 ± 3.14 years of age [mean ± SD]) after having signed informed consent based on the principles expressed in the declaration of Helsinki. Two participants had to be excluded because of excessive movement artefacts and one further participant because of extremely delayed response times (3 SD from the mean). Subsequently, the final sample size consisted of 34 participants (28 females; 21.62 ± 3.25 years of age [mean ± SD]). All participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), had no history of neurological and psychiatric disorders, and reported (corrected-to-) normal visual acuity. Participants were either awarded class credits or were reimbursed (24 Euros) for their participation. The study was approved by the Ethics Committee of the University of Munster (Department of Psychology).

Stimulus material and experimental design

Participants were presented with sequences of 20 recurring neutral face images (10 female) chosen from the Radboud Faces Database (RaFD; Langner et al., 2010). To limit the amount of eye movement, all images were scaled, using GIMP (GNU Image Manipulation Program), so that salient facial features, i.e., eye and mouth regions, aligned across images (Blais et al., 2008). Eight of these images (four male and four female images) were sorted into four reoccurring pairs, covering all possible paired-up combinations. Each individual participant was assigned a unique set of four pairs which were pseudorandomly presented within sequences of randomly reoccurring unpaired images. The face images (W = 9.5cm, H = 14cm) were depicted individually for 500ms in the centre of a grey background (subtending

visual angles of approx. 9° vertically and 6° horizontally). The depiction of these face images was immediately followed by a 2.5-second fixation period. A single trial was, therefore, a total of 3 seconds in length.

The experimental design consisted of two types of blocks, each occurring once during the training session and twice during the EEG-experiment. The blocks were shown in an alternating order, commencing with the first *Temporal Delay* (TD) block, and finishing with the second *Visual Interference* (VI) block. During the TD blocks each image was succeeded by an elongated fixation period of an additional 3 seconds. Hence, the timeframe between the onsets of two consecutive images was 6 seconds long (Figure 1). In contrast, the timeframe between the onsets of two face images in the VI blocks was only 3 seconds. The hidden face pairs in the VI blocks were, however, disjointed by the depiction of a randomly selected unpaired face image (*interference* image). Similar to the TD blocks, the interval between the paired images in the VI blocks was, subsequently, also 6 seconds in duration (Figure 1).

To balance the occurrences of each individual image, every face image was repeated twice during each of the four sequences making up a single TD block. After each sequence, a small break of one minute (at most) could be taken after which the next sequence would commence automatically. A longer self-determined break ensued upon completion of each block. With the additional 3-second fixation period within each trial, the TD blocks took approximately 16 – 19 minutes to complete, depending on whether participants made use of the entire one-minute break after completing each sequence. For the VI blocks, each image was repeated three times. In this case, each unpaired image occurred twice as a *random* and once as an *interference* image in each of the four sequences of a single VI block. Each VI block lasted approximately 12 – 15 minutes. This meant that together the two TD blocks comprised of 64 *predictive*, 64 *expected,* and 192 *random* trials and the two VI blocks of 96 *predictive*, 96 *expected*, 96 *interference,* and 192 *random* trials.

The experiment was programmed and presented using Presentation 18.1 (Neurobehavioral Systems, Dan Francisco, CA, USA).
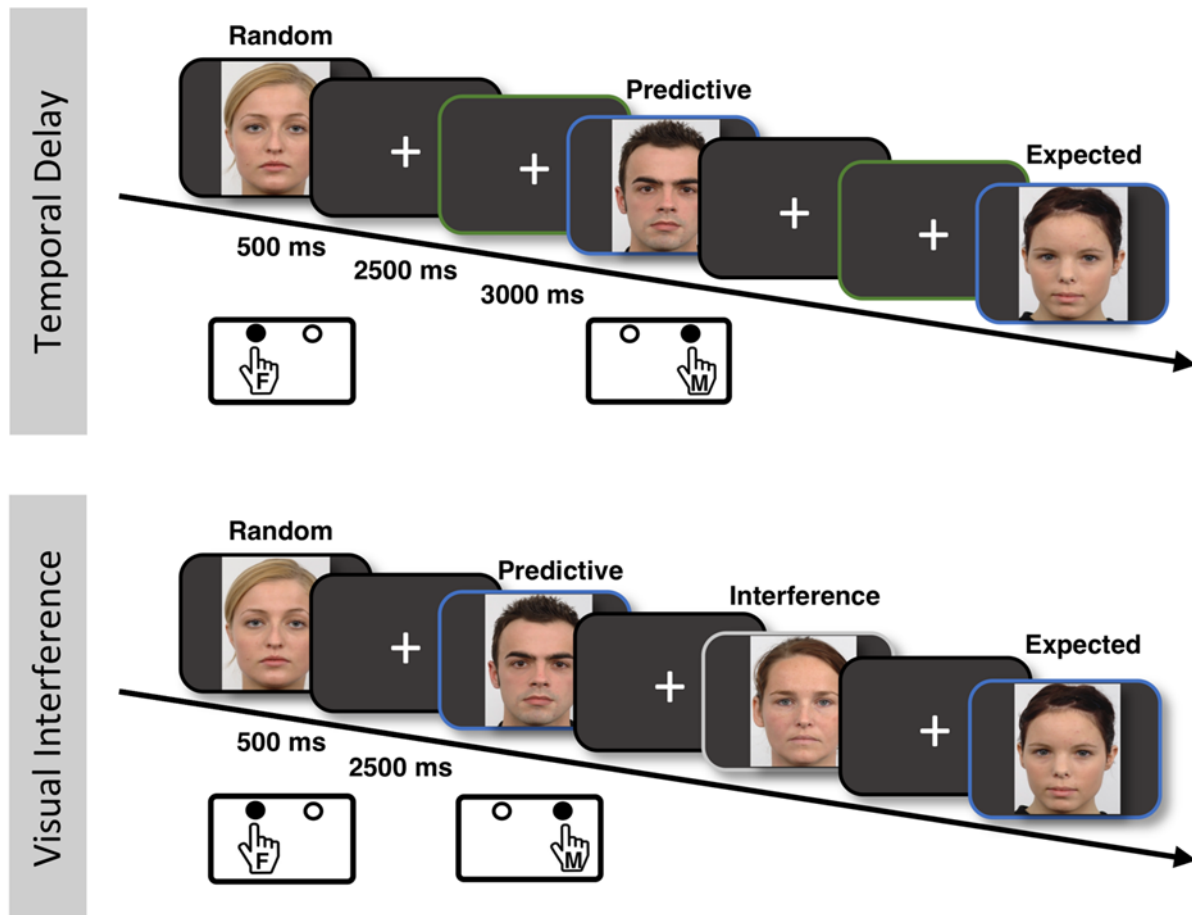

Figure 1 Schematic illustrations of the behavioural task and the sequential pattern of face images constituting the two types of blocks. The colours of the frames mark different event categories (blue: paired images; green: elongated ISI; light grey: interfering images).

Task

Prior to starting the experiment, participants were shown four individual face images (two male and two female faces) which they were asked to remember, as these would each be paired-up with a specific face. Participants then engaged in a classification task, in which they were instructed to distinguish between male and female faces as fast and as accurately as possible. In addition, they were required to learn and remember the identity of the faces which

immediately pursued each of the four remembered faces shown during the induction. For half of the participants, a left button press (left index finger) classified the depicted face as a female face and a right button press (right index finger) as a male face. This classification arrangement was reversed for the other half of participants. At the end of each experiment (training and EEG), the participants had to correctly identify each of the four image pairs.

Experimental procedure

The study took place on two consecutive days: a short behavioural training session was scheduled for the first day and the EEG-experiment for the following day. The training session allowed participants to become accustomed to the task at hand and explicitly learn the identity of the paired-up faces. During the 15-minute behavioural training, one TD and VI block were shown, each consisting of three sequences. At the end of the experiment, participants had to correctly identify all four of their personally tailored face pairs as a prerequisite to take part in the EEG-experiment the following day.

For the EEG-experiment, participants were comfortably seated in front of a response-box and screen in a dimly lit EEG booth. Over the duration of approximately an hour, two TD and VI blocks, each bearing four sequences, were shown in alternating order. Like before, at the end of the EEG-experiment, participants were asked to correctly classify the identity of their paired-up faces. At the end, a general questionnaire was carried out inquiring about participants' wakefulness and awareness.

EEG data acquisition and pre-processing

Scalp EEG was recorded using Brain Products' actiCAP snap system, combined with the BrainVision Recorder Software (Brain Products, Gilching, Germany). Sixty-two Ag/AgCl-electrodes were distributed on the cap according to the 10-20 system. Two further electrodes

served as electrooculograms and were placed above and beside the right eye to account for vertical and horizontal eye movements, respectively. Electrodes at FCz and FPz served as the online reference and ground, respectively, and were disregarded from all following analyses. EEG data was recorded at a sampling rate of 1kHz, with an applied online bandpass filter of 0.1 – 1000Hz. Electrode impedance was maintained to be below 10kΩ.

Recorded EEG data was pre-processed using MATLAB (R2017b) in combination with the EEGLAB toolbox (version 14.1.1b; Delorme & Makeig, 2004). Raw data was downsampled to 500Hz before applying a Butterworth bandpass filter (12 db/octave) with cut-offs at 0.1Hz and 30Hz for the ERP data and 0.5 and 40Hz for the time-frequency data, respectively. For the ERP analysis, continuous data was segregated into epochs extending from -250 to 600ms, locked to stimulus onset. To segregate continuous data into epochs of 3750s for the TF analysis, artificial triggers had to be added to the elongated timeframes separating each stimulus in the TD block. Here, the ISI was 6000ms seconds long instead of the 3000ms in the VI block. These artificial triggers were inserted 3000s after each image onset, allowing all continuous data-points to be separated into 3750ms epochs extending from -250 to 3500ms. The Gratton plug-in for EEGLAB was then applied to correct for ocular movement (Gratton et al., 1983). Noisy channels were semi-automatically inspected and interpolated if kurtosis criterion > 6. Of the ERP data, a total of 1% of electrodes were interpolated whereas 3.4% of electrodes were interpolated of the TF datasets. Artefacts were removed semi-automatically with the criteria that trials were discarded if artefacts exceeded an amplitude threshold of ± 75μV or conveyed fluctuations in voltage greater than 50μV respective to the previous sample point. Hereupon, trials were visually inspected and removed if containing any residual artefacts. Out of the initial 1136 trials (per participant), a mean number of 1081 trials remained of the ERP datasets and 873 trials of the TF datasets. Datasets were then re-referenced to a

common average and the number of random trials was reduced to match the number of predictive/interference/expected trials for the individual block types.

Statistical analysis

Behavioural analysis

Behavioural data was analysed using RStudio (version 3.6.0). For each individual participant, datasets were trimmed so that reaction times (RT) 3SD faster or slower than the mean were removed from all further analyses. For the RT analysis, any trials bearing missed or incorrect responses were also removed. The number of trials for each image category were then equalised; that is, the number of random images was reduced to match the number of predictive/interference/expected for each block type (TD block: $n \approx 64$ and VI block: $n \approx 96$). For the response time, an individual one-way, repeated-measures ANOVA was implemented for each of the two block types. A Bonferroni correction was applied to all *post hoc* comparisons. Given that the data for response accuracy was not normally distributed, non-parametric Friedman tests, along with *post hoc* Wilcoxon signed-rank tests, were applied to analyse the percentage of correct responses.

ERP analysis

The ERP datasets were averaged across each image category of interest (TD: expected and random; VI: expected, interference and random). Given that the ERP analysis was conducted to investigate the predictability of the different image types, the predictive images were disregarded because of their confounding informative, cue-like nature.

To measure the mean amplitude of the N170, the mean voltage within the timeframe of 140-180ms over electrodes P5/P6 and P7/P8 was calculated relative to the 250ms pre-stimulus

baseline (Ran et al., 2014). The mean amplitude was entered into a 2 x 2 repeated-measures ANOVA for the TD block with factors hemisphere (left vs. right) and image type (expected vs. random). For the VI block, a 2 x 3 repeated-measures ANOVA was applied with factors hemisphere (left and right) and image type (expected, interference and random). Where applicable, the degrees of freedom of the F-ratio were amended according to the Greenhouse-Geisser method.

Time-Frequency analysis

Spectral analyses were performed using MATLAB (R2020b) and the Fieldtrip toolbox (Oostenveld et al., 2011). To estimate spectral power, a fast Fourier Transform approach was applied to averaged trials. Here a Hanning taper was used for our frequencies of interest (2-30Hz), using a 500ms long sliding window which moved in fixed steps of 50ms and 1Hz increments.

As for the statistical analyses, cluster-based permutation tests were used to assess the differences in low frequency power between the different image conditions within each block type. First, time-frequency power was normalised by calculating the raw differences in power estimates between the predefined contrasts of interest, i.e., normalised difference $_{\text{expected vs random}}$ = (X-Y)/(X+Y) (Spaak et al., 2016). This normalised data of our predefined region of interest (O1/Oz/O2/PO7/PO8/PO4/PO3/POz) was then used for all statistical analyses and to generate time-frequency representations. For all planned contrasts, this normalised power was then subjected to Monte-Carlo randomisations using dependent sample t-tests and k =1000 permutations. Differences between image types were deemed significant with an alpha level below $\alpha = .05$.

A data-driven correlation was carried out to assess the relationship between the coexisting clusters, marking the immediate onset of the expected (in comparison to random)

faces of the VI block. For each participant (n = 34), the normalised power of the two observed clusters was averaged over channels, frequencies, and time. The averaged power of the beta suppression was then correlated with the averaged power of the alpha enhancement.

Results

Performance on classification task

The behavioural performance of the classification task was assessed in terms of response time and accuracy. Here we hypothesised that participants would respond and classify images faster and more accurately when the identity of the upcoming face was predictable. For the response time, both one-way, repeated-measures ANOVAs yielded a main effect for image types (TD block: $F(1.24, 40.97) = 304.67$, p < .001, $\eta_p^2 = .902$ [Greenhouse-Geisser corrected]; VI block: $F(1.21, 39.87) = 165.14$, p < .001, $\eta_p^2 = .833$ [Greenhouse-Geisser corrected]). In both cases, participants were able to classify expected images significantly faster than predictive (TD: $t(66) = -21.41$, p < .0001, d = -2.56; VI: $t(99) = -18.87$, p < .0001, d = -2.56), random (TD: $t(66) = -21.34$, p < .0001, d = -2.55; VI: $t(99) = -18.60$, p < .0001, d = -2.53), and interference images (VI: $t(99) = -16.76$, $p < .0001$, $d = -2.28$; Figure 2). The remaining contrasts yielded no significant differences in response time ($p > .05$). Similarly, the accuracy of the behavioural performances significantly differed between the image types regardless of the block type (TD: $\chi^2 (2) = 19.98$, $p < .0001$; VI: $\chi^2 (3) = 37.92$, $p < .0001$). It appears that fewer erroneous responses occurred during the classification of expected in comparison to predictive (TD: $p < .001$, $r = -0.38$; VI: $p < .0001$, $r = -0.36$), random (TD: $p < .0001$, $r = -0.40$; VI: $p = .002$, $r = -0.27$), and interference images (VI: $p < .0001$, $r = -0.38$; Figure 2). The remaining comparisons showed no substantial differences in accuracy between the image types ($p > .05$). A Bonferroni correction was applied to all *post hoc* comparisons.
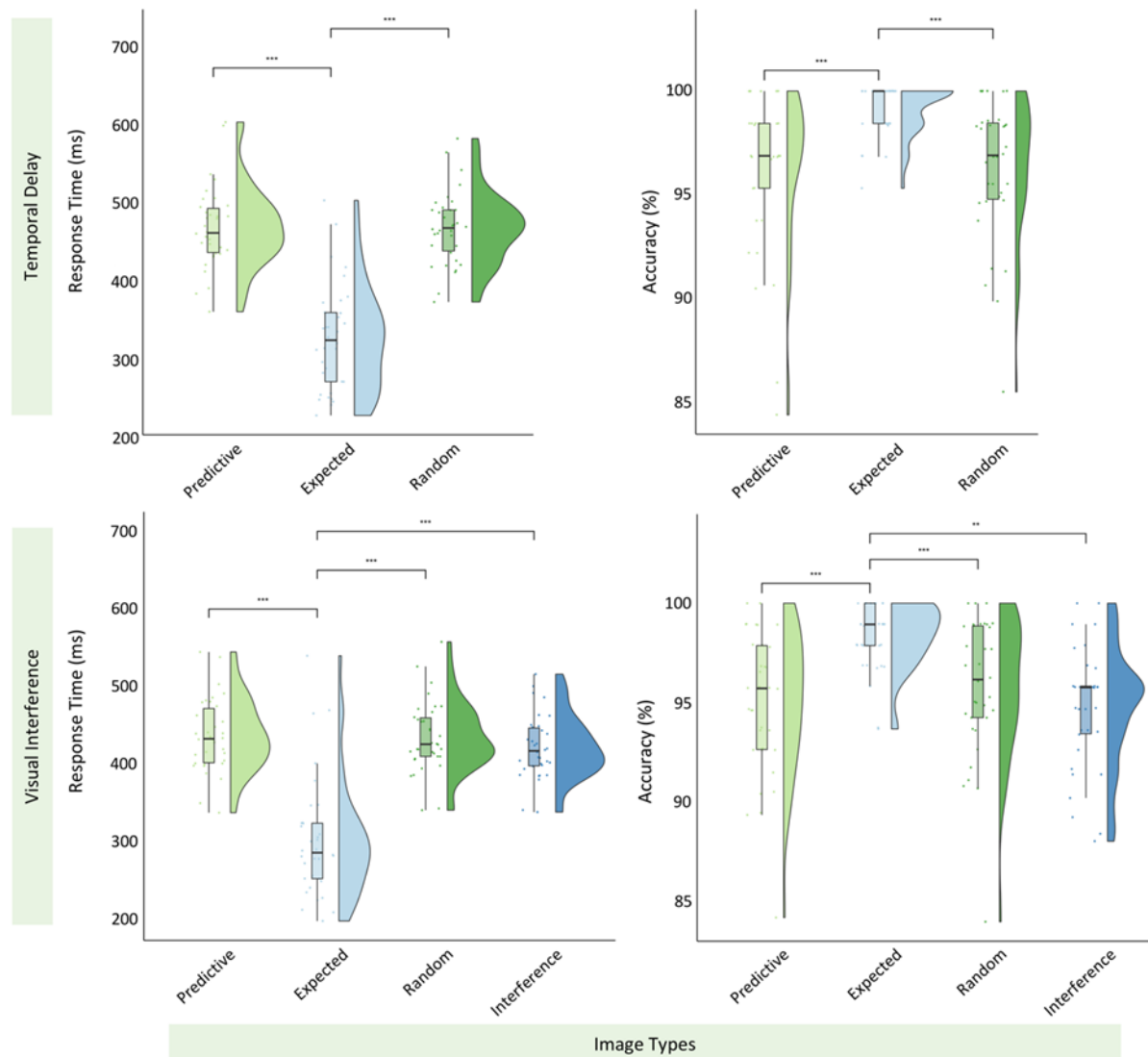
Figure 2 Behavioural performance for each type of image present in the two blocks. Significant differences ($\alpha \leq .05$) in response time (ms) and accuracy (%) are marked accordingly (*).

N170 responses

The modulation of the N170 component was analysed to investigate whether, in both block types, perceptual processing of predictable images was aided by top-down activity (Figure 3). It was hypothesised that in comparison to unpredictable images, fewer resources would be required to process cued images. The expected images were, thus, predicted to evoke a reduced N170 response compared to images where the identity of an upcoming face was not foretold by a certain cue.
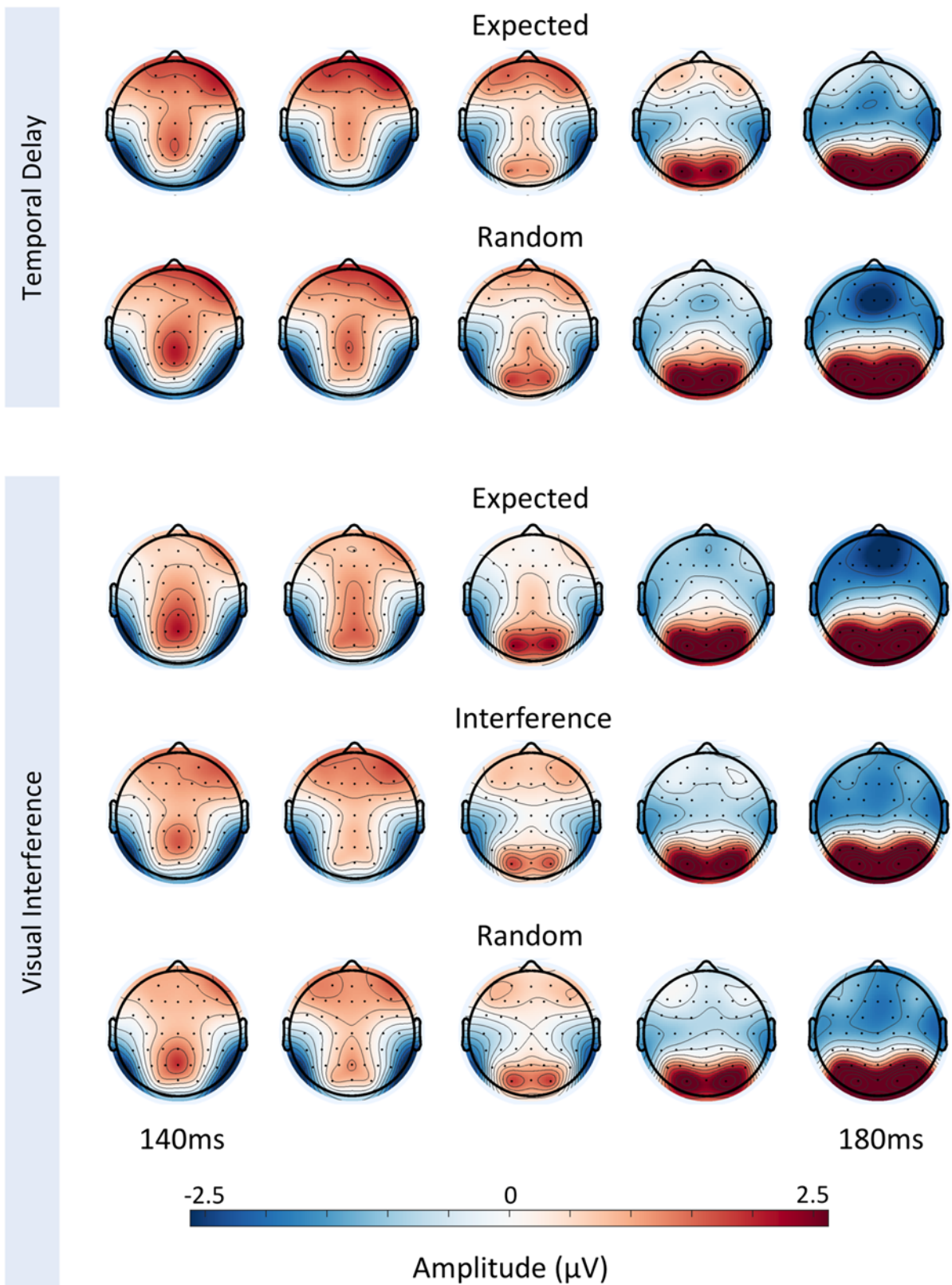
Figure 3 Topographies for each image condition of the two block types. The time extends from 140ms to 180ms in 10ms increments and depicts the period that was averaged to analyse the N170 component.

For the TD block, the 2 x 2 repeated-measures ANOVA yielded a significant main effect for image type (F(1, 33) = 5.95, p = .020, η_p^2 = .153) and no interaction between hemisphere and image type (F(1, 33) = 1.68, p = .204, η_p^2 = .049). More precisely, expected images reflected a significantly diminished response in contrast to random images (one-sided: t(33) = 2.44, p = .010, d = 0.42; Table 1). Interestingly, for the VI block, the 2 x 3 repeated-measures ANOVA yielded no significant main effect for hemisphere (F(1,33) = 0.20, p = .657, η_p^2 = .006) and image type (F(1.71, 56.42) = 0.20, p = .785, η_p^2 = .006 [Greenhouse-Geisser corrected]), nor a significant interaction between the two (F(2.00, 65.87) = 0.15, p = .864, η_p^2 = .004 [Greenhouse-Geisser corrected]). Hence, a significant reduction in the N170 was only observed when a predictable image immediately ensued its corresponding cue.

Table 1. N170 Amplitude (Mean±SD; μV).

Channel	Temporal Delay		Visual Interference		
	Expected	Random	Expected	Random	Interference
P7	-2.16±4.75	-2.26±4.44	-1.65±4.30	-1.52±4.34	-1.61±4.09
P8	-2.03±5.30	-2.30±5.34	-1.46±4.94	-1.40±4.94	-1.43±4.97
P5	-0.10±4.70	-0.36±4.48	0.43±4.29	0.22±4.38	0.26±4.39
P6	0.29±4.84	-0.37±5.05	0.84±4.75	0.51±4.91	0.56±4.74

Ongoing modulations of pre- and post-stimulus alpha/beta power

In a previously carried out study, we observed that alpha/beta power enhancements, extending from the onset of the predictive until the onset of the expected image, revealed an optimal state that prioritised top-down processes (Roehe et al., 2021). Based on these findings, we now hypothesised that a similar alpha/beta enhancement should be evident within the pre-stimulus timeframe prior to an expected image, regardless of the block type. However, both temporal delays and visual interferences may impede an elongated enhancement in alpha/beta

power that extends throughout the entire period, stretching from the onset of the cue until the presentation of the expected image.

For the TD block, the entire 6-second ISI was analysed as two succeeding 3-second timeframes and contrasted with the 6-second ISI between two random images. In the first 3-second timeframe, a distinctive negative cluster, encompassing both alpha and beta frequencies, marked the approximate timeframe of the behavioural responses classifying predictive images ($p < .001$; Figure 4). Considering the sizable differences in power marked by the first cluster and its subsequent impact on rendering smaller differences insignificant ($p = .072$), we readjusted the analysed time-window so that neural activity occurring during the period at which most behavioural responses occurred was disregarded. Analysing the timeframe from 1000 to 3000ms post-stimulus onset (predictive > random) consequently yielded a significant enhancement in alpha/low beta power for predictive images (relative to random images; $p = .046$). The second timeframe showed a late negative cluster just prior to the onset of the expected/random image ($p < .001$; Figure 4).

A very similar pattern in spectral power was observed for the VI block. Here, the onset of the predictive and interference images also evoked an alpha/beta suppression, relative to random images, at the time corresponding to the behavioural responses (predictive: $p = .002$; interference: $p = .002$). Once resizing the time-window to extend from 1000 to 3000ms post-stimulus onset, substantial enhancements in alpha/beta power succeeded the negative clusters (predictive > random: $p = .047$; interference > random: $p = .046$). Intriguingly, whilst the alpha/beta enhancement after the onset of the predictive image stopped near to 500ms before the onset of the interference image, the enhancement after the onset of the interference image remained until the presentation of the expected image. Similar to the TD block, the onset of the expected images was met by a suppression of largely beta power that commenced more than 1500ms prior to stimulus onset. Ultimately, we analysed the relationship of the two concurring

clusters leading up to the onset of the expected images. Interestingly, we observed a positive correlation between the suppression of high beta and the coinciding augmentation of alpha/low beta activity (Spearman's rho = .36, p = .035, 95% CI [0.03 0.63]).

Collectively, to ensure that these substantial enhancements in alpha/beta power (1000 – 3000ms post-stimulus onset) can indeed be linked to top-down processes reflecting expectations regarding the identity of the expected images, we analysed the timeframe covering the ISI between the onset of the expected and the ensuing random image. Like the previously stated results, the onset of the expected images also reflected a substantial suppression of alpha/beta power around the time of the behavioural response, irrespective of the block type (TD: $p < .001$; VI: $p < .001$). However, diverging from the earlier findings, no significant enhancements in alpha/beta power followed these suppressions. Instead, these suppressions seemed to persist for almost half the ISI (Figure 4).

Finally, we created data-driven correlation matrices for each of the eight predetermined parieto-occipital channels to analyse the relationship between the observed positive cluster and the significant N170 attenuation of the TD block. For each participant, the magnitude of the N170 reduction was correlated with each frequency and time point for each individual channel. Results revealed a positive relationship between the enhancement in alpha/beta power and the reduction in the N170 at two electrodes (PO7 and POz; $p < .05$; see Figure S1). Hence, these observations do not allow us to draw robust conclusions about the association between these two individual effects.
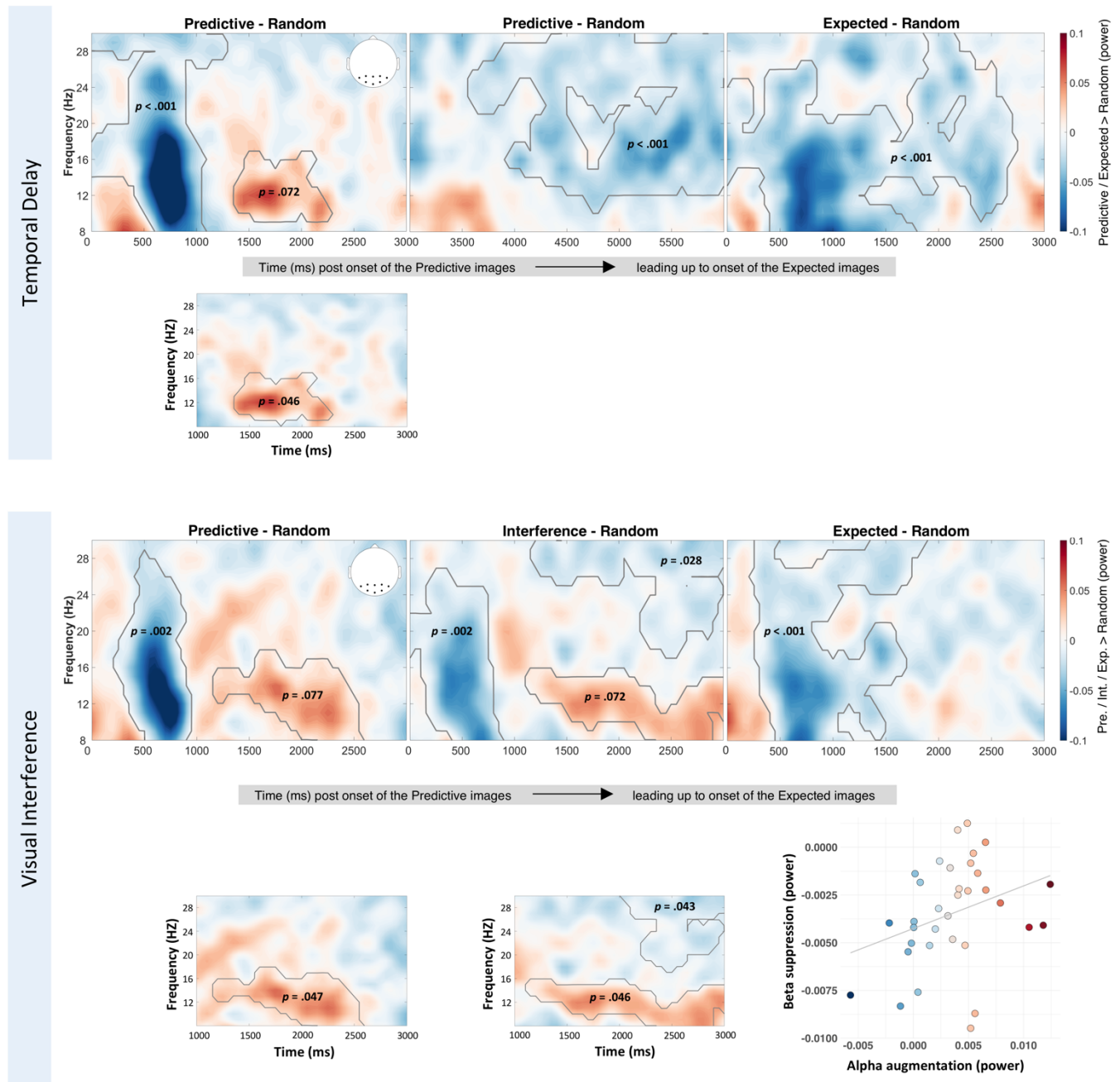
Figure 4 Time-frequency representations (TFRs) of dissimilarities in spectral power amongst the different image conditions of each block type. For the Temporal Delay block, the timeframe depicted stretches from the onset of the predictive image to the onset of the expected image. For the Visual Interference block, the timeframe extends from the onset of the predictive image to the onset of the expected image with the interference image occurring amid the two. For all TFRs, the timeframe between the onsets of two random images was used as a comparison. Subplots, representing a smaller timeframe (1000ms – 3000ms), are depicted below their original 3000ms counterparts. Clusters of interest, marking considerable differences in power between the chosen contrasts, are outlined in grey. The positive relationship between the beta suppression and alpha enhancement, reflected in the timeframe extending from 1000ms after onset of the interference/random images, is illustrated in the scatter plot.

Discussion

Ideally, an expected event would shortly ensue after being foretold by a cue. However, every now and then we are left waiting for an anticipated stimulus to occur and are sometimes even faced with processing other percepts in the meanwhile. In the current study, we looked at the N170 component in combination with spectral changes in alpha and beta frequencies to investigate how such temporal delays and visual interferences impact face-related expectations.

In the timeframe leading up to the depiction of expected images (relative to random images), we observed enhancement in both alpha and low beta oscillations, suggesting increased inhibition of incoming information, followed by alpha and beta suppressions, suggesting a release from this inhibition. These fluctuations in alpha/beta power conveyed different spectral patterns depending on whether a temporal delay in stimulus onset occurred or an interfering face image was presented in between the predictive and expected images. Moreover, we observed that time-resolved neural responses for expected images also showed dissimilar expressions depending on the block type. As such, a reduction in the N170 component was observed if the expected images followed the predictive faces, despite a relatively long temporal delay of 6 seconds, but vanished when preceded by a contextually relevant face image in the visual interference condition. Irrespective of the block type, behavioural measures confirmed that the identity of the cued face images was learned and could be predicted. As hypothesised, this led to a decrease in response time and an increase in overall accuracy.

Suppressions in alpha/beta power reflect a neural state optimal for bottom-up processes

Firstly, we observed suppressions encompassing alpha and beta frequencies during the first 1000ms after image onset for all image categories in contrast to random faces (Figure 4).

Given that both the predictive and expected images share an informative nature, although of different means, the observed decline in alpha/beta power seems to be in line with the previously established premise that tasks which require greater engagement also seem to evoke a greater alpha/beta power decrease (Griffiths et al., 2019; Lebar et al., 2017). Broadly, these studies build upon the notion that low frequency oscillations, predominantly alpha, are a marker for sensory inhibition and that decreases in alpha power reflect a release from this inhibition (Klimesch, 2011). Under this framework, enhancements in alpha/beta power would be linked to prioritising top-down processes, whilst a decline in these frequency ranges would shift priority to bottom-up processes. Notably, these task-related decreases in alpha/beta power extend across various tasks (Lebar et al., 2017; Pfurtscheller et al., 1994), sensory modalities, such as visual and auditory (Griffiths et al., 2019), and somatosensory (Lebar et al., 2017), as well as various species, including humans (Griffiths et al., 2019; Pfurtscheller et al., 1994), macaques (Haegens et al., 2011), and rodents (Wiest & Nicolelis, 2003). The omnipresence of this pattern in low frequency power, therefore, seems to hint towards a more general process beneficial for processing incoming information, rather than reflecting actual sensory information itself (Griffiths et al., 2019). We thus propose that in the current study, alpha and beta suppressions, associated with the predictive and expected images (relative to random images), signalled augmented contextual relevance.

Strikingly, we observed an identical alpha/beta response within a similar timeframe (~0 – 1000ms) for interfering images. One may question the sizable difference in alpha/beta power between interference and random images considering that the interference images are effectively just arbitrarily selected random images. Here we propose that the interfering images become an unintentional temporal cue for the onset of the expected images (Xu et al., 2021). Having learned the sequential structure of the VI block will have provided participants with the opportunity to anticipate that the onset of the expected image will ensue 3 seconds after the

onset of the interference image. Thus, although the interference images convey little to no differences in behavioural and time-resolved neural responses when compared to random images (Figure 2, Figure 3), their temporal station seems to be contextually relevant for predicting the imminent onset of anticipated faces. Given the distinctive attributes of predictive, expected, and interference images, the mutual decline in alpha/beta power, within the first second after stimulus onset, seems to coincide with the suggestion that this spectral modulation reflects a more generic neural state which boosts the ability to process contextually relevant information (Griffiths et al., 2019).

Enhancements in alpha/beta power reflect a neural state optimal for top-down processes

Extending the proposition raised above, an enhancement in alpha/beta power may reflect a contrasting neural state which is optimal for top-down processes, such as reflecting the activation of prior knowledge (Brodski-Guerniero et al., 2017; Mayer et al., 2016) and gating the gain and precision of neural communication (Lebar et al., 2017; Limanowski et al., 2020). Our findings revealed momentary enhancements in alpha/beta power within the timeframe ranging from the onset of the predictive to the onset of the expected image (in contrast to random images). Here we put forth the notion that like the alpha/beta suppressions, these enhancements do not, in fact, carry specific information regarding the anticipated face, but instead, create an optimal neural condition that is favourable for top-down processes. With this interpretation, we intend to unify some of the widely held theories regarding the role of alpha/beta frequencies. Brodski-Guerniero and colleagues (2017), for instance, conveyed that alpha and beta frequencies index the activation of prior face-related knowledge. More specifically, they observed that alpha/beta frequencies correlated with the amount of activated prior knowledge in face-specific brain regions, such as the fusiform face area (FFA). Likewise,

Mayer and colleagues (2016) showed that an increase in pre-stimulus alpha power was associated with the activation of former knowledge about previously observed letters. These observations fit well with the notion that a neural state ideal for top-down processes could promote access to activated neural representations whilst suppressing other less relevant external input. As such, fluctuations of alpha and beta power appear to reflect continuous shifts in gating inhibition of bottom-up processes whilst systematically giving rise to top-down processes. This suggestion provides a seamless transition to the proposal that alpha/beta power have been associated with gating neural communication (Lebar et al., 2017; Limanowski et al., 2020). Findings of these two studies revealed that beta power in occipital regions decreased when vision was task-relevant and increased when visual input was ignored. Therefore, these studies suggest that modulations of beta power gate to what extent a particular visual stimulus is processed at a given moment. This foregoing argument assumes that there is a systematic relationship between beta and alpha power. In other words, one would expect an increase in beta power to be accompanied by an increase in alpha power. In turn, the established neural state would be favourable for the facilitation of top-down processes, i.e., the activation of prior knowledge. Our results support such a relationship by revealing a correlation between the co-occurring beta suppression and alpha enhancement just prior to the presentation of expected (relative to random) images in the VI blocks (Figure 4). These findings would suggest that the beta suppression restricts top-down processes, yielding confined anticipatory processes. Arguably, this could indicate that in the VI blocks the pre-activated neural representation of the upcoming expected image is suppressed or dismissed in order to unbiasedly process the upcoming, contextually relevant interfering face (Blom et al., 2020). Hence, it appears that the underlying predictive hierarchical model is modified accordingly to account for the contextually relevant visual interferences.

On a related note, this spectral pattern of a coexisting beta suppression and alpha power enhancement was not observed in the TD block. Instead, the onset of the expected (relative to random) image was met by a drawn-out suppression in both alpha and beta power. Here we propose that the delayed onset of the anticipated image provided an elongated timeframe in which the brain is left 'waiting' for this upcoming event. Considering that the delay in stimulus onset remained consistent throughout the TD blocks, rather than keeping the representation for the predicted image active throughout the 6 second ISI, which could be relatively taxing, the brain efficiently shifts between neural states optimal for the current contextual setting. Namely, our results suggest that a temporary facilitation of relevant top-down processes shortly after the offset of the predictive images would suffice for the present context, before shifting to a neural state optimal for bottom-up processes in preparation for the upcoming sensory input.

Neural and behavioural signatures of anticipatory processes

Foremost, we observed that behavioural responses were significantly faster for anticipated faces compared to faces which were not foretold by a corresponding predictive face (Figure 2). In addition, significantly fewer erroneous responses were made when classifying a predicted in comparison to an unpredicted face. These anticipation-facilitated behavioural responses were evident for both the temporal delay and visual interference conditions. In line with previous studies, these behavioural effects confirm that top-down activity, such as explicit or implicit expectations, boosts behavioural responses (Ran et al., 2014; Turk-Browne et al., 2010).

Likewise, cued expectations have also been shown to influence time-resolved neural responses (Johnston et al., 2016; Ran et al., 2014). As hypothesised, we observed that the face-sensitive N170 was significantly diminished (reduced in negativity) for the four predictable face images of the TD block (Table 1). Notably, this neural activity in response to these

predictable images did not reach significance in the VI block. Previous studies have conveyed that the N170 diminishes for contiguous depictions of the same face (Caharel et al., 2009; Campanella et al., 2000; Ran et al., 2014). In these cases, the neural correlate of the identity of a particular face was available to be drawn upon to aid visual processing of the succeeding image. As such, fewer cognitive resources were required to process and respond to these predictable faces. In turn, this would be reflected in a diminished neural response, such as a reduction in the N170. The design of our TD block allowed predictive images to pre-activate a representation of the expected images which, in a top-down fashion, would be available to facilitate early processing of the directly ensuing expected image. On the contrary, given that in the VI block the predictive and expected images were segregated by an interfering image, the cue-triggered neural representation of the expected image might be temporally overwritten when the new sensory information of the interfering face becomes available. Especially considering that unlike other visual 'distractor' paradigms, the interference images in the current study were relevant to the task at hand and required visual processing. This reasoning is supported by findings showing that the brain regions involved in actively upholding face-related neural templates are also the regions processing this context-specific information (Brodski-Guerniero et al., 2017). Contextual relevance, thus, appears to play a fundamental role in selecting the most efficient forthcoming neural state. This line of thought is based on a related suggestion claiming that when multiple target representations are active simultaneously, trial-by-trial changes in environmental context play a considerable role in regulating the attentional-weight attributed to them individually (van Driel et al., 2019). The previously observed fluctuations in alpha and beta power provide confirmation that a goal-directed shift in neural states takes place between top-down and bottom-up processes throughout both block types. In addition, the interplay between the coexisting alpha enhancement and beta suppression in the visual interference condition provides an explanation as to why we observed

significant expectation-facilitated behavioural responses but no substantial differences in the N170 component between expected and random images. As mentioned previously, the beta suppression seems to restrict anticipatory process. Hence, it appears that lower sensory levels within the predictive hierarchical model are fine-tuned to account for the contextually relevant visual interferences whilst higher levels within this hierarchical predictive model remain stable (Long & Kuhl, 2018). A sustained maintenance of the anticipated face's sensory template is subsequently impeded, and the predictive model no longer provides a valuable source to draw identity-related expectations from ahead of its subsequent afferent sensory input. Access to higher cortical levels, for instance representing the learned associates between expected images and their corresponding behavioural responses, would, however, continue to enhance the propagation of specific behavioural predictions albeit the lack of an actively maintained face-related representation. As such, lower levels representing face-related templates could be overwritten by incoming visual information without compromising expectation-facilitated behavioural measures. This opens an exciting line of further investigations which could combine M/EEG and multivariate pattern analysis (Barne et al., 2020; Blom et al., 2020) to decode the amount of face-specific information activated ahead of its afferent sensory input after having attended to visual interferences.

Lastly, we corroborated that the observed enhancements in alpha/beta power are indeed neural signatures of a generic neural state which allow face-related neural patterns to emerge instead of representing face-specific information themselves. This interpretation was drawn from data-driven correlation matrices which merely provided moderate evidence to suggest that the enhancement in alpha/beta power for expected relative to random images (cluster in timeframe predictive > random) correlated with the significant modulation of the N170 obtained in the temporal delay condition (Figure S1). A question that remains, however, is that if these enhancements in power signal a general neural state that is beneficial as a means of

boosting top-down processes, what neural signatures do then carry actual stimulus specific information? Griffiths and colleagues (2019) put forth the notion that since the phase and power of a given oscillation are mathematically distinct, they may also have independent facilitatory purposes. This theoretical suggestion is supportive of previous findings revealing that the phase of low frequency oscillations (~8Hz) appears to carry information about a given stimulus (Michelmann et al., 2016). Note, however, that more evidence is required to conclusively attribute distinctive, yet complimentary, neural purposes to these two oscillation components.

Conclusion

In summary, we obtained novel findings which demonstrated that the brain shifts between neural states to optimise hierarchical predictive models and subsequent contextually relevant anticipatory processes. In both the TD blocks and VI blocks, we found indications of a neural state beneficial for top-down processes, i.e., granting early access to cued neural representations. Nevertheless, if the onset of the anticipated face was interrupted by the depiction of a distracting yet relevant image, priority shifted to processing the interfering visual input before giving restricted access to contextually relevant properties of the formerly cued neural representation (in the current study: the gender/sex of the expected face). In line with a growing body of literature, these fluctuating shifts boosting access to either internal representations or external stimulus specific information were mediated by modulations of alpha and beta power (Benwell et al., 2021; Brodski-Guerniero et al., 2017; Griffiths et al., 2019; Lebar et al., 2017, 2017; Limanowski et al., 2020; van Moorselaar et al., 2020). Our observations suggest that lower sensory levels within these predictive models are continuously revised, granting us to constantly adapt to the fluidity of our surroundings. Notably, neither a temporal delay in stimulus onset nor visual interferences negatively impacted expectation-facilitated behavioural responses. The brain, thus, appears to fine-tune different levels within

the hierarchical predictive model to different degrees. Whilst lower levels are revised and overwritten to allow us to have the most contextually adequate representation of our external environment at a given moment, higher levels appear to remain intact to aid higher cognitive functions. Ultimately, our findings fit neatly within the predictive processing framework by corroborating that the brain continuously adapts internal predictive architectures, and subsequent predictions, to optimise contextually relevant behaviours.

Acknowledgements

Declaration of interest

The authors declare no conflict of interest.

Authors contributions

Marlen A. Roehe: Conceptualization, Project Administration, Methodology, Software, Formal Analysis, Visualization, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing; **Daniel S. Kluger:** Conceptualization, Methodology, Software, Formal Analysis, Writing – Review & Editing; **Ricarda I. Schubotz:** Conceptualization, Project Administration, Methodology, Resources, Writing – Review & Editing, Supervision, Funding Acquisition.

Data availability statement

The data employed in this article can be found via OSF and will be made public after acceptance for publication.

Supporting Information

Please see **Figure S1** for additional information.

References

Arnal, L. H., & Giraud, A.L. (2012). Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences*, *16*(7), 390–398. https://doi.org/10.1016/j.tics.2012.05.003

Barne, L. C., de Lange, F. P., & Cravo, A. M. (2020). Prestimulus alpha power is related to the strength of stimulus representation. *Cortex*, *132*, 250–257. https://doi.org/10.1016/j.cortex.2020.08.017

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

Bauer, M., Stenner, M. P., Friston, K. J., & Dolan, R. J. (2014). Attentional Modulation of Alpha/Beta and Gamma Oscillations Reflect Functionally Distinct Processes. *Journal of Neuroscience*, *34*(48), 16117–16125. https://doi.org/10.1523/JNEUROSCI.3474-13.2014

Benwell, C. S. Y., Coldea, A., Harvey, M., & Thut, G. (2021). Low pre-stimulus EEG alpha power amplifies visual awareness but not visual sensitivity. *European Journal of Neuroscience*, ejn.15166. https://doi.org/10.1111/ejn.15166

Blais, C., Jack, R. E., Scheepers, C., Fiset, D., & Caldara, R. (2008). Culture shapes how we look at faces. *PLoS ONE*, *3*(8), e3022. https://doi.org/10.1371/journal.pone.0003022

Blom, T., Feuerriegel, D., Johnson, P., Bode, S., & Hogendoorn, H. (2020). Predictions drive neural representations of visual events ahead of incoming sensory information. *Proceedings of the National Academy of Sciences*, *117*(13), 7510–7515. https://doi.org/10.1073/pnas.1917777117

Brodski-Guerniero, A., Paasch, G. F., Wollstadt, P., Özdemir, I., Lizier, J. T., & Wibral, M. (2017). Information-Theoretic Evidence for Predictive Coding in the Face-Processing

System. *The Journal of Neuroscience, 37*(34), 8273-8283.

https://doi.org/10.1523/JNEUROSCI.0614-17.2017

Caharel, S., D'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to

repeated unfamiliar faces across viewpoint changes in the right hemisphere: Evidence

from the N170 ERP component. *Neuropsychologia*, *47*(3), 639–643.

https://doi.org/10.1016/j.neuropsychologia.2008.11.016

Campanella, S., Hanoteau, C., Dépy, D., Rossion, B., Bruyer, R., Crommelinck, M., &

Guérit, J. M. (2000). Right N170 modulation in a face discrimination task: An

account for categorical perception of familiar faces. *Psychophysiology, 37*(6), 796-

806. https://doi.org/10.1017/S0048577200991728

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of

cognitive science. *Behavioral and Brain Sciences*, *36*(3), 181–204.

https://doi.org/10.1017/S0140525X12000477

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-

trial EEG dynamics including independent component analysis. *Journal of*

Neuroscience Methods, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal*

Society B: Biological Sciences, *360*(1456), 815–836.

https://doi.org/10.1098/rstb.2005.1622

Gordon, N., Tsuchiya, N., Koenig-Robert, R., & Hohwy, J. (2019). Expectation and attention

increase the integration of top-down and bottom-up signals in perception through

different pathways. *PLoS Biology*, *17*(4), 1–28.

https://doi.org/10.1371/journal.pbio.3000233

Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*(4), 468–484. https://doi.org/10.1016/0013-4694(83)90135-9

Griffiths, B. J., Mayhew, S. D., Mullinger, K. J., Jorge, J., Charest, I., Wimber, M., & Hanslmayr, S. (2019). Alpha/beta power decreases track the fidelity of stimulus specific information. *ELife*, *8*. https://doi.org/10.7554/eLife.49562

Haegens, S., Nácher, V., Luna, R., Romo, R., & Jensen, O. (2011). α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(48), 19377–19382. https://doi.org/10.1073/pnas.1117190108

Johnston, P., Overell, A., Kaufman, J., Robinson, J., & Young, A. W. (2016). Expectations about person identity modulate the face-sensitive N170. *Cortex, 85,* 54-64. https://doi.org/10.1016/j.cortex.2016.10.002

Kaiser, J., & Lutzenberger, W. (2005). Human gamma-band activity: A window to cognitive processing. *NeuroReport*, *16*(3), 207–211. https://doi.org/10.1097/00001756-200502280-00001

Klimesch, W. (2011). Evoked alpha and early access to the knowledge system: The P1 inhibition timing hypothesis. *Brain Research*, *1408,* 52-71. https://doi.org/10.1016/j.brainres.2011.06.003

Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D. H. J., Hawk, S. T., & van Knippenberg, A. (2010). Presentation and validation of the radboud faces database. *Cognition and Emotion*, *24*(8), 1377–1388. https://doi.org/10.1080/02699930903485076

Lebar, N., Danna, J., Moré, S., Mouchnino, L., & Blouin, J. (2017). On the neural basis of sensory weighting: Alpha, beta and gamma modulations during complex movements. *NeuroImage*, *150*, 200–212. https://doi.org/10.1016/j.neuroimage.2017.02.043

Ligeza, T. S., Tymorek, A. D., & Wyczesany, M. (2017). Top-down and bottom-up competition in visual stimuli processing. *Acta Neurobiologiae Experimentalis*, *77*(4), 305–316. PMID: 29369296

Limanowski, J., Litvak, V., & Friston, K. (2020). Cortical beta oscillations reflect the contextual gating of visual action feedback. *NeuroImage*, *222*, 117267. https://doi.org/10.1016/j.neuroimage.2020.117267

Long, N. M., & Kuhl, B. A. (2018). Bottom-Up and Top-Down Factors Differentially Influence Stimulus Representations Across Large-Scale Attentional Networks. *The Journal of Neuroscience*, *38*(10), 2495–2504. https://doi.org/10.1523/JNEUROSCI.2724-17.2018

Mayer, A., Schwiedrzik, C. M., Wibral, M., Singer, W., & Melloni, L. (2016). Expecting to see a letter: Alpha oscillations as carriers of top-down sensory predictions. *Cerebral Cortex, 26*(7), 3146-3160. https://doi.org/10.1093/cercor/bhv146

Michelmann, S., Bowman, H., & Hanslmayr, S. (2016). The Temporal Signature of Memories: Identification of a General Mechanism for Dynamic Memory Replay in Humans. *PLOS Biology*, *14*(8), e1002528. https://doi.org/10.1371/journal.pbio.1002528

Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.M. (2011). FieldTrip: Open Source Software for Advanced Analysis of MEG, EEG, and Invasive Electrophysiological Data. *Computational Intelligence and Neuroscience*, *2011*, 1–9. https://doi.org/10.1155/2011/156869

Pfurtscheller, G., Neuper, C., & Mohl, W. (1994). Event-related desynchronization (ERD) during visual processing. *International Journal of Psychophysiology: Official Journal of the International Organization of Psychophysiology*, *16*(2–3), 147–153. https://doi.org/10.1016/0167-8760(89)90041-x

Ran, G., Zhang, Q., Chen, X., & Pan, Y. (2014). The effects of prediction on the perception for own-race and other-race faces. *PloS One*, *9*(11), 1–15. https://doi.org/10.1371/journal.pone.0114011

Roehe, M. A., Kluger, D. S., Schroeder, S. C. Y., Schliephake, L. M., Boelte, J., Jacobsen, T., & Schubotz, R. I. (2021). Early alpha/beta oscillations reflect the formation of face-related expectations in the brain. *PLOS ONE*, *16*(7), e0255116. https://doi.org/10.1371/journal.pone.0255116

Spaak, E., Fonken, Y., Jensen, O., & de Lange, F. P. (2016). The Neural Mechanisms of Prediction in Visual Search. *Cerebral Cortex*, *26*(11), 4327–4336. https://doi.org/10.1093/cercor/bhv210

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

van Driel, J., Ort, E., Fahrenfort, J. J., & Olivers, C. N. L. (2019). Beta and theta oscillations differentially support free versus forced control over multiple-target search. *The Journal of Neuroscience*, *39*(9), 1733–1743. https://doi.org/10.1523/JNEUROSCI.2547-18.2018

van Moorselaar, D., Lampers, E., Cordesius, E., & Slagter, H. A. (2020). Neural mechanisms underlying expectation-dependent inhibition of distracting information. *ELife*, *9*, e61048. https://doi.org/10.7554/eLife.61048

Wiest, M. C., & Nicolelis, M. A. L. (2003). Behavioral detection of tactile stimuli during 7-12 Hz cortical oscillations in awake rats. *Nature Neuroscience*, *6*(9), 913–914. https://doi.org/10.1038/nn1107

Xu, Z., Ren, Y., Guo, T., Wang, A., Nakao, T., Ejima, Y., Yang, J., Takahashi, S., Wu, J., Wu, Q., & Zhang, M. (2021). Temporal expectation driven by rhythmic cues compared to that driven by symbolic cues provides a more precise attentional focus in time. *Attention, Perception, & Psychophysics*, *83*(1), 308–314. https://doi.org/10.3758/s13414-020-02168-y
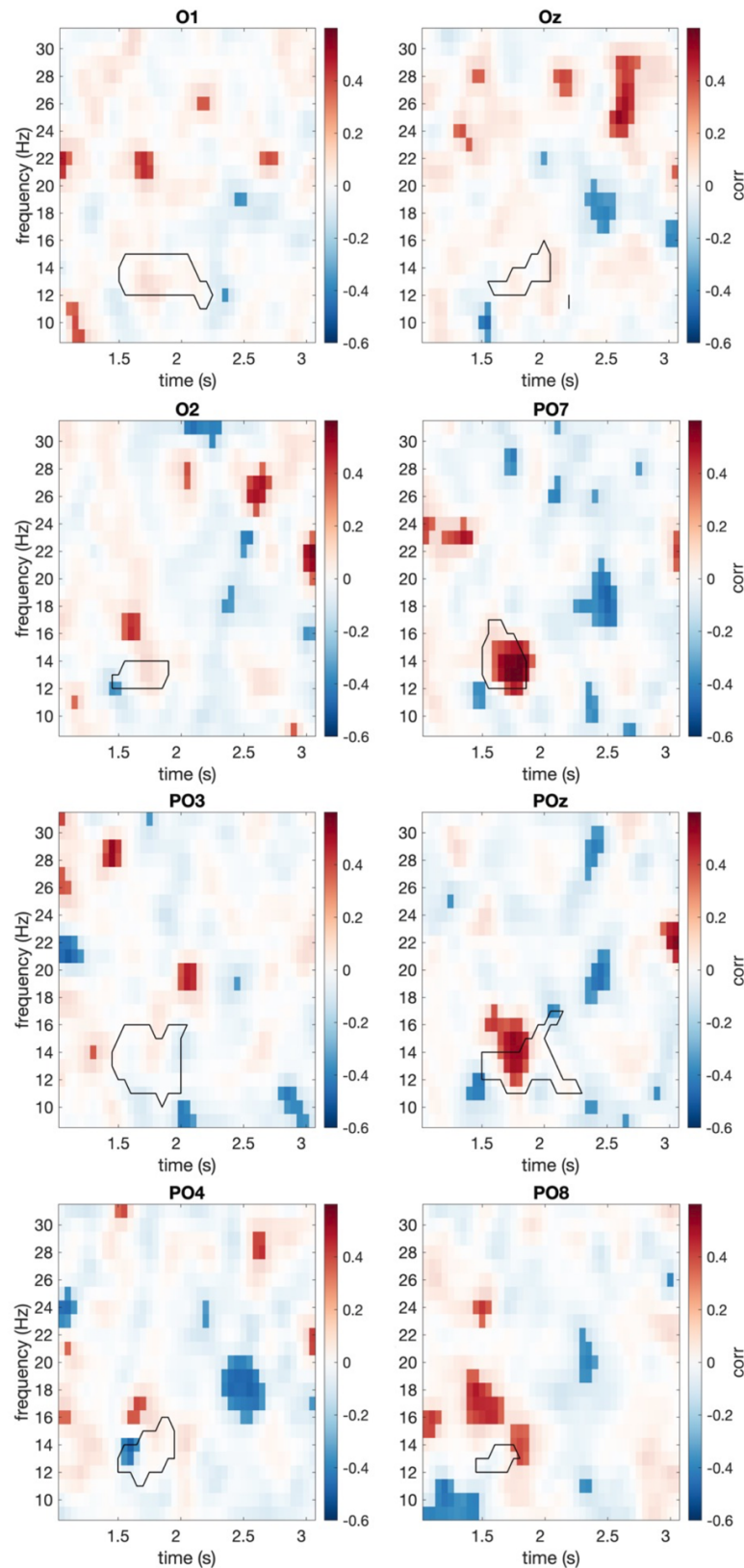
Figure S1 Correlation matrices showing the relationship between the underlying alpha/beta power differences of the positive cluster (Predictive > Random) and the reduced N170 response for the upcoming Expected image for each predetermined channel (TD block). Significant time and frequency points are marked opaque (correlation coefficient). The positive cluster of the substantial alpha/beta enhancement after the onset of the Predictive image (relative to Random images) is outlined in black.

2.3 Study III: The brain downregulates higher cognitive processes to compensate for processing contextually relevant interferences

Marlen A. Roehe[a,b*], Daniel S. Kluger[b,c], and Ricarda I. Schubotz[a,b,d]

[a]Department of Psychology, University of Munster, Germany

[b]Otto-Creutzfeldt-Centre for Cognitive and Behavioural Neuroscience, University of Munster, Germany

[c]Institute for Biomagnetism and Biosignal Analysis, University of Munster, Germany

[d]Department of Neurology, University Hospital Cologne, Germany

To be submitted

Abstract

The environmental context plays a crucial role in assisting the brain to compartmentalise which sensory information to select as contextually relevant or disregard as contextually irrelevant. In the present electroencephalography study, we examined how the brain compensates for processing contextually relevant information which disrupts prior activated predictions. Thirty-four participants were instructed to memorise an individualised set of eight sequential pairs. Although the first image of each memorised pair acted as a cue for its expected counterpart, these images were not presented in immediate succession. Instead, an unpaired image was pseudorandomly selected and presented amidst these pairs. To keep participants engaged throughout the experiment, they were instructed to correctly classify the sex of each face image as fast as possible without compromising accuracy. We obtained evidence to suggest that visually processing contextually relevant interferences was assisted by an enhanced suppression in alpha/beta power. This suppression in alpha/beta power has been shown to reflect a neural state optimal for processing incoming information. Time-resolved neural responses, in contrast, appeared to be downregulated for these interferences as revealed by a diminished P3b response when compared to cue and unpaired images. Interestingly, we observed that a larger reduction in the P3b responses (compared to unpaired images) was linked to a faster classification of the impending predictable images. These observations imply that the brain compensates for processing contextually relevant interferences by downregulating higher cognitive processes that are dispensable to the present context and its behavioural requirements.

Introduction

The brain's ability to select relevant and disregard irrelevant afferent sensory information is essential for perceiving and processing the world around us (Ligeza et al., 2017; van Moorselaar et al., 2020). Instead of focusing on a binary process that classes information as either relevant or irrelevant, a stimulating objective would be to examine whether the brain progressively censors incoming information of diminishing importance, and vice versa. Here, the current context would play a pivotal role in assisting the brain to compartmentalise which sensory input to prioritise over others (Limanowski et al., 2020). More specifically, the context aids in isolating the most "newsworthy" and relevant sensory events which are then processed and assembled into adequate internal representations of the external environment. According to *predictive processing* accounts, these representations are constructed as hierarchical models (Clark, 2013; Friston, 2005). Each level is consistently updated, whereby incoming sensory information regarding the present setting is compared to sensory predictions derived from prior knowledge. In terms of perception, a mismatch between the bottom-up driven sensory input and the top-down transmitted prediction generates prediction errors which prompt the revision of the subsequent representation. These distinct, yet complementary, sensory signals are reflected by contrasting neural signatures: whilst bottom-up processes are reflected by high-frequency gamma oscillations (Bastos et al., 2015; see also Kaiser & Lutzenberger, 2005), top-down processes are marked by low-frequency alpha/beta oscillations (Arnal & Giraud, 2012; Bastos et al., 2015). A growing body of studies has shown that enhancements in alpha/beta power demonstrate the inhibition of incoming sensory information (Haegens et al., 2011; Mathewson et al., 2011). That is, the brain suppresses incoming sensory information to give priority to top-down processes such as pre-activating representations of existing knowledge and subsequent predictions (Brodski-Guerniero et al., 2017; Mayer et al., 2016). In contrast, the release of such sensory inhibition is reflected by the suppression of alpha/beta power

(Houshmand Chatroudi et al., 2021; Klimesch, 2011). More generally, it has recently been proposed that modulations in alpha/beta power represent polar opposite neural states that either facilitate bottom-up or top-down processes (Griffiths et al., 2019; Roehe et al., 2021). Highly predictable environments, for instance, would be represented by neural states optimal for top-down processes (enhancement in alpha/beta power) which boost (i) the pre-activation of previously assembled representations and (ii) context-specific predictions. In a less familiar or erratic setting on the other hand, priority should be attributed to incoming afferent information (suppression of alpha/beta power) to enable us to efficiently interact with our environment.

This interplay between bottom-up and top-down signals is also evident in event-related potentials (ERPs). Past literature has shown that the face-sensitive N170 component is influenced by familiarity (Johnston et al., 2016; Ran et al., 2014; Roehe et al., under review) and whether the same face was shown consecutively (Caharel et al., 2009; Campanella et al., 2000). In contrast, the P3b component (a subcomponent of the P300 that is characterised by a centro-parietal scalp distribution in response to target stimuli) has been associated with surprise (Saurels et al., 2022; Valakos et al., 2020), an evaluation process assessing a signal's informative nature (Kluger et al., 2019), and the process of updating internal models (Donchin, 1981; Fonken et al., 2020).

Although all the findings mentioned above shine light on the dynamic nature of neural signatures underlying perception, little is known about how contextually relevant interferences are processed. Namely, in a natural setting, a sensory cue is not always pursued by a single expected event. Instead, we are commonly left to process several sensory signals whilst waiting for the anticipated event to occur. In a previous study we found evidence to suggest that the brain shifts between neural states that are optimal for bottom-up and top-down processes (Roehe et al., under review). These fluctuations in alpha/beta power indicated that the brain adapts internal representations to account for temporal changes in the environment and for

contextually relevant visual interferences. It was observed that if anticipatory processes were interrupted by a distracting but contextually relevant visual stimulus, the brain prioritised processing the interfering image above actively maintaining the representation of the expected event. This was demonstrated by the insignificant difference in the N170 amplitude between expected, arbitrary, and interfering images (Figure 1B). Intriguingly, it was concluded that not the entire predictive model of the expected stimulus was revised. Behavioural effects showed that even though the N170 component was impacted by processing interfering images, participants continued to respond to expected events substantially faster than to arbitrary and interfering events (Figure 1A). Thus, it was concluded that whilst the brain revises lower visual
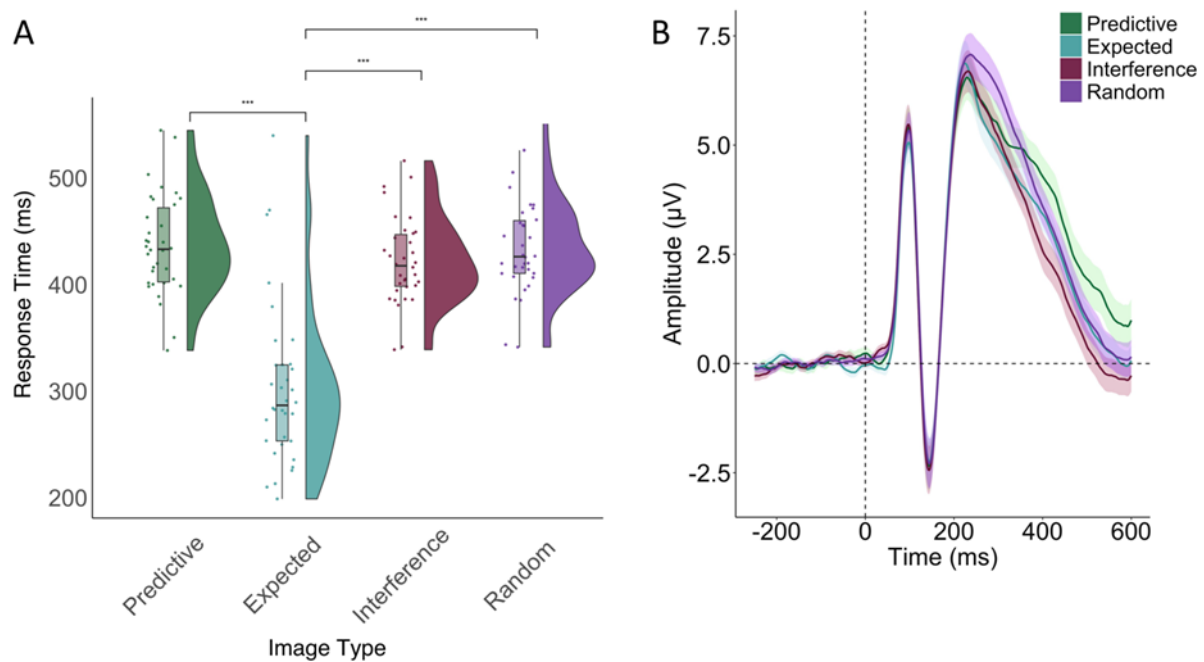

Figure 1 Overview of behavioural and ERP responses from Roehe et al., (under review). **(A)** Time taken to correctly categorise images as either male or female faces. **(B)** Grand-average waveforms depicting the N170 response across electrodes P5/6 and P7/8 for each of the four types of images (predictive, expected, interference, and random) relative to a 250ms pre-stimulus baseline. Figure was adapted from Roehe et al. (under review).

levels within the respective hierarchical model, higher cognitive levels remained intact to continue to aid anticipatory-facilitated behaviour. One question that subsequently arises is: how does the brain compensate for processing contextually relevant events in order to maintain such anticipation-facilitated behavioural effects? With this being the focal aim of the present study, we re-analysed the neural data of the previous electroencephalography (EEG) study (Roehe et al., under review), this time focusing on the perceptual processes of interfering images.

Foremost, we expected that the unpaired images, arbitrarily selected to act as *interference* images, would require more bottom-up processing than the explicitly learned sequential pairs. As such, we hypothesised that interference images would be marked by a stronger peri-stimulus alpha/beta suppression than *predictive* and *expected* images. Since the interference images were contextually relevant and required a certain behavioural response, we did not expect modulations in neural activity resulting from 'surprise' or distractor suppression. This foregoing hypothesis was based on previous research stating that the interference by distracting stimuli was greatly diminished if the temporal and spatial presentation of these images was highly foreseeable (van Moorselaar et al., 2020). Furthermore, we hypothesised that higher cognitive processes would be stifled or even impeded for interference images to allow expectation-facilitated behavioural responses for expected images to be maintained. A reduced P3b component was therefore expected to be evoked by the interference images relative to unexpected (*random*) and predictive images. In turn, we anticipated that diminished P3b responses (compared to random images) would be associated with faster behavioural responses for upcoming expected images (Figure 1A). Succinctly, the present study would convey novel insight into how the brain deals with contextually relevant interferences that disrupt visual anticipatory processes.

Materials and methods

Data statement

The data analysed here were taken from a previous dataset (Roehe et al., under review).

Participants

A total of 37 participants took part in the study (31 female; 21.57 ± 3.14 years of age [mean $\pm$ SD]), all of whom signed informed consent based on the principles expressed in the declaration of Helsinki. Two participants had to be excluded due to excessive movement artefacts and one additional participant because of prolonged reaction times (3 SD from the mean). The final sample size consisted of 34 participants (28 female; 21.62 ± 3.25 years of age [mean $\pm$ SD]). All participants were right-handed as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971), and reported (corrected-to-) normal visual acuity and no history of neurological and psychiatric disorders. Participants were either awarded class credits or were reimbursed for their participation. Ethical approval was granted by the Ethics Committee of the University of Munster (Department of Psychology).

Stimulus material

Twenty neutral face images (10 female) were selected from the Radboud Faces Database (RaFD; Langner et al., 2010). To limit eye movements, all images were scaled and cropped so that salient facial features, i.e., eye and mouth regions, generally aligned across images (Blais et al., 2008). For each participant, eight of these images (four male, four female) were randomly selected and sorted into four reoccurring pairs, covering all possible paired-up combinations.

Task and experimental design

Prior to the experiment, participants were shown four individual face images (two male, two female), i.e., one from each of the four pairs, which they were asked to memorise. During a training session, they were informed that these particular *predictive* images would each be paired-up with a specific *expected* face which they would have to correctly identify at the end of each experiment (training and EEG). During the task, face images were presented individually in portrait orientation (subtending visual angles of approx. 9° vertically and 6° horizontally) in the centre of a grey background. Learnt paired-up images were pseudorandomly presented within sequences of randomly reoccurring unpaired (*random*) images. Instead of presenting the paired-up faces in succession, an unpaired *interference* image was depicted in the timeframe after the predictive image and before the expected image (Figure 2). In other words, the participants were required to learn the identity of the faces which pursued immediately after having seen both the predictive (one of the four memorised faces shown during the induction) and interference image (arbitrarily selected unpaired image acting as a 'distractor'; Figure 2). To keep the participants engaged, they were instructed to distinguish between male and female faces as fast as possible without compromising accuracy. For the classification task, participants could answer by pressing a corresponding button using their right and left index fingers. The assignment of the male/female responses to the right/left index fingers was counterbalanced across participants but fixed for each participant.

Each face image was depicted for 500ms followed by a fixation period of 2500ms; hence, yielding trials of 3 seconds in length. For consistency purposes, each image was repeated three times to form sequences of approximately 3 minutes. In this case, each unpaired image occurred twice as a random and once as an interference image in each of the four sequences that made up a single experimental block. After each sequence, participants were given the option to either proceed immediately onto the next sequence or take a timed break of one

minute. After this one-minute break, the next sequence would commence automatically. Between the experimental blocks, participants took a self-determined break. Overall, the two blocks lasted approximately 12 – 15 minutes each and comprised of 96 *predictive*, 96 *expected*, 96 *interference,* and 192 *random* trials.

The experiment was programmed and presented using Presentation 18.1 (Neurobehavioral Systems, Dan Francisco, CA, USA).
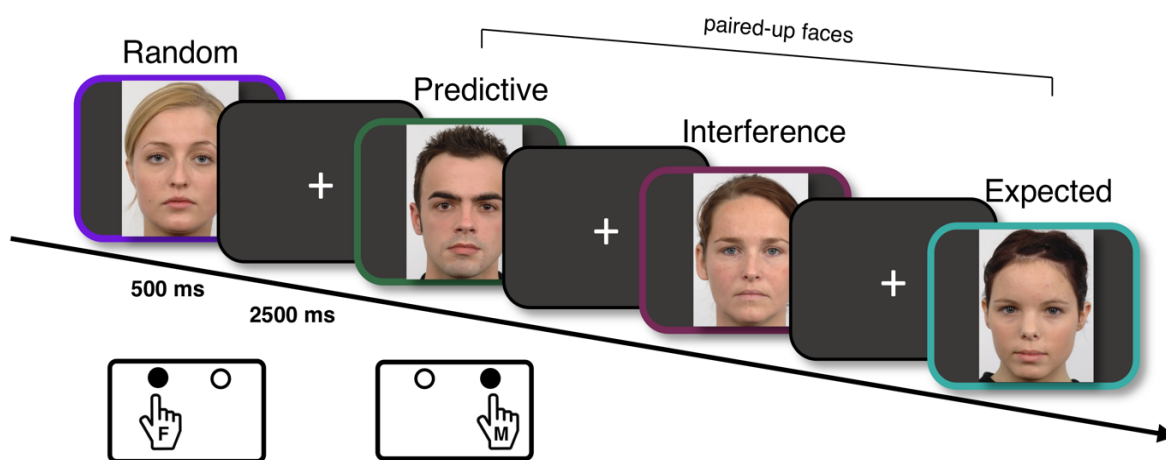

Figure 2 Schematic diagram of the experimental task. The colours of the frames mark different image categories (purple: random images; green: predictive images; burgundy: interference images; turquoise: expected images).

Experimental procedure

The study took place on two consecutive days: a short behavioural training session took place on day one and the EEG recording was scheduled for the following day. During this training session, three of the sequences were shown (approximately 9 minutes). The training session allowed participants to explicitly learn the identity of their individualised paired-up faces and become accustomed to the task at hand. At the end of the experiment, participants had to correctly identify all four pairs as a prerequisite for taking part in the EEG recording the following day.

For the EEG recording, participants were comfortably seated in front of a response-box and screen in a dimly lit EEG booth. Here, two experimental blocks, each bearing four sequences, were presented (approximately 24 – 30 minutes). Like before, participants engaged in a classification task. After completing the EEG recording, a general questionnaire was carried out inquiring about participants' wakefulness and awareness.

EEG data acquisition and pre-processing

Scalp EEG was recorded using Brain Products' actiCAP snap system, combined with the BrainVision Recorder Software (Brain Producted, Gilching, Germany). An elastic cap with sixty-two Ag/AgCl-electrodes (distributed according to the 10-20 system) was used for the recording. To record vertical and horizontal eye movements, two further electrodes were placed above and beside the right eye, respectively. FCz and FPz served as the online reference and ground, respectively. Continuous EEG data were recorded at a sampling rate of 1000Hz and with an online bandpass filter of 0.1 – 1000Hz. Electrode impedance was maintained to be below 10kΩ.

Continuous EEG data were pre-processed using MATLAB (R2017b) in combination with the EEGLAB toolbox (version 14.1.1b; Delorme & Makeig, 2004) and custom scripts. Raw data were downsampled to 500Hz before applying a Butterworth bandpass filter (12 db/octave) with cut-offs at 0.1Hz and 30Hz for the ERP data and 0.5 and 40Hz for time-frequency (TF) data, respectively. For the ERP analysis, continuous data were epoched around stimulus onset, i.e., extending from -250 to 600ms with the -250 – 0ms timeframe acting as a baseline for each trial. For the TF analyses, continuous datasets were segregated into 3750ms epochs extending from -250 to 3500ms (relative to stimulus onset). Next, the Gratton plug-in for EEGLAB was applied to eliminate ocular-movement artefacts (Gratton et al., 1983). Noisy channels were then semi-automatically inspected and interpolated if the kurtosis criterion > 6

(ERP data: M = 0.62 ± 1.16 interpolated channels; TF data: M = 2.15 ± 2.60 interpolated channels). Movement artefacts were removed semi-automatically with the criteria that trials were discarded if peak-to-peak fluctuations exceeded an amplitude threshold of ± 75μV or caused alterations in voltage greater than 50μV/ms. Hereupon, trials were visually inspected and removed if containing any residual artefacts. Datasets were then re-referenced to a common average and the number of random trials was reduced (every second random image was selected) to match the number of predictive/interference/expected trials.

Statistical analysis

Time-Frequency analysis

Spectral analyses were performed using the Fieldtrip toolbox (Oostenveld et al., 2011) for MATLAB (R2020b). A fast Fourier Transform approach was applied to averaged trials to estimate spectral power. For our frequencies of interest (2-30Hz), a Hanning taper was used with a 500ms long sliding window which moved in fixed steps of 50ms and 1Hz increments.

First, time-frequency power was normalised by calculating the raw differences in power estimates between the predefined contrasts of interest, i.e., normalised difference $_{\text{expected vs random}}$ = (X-Y)/(X+Y) (Roehe et al., 2021; Spaak et al., 2016). The normalised data of our predetermined region of interest (O1/Oz/O2/PO7/PO3/POz/PO4/PO8; Houshmand Chatroudi et al., 2021) were then used for all statistical analyses and to create time-frequency representations. The normalised data were analysed in R (R Core Team, 2014) using linear mixed-effect models (nlme package). The variance across participants was accounted for by including the participant as a random effect in the model. Having included this random effect, the maximum likelihood estimations were obtained for the fixed effects image contrasts (*predictive vs. random*, *interference vs. random*, and *expected vs. random*) and for frequency

bands (*alpha* and *beta* frequencies), which was considered as a nuisance predictor (Model 1). After considering the full model, non-significant interactions between fixed effects were identified through stepwise model comparisons and not included in the final model that best explained our dependent variable:

Model 1: Power ∼ Contrasts + Frequency + (∼1|Participants)

Tukey's method was used for all post hoc comparisons in order to account for multiple comparisons.

ERP analysis

The ERP datasets were averaged for each participant and each image category of interest (predictive, expected, interference, and random). To determine the mean amplitude of the P3b, the mean voltage within the timeframe of 300-600ms at electrodes CPz/CP1/CP2 and Pz/P1/P2 was calculated (Kluger et al., 2019; Valakos et al., 2020). These averaged voltage datasets were then analysed in R using linear mixed-effect models. The image category (*predictive*, *expected*, *interference*, and *random* images) was considered as a fixed predictor of voltage variance and the electrode distribution (*CPz, CP1, CP2, Pz, P1*, and *P2*) was fitted as a nuisance predictor (Model 2). Similar to the ERP analysis, participants were modelled as a random effect. Stepwise model comparisons were used to identify and remove non-significant interactions between fixed effects after having considered the full model.

Model 2: Voltage ∼ Category + Electrode + (∼1|Participants)

For all planned contrasts, Tukey's method was applied to account for multiple comparisons. Lastly, we assessed whether a reduced P3b response for interference images –

relative to random images – was linked to a faster classification of the upcoming expected image. For each participant, the voltage was averaged over the electrodes and timeframe of interest for the P3b component. The difference in mean voltage was then calculated between the interference and random images and correlated with the mean response time for the expected images using a Spearman's rank correlation test.

Results

Peri-stimulus alpha/beta power

To examine differences in early visual processing, we analysed the peri-stimulus alpha and beta power of the image types predictive (M: $0.66^{-2} \pm 0.03$ power), interference (M: $-1.66^{-2} \pm 0.03$ power), and expected (M: $0.99^{-2} \pm 0.04$ power), which was normalised relative to random images. The linear mixed-effect model identified the fixed effect image category to be significant ($F(2, 167) = 13.40$, $p < .0001$). As hypothesised, peri-stimulus alpha/beta power was reduced upon visually processing interference images in contrast to predictive and expected images (interference-random vs. predictive-random: $z = -4.13$, $p = <.0002$, 95% CI = [-0.04; -0.01], $d' = -0.72$; interference-random vs. expected-random: $z = -4.70$, $p = <.0001$, 95% CI = [-0.04; -0.01], $d' = -0.81$; Figure 3). No substantial difference in alpha/beta power was observed between predictive-random and expected-random images ($z = -0.57$, $p = .836$, 95% CI = [-0.02; 0.01], $d' = -0.1$).
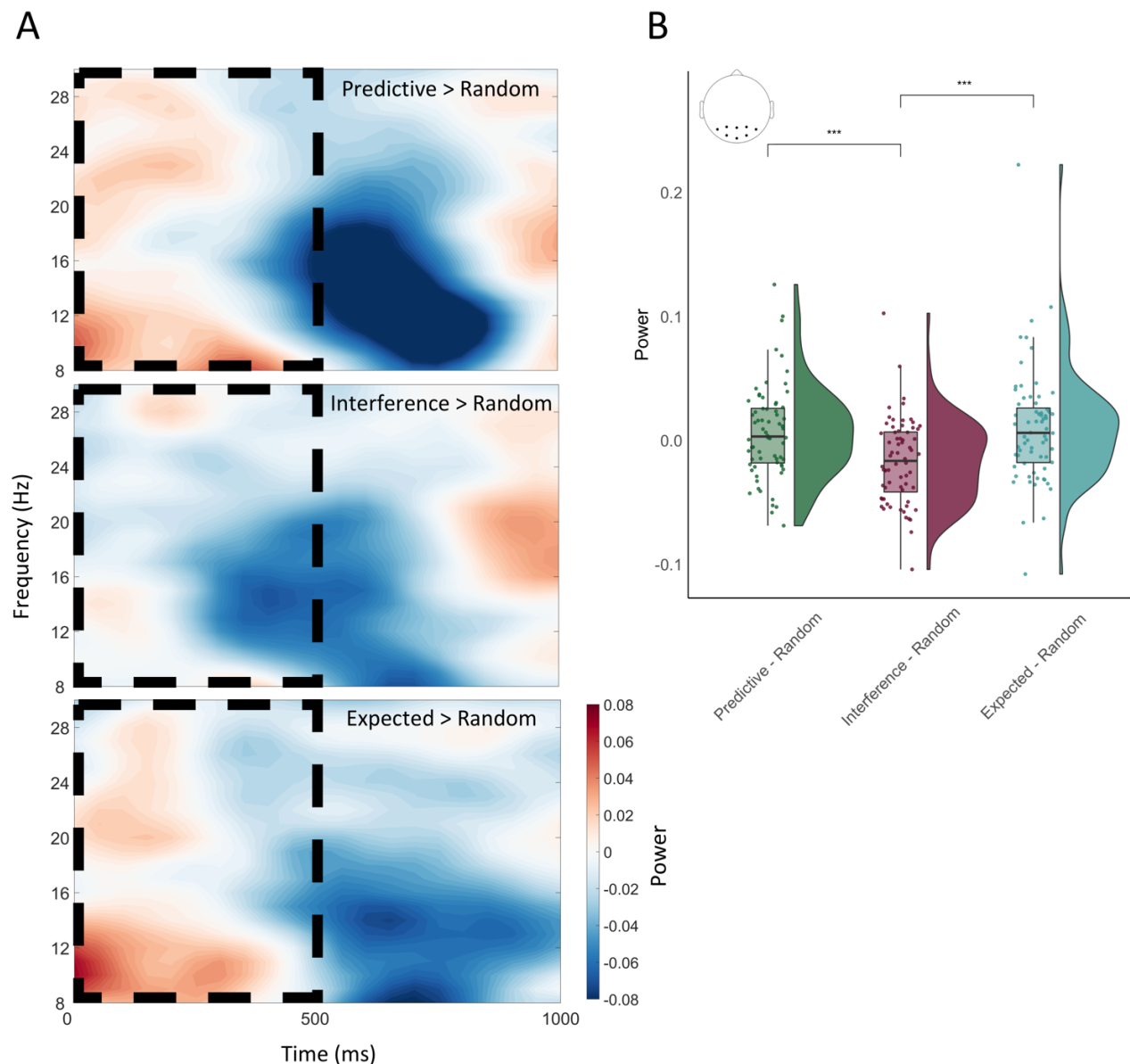
Figure 3 Normalised alpha/beta power modulations for Predictive, Interference and Expected images extending from stimulus onset to 1000ms post-stimulus onset. (A) Time-frequency representations of estimated power changes in alpha and beta frequency ranges. The dashed frame highlights the 500ms during which images were presented. Observed fluctuations in estimated power is relative to random images (see Materials and methods for a detailed explanation regarding the normalisation applied here). **(B)** Differences in normalised peri-stimulus alpha/beta power (0 – 500ms) between the image types: Predictive, Interference, and Expected. The scalp map depicts the parieto-occipital region of interest. All power estimates used for analyses and to create illustrations were averaged across those electrodes. Significant differences in alpha/beta power are marked accordingly (Note: * p < .05; ** p < .01, *** p < .001).

P3b response

The P3b response was analysed to determine to what extent higher cognitive processes differed amongst the image types (predictive, interference, expected, and random images). It was hypothesised that whilst highly informative images, i.e., predictive images, are likely to elicit a large P3b response, predictable (expected images) and less informative images (interference images) would elicit a diminished P3b response.

We identified the fixed effect for image category to be significant ($F(3, 369) = 68.48$, $p < .0001$). The obtained results revealed that predictive images evoked the largest P3b response ($\mu = 4.69\mu V$), followed by random ($\mu = 4.14\mu V$), interference ($\mu = 3.54\mu V$), and expected images ($\mu = 2.99\mu V$; Figure 4). The estimated differences between the different image types, as well as their corresponding 95% confidence intervals, are presented in Table 1. The post hoc analyses conveyed significant differences between all image types (Table 1).

Table 1 Estimates, corresponding 95% confidence intervals, SE, z-statistic, effect size, and *p*-values of the contrasts corresponding to the fixed effect *category* of the P3b linear mixed effect model: * p < .05, ** p < .01, *** p < .001

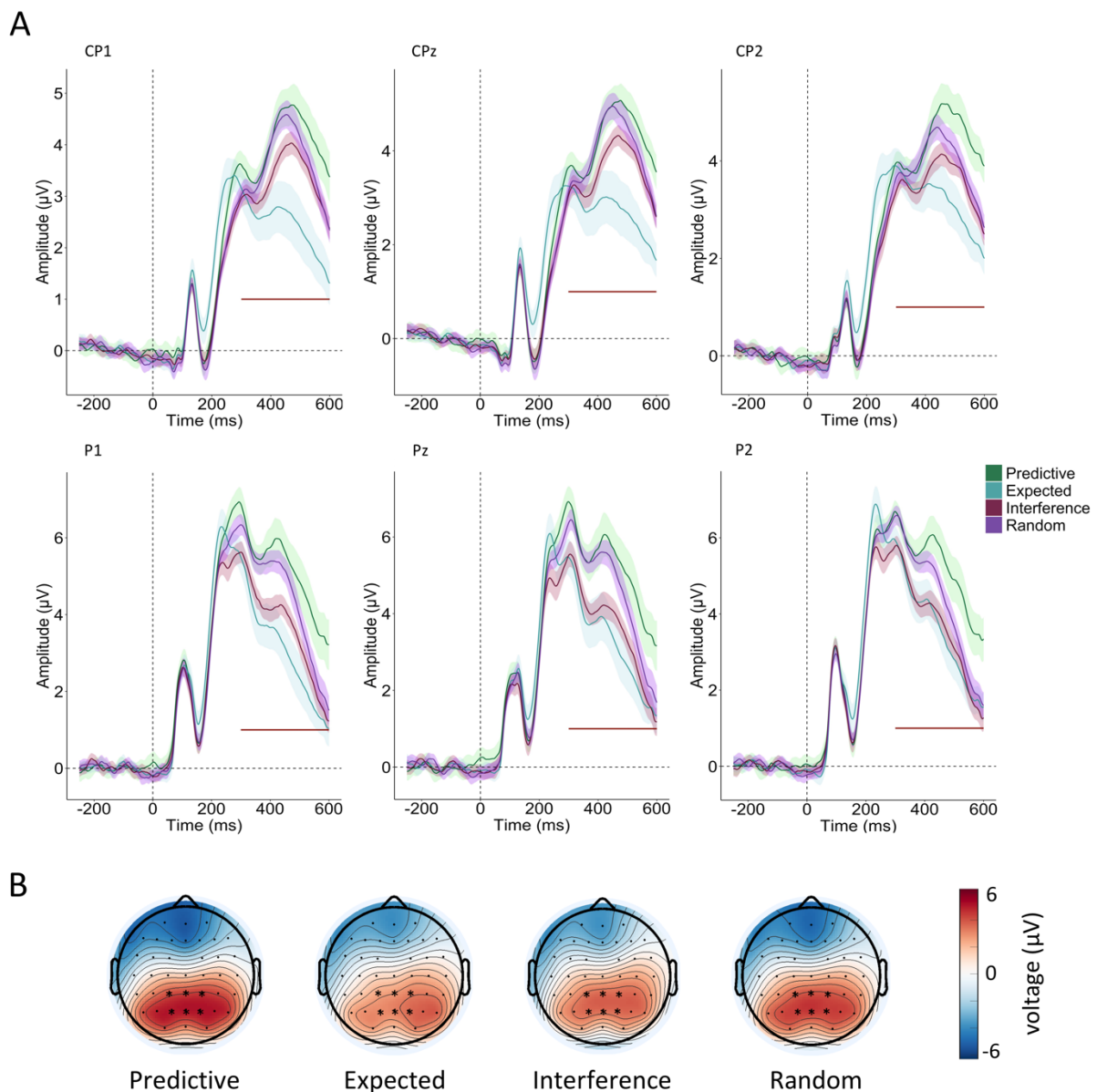|		95% CI					
Contrasts	Estimate	Lower	Upper	SE	z	Effect size	p
Interference – Expected	0.55	0.26	0.84	0.11	4.37	0.48	<.0001 ***
Predictive – Expected	1.70	1.41	2.00	0.11	13.51	1.49	<.0001 ***
Random – Expected	1.15	0.86	1.44	0.11	9.16	1.01	<.0001 ***
Predictive – Interference	1.15	0.86	1.44	0.11	9.14	1.01	<.0001 ***
Random – Interference	0.60	0.31	0.89	0.11	4.78	0.53	<.0001 ***
Random – Predictive	-0.55	-0.84	-0.26	0.11	-4.35	-0.48	<.0001 ***

Figure 4 Illustrations of the P3b component for each image type (Predictive, Expected, Interference, and Random). (A) Grand-average ERP waves expressed at each of the six pre-selected centro-parietal electrodes. Red horizontal lines highlight the timeframe in which the amplitude of the P3b component was analysed (300 – 600ms). **(B)** Grand-average ERP topographies for each image type averaged across 300 – 600ms post-stimulus onset. The centro-parietal ROI of the P3b is highlighted by asterisks (*). Both **(A)** and **(B)** show that predictive images evoked the largest P3b response, followed by predominantly random, interference, and lastly expected images.

Correlation between P3b and expectation-facilitated behavioural responses

Lastly, we examined whether the suppression of higher cognitive processes, reflected by the diminished P3b for interference relative to random images, would allow expectation-facilitated behavioural responses for expected images to be maintained. Thus, we assessed the relationship between the magnitude of the diminished P3b response for interference relative to random images and the time taken to correctly classify the succeeding expected image. A substantial negative correlation was identified (Spearman's rho = -.44, p = .010, 95% CI [-0.68 -0.12]). Hence, the larger the P3b amplitude for interference (versus random) images, the slower the classification response for the ensuing expected images (Figure 5).
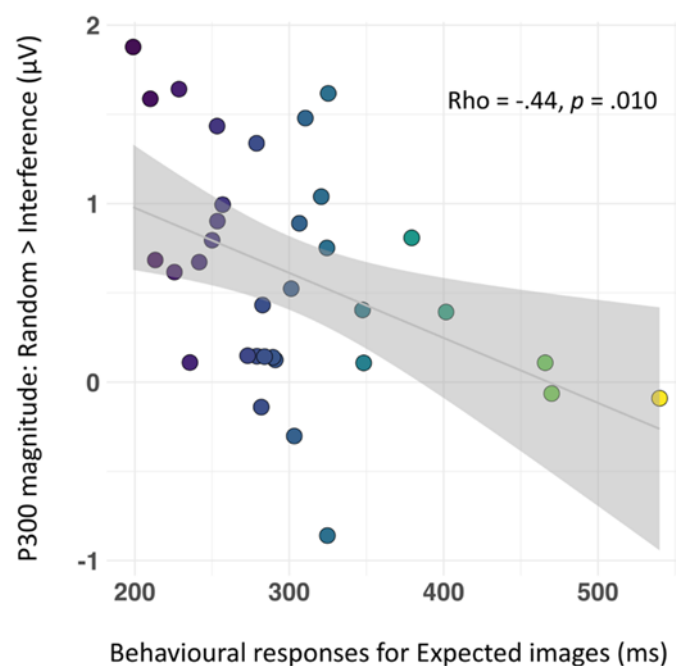

Figure 5 Correlation between the diminished P3b response (µV) for interference images and the expectation-facilitated behavioural response (ms) for ensuing expected images. Spearman's rho and the respective p-value are reported in the top right-hand corner. The shaded area represents the 95% confidence intervals.

Discussion

In the present study, we investigated how the brain compensates for having to process contextually relevant visual stimuli that interfere with an overarching goal. Given that these visual interferences were relevant to the current context, one would expect early visual processes to remain intact in order to maintain an up-to-date representation of the present setting. Processes reflecting higher cognitive functions may, however, be dampened or altogether repressed to allow expectation-facilitated behavioural requirements, associated with the ensuing target image (expected image), to be successfully met. In line with such notions, we investigated early visual processes reflected by fluctuations of alpha/beta power in addition to later cognitive measures characterised by the parietal P3b and behavioural responses. Indeed, we found evidence suggesting that visually processing contextually relevant interferences remained unhindered. Hence, the forward flow of sensory signals was facilitated by the suppression of alpha/beta power (relative to random images). This decrease in parieto-occipital alpha/beta power is considered to create the optimal neural state for processing incoming visual information. Higher cognitive processing of interfering stimuli, on the other hand, appeared to be downregulated as revealed by a diminished P3b response for interference compared to predictive and random images. Notably, we observed that a more diminished P3b response for interference images (relative to random images) was associated with a faster behavioural response for the ensuing expected image.

Facilitation of early visual processes

Fluctuations in alpha/beta power have been recognised to affect the flow of incoming sensory information to higher cognitive levels (Houshmand Chatroudi et al., 2021; Klimesch et al., 2007; Roehe et al., under review). More precisely, enhancements in alpha/beta power

have been associated with the inhibition of bottom-up projected afferent information (Haegens et al., 2011; Mathewson et al., 2011), whereas an alpha/beta suppression reflects a release from this inhibition (Griffiths et al., 2019; Klimesch, 2011). Recent advances have put forth the notion that this interplay in low frequency power serves as a dynamic neural state that, in turn, prioritises either bottom-up or top-down processes depending on the contextual setting (Griffiths et al., 2019; Roehe et al., 2021). As such, a neural state established by predominantly alpha/beta enhancements allows for top-down processes to dominate whilst bottom-up processes are stifled (and vice versa). Expectedly, the alpha/beta activity observed for the interference images in the present study appeared to provide a neural state marked by the decrease in alpha/beta power. Although disrupting the underling anticipatory processes of the upcoming expected images (Roehe et al., under review), processing the interference images was a necessity for the behavioural task. Hence, these images could not be fully ignored as customary in traditional 'distractor suppression' paradigms. They were essentially pseudorandomly selected random images and, therefore, unlikely to be predicted in advance. As such, these images were consequently marked by a more prominent suppression in alpha/beta power than the explicitly learned sequential pairs (Figure 3). As for these explicitly learned images, top-down processes could have aided visual processing by retrieving relevant face-related information from working memory (Brodski-Guerniero et al., 2017).

The observation that early visual processes underlying the interfering faces are not hindered by the overarching goal of predicting the identity of the upcoming expected image aligns nicely with previous findings (Roehe et al., under review). In fact, these results suggested that actively processing interfering faces disrupted the maintenance of the expected face's internal representation by temporally overwriting it (Roehe et al., under review). Hereupon, the neural templates representing identity-related information of expected images were unable to be drawn upon prior to stimulus onset. This was expressed by the insignificant differences of

the N170 amplitude amongst expected, random and interference images (Figure 1B). Behavioural responses for expected images, however, continued to be accelerated even after processing interference images (Figure 1A; Roehe et al., under review). Thus, our results propose that whilst lower visual levels within the respective hierarchical generative model (evoked by predictive images) are updated, higher levels appear to remain intact to aid expectation-facilitated behaviours. This, in turn, begs the question of whether higher cognitive processes relating to processing interference images are inhibited to allow for these expectation-facilitated behavioural effects.

Suppression of higher cognitive processes

The P3b has been proposed to reflect a plethora of higher cognitive processes including a mismatch between sensory input and internal expectations (Saurels et al., 2022; Valakos et al., 2020), inhibition of irrelevant neural networks (Elbert, 1993; Houshmand Chatroudi et al., 2021; Polich, 2007), and an evaluation process during which the informative nature of incoming sensory input is assessed (Kluger et al., 2019; Polich, 2007) and the internal representation updated (Donchin, 1981; Fonken et al., 2020). In the present study, we observed that the informative cues elicited an enhanced P3b response whilst the interfering faces were marked by a noticeably diminished response relative to random images (Figure 4). These observations appear to align more with the notion that the P3b reflects an evaluation process, determining the significance of a given sensory input, rather than reflecting an 'error signal' arising from a sensory discrepancy. Kluger and colleagues (2019), for instance, showed that sequential informative events, coined 'checkpoints', expressed a substantial P3b response similar to events that violated cue-based expectations. The key difference was that events violating a prediction elicited a prediction error signal as reflected by a N400 evoked response. As such, the P3b was considered to be a neural correlate of processes regarding model

evaluation rather than model adaptation, which appears to occur at later stages (Kluger et al., 2019). This notion would also encompass the suggestion that the P3b indexes neural inhibition (Elbert, 1993). If incoming information is acknowledged as contextually informative, it would be propagated upward to the next higher level of the generative model (Clark, 2013; Friston, 2005). It would therefore seem practically sound to facilitate this feedforward transmission by inhibiting irrelevant neural networks and thus boosting the signal-to-noise ratio (Houshmand Chatroudi et al., 2021). In contrast, if a sensory input is reckoned uninformative for the current context, it would be inefficient to pass this information further up the hierarchy. The inhibition of irrelevant neural networks is thus unnecessary, resulting in a diminished P3b response. Collectively, these observations hint towards the proposal that the P3b component does not represent inhibition processes *per se*, but rather reflects a general evaluation process which then primes fundamental processes for model-updating, i.e., boosting the signal-to-noise ratio. The evoked neural responses we observed for the interfering and anticipated faces support this notion. Namely, the interfering faces acted as distractions and their lack of informative significance rendered them contextually invaluable after initial visual processing. Similarly, once the behavioural requirements were successfully met and the expected images correctly classified, these explicitly learned images no longer detained any further information relevant to contextually update the internal representation. In both cases, these stimuli did not require the current model to be updated, which was reflected by a reduced P3b response. On the contrary, the highly informative predictive images not only triggered temporal predictions regarding the sequential make-up of the image sequences (predictive, interference, and lastly expected images), but also triggered identity-related predictions of the expected faces in order to facilitate behaviour. The predictive trials were consequently marked as highly informative which was represented by the enhanced P3b response. Hence, these modulating P3b responses

appear to reflect an evaluation process that identifies whether a specific stimulus is sufficiently "newsworthy" to update the respective internal model.

Collectively, these results suggest that whilst sensory input that was deemed informative was passed on to and processed at higher cognitive levels (predictive images), the interference images appeared to be merely processed at lower visual levels. Our findings therefore suggest that these higher cognitive processes are, to some extent, suppressed for contextually relevant interferences (Figure 6). Interestingly, this suppression negatively correlated with the behavioural responses driven by anticipatory processes (Figure 5). These findings suggest that there is a relationship between the extent to which later cognitive processes of visual interferences are restricted and the accelerated response classifying the anticipated image. The current study, thus, provides a fundamental framework of how the brain compensates for processing contextually relevant interferences. Future studies combining MEG and multivariate pattern analysis (Barne et al., 2020; Blom et al., 2020) could build upon these findings by decoding the amount of face-related information that is passed on to higher levels for each image type (predictive, interference, and expected). Besides providing further evidence to reveal at what cost the brain processes contextually relevant interferences, this would also shed light on some of the neural regions involved.
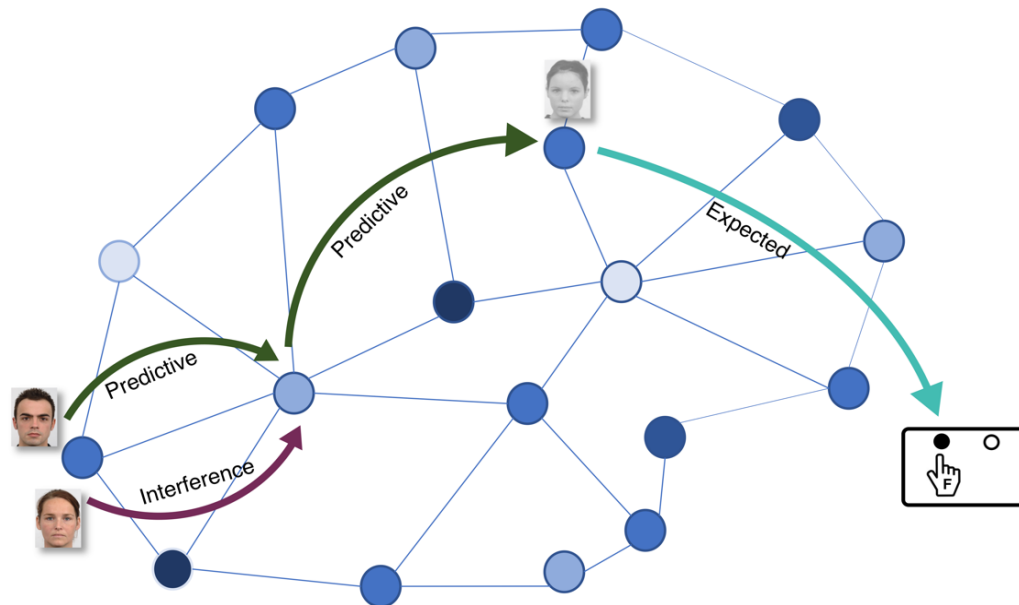
Figure 6 Simplified schematic diagram of how the brain compensated for processing contextually relevant visual interferences. Initially, predictive images are processed in early visual regions. Sensory information is then propagated upwards to trigger the pre-activation of existing knowledge regarding the upcoming expected image. This existing knowledge allows subsequent predictions of the expected image to be generated. These, in turn, facilitate respective behavioural requirements. In contrast, processing contextually relevant visual interferences seems to cease at visual regions within the hierarchy. In essence, the brain appears to downregulate the higher cognitive processes of the interference images to prevent them from hindering expectation-facilitated behavioural responses.

Conclusion

Overall, the findings of the present study demonstrated that the brain processes all contextually relevant sensory input to the extent that seems fit to the current setting. If a sensory stimulus is evaluated and deemed unnecessary for the current overarching goal, the brain appears to restrict or disregard further processing, i.e., passing on information further up the hierarchical model, and proceeds to processes regarded more critical to the task at hand. We can thus infer that the brain compensates for processing contextually relevant interferences by downregulating higher cognitive processes that are dispensable to the current environment and its behavioural requirements.

Acknowledgements

Funding

Declaration of interest

The authors declare no conflict of interest.

Author contributions

Marlen A. Roehe: Conceptualization, Project Administration, Methodology, Software, Formal Analysis, Visualization, Investigation, Data curation, Writing – Original Draft, Writing – Review & Editing; **Daniel S. Kluger:** Conceptualization, Methodology, Software, Formal Analysis, Writing – Review & Editing; **Ricarda I. Schubotz:** Conceptualization, Project Administration, Methodology, Resources, Writing – Review & Editing, Supervision, Funding Acquisition.

References

Arnal, L. H., & Giraud, A.-L. (2012). Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences*, *16*(7), 390–398. https://doi.org/10.1016/j.tics.2012.05.003

Barne, L. C., de Lange, F. P., & Cravo, A. M. (2020). Prestimulus alpha power is related to the strength of stimulus representation. *Cortex*, *132*, 250–257. https://doi.org/10.1016/j.cortex.2020.08.017

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

Blais, C., Jack, R. E., Scheepers, C., Fiset, D., & Caldara, R. (2008). Culture shapes how we look at faces. *PLoS ONE*, *3*(8), e3022. https://doi.org/10.1371/journal.pone.0003022

Blom, T., Feuerriegel, D., Johnson, P., Bode, S., & Hogendoorn, H. (2020). Predictions drive neural representations of visual events ahead of incoming sensory information. *Proceedings of the National Academy of Sciences*, *117*(13), 7510–7515. https://doi.org/10.1073/pnas.1917777117

Brodski-Guerniero, A., Paasch, G. F., Wollstadt, P., Özdemir, I., Lizier, J. T., & Wibral, M. (2017). Information-Theoretic Evidence for Predictive Coding in the Face-Processing System. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*. https://doi.org/10.1523/JNEUROSCI.0614-17.2017

Caharel, S., D'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: Evidence from the N170 ERP component. *Neuropsychologia*, *47*(3), 639–643. https://doi.org/10.1016/j.neuropsychologia.2008.11.016

Campanella, S., Hanoteau, C., Dépy, D., Rossion, B., Bruyer, R., Crommelinck, M., &

Guérit, J. M. (2000). Right N170 modulation in a face discrimination task: An

account for categorical perception of familiar faces. *Psychophysiology*.

https://doi.org/10.1017/S0048577200991728

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of

cognitive science. *Behavioral and Brain Sciences*, *36*(3), 181–204.

https://doi.org/10.1017/S0140525X12000477

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-

trial EEG dynamics including independent component analysis. *Journal of

Neuroscience Methods*, *134*(1), 9–21. https://doi.org/10.1016/j.jneumeth.2003.10.009

Donchin, E. (1981). Presidential address, 1980. Surprise!...Surprise? *Psychophysiology*,

18(5), 493–513. https://doi.org/10.1111/j.1469-8986.1981.tb01815.x

Elbert, T. (1993). Slow Cortical Potentials Reflect the Regulation of Cortical Excitability. In

W. C. McCallum & S. H. Curry (Eds.), *Slow Potential Changes in the Human Brain*

(pp. 235–251). Springer US. https://doi.org/10.1007/978-1-4899-1597-9_15

Fonken, Y. M., Kam, J. W. Y., & Knight, R. T. (2020). A differential role for human

hippocampus in novelty and contextual processing: Implications for P300.

Psychophysiology, *57*(7). https://doi.org/10.1111/psyp.13400

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal

Society B: Biological Sciences*, *360*(1456), 815–836.

https://doi.org/10.1098/rstb.2005.1622

Gratton, G., Coles, M. G. H., & Donchin, E. (1983). A new method for off-line removal of

ocular artifact. *Electroencephalography and Clinical Neurophysiology*, *55*(4), 468–

484. https://doi.org/10.1016/0013-4694(83)90135-9

Griffiths, B. J., Mayhew, S. D., Mullinger, K. J., Jorge, J., Charest, I., Wimber, M., & Hanslmayr, S. (2019). Alpha/beta power decreases track the fidelity of stimulus specific information. *ELife*, *8*. https://doi.org/10.7554/eLife.49562

Haegens, S., Nácher, V., Luna, R., Romo, R., & Jensen, O. (2011). α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(48), 19377–19382. https://doi.org/10.1073/pnas.1117190108

Houshmand Chatroudi, A., Rostami, R., Nasrabadi, A. M., & Yotsumoto, Y. (2021). Effect of inhibition indexed by auditory P300 on transmission of visual sensory information. *PLOS ONE*, *16*(2), e0247416. https://doi.org/10.1371/journal.pone.0247416

Johnston, P., Overell, A., Kaufman, J., Robinson, J., & Young, A. W. (2016). Expectations about person identity modulate the face-sensitive N170. *Cortex*. https://doi.org/10.1016/j.cortex.2016.10.002

Kaiser, J., & Lutzenberger, W. (2005). Human gamma-band activity: A window to cognitive processing. *NeuroReport*, *16*(3), 207–211. https://doi.org/10.1097/00001756-200502280-00001

Klimesch, W. (2011). Evoked alpha and early access to the knowledge system: The P1 inhibition timing hypothesis. *Brain Research*, *1408*. https://doi.org/10.1016/j.brainres.2011.06.003

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Kluger, D. S., Quante, L., Kohler, A., & Schubotz, R. I. (2019). Being right matters: Model-compliant events in predictive processing. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0218311

Langner, O., Dotsch, R., Bijlstra, G., Wigboldus, D. H. J. J., Hawk, S. T., & van Knippenberg, A. (2010). Presentation and validation of the radboud faces database. *Cognition and Emotion*, *24*(8), 1377–1388. https://doi.org/10.1080/02699930903485076

Ligeza, T. S., Tymorek, A. D., & Wyczesany, M. (2017). Top-down and bottom-up competition in visual stimuli processing. *Acta Neurobiologiae Experimentalis*, *77*(4), 305–316.

Limanowski, J., Litvak, V., & Friston, K. (2020). Cortical beta oscillations reflect the contextual gating of visual action feedback. *NeuroImage*, *222*, 117267. https://doi.org/10.1016/j.neuroimage.2020.117267

Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed Out of Awareness: EEG Alpha Oscillations Represent a Pulsed-Inhibition of Ongoing Cortical Processing. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00099

Mayer, A., Schwiedrzik, C. M., Wibral, M., Singer, W., & Melloni, L. (2016). Expecting to see a letter: Alpha oscillations as carriers of top-down sensory predictions. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhv146

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019

Ran, G., Zhang, Q., Chen, X., & Pan, Y. (2014). The effects of prediction on the perception for own-race and other-race faces. *PloS One*, *9*(11), 1–15. https://doi.org/10.1371/journal.pone.0114011

Roehe, M. A., Kluger, D. S., Schroeder, S. C. Y., Schliephake, L. M., Boelte, J., Jacobsen, T., & Schubotz, R. I. (2021). Early alpha/beta oscillations reflect the formation of face-related expectations in the brain. *PLOS ONE*, *16*(7), e0255116. https://doi.org/10.1371/journal.pone.0255116

Roehe, M. A., Kluger, D. S., & Schubotz, R. I. (under review). Fluctuations in alpha and beta power provide neural states favourable for contextually relevant anticipatory processes.

Saurels, B. W., Frommelt, T., Yarrow, K., Lipp, O. V., & Arnold, D. H. (2022). Neural prediction errors depend on how an expectation was formed. *Cortex*, *147*, 102–111. https://doi.org/10.1016/j.cortex.2021.10.012

Spaak, E., Fonken, Y., Jensen, O., & de Lange, F. P. (2016). The Neural Mechanisms of Prediction in Visual Search. *Cerebral Cortex*, *26*(11), 4327–4336. https://doi.org/10.1093/cercor/bhv210

Valakos, D., d'Avossa, G., Mylonas, D., Butler, J., Klein, C., & Smyrnis, N. (2020). P300 response modulation reflects breaches of non-probabilistic expectations. *Scientific Reports*, *10*(1), 10254. https://doi.org/10.1038/s41598-020-67275-0

van Moorselaar, D., Lampers, E., Cordesius, E., & Slagter, H. A. (2020). Neural mechanisms underlying expectation-dependent inhibition of distracting information. *ELife*, *9*, e61048. https://doi.org/10.7554/eLife.61048

3. General Discussion and Future Research

3.1 Summary of the presented studies

The collective aim of the presented studies was to determine some of the temporal aspects of anticipatory processes underlying visual perception. Foremost, the focal intention was to examine the process of expectation generation and how it is affected by 'sensory disruptions' commonly experienced within our natural habitat. Considering that contextually relevant disruptions are prone to require visual processing to some extent, we also investigated how the brain copes with processing these bottom-up signals whilst simultaneously anticipating upcoming visual events.

Study I explored the fundamental question: can the generation of cued expectations be confined to a particular timeframe? An implicit 'associative learning' paradigm was employed for participants to gain implicit knowledge of hidden sequential pairs by means of statistical learning. By exploiting the temporal advantages of EEG, we analysed alpha/beta power and N170 responses to mark the on- and offset of top-down processes. In line with previous research, we observed that bottom-up processes were downregulated for expected (versus random) images as reflected by a reduced response in the N170 and peri-stimulus gamma-band power. Furthermore, we obtained evidence to suggest that a neural state optimal for anticipatory top-down processes was established as soon as the predictive cue was observed. This was reflected by a continuous enhancement in alpha/beta power prevailing throughout the entire three second timeframe between the onset of the predictive cue and the expected image. The augmented alpha/beta power directly prior to the onset of the expected stimulus positively correlated with the modulation of the N170 amplitude (expected versus random images). Thus, suggesting that, at least to some extent, these early top-down processes provided anticipated

information prior to the presentation of the expected image. Surprisingly, we did not find expectation-facilitated behavioural effects. Nevertheless, this could be due to a ceiling effect given the simplicity and repetitiveness of the classification task. In summary, *Study I* provided evidence to suggest that anticipatory processes are activated as soon as being triggered by a respective cue and extend until the expected event occurs. These findings set the groundwork for the succeeding studies.

The main objective of *Study II* was to determine how different types of disturbances that we commonly face in our natural surroundings may impact the anticipatory processes observed in *Study I*. The two disturbances implemented here were: (a) a delay in the onset of the expected event, and (b) a visual interference, by which an additional face image was presented between the predictive cue and its expected counterpart. It was hypothesised that the delay in the onset of the expected stimulus would have minor impact on anticipatory processes. In contrast, considering that the visual interferences required a behavioural response (given the experimental context), it was proposed that subsequent bottom-up processes would interfere with early activated anticipatory processes for the upcoming expected image. In both cases, alpha/beta power suppressions as well as enhancements laced the interstimulus interval prior to the onset of the expected images. Thus, the brain appears to alternate between neural states facilitating either top-down or bottom-up processes at a given time. Additionally, we observed a reduction in the face-sensitive N170 component solely when an anticipated image directly ensued its corresponding predictive cue. This expectation-facilitated effect disappeared when the expected face was preceded by a distracting image. Interestingly, behavioural measures confirmed that neither a temporal delay in stimulus onset nor a visual interference negatively impacted explicit expectation-facilitated behavioural effects. Collectively, the findings of *Study II* provided evidence to suggest that the brain fine-tunes lower levels of the internal generative model to account for both temporal delays in stimulus onset and visual interferences. Higher

levels and their subsequent top-down predictions, however, seem to remain intact to facilitate higher cognitive functions, i.e., optimising expectation-facilitated behaviours.

Expanding upon the conclusions drawn in *Study II*, *Study III* was conducted to explore the influence of the current context on how visual interferences are processed. By re-analysing the EEG data recorded in *Study II,* we intended to investigate whether these contextually relevant interferences were processed only to the extent which was necessary for the current context. We observed that initial visual processing was facilitated as reflected by a peri-stimulus alpha/beta suppression (compared to random images). In contrast, higher cognitive processing of these visually interfering stimuli seemed to be downregulated as revealed by a diminished P3b response (relative to predictive and random images). Intriguingly, we observed that a more diminished P3b response for visual interferences (relative to random stimuli) was associated with a faster behavioural response for the ensuing expected stimulus. To this end, these findings show that the brain compensates for processing contextually relevant interferences by downregulating higher cognitive processes which are dispensable to the current context and task at hand.

In the following, key findings of the three aforementioned studies will be discussed within the predictive processing framework. My main aim is then to show that the fluctuating alpha/beta power observed in all three studies endorses the notion that the brain efficiently prioritises the most reliable or relevant sources of information at a given time. Drawing on our event-related potential findings will help interpret how this balance between weighting either top-down or bottom-up information will affect anticipatory processes, i.e., the early activation of prior knowledge and expectation-facilitated behaviours. By emphasising on the well-calibrated interplay between these findings, I will highlight some of the advantages that a predictive processing account of visual perception upholds.

3.2 Stability of cued face-related expectations

Based on the belief that the probabilistic brain uses prior knowledge to minimise prediction error (Clark, 2015; Friston, 2009), a neural pattern reflecting the downregulation of bottom-up signals should, in theory, emerge for predicted events. That is, neural signatures of expectation-facilitated suppressions should help distinguish expected from unexpected sensory signals (Johnston et al., 2016; Kok et al., 2012; Todorovic et al., 2011; Turk-Browne et al., 2010). In both *Study I* and *Study II* we established a stable experimental environment in which specific faces were reliably foretold by a predictive cue. Whilst *Study I* gave initial insight into the generation process of cued face-related expectations, *Study II* was conceptualised to examine how this process was influenced by (i) a temporal delay in the onset of the expected image or (ii) a visual interruption which segregated the expected image temporarily from its respective cue. In both studies, visually processing expected images appeared to be downregulated by anticipatory processes. Foremost, a suppression in gamma-band activity, associated with diminished bottom-up processes including the transfer of prediction errors (Arnal & Giraud, 2012; Bastos et al., 2012; Brodski et al., 2015), marked the depiction of the expected faces (relative to randomly occurring faces) in *Study I*. Relatedly, a unilateral (left) reduction in the N170 response was observed for these expected faces (relative to random faces). A similar expectation-facilitated response – this time bilaterally – was mirrored in *Study II* for the expected images that were temporally delayed (relative to random images)[1]. These observations align with previous findings conveying that anticipated faces, as a consequence of consecutive depictions, and familiar faces in general evoked a reduced N170 response (Caharel et al., 2009; Campanella et al., 2000; Johnston et al., 2016; Ran et al., 2014). In these

---

[1] Several factors which could have contributed to a unilateral instead of a bilateral modulation of the N170 have been discussed in *Study I*. Potential reasons why *Study I* and *Study II* expressed a different lateralisation of the expectation-facilitated N170 effect will be raised in the *Critical reflections and future directions* section.

examples, prior knowledge could be drawn upon to aid visual processing of subsequent faces. In other words, the predictions generated on the basis of this respective prior knowledge provide a match for incoming sensory evidence, leading to a decline in prediction errors. Indeed, recent findings have provided stimulating evidence to suggest that the N170 could be a prediction error signal, reflecting the conflict between top-down predictions and incoming sensory information (Baker et al., 2021; Johnston et al., 2017). The diminished N170 response and gamma-band activity for expected relative to random images observed in *Study I* endorse this assumption. Previous research investigating N170 and M170 [2] responses alongside gamma activity has shown that these neural responses may be tied to different stages within the face processing hierarchy (Gao et al., 2013; Zion-Golumbic & Bentin, 2007). Specifically, the N170/M170 appeared to be predominantly involved in face detection and classification. Gamma-band activity, on the other hand, appeared to be involved in updating respective pre-existing representations. In future, a cued expectation paradigm with varying degrees of face-related expectation violations could be implemented within a M/EEG setting to further illuminate if the N170/M170 response does indeed reflect a prediction error signal.

Referring back to *Study I* and *Study II*, the diminished N170 responses observed suggest that, at least to some extent, a neural template of the expected faces was activated ahead of its presentation to facilitate the generation of relatively precise predictions. The early activation of prior knowledge, which *Study I* has shown is triggered by the onset of the predictive cue, thus appears to assist in the maintenance of face-related predictions (Brodski-Guerniero et al., 2017). Interestingly, *Study II* showed that this process can withstand extensive timeframes of six seconds. As such, these cued expectations appear to remain stable even when confronted with temporal delays.

---

[2] A posterior face-sensitive component similar to the N170 found in MEG (Liu et al., 2000).

On the contrary, this early activation of prior knowledge seems to be impeded when the brain has to process other kindred visual stimuli before attending to the anticipated image. This assumption is centred around observations from *Study II.* Here, findings showed that when visually interfering images were presented between the predictive cue and its expected counterpart, the above mentioned N170 response disappeared. One has to bear in mind that these interfering images required a specific behavioural response, making them contextually relevant to the task at hand. Previous research has shown that motivational relevance influences visual processing (for a review, see Summerfield & Egner, 2009). In *Study II,* we therefore proposed that upon visually processing this type of interference, the pre-activated neural representation of the expected images (triggered by the cue) is temporarily overwritten in the process of updating the internal model. This assumption rests on the notion that lower levels within the visual system's hierarchy are updated more readily than higher cognitive levels (Long & Kuhl, 2018). In addition, on the grounds of predictive processing, the brain aims to acquire the most up-to-date model of the external world (Clark, 2013, 2015; Hohwy, 2013) and would subsequently update early visual levels to account for the visually interfering images that were attended to. Nevertheless, given that the main goal of the experimental context was to classify each image as quickly as possible, keeping the internal representation of the associated behavioural response for the expected image intact would have sufficed for the overarching task requirements. Indeed, *Study II* showed that even though the N170 responses during the visual interference condition did not portray signs of expectation-facilitation, the behavioural responses did. Based on these observations, we suggested that whilst the brain updates and revises lower levels within the hierarchical model that are dispensable to the contextual goal, higher cognitive levels remain unaffected by the visually interfering image. This would consequently ensure the facilitation of contextually relevant behavioural responses. As previously raised in *Study II,* this opens a stimulating line of future research which could

combine M/EEG and multivariate pattern analysis (Barne et al., 2020; Blom et al., 2020) to decode the amount of face-specific information activated ahead of the expected face's presentation after having attended to contextually relevant visual interferences.

Study III provided evidence to corroborate that higher cognitive processing of visually interfering images was downregulated to permit expectation-facilitated behavioural responses for the upcoming expected image. In other words, higher levels within the internal model appeared to be unaffected by revisions and model-updating after visually processing interfering images. This was shown by a diminished P3b response evoked by these interfering images relative to the predictive cues and randomly occurring unpaired images. Moreover, *Study III* convincingly showed a linear relationship between this diminished P3b response and the accelerated classification response for the ensuing expected image. These observations add to the literature supporting the notion that the P3b reflects an evaluation process in which the informative characteristics of a given bottom-up signal is assessed (Kluger et al., 2019; Polich, 2007). As such, a reduced response is typically evoked by less informative or expected events (Ran et al., 2014), whereas informative events evoke an enhanced P3b response that subsequently primes fundamental processes underlying model-updating (Donchin, 1981; Fonken et al., 2020), including the generation of prediction errors (Valakos et al., 2020), and silencing irrelevant neural networks (Elbert, 1993; Houshmand Chatroudi et al., 2021). By evaluating and restricting to what extent visual interferences are processed, the brain enables higher cognitive representations to remain stable which in turn aids the generation of predictions regarding upcoming responses.

Notably, neither the temporal delay nor the visual interference disruption appeared to negatively impact expectation-facilitated behaviours (*Study II*). In both cases, the response time and the overall accuracy of the classification response were substantially facilitated by anticipatory processes. Whilst a familiar expectation suppression pattern was observed for the

response time (Ran et al., 2014; Turk-Browne et al., 2010; Zhou et al., 2020), response accuracy showed an inverse pattern, i.e., accuracy increased with prior expectation (Auksztulewicz et al., 2017; Schliephake et al., 2021). Again, prior knowledge can be relied upon to guide precise predictions regarding the expected stimulus. Having explicitly learned the identity of the expected faces, participants would subsequently be less likely to accidentally misclassify the sex of these face images. In the same vein, behavioural responses could be prepared ahead of the depiction of the anticipated stimulus, resulting in an accelerated behavioural response.

In sum*, Study I* and *Study II* provide evidence to suggest that cued anticipatory processes, which are contextually relevant, remain stable even within dynamic environments. To achieve this, *Study III* showed that the brain appears to downregulate processes which might interfere with maintaining stable neural representations of the contextually relevant expected events. In turn, prior activation of these internal representations aids the facilitation of top-down predictions that more-or-less match the incoming signal, thus minimising prediction error signals.

3.3 A neural state favourable for anticipatory processes

Within all three studies comprising this thesis, experimental conditions were generated in which either top-down predictions or bottom-up sensory input played a more substantial role at a given time. So far, past research has associated the facilitation of top-down processes with increases in alpha/beta power and bottom-up processes with decreases in alpha/beta power (Arnal & Giraud, 2012). More specifically, whilst enhancements in occipital alpha power have been linked to the inhibition of incoming visual information (Haegens et al., 2011; Mathewson et al., 2011), a suppression in power within alpha ranges has been linked to the release from this inhibition (Klimesch, 2011). Contextually relevant decreases in alpha/beta power have also

been the subject of study in various tasks (Lebar et al., 2017; Pfurtscheller et al., 1996), sensory modalities (Griffiths et al., 2019; Lebar et al., 2017), and different species, such as humans (Griffiths et al., 2019; Lebar et al., 2017), macaques (Haegens et al., 2011), and rodents (Wiest & Nicolelis, 2003). In terms of anticipatory processes, enhancements in alpha/beta power have been associated with activating previously established knowledge and sensory predictions (Bastos et al., 2015; Brodski-Guerniero et al., 2017; Mayer et al., 2016). In brief, fluctuations in alpha and beta power appear to be associated with several features underlying both bottom-up and top-down processes. With the intention to incorporate these listed findings, *Study I* and *Study II* put forth the notion that modulations in alpha/beta power provide contrasting neural states that either facilitate bottom-up or top-down processes. This notion was first raised by Griffiths and colleagues (2019) with regard to suppressions in alpha/beta power. Here the authors suggested that instead of reflecting actual bottom-up prediction errors (or incoming signal), suppressions in alpha/beta power established a general neural state favourable for facilitating such mentioned bottom-up processes. To compliment this proposal, they speculated that stimulus-related information could, in turn, be carried by the phase of low alpha oscillations (Michelmann et al., 2016). Considerably more evidence is needed, however, to support this assumption.

Critically, if enhancements in pre-stimulus alpha/beta power were indeed a reflection of predictions carrying stimulus specific information one would anticipate: (i) an expectation-facilitated reduction in the N170 response for the expected (relative to random) images (Johnston et al., 2016; Ran et al., 2014), and (ii) a linear relationship between the pre-stimulus alpha/beta enhancement and peri-stimulus expectation-facilitated suppression in the N170. Expectation-facilitated modulations in the N170 response were observed in both *Study I* and *Study II*. Although in *Study II*, this only extended to the expected images which immediately ensued their respective cue. The expected images of the visual interference condition, however,

showed no expectation-facilitated effect in the N170, despite evident enhancements in alpha/beta power within the respective pre-stimulus timeframe (relative to random faces). Furthermore, both *Study I* and *Study II* (temporal delay condition) provided limited evidence of a positive linear relationship between the pre-stimulus enhancement in alpha/beta power and the modulation of the N170 response (reduced negative deflection) for expected relative to random faces. Instead of reflecting stimulus-related information of the expected face *per se*, the augmentation in pre-stimulus alpha/beta power seems to be more in line with the notion of a global neural state. Hence, *Study I* and *Study II* extend the concept of a neural state optimal for bottom-up processing (Griffiths et al., 2019) by adding an opposing neural state which is favourable for top-down processes.

In *Study I* and *Study II* a stable environment was established in which the expected faces could be reliably predicted. Hence, in both cases enhancements in alpha/beta power were observed within the pre-stimulus timeframe leading up to the onset of the expected face. Furthermore, *Study II* also revealed that in the timeframe extending past the expected face - leading up to a randomly occurring image - this enhancement in alpha/beta power was not observed. Instead, an elongated alpha/beta suppression appeared to dominate this timeframe. Thus, fluctuations in alpha/beta power seem to highlight at which point in time a neural state necessary for facilitating top-down versus bottom-up processes is established and vice versa. The idea of fluctuating between two neural states, one facilitating top-down processes and the other facilitating bottom-up processes, ties in somewhat neatly with the premise of precision-weighting. When more weight is attributed to top-down processes, an enhancement in alpha/beta power would be expected. In turn, when more weight is bestowed upon bottom-up processes, alpha/beta power is suppressed to establish a neural state optimal for bottom-up processes. On these grounds, one would expect an interchanging interplay between these two

neural states, regulated by the sensory signals that are estimated to provide the most relevant information given the current context (Clark, 2017b; Lupyan & Clark, 2015).

3.4 Efficiency of weighting contextually relevant information

A cornerstone of predictive processing is the view that the predictive properties of the brain can be amplified or muted by means of increasing the weight assigned to either internal predictions or incoming signals, respectively (Clark, 2015; Yon & Frith, 2021). In an exceedingly dynamic world like ours, these contextually driven patterns of weightings allow predictive models to determine which signals should predominantly guide perceptual inferences (Clark, 2017b, 2022; O'Reilly, 2013). This would amount to fluidly altering between assigning more weight to top-down predictions in familiar surroundings and more weight to bottom-up signals in territories where contingencies are less predictable. Hence, the contextual setting plays a crucial role in determining how far predictive perceptual systems rely on prior knowledge and subsequent predictions (Summerfield & Egner, 2009).

The findings observed in *Study II* and *Study III* were facilitated by an explicit cueing paradigm, i.e., the participants explicitly learned their unique sets of sequential pairs. Hence, explicit expectations regarding predefined regularities were generated whilst also enhancing the cue and target's saliency (Kok et al., 2012). As a result, these stimuli may attract more attention and engagement than the random (less contextually relevant) images, given their contextual significance (Griffiths et al., 2019; Lebar et al., 2017). Classically, attention can be categorised into two types. Bottom-up attention (stimulus-driven), in which a particularly salient stimulus captures perceptual resources, i.e., a sudden movement or loud noise, and top-down attention (goal-driven), which is guided by higher level cognition, such as prior knowledge and contextual goals (Summerfield & Egner, 2009; Vanunu et al., 2021). In terms of predictive processing accounts, attention is hypothesised to increase the weight on prediction

error signals to facilitate efficient model-revision and updating (Feldman & Friston, 2010; Jiang et al., 2013; Smout et al., 2019). Although this is a sound interpretation of how bottom-up attention should in principle work, top-down attention regarding visual perception is less well understood. The general argument here pushes the notion that assigning more weight to top-down predictions regarding task-relevant information renders us more sensitive to a given sensory stimulus (Yon & Frith, 2021). This sensory signal therefore 'stands out' from task-irrelevant signals (Clark, 2017b). The incoming signal from this given stimulus is then drawn upon to facilitate efficient updating of the internal model. However, the underlying mechanisms that enable such enhanced sensitivity to task-relevant stimuli are not well understood as to date and require more research in future.

Although all images within the three studies were equally relevant to the task requirements (sex-classification task), explicit knowledge of the sequential pairs may have rendered them more salient. In other words, given the current context, these images 'stood out' from the rest of the randomly occurring faces. The fluctuations between alpha/beta power which we observed in *Study II* appear to be in line with the notion that these images required more engagement than the random (less contextually relevant) images, as marked by alpha/beta power suppressions following stimulus presentation (Griffiths et al., 2019; Lebar et al., 2017; Limanowski et al., 2020). In addition, we observed the same alpha/beta suppression for interference (versus random) images. Considering that the interference images were effectively arbitrarily selected random images, we proposed that these images were also enhanced in saliency because the participants had explicitly learned the sequential make-up of the visual interference blocks. As such, the interfering images became an unintentional temporal cue for the temporal onset of the approaching expected images (Xu et al., 2021).

In addition, findings of *Study III* showed that the onset of the interference images was marked by an enhanced suppression in alpha/beta power relative to the predictive and expected

images. This neural state favourable to bottom-up processing will have facilitated the forward flow of incoming information (Griffiths et al., 2019; Houshmand Chatroudi et al., 2021), and subsequently the revision of lower levels within the visual system (Long & Kuhl, 2018). Specifically, Long & Kuhl (2018) showed that whilst visual interruptions in the form of scrambled facial features primarily influenced representations within the visual system, modulations such as a switch in goal or task relevance influenced representations in frontoparietal networks. This is in line with our previous suggestion (*Study II*) that the interfering images appeared to affect the stable maintenance of a face-related template of the expected images; hence, the insignificant expectation-facilitated N170 effect. However, the diminished P3b response for the interfering images (relative to random images) showed that although processed at lower visual levels, these bottom-up signals do not appear to interfere with higher cognitive levels that facilitate contextually relevant behaviours (*Study III*). That is, the brain appears to give more weight to bottom-up processes to efficiently update the internal model to account for visually interfering images before giving weight to top-down processes to efficiently assist expectation-facilitated behaviours (*Study II* and *Study III*). Similarly, temporal delays in stimulus onset were accounted for by first providing a neural state optimal for top-down processes to activate respective prior knowledge (*Study II*). Once this had been achieved, a pre-stimulus neural state was established favouring bottom-up processes in anticipation of the delayed salient expected image. The brain, thus, seems to fluctuate between these two neural states to flexibly give weight to either top-down or bottom-up processes. Critically, this is not to say that fluctuating between neural states reflects precision-weighting *per se*. Instead, these neural states index whether top-down or bottom-up processes have been bestowed more weight given the present context. Promising studies narrowing in on how specific neuromodulators shape to what extent the brain relies on either top-down or bottom-up signals might enrich our understanding of the mechanisms underlying precision-weighting

in visual perception (Lawson et al., 2021; Yu & Dayan, 2005). Lawson and colleagues (2021), for instance, examined the speeded response of participants taking noradrenaline-blocking medication (Propranolol) during a classification task (faces versus houses). They conveyed that these participants were more likely to trust their internal top-down predictions during conditions of high uncertainty. That is, under the influence of Propranolol, they responded faster to 'noisy' expected stimuli than the participants of the placebo group; thus, implying that increased weight was given to top-down predictions. By altering the predictive contingencies in the experiment, Lawson and colleagues (2021) were also able to show that these participants were slower to update their internal model when confronted with new regularities. Hence, noradrenaline is believed to encode the (un)certainty of our predictions and subsequently plays a role in assigning more weight to incoming information when our surroundings are estimated to be more volatile. That means, when our environments are more probable to change, we tend to rely more heavily on incoming signals to update our internal model considering that our prior representations are quickly outdated (Yon, 2021). By suppressing noradrenergic circuits, the above-mentioned results propose that more weight is afforded to our prior beliefs even in the face of constant change. An interesting notion would be to examine (i) if visual interferences are as readily accounted for in internal models of participants whose noradrenergic circuits have been suppressed, and (ii) if enhanced weight assigned to top-down processes is reflected by an elongated augmentation in alpha/beta power throughout the pre-stimulus timeframe of the expected stimuli. This would further substantiate the assumption that alpha/beta enhancements reflect a neural state optimal for top-down processes.

In *Study I*, implicit expectations guided top-down processes which prevailed from the onset of the cue to the presentation of the expected image[3]. Here, the whole brain analysis suggests that not only top-down related processes regarding the visual system appear to play a role in generating and maintaining cued expectations. Instead, a whole network of regions appears to be involved in establishing an overall neural state optimal for top-down processes.

Overall, all three studies show that the brain prioritises either top-down or bottom-up states depending on which signal is contextually relevant at a given point in time. Fluctuations between these two neural states, for example, facilitate optimal conditions for keeping contextually relevant knowledge intact whilst also updating lower visual levels to account for different interferences which we face in everyday life. By weighting which information is most relevant, the brain can efficiently compensate for processing different interferences whilst continuing to drive expectation-facilitated behaviours.

3.5 Critical reflections and future directions

The three studies comprising this thesis collectively aimed to deepen our understanding of the generation, maintenance, and development of cued face-related expectations. In hindsight, several factors have been brought to light which impacted how the results were interpreted.

One major difference between the experimental paradigms of *Study I* and *Study II* was that different types of expectations were elicited. That is, in *Study I*, implicit expectations were generated as a result of statistical learning, whereas in *Study II*, participants were explicitly

---

[3] We conducted a whole brain analysis in *Study I* to gain initial insight into the formation and development of cued face-related expectations. In contrast, the region of interest (ROI) was narrowed down to parieto-occipital electrodes in *Study II*, because one of our main points of interest rested on the influence of visual interferences on the development of face-related expectations. We subsequently chose a ROI commonly used in literature to examine visual perception. The averaged spectral patterns in pre-stimulus alpha/beta power observed in these two studies consequently differ primarily because different ROIs were implemented.

primed to learn their unique sets of paired-up faces during a training session. The use of a statistical learning paradigm in *Study I* may have contributed to the ceiling effect observed in the behavioural responses. Especially the simplicity and the repetitiveness of the classification task could have allowed participants to quickly reach optimal proficiency[4]. It is noteworthy to mention here that how the participants are instructed during the induction period can impact and even confound expectation-facilitated responses. Prior to commencing a statistical learning experiment, Zhou and colleagues (2020), for instance, informed participants that the upcoming sequences were to comprise a predictive structure (the exact pairwise relationship between certain images was not conveyed). Being orientated towards the presence of sequential pairs may however tilt the balance towards eliciting explicit rather than implicit expectations. In future, it would be interesting to examine if implicit and explicit face-related expectations reflect expectation-facilitated responses to varying degrees. This could also provide an assumption why *Study I* and *Study II* expressed a different lateralisation of the expectation-facilitated N170 effect. The rationale behind this speculation is based on conflicting findings concerning the enhanced facilitation of explicit versus implicit cueing on expectation-facilitated behavioural responses, i.e., response times regarding temporal expectations (c.f. Ball et al., 2020; Menceloglu et al., 2017).

Relatedly, a limitation between *Study I* and *Study II* is that different ROIs were used to analyse the N170. Due to the Covid pandemic all our participants were required to wear a FFP2 face covering during the EEG-recording. Given the close proximity of electrodes TP7/8 and the mask's elastic fastening behind each ear, their signals were contaminated with artefacts. These electrodes were thereupon not included in the analysis of the N170 component in *Study II*. Naturally, this could also have contributed to the different lateralisation of the diminished N170 effects observed between *Study I* and *Study II*.

---

[4] For a more detailed critical reflection of the behavioural results obtained in *Study I*, see *Discussion* of *Study I*.

4. Conclusion

The view that the brain is a 'prediction engine' which actively anticipates its natural environments has transformed the way it has been studied, empirically as well as philosophically, over the past decades. Given that at the heart of predictive processing lies the notion that the brain persistently generates top-down predictions regarding up- and incoming sensory information and their reliability given the current context, it was our intention to gain deeper insight into the temporal aspects encompassing the generation, maintenance, and development of such expectations. In *Study I* we obtained evidence to suggest that anticipatory processes are initiated the moment a predictive cue is observed. *Study II* extended on this by conveying that these anticipatory processes are not hindered by temporal delays in the onset of the expected image but, to some extent, by visual interferences. The notion that the brain compensates for processing visual interferences by mitigating their influence on higher cognitive levels was subsequently indicated in *Study III*.

In this thesis, I examined some of the fundamental underpinnings of the predictive brain with the aim to highlight their benefits within a visual perception framework. Thus, if the brain truly is a prediction engine, the aforementioned studies collectively showed that it consistently predicts and calibrates the relevance of internal predictions versus incoming signals. Depending on which way the balance sways, we rely more heavily on prior knowledge and top-down predictions, or bottom-up information to influence how far our internal model is updated. To date, this appears to be a lucrative interaction between our internal predictive model and the external world that, nevertheless, provides plenty of fascinating conundrums waiting to be resolved in future.

References

Alink, A., Schwiedrzik, C. M., Kohler, A., Singer, W., & Muckli, L. (2010). Stimulus Predictability Reduces Responses in Primary Visual Cortex. *Journal of Neuroscience*, *30*(8), 2960–2966. https://doi.org/10.1523/JNEUROSCI.3730-10.2010

Arnal, L. H., & Giraud, A.-L. (2012). Cortical oscillations and sensory predictions. *Trends in Cognitive Sciences*, *16*(7), 390–398. https://doi.org/10.1016/j.tics.2012.05.003

Auksztulewicz, R., Friston, K. J., & Nobre, A. C. (2017). Task relevance modulates the behavioural and neural effects of sensory predictions. *PLOS Biology*, *15*(12), e2003143. https://doi.org/10.1371/journal.pbio.2003143

Baker, K. S., Pegna, A. J., Yamamoto, N., & Johnston, P. (2021). Attention and prediction modulations in expected and unexpected visuospatial trajectories. *PLOS ONE*, *16*(10), e0242753. https://doi.org/10.1371/journal.pone.0242753

Ball, F., Groth, R.-M., Agostino, C. S., Porcu, E., & Noesselt, T. (2020). Explicitly versus implicitly driven temporal expectations: No evidence for altered perceptual processing due to top-down modulations. *Attention, Perception, & Psychophysics*, *82*(4), 1793–1807. https://doi.org/10.3758/s13414-019-01879-1

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., Hämäläinen, M. S., Marinkovic, K., Schacter, D. L., Rosen, B. R., & Halgren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences*, *103*(2), 449–454. https://doi.org/10.1073/pnas.0507062103

Barne, L. C., de Lange, F. P., & Cravo, A. M. (2020). Prestimulus alpha power is related to the strength of stimulus representation. *Cortex*, *132*, 250–257. https://doi.org/10.1016/j.cortex.2020.08.017

Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., & Friston, K. J.

(2012). Canonical microcircuits for predictive coding. *Neuron*, *76*(4), 695–711.

https://doi.org/10.1016/j.neuron.2012.10.038

Bastos, A. M., Vezoli, J., Bosman, C. A., Schoffelen, J.-M., Oostenveld, R., Dowdall, J. R.,

De Weerd, P., Kennedy, H., & Fries, P. (2015). Visual Areas Exert Feedforward and

Feedback Influences through Distinct Frequency Channels. *Neuron*, *85*(2), 390–401.

https://doi.org/10.1016/j.neuron.2014.12.018

Bauer, M., Stenner, M.-P., Friston, K. J., & Dolan, R. J. (2014). Attentional Modulation of

Alpha/Beta and Gamma Oscillations Reflect Functionally Distinct Processes. *Journal

of Neuroscience*, *34*(48), 16117–16125. https://doi.org/10.1523/JNEUROSCI.3474-

13.2014

Berger, H. (1930). Über das Elektroenzephalogramm des Menschen II. J. Psychol. Neurol.

40, 160-179.

Bestmann, S., Harrison, L. M., Blankenburg, F., Mars, R. B., Haggard, P., Friston, K. J., &

Rothwell, J. C. (2008). Influence of Uncertainty and Surprise on Human Corticospinal

Excitability during Preparation for Action. *Current Biology*, *18*(10), 775–780.

https://doi.org/10.1016/j.cub.2008.04.051

Blom, T., Feuerriegel, D., Johnson, P., Bode, S., & Hogendoorn, H. (2020). Predictions drive

neural representations of visual events ahead of incoming sensory information.

Proceedings of the National Academy of Sciences, *117*(13), 7510–7515.

https://doi.org/10.1073/pnas.1917777117

Brodski, A., Paasch, G.-F. G. F., Helbling, S., & Wibral, M. (2015). The Faces of Predictive

Coding. *Journal of Neuroscience*, *35*(24), 8997–9006.

https://doi.org/10.1523/JNEUROSCI.1529-14.2015

Brodski-Guerniero, A., Paasch, G. F., Wollstadt, P., Özdemir, I., Lizier, J. T., & Wibral, M. (2017). Information-Theoretic Evidence for Predictive Coding in the Face-Processing System. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*. https://doi.org/10.1523/JNEUROSCI.0614-17.2017

Caharel, S., D'Arripe, O., Ramon, M., Jacques, C., & Rossion, B. (2009). Early adaptation to repeated unfamiliar faces across viewpoint changes in the right hemisphere: Evidence from the N170 ERP component. *Neuropsychologia*, *47*(3), 639–643. https://doi.org/10.1016/j.neuropsychologia.2008.11.016

Campanella, S., Hanoteau, C., Dépy, D., Rossion, B., Bruyer, R., Crommelinck, M., & Guérit, J. M. (2000). Right N170 modulation in a face discrimination task: An account for categorical perception of familiar faces. *Psychophysiology*. https://doi.org/10.1017/S0048577200991728

Cao, L., Thut, G., & Gross, J. (2017). The role of brain oscillations in predicting self-generated sounds. *NeuroImage*, *147*, 895–903. https://doi.org/10.1016/j.neuroimage.2016.11.001

Clark, A. (2013). Whatever next? Predictive brains, situated agents, and the future of cognitive science. *Behavioral and Brain Sciences*, *36*(3), 181–204. https://doi.org/10.1017/S0140525X12000477

Clark, A. (2015). Radical Predictive Processing: Radical Predictive Processing. *The Southern Journal of Philosophy*, *53*, 3–27. https://doi.org/10.1111/sjp.12120

Clark, A. (2017a). Busting Out: Predictive Brains, Embodied Minds, and the Puzzle of the Evidentiary Veil. *Nous*, *51*(4), 727–753. https://doi.org/10.1111/nous.12140

Clark, A. (2017b). Predictions, precision, and agentive attention. *Consciousness and Cognition*, *56*, 115–119. https://doi.org/10.1016/j.concog.2017.06.013

Clark, A. (2022). Extending the Predictive Mind. *Australasian Journal of Philosophy*, 1–12. https://doi.org/10.1080/00048402.2022.2122523

Den Ouden, H. E. M., Kok, P., & de Lange, F. P. (2012). How prediction errors shape perception, attention, and motivation. *Frontiers in Psychology*, *3*(DEC). https://doi.org/10.3389/fpsyg.2012.00548

Diederen, K. M. J., Ziauddeen, H., Vestergaard, M. D., Spencer, T., Schultz, W., & Fletcher, P. C. (2017). Dopamine Modulates Adaptive Prediction Error Coding in the Human Midbrain and Striatum. *The Journal of Neuroscience*, *37*(7), 1708–1720. https://doi.org/10.1523/JNEUROSCI.1979-16.2016

Donchin, E. (1981). Presidential address, 1980. Surprise!...Surprise? *Psychophysiology*, *18*(5), 493–513. https://doi.org/10.1111/j.1469-8986.1981.tb01815.x

Egner, T., Monti, J. M., & Summerfield, C. (2010). Expectation and Surprise Determine Neural Population Responses in the Ventral Visual Stream. *Journal of Neuroscience*, *30*(49), 16601–16608. https://doi.org/10.1523/JNEUROSCI.2770-10.2010

Elbert, T. (1993). Slow Cortical Potentials Reflect the Regulation of Cortical Excitability. In W. C. McCallum & S. H. Curry (Eds.), *Slow Potential Changes in the Human Brain* (pp. 235–251). Springer US. https://doi.org/10.1007/978-1-4899-1597-9_15

Feldman, H., & Friston, K. J. (2010). Attention, Uncertainty, and Free-Energy. *Frontiers in Human Neuroscience*, *4*. https://doi.org/10.3389/fnhum.2010.00215

Fonken, Y. M., Kam, J. W. Y., & Knight, R. T. (2020). A differential role for human hippocampus in novelty and contextual processing: Implications for P300. *Psychophysiology*, *57*(7). https://doi.org/10.1111/psyp.13400

Friston, K. (2003). Learning and inference in the brain. *Neural Networks*, *16*(9), 1325–1352. https://doi.org/10.1016/j.neunet.2003.06.005

Friston, K. (2005). A theory of cortical responses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *360*(1456), 815–836. https://doi.org/10.1098/rstb.2005.1622

Friston, K. (2009). The free-energy principle: A rough guide to the brain? *Trends in Cognitive Sciences*, *13*(7), 293–301. https://doi.org/10.1016/j.tics.2009.04.005

Gao, Z., Goldstein, A., Harpaz, Y., Hansel, M., Zion-Golumbic, E., & Bentin, S. (2013). A magnetoencephalographic study of face processing: M170, gamma-band oscillations and source localization. *Human Brain Mapping*, *34*(8), 1783–1795. https://doi.org/10.1002/hbm.22028

Griffiths, B. J., Mayhew, S. D., Mullinger, K. J., Jorge, J., Charest, I., Wimber, M., & Hanslmayr, S. (2019). Alpha/beta power decreases track the fidelity of stimulus specific information. *ELife*, *8*. https://doi.org/10.7554/eLife.49562

Haarsma, J., Fletcher, P. C., Griffin, J. D., Taverne, H. J., Ziauddeen, H., Spencer, T. J., Miller, C., Katthagen, T., Goodyer, I., Diederen, K. M. J., & Murray, G. K. (2021). Precision weighting of cortical unsigned prediction error signals benefits learning, is mediated by dopamine, and is impaired in psychosis. *Molecular Psychiatry*, *26*(9), 5320–5333. https://doi.org/10.1038/s41380-020-0803-8

Haegens, S., Nácher, V., Luna, R., Romo, R., & Jensen, O. (2011). α-Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(48), 19377–19382. https://doi.org/10.1073/pnas.1117190108

Helmholtz, H. von. (1948). Concerning the perceptions in general, 1867. In W. Dennis (Ed.), *Readings in the history of psychology.* (pp. 214–230). Appleton-Century-Crofts. https://doi.org/10.1037/11304-027

Hohwy, J. (2013). *The Predictive Mind*. Oxford University Press.

https://doi.org/10.1093/acprof:oso/9780199682737.001.0001

Houshmand Chatroudi, A., Rostami, R., Nasrabadi, A. M., & Yotsumoto, Y. (2021). Effect of

inhibition indexed by auditory P300 on transmission of visual sensory information.

PLOS ONE, *16*(2), e0247416. https://doi.org/10.1371/journal.pone.0247416

Huang, Y., & Rao, R. P. N. (2011). Predictive coding. *WIREs Cognitive Science*, *2*(5), 580–

593. https://doi.org/10.1002/wcs.142

Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey

striate cortex. *The Journal of Physiology*, *195*(1), 215–243.

https://doi.org/10.1113/jphysiol.1968.sp008455

Jiang, J., Summerfield, C., & Egner, T. (2013). Attention Sharpens the Distinction between

Expected and Unexpected Percepts in the Visual Brain. *Journal of Neuroscience*,

33(47), 18438–18447. https://doi.org/10.1523/JNEUROSCI.3308-13.2013

Johnston, P., Overell, A., Kaufman, J., Robinson, J., & Young, A. W. (2016). Expectations

about person identity modulate the face-sensitive N170. *Cortex*.

https://doi.org/10.1016/j.cortex.2016.10.002

Johnston, P., Robinson, J., Kokkinakis, A., Ridgeway, S., Simpson, M., Johnson, S.,

Kaufman, J., & Young, A. W. (2017). Temporal and spatial localization of prediction-

error signals in the visual brain. *Biological Psychology*, *125*, 45–57.

https://doi.org/10.1016/j.biopsycho.2017.02.004

Klimesch, W. (2011). Evoked alpha and early access to the knowledge system: The P1

inhibition timing hypothesis. *Brain Research*, *1408*.

https://doi.org/10.1016/j.brainres.2011.06.003

Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in Cognitive Sciences*, *16*(12), 606–617. https://doi.org/10.1016/j.tics.2012.10.007

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, *53*(1), 63–88. https://doi.org/10.1016/j.brainresrev.2006.06.003

Kluger, D. S., Quante, L., Kohler, A., & Schubotz, R. I. (2019). Being right matters: Model-compliant events in predictive processing. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0218311

Kok, P., Jehee, J. F. M., & de Lange, F. P. (2012). Less Is More: Expectation Sharpens Representations in the Primary Visual Cortex. *Neuron*, *75*(2), 265–270. https://doi.org/10.1016/j.neuron.2012.04.034

Kropotov, J. D. (2009). Alpha Rhythms. In *Quantitative EEG, Event-Related Potentials and Neurotherapy* (pp. 29–58). Elsevier. https://doi.org/10.1016/B978-0-12-374512-5.00002-5

Kutas, M., & Hillyard, S. A. (1980). Reading Senseless Sentences: Brain Potentials Reflect Semantic Incongruity. *Science*, *207*(4427), 203–205. https://doi.org/10.1126/science.7350657

Lawson, R. P., Bisby, J., Nord, C. L., Burgess, N., & Rees, G. (2021). The Computational, Pharmacological, and Physiological Determinants of Sensory Learning under Uncertainty. *Current Biology*, *31*(1), 163-172.e4. https://doi.org/10.1016/j.cub.2020.10.043

Lebar, N., Danna, J., Moré, S., Mouchnino, L., & Blouin, J. (2017). On the neural basis of sensory weighting: Alpha, beta and gamma modulations during complex movements. *NeuroImage*, *150*, 200–212. https://doi.org/10.1016/j.neuroimage.2017.02.043

Lee, T. S., & Mumford, D. (2003). Hierarchical Bayesian inference in the visual cortex. *Journal of the Optical Society of America A*, *20*(7), 1434. https://doi.org/10.1364/JOSAA.20.001434

Ligeza, T. S., Tymorek, A. D., & Wyczesany, M. (2017). Top-down and bottom-up competition in visual stimuli processing. *Acta Neurobiologiae Experimentalis*, *77*(4), 305–316.

Limanowski, J., Litvak, V., & Friston, K. (2020). Cortical beta oscillations reflect the contextual gating of visual action feedback. *NeuroImage*, *222*, 117267. https://doi.org/10.1016/j.neuroimage.2020.117267

Liu, J., Higuchi, M., Marantz, A., & Kanwisher, N. (2000). The selectivity of the occipitotemporal M170 for faces: *NeuroReport*, *11*(2), 337–341. https://doi.org/10.1097/00001756-200002070-00023

Long, N. M., & Kuhl, B. A. (2018). Bottom-Up and Top-Down Factors Differentially Influence Stimulus Representations Across Large-Scale Attentional Networks. *The Journal of Neuroscience*, *38*(10), 2495–2504. https://doi.org/10.1523/JNEUROSCI.2724-17.2018

Luck, S. J. (2014). *An introduction to the event-related potential technique* (Second edition). The MIT Press.

Lupyan, G., & Clark, A. (2015). Words and the World: Predictive Coding and the Language-Perception-Cognition Interface. *Current Directions in Psychological Science*, *24*(4), 279–284. https://doi.org/10.1177/0963721415570732

Mathewson, K. E., Lleras, A., Beck, D. M., Fabiani, M., Ro, T., & Gratton, G. (2011). Pulsed Out of Awareness: EEG Alpha Oscillations Represent a Pulsed-Inhibition of Ongoing Cortical Processing. *Frontiers in Psychology*, *2*. https://doi.org/10.3389/fpsyg.2011.00099

Mayer, A., Schwiedrzik, C. M., Wibral, M., Singer, W., & Melloni, L. (2016). Expecting to see a letter: Alpha oscillations as carriers of top-down sensory predictions. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhv146

Menceloglu, M., Grabowecky, M., & Suzuki, S. (2017). Comparing the effects of implicit and explicit temporal expectation on choice response time and response conflict. *Attention, Perception, & Psychophysics*, *79*(1), 169–179. https://doi.org/10.3758/s13414-016-1230-4

Michelmann, S., Bowman, H., & Hanslmayr, S. (2016). The Temporal Signature of Memories: Identification of a General Mechanism for Dynamic Memory Replay in Humans. *PLOS Biology*, *14*(8), e1002528. https://doi.org/10.1371/journal.pbio.1002528

O'Reilly, J. X. (2013). Making predictions in a changing world—Inference, uncertainty, and learning. *Frontiers in Neuroscience*, *7*. https://doi.org/10.3389/fnins.2013.00105

Pfurtscheller, G., Stancák, A., & Neuper, C. (1996). Event-related synchronization (ERS) in the alpha band—An electrophysiological correlate of cortical idling: A review. *International Journal of Psychophysiology*, *24*(1–2), 39–46. https://doi.org/10.1016/S0167-8760(96)00066-9

Polich, J. (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology: Official Journal of the International Federation of Clinical Neurophysiology*, *118*(10), 2128–2148. https://doi.org/10.1016/j.clinph.2007.04.019

Ran, G., Zhang, Q., Chen, X., & Pan, Y. (2014). The effects of prediction on the perception for own-race and other-race faces. *PloS One*, *9*(11), 1–15. https://doi.org/10.1371/journal.pone.0114011

Rao, R. P. N., & Ballard, D. H. (1999). Predictive coding in the visual cortex: A functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience*, *2*(1), 79–87. https://doi.org/10.1038/4580

Schliephake, L. M., Trempler, I., Roehe, M. A., Heins, N., & Schubotz, R. I. (2021). Positive and negative prediction error signals to violated expectations of face and place stimuli distinctively activate FFA and PPA. *NeuroImage*, *236*, 118028. https://doi.org/10.1016/j.neuroimage.2021.118028

Schubotz, R. I. (2007). Prediction of external events with our motor system: Towards a new framework. *Trends in Cognitive Sciences*, *11*(5), 211–218. https://doi.org/10.1016/j.tics.2007.02.006

Smout, C. A., Tang, M. F., Garrido, M. I., & Mattingley, J. B. (2019). Attention promotes the neural encoding of prediction errors. *PLoS Biology*, *17*(2), e2006812. https://doi.org/10.1371/journal.pbio.2006812

Summerfield, C., & Egner, T. (2009). Expectation (and attention) in visual cognition. *Trends in Cognitive Sciences*, *13*(9), 403–409. https://doi.org/10.1016/j.tics.2009.06.003

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M.-M., & Egner, T. (2008). Neural repetition suppression reflects fulfilled perceptual expectations. *Nature Neuroscience*, *11*(9), 1004–1006. https://doi.org/10.1038/nn.2163

Todorovic, A., van Ede, F., Maris, E., & de Lange, F. P. (2011). Prior Expectation Mediates Neural Adaptation to Repeated Sounds in the Auditory Cortex: An MEG Study. *Journal of Neuroscience*, *31*(25), 9118–9123. https://doi.org/10.1523/JNEUROSCI.1425-11.2011

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

Valakos, D., d'Avossa, G., Mylonas, D., Butler, J., Klein, C., & Smyrnis, N. (2020). P300 response modulation reflects breaches of non-probabilistic expectations. *Scientific Reports*, *10*(1), 10254. https://doi.org/10.1038/s41598-020-67275-0

van Moorselaar, D., Lampers, E., Cordesius, E., & Slagter, H. A. (2020). Neural mechanisms underlying expectation-dependent inhibition of distracting information. *ELife*, *9*, e61048. https://doi.org/10.7554/eLife.61048

van Pelt, S., Heil, L., Kwisthout, J., Ondobaka, S., van Rooij, I., & Bekkering, H. (2016). Beta- and gamma-band activity reflect predictive coding in the processing of causal events. *Social Cognitive and Affective Neuroscience*, *11*(6), 973–980. https://doi.org/10.1093/scan/nsw017

Vanunu, Y., Hotaling, J. M., Le Pelley, M. E., & Newell, B. R. (2021). How top-down and bottom-up attention modulate risky choice. *Proceedings of the National Academy of Sciences*, *118*(39), e2025646118. https://doi.org/10.1073/pnas.2025646118

Wiest, M. C., & Nicolelis, M. A. L. (2003). Behavioral detection of tactile stimuli during 7-12 Hz cortical oscillations in awake rats. *Nature Neuroscience*, *6*(9), 913–914. https://doi.org/10.1038/nn1107

Xu, Z., Ren, Y., Guo, T., Wang, A., Nakao, T., Ejima, Y., Yang, J., Takahashi, S., Wu, J., Wu, Q., & Zhang, M. (2021). Temporal expectation driven by rhythmic cues compared to that driven by symbolic cues provides a more precise attentional focus in time. *Attention, Perception, & Psychophysics*, *83*(1), 308–314. https://doi.org/10.3758/s13414-020-02168-y

Yon, D. (2021). Prediction and Learning: Understanding Uncertainty. *Current Biology*, *31*(1), R23–R25. https://doi.org/10.1016/j.cub.2020.10.052

Yon, D., & Frith, C. D. (2021). Precision and the Bayesian brain. *Current Biology*, *31*(17), R1026–R1032. https://doi.org/10.1016/j.cub.2021.07.044

Yu, A. J., & Dayan, P. (2005). Uncertainty, Neuromodulation, and Attention. *Neuron*, *46*(4), 681–692. https://doi.org/10.1016/j.neuron.2005.04.026

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

Zion-Golumbic, E., & Bentin, S. (2007). Dissociated Neural Mechanisms for Face Detection and Configural Encoding: Evidence from N170 and Induced Gamma-Band Oscillation Effects. *Cerebral Cortex*, *17*(8), 1741–1749. https://doi.org/10.1093/cercor/bhl100

List of Figures

Abbreviations

ANOVA   Analysis of Variance

EEG   Electroencephalography

ERPs   Event-Related Potentials

EOG   Electrooculogram

fMRI   functional Magnetic Resonance Imaging

ISI   Interstimulus Interval

MEG   Magnetoencephalography

RaFD   Radboud Faces Database

ROI   Region of Interest

RT   Reaction Time

TD   Temporal Delay block

TF   Time-Frequency

VI   Visual Interference block

V1   Visual area 1

V2   Visual area 2

V4   Visual area 4

Curriculum Vitae

Marlen A. Roehe

10.04.1993

Guelph, Ontario, Canada

Academic Career

2017 – present	***Ph.D.***, Westfälische Wilhelms-Universität, Münster, Biological Psychology and Otto Creutzfeldt Centre for Cognitive and Behavioural Neuroscience
	Ph.D. Thesis: Measures and content of anticipation in the brain. (Supervisor: Prof. R. I. Schubotz)
2015 – 2016	***M.Sc.***, University of Edinburgh, Edinburgh, School of Philosophy, Psychology and Language Sciences
	Master Thesis: The therapeutic impact of music on predictive processes underlying mentalisation and social-bonding in children with autism. (Supervisor: Prof. A. Clark)
2011 – 2015	***B.Mus.***, (with Honours), University of Edinburgh, Edinburgh, Reid School of Music
	Bachelor Thesis: Does musical activity have the potential to be of therapeutic benefit for patients with frontotemporal dementia? (Supervisor: Prof. R. MacDonald)

Awards

2016	Highly Commended Dissertation Award, University of Edinburgh

Teaching Experience

2020	Empirical Research Skills, B.Sc. Psychology
2019	Empirical Research Skills, B.Sc. Psychology

2018	Empirical Research Skills, B.Sc. Psychology
2017	Biological Psychology Seminar, B.Sc. Psychology
2014	***Student Research Assistant.*** Institute for Music in Human and Social Development and Clinical Research Imaging Centre, University of Edinburgh. Digitising and analysing behavioural data.

Publications - Scientific Papers

Roehe, M. A., Kluger, D. S., & Schubotz, R. I. (2022). Fluctuations in alpha and beta power provide neural states favourable for contextually relevant anticipatory processes. (under review).

Roehe, M. A., Kluger, D. S., Schroeder, S. C. Y., Schliephake, L. M., Boelte, J., Jacobsen, T., & Schubotz, R. I. (2021). Early alpha/beta oscillations reflect the formation of face-related expectations in the brain. *PLoS ONE, 16(7),* e0255116.

Schliephake, L. M., Trempler, I., ***Roehe, M. A.,*** Heins, N., & Schubotz, R. I. (2021). Positive and negative prediction error signals to violated expectations of face and place stimuli distinctively activate ffa and ppa. *NeuroImage*, *236*(2021), 118028.

Kluger, D. S., Broers, N., ***Roehe, M. A.,*** Wurm, M. F., Busch, N. A., & Schubotz, R. I. (2020). Exploitation of local and global information in predictive processing. *PLoSONE*, *15*(4), e0231021.

Conference Presentations

Roehe, M. A., Kluger, D. S., Schroeder, S. C. Y., Schliephake, L. M., Boelte, J., Kohler, A., & Schubotz, R. I. (2020). Formation of face-related predictions: An interplay of pre-stimulus alpha/beta enhancement and peri-stimulus n170 diminution. In *Cognitive Neuroscience Society 2020 Virtual Meeting* (p. 92). Boston, USA.

Declarations

Declarations by the candidate documenting **open-science activities** and **on the consideration of ethical aspects** as part of the doctoral process and disclosure of **personal contribution** for manuscripts completed by two or more authors (cumulative dissertations)

Doctoral candidate: **Marlen A. Roehe**

Title of dissertation: **Measures and Content of Anticipation in the Brain**

1. Documentation of **open-science activities**

Manuscript 1

	yes	no	If yes, please specify the source
Pre-registration	◯	◉	
Publication of data	◉	◯	Open Science Framework (https://osf.io/vxqrh/)
Publication of analysis scripts	◯	◉	
Publication of materials	◯	◉	
Open access publication	◉	◯	
If applicable, (voluntary) statement as to why open-science activities played little or no role in this study:			

Manuscript 2

	yes	no	If yes, please specify the source
Pre-registration	◯	◉	
Publication of data	◯	◉	
Publication of analysis scripts	◯	◉	
Publication of materials	◯	◉	
Open access publication	◯	◉	
If applicable, (voluntary) statement as to why open-science activities played little or no role in this study:			

Manuscript 3

	yes	no	If yes, please specify the source
Pre-registration	◯	⦿	
Publication of data	◯	⦿	
Publication of analysis scripts	◯	⦿	
Publication of materials	◯	⦿	
Open access publication	◯	⦿	
If applicable, (voluntary) statement as to why open science activities played little or no role in this study:			

2. Declaration on **the consideration of ethical aspects**

Study number	Source (manuscript / chapter of dissertation): e.g. study 1 in paper 2, study 1 described in chapter 4	Was the study reviewed by an ethics commission?	
		yes	no
1	Manuscript 1	⦿	◯
2	Manuscript 2 & 3	⦿	◯
		◯	◯
		◯	◯
		◯	◯
If applicable, (voluntary) statement describing how ethical aspects were considered in planning and conducting the studies:			

3. **Declaration** of one's **personal contribution** to the submitted academic manuscripts by two or more authors

Manuscript 1

Title	Early alpha/beta oscillations reflect the formation of face-related expectations in the brain
Author(s)	Marlen Roehe, Daniel Kluger, Svea Schroeder, Lena Schliephake, Jens Boelte, Thomas Jacobsen & Ricarda Schubotz

Publication status:	not yet submitted	◯	(please mark with X)
	submitted	◯	
	in review	◯	
	in revision	◯	
	accepted	◯	
	published	⊙	

Journal	PLoS ONE
Year of publication	2021

Description of your own contribution in the case of joint authorship:

*partly responsible for conceptualising and designing the study
*mainly responsible for data collection and curation
*responsible for formal analyses and data interpretation
*mainly responsible for writing and revising the manuscript
*corresponding author

Manuscript 2

Title	Fluctuations in alpha and beta power provide neural states favourable for contextually relevant anticipatory processes
Author(s)	Marlen Roehe, Daniel Kluger & Ricarda Schubotz

Publication status:	not yet submitted ○	(please mark with X)
	submitted ○	
	in review ○	
	in revision ◉	
	accepted ○	
	published ○	

Journal	European Journal of Neuroscience
Year of publication	

Description of your own contribution in the case of joint authorship:

*partly responsible for conceptualising and designing the study
*mainly responsible for data collection and curation
*responsible for formal analyses and data interpretation
*mainly responsible for writing and revising the manuscript
*corresponding author

Manuscript 3

Title	The brain downregulates higher cognitive processes to compensate for processing contextually relevant interferences
Author(s)	Marlen Roehe, Daniel Kluger & Ricarda Schubotz

Publication status:		
not yet submitted	⦿	(please mark with X)
submitted	◯	
in review	◯	
in revision	◯	
accepted	◯	
published	◯	

Journal	
Year of publication	

Description of your own contribution in the case of joint authorship:

*partly responsible for conceptualising and designing the study
*mainly responsible for data collection and curation (same data as for manuscript 2)
*responsible for formal analyses and data interpretation
*mainly responsible for writing and revising the manuscript
*corresponding author

Please attach additional tables if the dissertation comprises more than three academic manuscripts.

Place, Date
candidate

Signature of the doctoral

Pernitz, 31.01.2023