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One thing leads to another:
anticipating visual object identity based on associative-memory templates

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Running Title: Anticipating object identity based on memory

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Abstract

Probabilistic associations between stimuli afford memory templates that guide perception through pro-active anticipatory mechanisms. A great deal of work has examined the behavioural consequences and human electrophysiological substrates of anticipation following probabilistic memory cues that carry spatial or temporal information to guide perception. However, less is understood about the electrophysiological substrates linked to anticipating the sensory content of events based on recurring associations between successive events. Here, we demonstrate behavioural and electrophysiological signatures of utilising associative-memory templates to guide perception, while equating spatial and temporal anticipation (Experiment 1 and 2), as well as target probability and response demands (Experiment 2). By recording the electroencephalogram (EEG) in the two experiments (N=55; 24 Female), we show that two markers in human electrophysiology implicated in spatial and temporal anticipation also contribute to anticipation of perceptual identity: attenuation of alpha band oscillations and the contingent negative variation (CNV). Taken together, our results show that memory-guided identity templates proactively impact perception and are associated with anticipatory states of attenuated alpha oscillations and the CNV. Furthermore, by isolating object-identity anticipation from spatial and temporal anticipation, our results suggest a role for alpha attenuation and the CNV in specific visual content anticipation beyond general changes in neural excitability or readiness.

Significance Statement

Probabilistic associations between stimuli afford memory templates that guide perception through pro-active anticipatory mechanisms. The current work isolates the behavioural benefits and electrophysiological signatures of memory-guided identity-based anticipation – while equating anticipation of space, time, motor responses, and task-relevance. Our results show that anticipation of the specific identity of a forthcoming percept impacts performance and is associated with states of attenuated alpha oscillations and the contingent negative variation (CNV) – extending previous work implicating these neural substrates in spatial and temporal preparatory attention. Taken together this work bridges fields of attention, memory, and perception, providing new insights into the neural mechanisms that support complex attentional templates.
Introduction

Probabilistic associations between stimuli can lead to memory-based templates that impact perceptual performance through anticipation of the location, temporal onset, identity, or features of anticipated sensory events. Early studies relied on relatively simple symbolic cues (e.g., arrows) to demonstrate that attention can be guided in space, time, and across features to facilitate performance (Coull & Nobre, 1998; Posner, 1980; Treue & Martinez Trujillo, 1999).

More recently, studies have considered attentional orienting in more naturalistic tasks, in which the contents of long-term memory, often probabilistic in nature, guide the processing of incoming stimuli (Hutchinson & Turk-Browne, 2012). The bulk of the studies investigating memory-guided attention have focused primarily on anticipating spatial location (Awh, Belopolsky, & Theeuwes, 2012; Chun & Jiang, 1998; Goldfarb, Chun, & Phelps, 2016; Jiang, 2018; J. J. Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006) and the expected temporal onset of items (Cravo, Rohenkohl, Santos, & Nobre, 2017; Olson & Chun, 2001). However, in addition, there is mounting interest in investigating mechanisms that support memory-based anticipation of the identity of upcoming percepts (Kok, Jehee, & de Lange, 2012; Peelen & Kastner, 2014; Stokes, Myers, Turnbull, & Nobre, 2014; C. Summerfield, Tritschuh, Monti, Mesulam, & Egner, 2008; Turk-Browne, Isola, Scholl, & Treat, 2008; Turk-Browne, Scholl, Johnson, & Chun, 2010).

Identity anticipation through ‘perceptual templates’ plays a central role in theories of attention (e.g. Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Wolfe, 1994). In much of the work examining perceptual templates to date observers are explicitly provided with the template of the forthcoming target. That is, they are shown a particular object which they must subsequently match or search, such as in delayed-match-to-sample or visual search tasks (Carlisle, Arita, Pardo, & Woodman, 2011; Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993; van Driel, Gunseli, Meeter, & Olivers, 2017). Though this can be informative in assessing perceptual templates, it fails to capture a common everyday experience in building memory templates. Outside of the laboratory, frequent associations between successive different stimuli support the establishment of memory templates. Building on previous work investigating associative memory templates (Higuchi & Miyashita, 1996; Kok, Failing, & de Lange, 2014; Kok et al., 2012; Kok, Mostert, & De Lange, 2017; Rainer, Rao, & Miller,
1999; Turk-Browne et al., 2008, 2010), we here targeted two specific human electrophysiological substrates of associative memory templates during the anticipatory period.

We developed a task to investigate the anticipation of visual-identity information based on probabilistic associative memory. We report robust behavioral benefits on target perception in the context of a demanding visual identification task. We also investigated the electrophysiological markers linked to proactive template-based anticipation, specifically testing for the involvement of two canonical neural markers of anticipation from the spatial and temporal orientating literatures – the modulation of alpha-band oscillations and the Contingent Negative Variation (CNV).

Alpha attenuation has been associated with both spatial (Haegens, Nacher, Luna, Romo, & Jensen, 2011; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; van Ede, 2018; Worden, Foxe, Wang, & Simpson, 2000) and temporal (Heideman et al., 2018; Rohenkohl & Nobre, 2011; van Ede, Niklaus, & Nobre, 2017; Zanto et al., 2011) orienting of attention, including during long-term-memory-guided anticipation (Stokes, Atherton, Patai, & Nobre, 2012). Likewise, the CNV is an ERP component classically associated with temporal anticipation (Cravo, Rohenkohl, Wyart, & Nobre, 2011; Los & Heslenfeld, 2005; Miniussi, Wilding, Coull, & Nobre, 1999; Nobre, 2001; Pfeuty, Ragot, & Pouthas, 2005; Praamstra, Kourtis, Kwok, & Oostenveld, 2006), also in the context of long-term-memory-guided anticipation (Cravo et al., 2017). Probing the involvement of these electrophysiological signatures during object-identity anticipation is important to inform a relevant and current theoretical debate about the nature of such markers. Alpha and CNV modulations during anticipation in space and time may purely reflect changes in the excitability of underlying neuronal populations (Benwell et al., 2017; Lemi, Chaumon, Crouzet, & Busch, 2017; Romei et al., 2008; Romei, Gross, & Thut, 2010; Samaha, Gosseries, & Postle, 2017), independent of “informational content”. In the current work, we isolate identity anticipation and control for general “readiness” or “excitability” by equating spatial and temporal anticipation as well as target and response probabilities. If alpha and CNV modulations nevertheless still occur under these conditions, this would provide evidence that they also play a role in the anticipation of visual content.
Methods

Participants

In both experiments, all participants were right-handed with normal/corrected-to-normal vision had no history of neurological disorders, and were not taking any neurological medication. All participants gave informed written consent, and were compensated £15 per hour for a total of £45. The experiments were approved by the Oxford Central University Research Ethics Committee.

In Experiment 1, thirty volunteers participated. Out of the 30 participants, 5 of the participants missed > 80% of the difficult targets preceded by a non-predictive S1. On this basis, these participants were excluded from the analysis. Of the twenty-five remaining participants the average age was 24.2 (18-33) and there were 9 females.

In Experiment 2, thirty-six volunteers participated. Out of the 36 participants, 6 of the participants performed at chance for targets on non-predictive S1 trials. On this basis, these participants were excluded from the analysis. Of the remaining thirty participants the average age was 27.1 (20-34) and 15 were female.

Procedures

Participants sat in a dimly-lit booth at a distance of 100 cm from the monitor (22 inch Samsung SyncMaster 2233; resolution: 1680 × 1050 pixels; refresh rate: 100 Hz; screen width: 47 cm). The experimental script was generated using Psychophysics Toolbox (Brainard, 1997) on MATLAB (version 2014b, The Mathworks Inc., Natick, NA, USA). Participants were instructed to refrain from excessive blinking and to keep their face as relaxed as possible to avoid muscular artifacts in the EEG recordings.

Experiment 1

The structure of Experiment 1 is shown in Figure 1. Participants were shown a random sequence of objects taken from a set of 14 objects from the Novel Object and Unusual Name database (NOUN) (Horst & Hout, 2016). Among these objects there were four critical objects: easy S1, easy target, difficult S1, and difficult target, and ten neutral objects. These four objects were
randomly allocated to every fourth participant and then counter-balanced for subsequent participants such that for each random allocation of four objects, each object held each of the four critical roles. Participants’ task was to press a corresponding key (either “m” or “x” key) whenever they detected a target. The targets switched their association with the keys randomly between blocks, such that each target was associated with the “x” and “m” buttons for half of the blocks.

Before the start of the task, observers were informed about the S1 objects. Specifically, they were told that following the presentation of a predictive S1 there was a 70% probability that the next item would be the corresponding target (i.e. the paired associate). Therefore, within the stream, specific S1 identities would predict specific target identities. In the other 30% of the trials each of the other items was equiprobable.

A single trial consisted of the following sequence: stimulus 1 (S1), blank, stimulus 2 (S2), and a mask. S1 could either be a predictive or a non-predictive and was always presented for 250 ms. S2 could either be one of the targets or a foil object. S2 was immediately followed by a 100-ms mask that consisted of patches drawn randomly from the potential target items. For each set of objects 3 of these masks were created and used randomly throughout the experiment. Target difficulty was determined by its exposure duration. The easy target was always presented for 150 ms before the mask, whereas the difficult target was presented for only 25 ms before the mask. The neutral objects were shown for either 150 or 25 ms equiprobably, i.e. any particular neutral object would be shown for 150 and 25 ms half of the time. The mask was followed by a 1000-ms blank before the next trial began. With this design the appearance of S2 was completely predictable in space and time. Participants completed 14 blocks of 100 trials in total.

**Experiment 2**

The structure of Experiment 2 is shown in Figure 4. The stimuli, experimental set up, and EEG procedures were the same as in Experiment 1. A trial was similar to that of Experiment 1, with a few critical changes. On each trial, participants first saw S1 (250 ms) which again could be a predictive or an non-predictive S1 with equal probability. This was followed by a 750-ms blank and the quick presentation of one of three targets (30 ms) – we will refer to these targets as
target A, B, or C. That is, there was a task-relevant item presented on every trial. Critically, two of these items (target A and target B) were predictable based on S1, whereas the other item (target C) was always equally probable after all S1 stimuli. Following the presentation of the target and a mask (100 ms), all three potential targets appeared on the screen and observers used the left, down, and right arrow keys to indicate which object they had just seen. The position of the three targets was randomized across trials such that observers could not prepare their response before the response screen. The stimuli were randomly allocated to each participant. With these changes to the design, every trial and item was task relevant, and participants could not prepare a specific response during the period after S1. Here, therefore, predictive and non-predictive S1s differed only with regard to its ability vs inability to form a specific target template in anticipation of S2.

The relationships between the S1 and target items were explicitly detailed to the participants before the experiment. In total there were eight potential S1 items. Four of these items were predictive and four were non-predictive. Of the four predictive S1s, two predicted target A and two predicted target B. That is if one of these predictive S1 objects appeared the associated target would follow in 2/3 of the trials. In the remaining 1/3 of the trials Target C would appear. On non-predictive S1 trials all targets were equally likely. As such, throughout the experiment, all three targets were equally likely to appear such that there was no higher probability of a predictable target.

**Behavioral analysis (Experiment 1 & 2)**

Behavioral data were analyzed using R (R Core Team, 2018). Reaction times and error rates were submitted to an ANOVA implemented in the ez package (Lawrence, 2013) and t-tests implemented in lsr (Navarro, 2015). Effect size estimates (η^2 \& d) are provided for all effects. Plotting was completed using the ggplot2 package in R (Wickham, 2009).

**EEG Acquisition (Experiment 1 & 2)**

We acquired EEG using Synamps amplifiers and Neuroscan data acquisition software (Compumedics). Sixty-one electrodes were distributed across the scalp using the international
10–10 positioning system. The left mastoid was used as the active reference, and we included a right mastoid measurement to derive an average-mastoid reference offline. The ground was placed on the left upper arm. Additionally, vertical and horizontal EOG electrodes were used to monitor for eye blinks and eye movements. During acquisition, data were low-pass filtered by an anti-aliasing filter (250-Hz cutoff), digitized at 1000 Hz, and stored for offline analysis.

**EEG Preprocessing (Experiment 1 & 2)**

The preprocessing and analysis scripts for both experiments can be found as html files and as reproducible scripts (jupyter notebooks; (Kluyver et al., 2016) at https://github.com/SageBoettcher/identityTemplates. The preprocessing pipeline is modified from the analysis pipeline used by Draschkow and colleagues (Draschkow et al., 2018). All EEG data analysis was conducted in MNE-Python (Gramfort et al., 2013). The data were downsampled to 200 Hz, and high-pass filtered at 0.1 Hz. To regress out eye-movement activity, an Independent component analysis (ICA; Jung et al., 2000) was used to decompose the data – which was high-pass filtered at 1 Hz – into sixty temporally independent components. Eye-movement components were detected by first correlating the filtered data with the electrooculography (EOG) and subsequently, when needed, manually selecting a subset of typical component maps and identifying the best group match to them (Viola et al., 2009). Selected components were then removed from the data. Trials were segmented from -200 ms to +750 ms (Experiment 1) or +1000 ms (Experiment 2) relative to the onset of S1. Average activity over the 200 ms preceding the stimulus onset was used as a baseline against which all amplitudes were calculated. Finally, epochs with especially high variance were discarded. These epochs were detected through a generalized extreme studentized deviate (ESD) test for outliers with an alpha value of .05 and discarded from the analysis. On average 34 trials out of 1400 were discarded in the manner.

**EEG Data Analysis (Experiments 1 & 2)**

Alpha
For the time-frequency analysis, we used epochs from -200 to 1000 ms. Morlet wavelets were convolved with the data between 3 and 40 Hz. For each frequency, we used a fixed 400-ms time window such that the number of cycles changed with the frequency. After the time frequency transformation, activity was averaged over all posterior electrodes (P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO7, PO3, POz, PO4, PO8, O1, Oz, O2) and contrasted between predictive and non-predictive trials (separately for the easy and difficult conditions in Experiment 1). We expressed this as a normalised difference \(((\text{predictive minus non-predictive}) / (\text{predictive plus non-predictive})) \times 100\).

ERPs

The event-related potentials (ERPs) were calculated by averaging trials within a participant and then subsequently averaging these waveforms across participants separately for each condition. The ERPs were averaged across a predefined set of central-posterior electrodes (‘P1’, ‘Pz’, ‘P2’, ‘CPz’, ‘POz’) as well as central-frontal electrodes (‘F1’, ‘Fz’, ‘F2’, ‘AFz’, ‘FCz’). These electrodes were chosen based on previous work showing peak amplitude for the CNV at electrode Fz and peak amplitude for potentials linked to retrieval at electrode Pz. We focused our analyses on these electrodes and included the immediately surrounding electrodes to increase potential sensitivity.

EEG statistical analysis

Inferential claims about differences between conditions were based on cluster-based permutation test (Maris & Oostenveld, 2007) and reported according to recommendations by Sassenhagen & Draschkow (2019).

Results

Experiment 1: Target Templates and Target Difficulty

In Experiment 1 we investigated whether identity templates from associative memory impact perception, as well as the neural markers that may be involved in this template-based anticipation. To evaluate the adaptive utility of the identity template, we additionally asked to
what extent these hypothesized effects depend on the anticipated perceptual difficulty of the
target.

The structure of the experiment is shown in Figure 1. On each trial, participants saw two
sequential objects (S1 & S2) followed by a mask. Whenever participants saw one of their two
potential targets – always in the S2 position – they responded with a corresponding button press
on a keyboard (m or x, counterbalanced across blocks). The S1 item could either be predictive or
non-predictive of the identity of the upcoming item. Predictive S1s were followed by their
respective S2-target in 70% of trials. Spatial and temporal predictions were fixed with
presentation always appearing in the center of the screen after 750 ms; therefore, predictive
and non-predictive S1s differed in that only predictive S1s enabled participants to anticipate the
identity of the upcoming S2 stimuli.

Figure 1. Trial schematic and behavioral data from Experiment 1. (A) an example of the trial sequence
from Experiment 1. On each trial, participants saw stimulus 1 (S1) which could either be predictive or
non-predictive about the following stimulus 2 (S2) which could be an easy target (150 ms), a difficult
target (25 ms), or a foil (25 or 150 ms). S2 was immediately followed by a mask. Participants were
instructed to respond to the targets (but not the foils) with the corresponding button as quickly as
possible. (B) The probability of a specific S2 target following a predictive S1 was 70%, whereas non-
predictive S1s were equally likely to be followed by either of the two potential targets, or either of the
4 foils. S1-S2 relationships were made explicit to participants before starting the experiment. (C)
Participants responded more quickly and more accurately to targets preceded by a predictive S1 as
well as to easy targets. Additionally, there was a significant interaction in both RT and percent error
indicating that predictive S1s had a larger benefit in the difficult-target trials.

Behavioral Results
To assess whether predictive S1s impact performance and whether this effect was modulated by
the expected target difficulty, we conducted repeated-measures ANOVAs on RT and error rates
with S1 type (predictive and non-predictive) and target difficulty (easy and difficult) as factors.
Behavioral results are depicted in Figure 1C. Target difficulty and S1 type interacted significantly
in both RT ($F(1,24) = 5.4, p = .03, \eta_g^2 = .002$) as well as error rates ($F(1,24) = 12.0, p = .002, \eta_g^2 =
.08$). Moreover, we found main effects of S1 type and target difficulty for both RT (S1 effect:
$F(1,24) = 87.3, p < .001, \eta_g^2 = .41$; difficulty effect: $F(1,24) = 7.9, p = .009, \eta_g^2 = .01$) and error
rates (S1 effect: $F(1,24) = 29.5, p < .001, \eta_g^2 = .21$; difficulty effect: $F(1,24) = 15.4, p < .001, \eta_g^2$
= .28). Paired samples t-tests (Bonferroni corrected p-values) revealed a significant RT benefit
(i.e., faster RTs) of the predictive S1 for both easy and difficult targets (easy: $t(24) = 9.17, p <$
.001, $d = 1.83$; difficult: $t(24) = 9.11, p < .001, d = 1.82$), and that the benefit of the predictive S1 was larger for difficult targets ($t(24) = 2.33, p = .03, d = .47$). The same pattern occurred for error rates, with a significant benefit (i.e., lower errors) following predictive vs. non-predictive S1 items in trials with an easy target ($t(24) = 2.9, p = .01, d = .59$) as well as trials with a difficult target ($t(24) = 4.93, p < .001, d = .99$). Once again this benefit of predictive S1s was larger for difficult targets ($t(24) = 3.46, p = .002, d = .69$). Thus, predictive objects impact performance on the target, and this benefit was particularly pronounced when the targets were difficult to perceive.

The above results considered only target-present trials. For completeness, we also analyzed foil trials to determine if predictive S1s also led to more false alarms. We found that observers were indeed more likely to false alarm to a foil following a predictive compared to a non-predictive S1 ($t(24) = 3.14, p = .004, d = .62; 14.5\% \text{ vs. } 1.5\% \text{ false alarms}$). Because the probability that a target would appear after an informative S1 was higher than the probability that a non-target would appear (in Experiment 1, but not Experiment 2 as we return to later), this increase in false-alarms following predictive S1s may simply reflect a strategic decision of participants to report the target when unsure.

**EEG Results**

**Alpha**

To assess the effect of a predictive vs. non-predictive S1s on induced brain activity, we first compared time- and frequency-resolved maps of power (collapsed over all posterior electrodes; see insets Figure 2A,B) from the onset of S1 until 250 ms after the onset of the S2 as seen in Figure 2. More specifically, we directly contrasted trials with a predictive and a non-predictive S1. We did so separately for trials with a predictive S1 that predicted an easy target (predictive-easy S1) and trials with a predictive S1 that predicted a difficult target (predictive-difficult S1). The same non-predictive-S1 trials were used for both comparisons. Significant clusters emerged following both the predictive-easy S1 (Fig. 2A, $p < .001$) and following the predictive-difficult S1 (Fig. 2B, $p < .001$) in comparison to following the non-predictive S1. The maximal attenuation within these clusters for both the easy and difficult S1 occurred around 11 Hz and 600 ms after S1 onset, i.e. mostly concentrated within the alpha band. A topographic inspection confirmed
that these effects had a clear posterior topography in line with a visual preparation effect. There were no significant clusters when directly contrasting easy to difficult S1s (all cluster ps > .13).

To have a clearer understanding of the time course of the alpha attenuation, we also averaged these effects along the classical alpha band (8-12 Hz; Fig. 2C). Once again, we found a significant cluster for both the easy (p < .001) and the difficult S1s (p < .001); with no significant difference according to the difficulty levels during the anticipation period (p = .14, with the only cluster forming after the onset of the target).

Figure 2. Alpha attenuation following predictive vs. non-predictive S1s in Experiment 1. (A) Time frequency results for posterior electrodes shows alpha attenuation in the predictive easy S1 trials vs. the non-predictive trials, as well as in the predictive difficult S1 trials vs. the non-predictive S1 trials (B). The topographies are plotted on the same scale as the above time frequency plot. C) shows the time course of the alpha attenuation averaged between 8 and 12 Hz. Vertical lines at 750 ms show the onset of the S2 target. Significant clusters with a p value < .05 are denoted with the black outline (panels A and B) and as horizontal lines in panel C. Shaded areas represent ± 1 SEM (68% confidence intervals).

**ERPs**

To investigate the anticipatory nature of identity-based templates, we additionally investigated event-related-potentials (ERPs) locked to the onset of predictive-easy S1s, predictive-difficult S1s, and non-predictive S1s for predefined clusters of frontal and posterior electrodes. The results are depicted in Figure 3. We were specifically interested in testing if these identity-based predictions also produce a CNV – a frontal negativity – in the pre-defined frontal electrodes.

We first considered the frontal electrode cluster (Fig. 3A). For both the predictive-easy and the predictive-difficult S1 cues, we found a significantly larger negativity in the late S1-S2 cue-target interval, compared to the non-predictive S1 cues (easy: p<.001, difficult: p<.001). These negativities were associated with a frontal topography characteristic of the CNV (Fig. 3C).

In the S1-predictive-easy condition we additionally found an early positivity (p = .004) that is likely a spillover effect from an earlier more posterior positivity that we return to below (as also confirmed by the time-resolved topographical analysis presented in Figure 3C). There were no significant clusters when contrasting the easy and difficult S1s (ps > .43).

When comparing effects for predictive vs. non-predictive S1 cues in the predefined posterior electrodes (Fig. 3B) a significant cluster was identified from around 200 to 600 ms for both easy and difficult (ps < .01) The effect reflected a late positive potential elicited by
predictive cues. Topographical analysis confirmed the potential was centrally distributed over
the posterior scalp (Fig. 3C). As with the alpha modulations and the CNV, there were no
significant clusters when comparing the easy and difficult predictive S1s (all cluster ps > .43).
These effects were confirmed, and also nicely demonstrated, by the time-resolved
topographies of predictive vs. non-predictive S1 (separated by the easy and difficult conditions),
as depicted in Figure 3C.

Figure 3. Posterior positivity and frontal negativity following predictive vs. non-predictive S1s in
Experiment 1. (A) ERPs locked to the onset of S1 and averaged across a subset of frontal electrodes
(‘F1’, ‘Fz’, ‘F2’, ‘AFz’, ‘FCz’). Predictive S1s show a late frontal negativity relative to non-predictive S1s,
while difficulty did not significantly modulate this effect. (B) ERPs locked to the onset of S1 and
averaged across a subset of posterior electrodes (‘P1’, ‘Pz’, ‘P2’, ‘CPz’, ‘POz’). The predictive S1s show a
clear positive deflection from the non-predictive S1, while difficulty did not significantly modulate this
effect. (C) Topographies of the ERP effects (predictive easy/difficult vs. non-predictive) over time show
an early posterior positivity followed by a late frontal negativity. Significant clusters with a p value < .05
are denoted with horizontal lines in panels A and B. Shaded areas represent ± 1 SEM (68% confidence
intervals).

Experiment 2: Target Templates While Equating Target and Response Probabilities
In Experiment 1, the pattern of behavioral data was suggestive of proactive and flexible template
utilisation, resulting in larger performance benefits when target discrimination was difficult.
Proactive memory-based expectation was also suggested by alpha attenuation and a CNV
following predictive vs. non-predictive S1 objects. These predictive S1s allowed participants to
prepare for the identity of the upcoming stimulus, while controlling for spatial and temporal
expectations that were matched between the S1 objects.

Although neural markers clearly signaled target anticipation, it was not possible to
conclude that the neural effects were specifically related to the perceptual identity of the
anticipated target. On average, task-relevant items (targets) were also more likely following
predictive vs. non-predictive S1s, which may have led to differential motor anticipation, or states
of attention. Because responses were only required to the target stimuli, during predictive S1
trials observers could not only prepare for a task-relevant visual target, but possibly also for the
associated motor response. The neural effects may thus reflect general task readiness (or
“excitability”), rather than template-specific anticipation of visual identity. To rule out this
potential interpretation, we designed Experiment 2 (Fig. 4).
In Experiment 2, we equated these other forms of anticipation by making S2 a task-relevant stimulus on every trial. Specifically, participants were always tasked with discriminating S2, but only a subset of S1 stimuli predicted the identity of S2. Therefore, the only difference between predictive and non-predictive S1s was the likelihood of a specific target appearing. As such, differences between the S1 conditions must be attributed to proactive target template activation. Participants once again saw predictive and non-predictive S1s (Fig. 4B) which were equated for their spatial and temporal predictions, as well as motor affordances. Three stimuli served as S2, two of which were predicted by a subset of S1 stimuli and one of which was completely unpredictable. Participants responded to S2 in a 3-alternative forced choice (3AFC) design. To eliminate anticipation of specific motor responses, response mappings were random on every trial. Across the experiment, all three targets were equally probable and potential differences in the preparatory period can no longer be attributed to differences in target probability or response preparation. In Experiment 2, all trials had the same difficulty level, allowing us to focus exclusively on the central question of identity anticipation.

**Figure 4.** Trial schematic and behavioral data from Experiment 2. (A) Schematic of an example non-predictive trial in Experiment 2. Participants’ task was to always report the second S2 object. The paradigm is very similar to experiment 1 with the exception that participants must respond on every trial (i.e., each S2 is a target). Probabilities of each S2 target given the preceding S1 are shown in panel (B). In (C) we see that there is a significant effect of the predictive S1 on error rates. Because this task was a delayed forced choice, reaction times were no longer informative.

**Behavioral Results**

To test for a benefit to the predictive S1s in the error rates, we used a paired samples t-test. As seen in Figure 4C, targets preceded by a predictive S1 were again detected more accurately ($t(29) = 4.16, p < .001, d = .76$). Because participants gave a 3AFC response after an imposed delay, reaction times were not considered informative of perceptual processing in Experiment 2 and were therefore not analysed.

**EEG Results**

**Alpha**

To assess the alpha attenuation following predictive vs. non-predictive S1s, we compared the time-frequency maps in the period between the onset of S1 and the onset of S2. As shown in
Figure 5A, we observed a significant cluster ($p = .005$), with a qualitatively similar profile (in terms of time range, frequency-range, sign, and topography) as in Experiment 1. The peak attenuation in this cluster was found at 11 Hz and 610 ms post S1. As in Experiment 1, this attenuation was associated with a predominantly posterior topography (Fig. 5A). When focusing on the predefined 8-12 Hz alpha band (Fig. 5B), we found a significant cluster ($p = .01$), which spanned a similar time range as in Experiment 1.

**Figure 5.** Alpha attenuation following predictive vs. non-predictive S1 in Experiment 2. (A) Time-frequency results for posterior electrodes show alpha attenuation following the predictive S1 relative to the non-predictive S1, with a peak negativity at 610 ms post S1 at 11 Hz. (B) Time course of the alpha attenuation, averaged between 8 and 12 Hz. Vertical line at 1000 ms shows the onset of the target. Significant clusters with a $p$ value < .05 are denoted with the black outline in panel A, and by the horizontal line in panel B. Shaded area represents ± 1 SEM (68% confidence interval).

**ERPs**

As in Experiment 1, we also investigated ERPs locked to the onset of S1 in the pre-defined frontal and posterior electrode clusters (Fig. 6). In the frontal electrode cluster (Fig. 6A), we again observed a CNV – a larger negativity following predictive S1s just before the onset of S2 (cluster $p = .04$). Like in Experiment 1, we also found a significant positive cluster in the frontal electrodes between about 300 and 450 ms ($p = .01$), which again likely involved a spillover from a more posterior effect (Fig. 6C). Indeed, in the posterior cluster (Fig. 6B), predictive S1s again elicited a larger positive potential from about 300 ms until around 550 ms, yielding a significant cluster ($p = .001$).

The topographies again demonstrate how the effects of the predictive vs. non-predictive S1s develop over time and space (Fig. 6C), and revealed a qualitatively similar spatial-temporal progression as observed in Experiment 1.

**Figure 6.** Posterior positivity and frontal negativity following predictive vs. non-predictive S1 in Experiment 2. A) ERPs locked to the onset of S1 and averaged across a subset of frontal electrodes. Predictive S1s show a late frontal negativity relative to non-predictive S1s. B) ERPs locked to the onset of S1 and averaged across a subset of posterior electrodes. The predictive S1s show a clear positive deflection from the non-predictive S1s. C) Topographies of the ERP effects (Predictive vs. Non-predictive) show an early posterior positivity followed by a late frontal negativity. Significant clusters with a $p$ value < .05 are denoted with horizontal lines in panels A and B. Shaded areas represent ± 1 SEM (68% confidence intervals).
The tightly controlled identity-expectation manipulation in Experiment 2 also enabled us to investigate whether the proactive deployment of probabilistic associative-memory templates based on S1 improved neural processing of S2 during perceptual analysis (i.e., post S2 target onset). Unlike in Experiment 1, the S1 items were all followed by target items, thus equating motor demands and degree of preparation. Presentation duration of S2 was also equated. To test for qualitative changes in sensory processing, we applied linear discriminant analysis to decode the content of the two predictable targets in posterior electrodes when they were preceded either by a predictive or a non-predictive S1 (Fig. 7). Cluster-based permutations that considered the first 300 ms of target processing showed a single cluster of better decoding for predictable compared to unpredictable targets, though this did not survive cluster-correction (p = .09). When we considered only the peak decoding period of all targets (at 145ms; Fig. 7B) we found better decoding for predicted vs. unpredicted targets (t(29) = 2.89, p = .007). However, because this effect was not particularly strong (Fig. 7), we would like to present this as a tentative result in the hope that it will motivate further investigation, without further elaboration in the discussion.

Discussion

Our results provide evidence that identity templates based on probabilistic associative memory impact perception. Furthermore, these templates are associated with proactive states of attenuated alpha oscillations and the CNV, even when controlling for differences in spatial and temporal anticipation as well as response and target probabilities.

Our behavioral and EEG results build on and extend earlier work on memory-guided attentional orienting and perceptual identity templates in several ways. When considering memory-guided anticipation, we have focused here on perceptual consequences and the electrophysiological signatures of memory-guided predictions based on identity, as opposed to...
anticipation in space and time (Awh et al., 2012; Chun & Jiang, 1998; Cravo et al., 2017; Goldfarb et al., 2016; Jiang, 2018; Olson & Chun, 2001; J. J. Summerfield et al., 2006). We have studied this in a context where the templates must be retrieved from complex probabilistic associations in memory templates (Higuchi & Miyashita, 1996; Kok et al., 2014, 2012, 2017; Rainer et al., 1999; Stokes, Thompson, Nobre, & Duncan, 2009; Turk-Browne et al., 2008, 2010) – rather than being explicitly provided (Carlisle et al., 2011; Chelazzi et al., 1993; van Driel et al., 2017) – and have focused specifically on the anticipatory electrophysiological substrates associated with such templates.

This work also expands upon prior work that has used similar paired-associate tasks as the one here (Brincat & Miller, 2015; Gallistel, 1990; Higuchi & Miyashita, 1996; Rose, Verleger, & Wascher, 2001; Stokes et al., 2014), but where the focus was on learning. In the current study, the focus was not on the learning of the S1-S2 associations, but rather on the exploitation of previously learned information in service of guiding ensuing behavior (see also Rainer, Rao, & Miller, 1999; Stokes et al., 2013, 2014), here in a demanding perceptual task with masked visual targets. Doing so, we report that participants are able to utilise learned identity associations to impact perception.

A major empirical contribution of our study was to identify electrophysiological markers for the anticipation of identity-related informational content in the human brain that we discuss next in turn.

**Alpha attenuation**

In previous work, alpha attenuation has been noted during anticipatory periods for both spatially and temporally predictable targets (Heideman et al., 2018; Rohenkohl & Nobre, 2011; Sauseng et al., 2005; Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Thut et al., 2006; van Ede, de Lange, Jensen, & Maris, 2011; Worden et al., 2000; Zanto et al., 2011). In this context, alpha attenuation has been theorized to reflect engagement of sensory processing areas in preparation for a task-relevant event, in line also with the notion that alpha is inversely related to firing-rates (Haegens et al., 2011) and/or processing capacity (Hanslmayr, Staresina, & Bowman, 2016) of the underlying populations. In our results, we have shown alpha attenuation...
when S1 specifically predicts the identity of an upcoming target over and above its location and
temporal onset. Accordingly, we propose that the alpha attenuation also reflects engagement
with visual processing areas to prepare a specific target template. As such, the alpha
modulations reported here complement recent work showing that lower alpha power is
associated with higher fidelity of stimulus-specific information (Barne, Lange, & Cravo, 2020;
Griffiths et al., 2019; van Ede, Chekroud, Stokes, & Nobre, 2018). In this light, it is interesting to
note that alpha-band oscillations were not significantly modulated by the anticipated perceptual
difficulty in identifying the target, as might be expected from a pure “excitability” account (e.g.
Benwell et al., 2017; Lemi et al., 2017; Romei et al., 2008, 2010; Samaha et al., 2017). Rather, at
least in our task, the observed alpha attenuation appears to reflect anticipation of specific visual
content related to target identity, though we note that visual content in our task entailed
different shapes across objects, and thus included some spatial attributes.

When templates are separated by space and time, template preparation has previously
been associated with spatially lateralized contralateral alpha attenuation relative to the
memorized location of the template (de Vries, van Driel, & Olivers, 2017; van Driel et al., 2017).
Our findings complement this recent work by isolating template identity, while controlling for
spatial attention associated with the template. Moreover, as emphasized earlier, we here show
this in a context in which the template was not presented to participants, but had to be retrieved
from long-term memory based on a known probabilistic association between S1 and S2.

Snyder and Foxe (2010) demonstrated that when participants were cued to a relevant
non-spatial feature-dimension of a target stimulus (color or motion), alpha power was relatively
attenuated in the area coding for the relevant feature dimension (dorsal visual stream regions
for motion and ventral visual stream regions for color). This complements the idea that alpha-
attenuation may serve as a general attentional mechanism in perception. However, because this
previous work cued feature dimensions (e.g., colour) rather than feature values (e.g., red), it
does not address whether alpha is also a relevant mechanism for expected identity or ‘template’
preparation.

Interestingly, a previous study in which participants could prepare for a specific defining
feature of a forthcoming target grating (Wildegger, van Ede, Woolrich, Gillebert, & Nobre, 2017)
found no evidence for modulations within the alpha-band. The apparent discrepancy with the
current finding could be due to statistical variability (i.e. a false negative in previous work), or
reflect crucial task dependencies. For example, our task utilised complex stimuli, memory
associations, and targets that were always presented centrally whereas the previous work used
simple orientations, symbolic cues, and uncertainty about target location.

In the current work, we focused on the process of template-guided attention. The
instantiation of the target template putatively involves a process of retrieval from long-term
memory, possibly followed by storage in visual working memory and accompanied by visual
imagery. Retrieval from long-term memory (Fukuda & Woodman, 2017; Hanslmayr et al., 2016;
Staresina et al., 2016; Waldhauser, Braun, & Hanslmayr, 2016); storage, and prioritization of
perceptual representations in working memory (Fukuda & Woodman, 2017; van Ede, 2018; van
Ede, Jensen, & Maris, 2017); and visual imagery (Barrett & Ehrlichman, 1982; Salenius, Kajola,
Thompson, Kosslyn, & Hari, 1995; Slatter, 1960), have all previously been associated with
attenuation of alpha oscillations. Our findings are thus in line with this large body of prior work.

In contrast to this work, in the current study, these individual processes were never explicitly
tasked to the participants. Rather, here, these processes may constitute the natural chain of
events that support adaptive memory-guided perceptual anticipation.

ERPs

In addition to the alpha effects, Experiments 1 and 2 each also revealed significant ERPs
associated with target-identity anticipation. Moreover, like the alpha modulation, these
potentials did not differ significantly between the predictive-easy and difficult S1s in Experiment
1. The two ERP effects consisted of a CNV and a late posterior potential. Both of these have been
previously found in associative learning tasks (Rose et al., 2001; Stokes et al., 2014). However, in
this previous work, S1 predictions were coupled to response probabilities, a confound we ruled
out in Experiment 2.

The CNV is a classic signature of temporal and response anticipation (Donchin, Tueting,
Ritter, Kutats, & Heffley, 1975; Walter, Cooper, Aldridge, McCallum, & Winter, 1964), and is likely
to reflect the anticipation of the target – here shown to be strengthened by foreknowledge of
the identity of the ensuing target.

Our late posterior positive potential may relate to the processing of S1 when it predicts a
specific target, or serve as a link between the S1 and the S2 item. The exact functional
contribution of the late positive potential in our task is difficult to pinpoint. Its posterior
topography and time course are compatible with a few different possibilities. Identification of
the S1 as a relevant, predictive stimulus may have triggered a P300, which has a long history as a
marker of stimulus relevance or meaning (Johnson, 1986; Polich, 2007; Squires, Squires, &
Hillyard, 1975). Alternatively, it may have reflected the process of recalling the associated target
(Donaldson & Rugg, 1999), therefore providing a link between S1 and S2. A similar potential has
also been noted during the orienting of spatial attention (Brignani, Lepsien, Rushworth, & Nobre,
2009), raising the possibility of an analogous mechanism for orienting attention to identity-
defining stimulus attributes.

Importantly, in Experiment 2, both the predictive and non-predictive S1 indicate that a
task-relevant target would appear in 1000 ms in the center of the screen, and all trials required a
response. The only difference was that the predictive S1 indicates which item is likely to appear.
Accordingly, this provides compelling evidence that these ERPs, like the alpha attenuation, are
sensitive to the expectation of the particular identity of the forthcoming item.

It remains to be investigated whether the effects shown here are contingent on
knowledge of the location and timing of an upcoming event. By design, space and time were
always reliable in the current work. While contrasts with non-predictive S1s allowed us to
eliminate any neural correlates that were attributable to purely spatial and temporal predictions,
we cannot rule out that the observed modulations might still reflect the interaction between
identity-based anticipation and the known spatial and temporal attributes of the anticipated
stimulus. That is to say, it is of yet unclear whether the same results would be obtained for
identity-based predictions in the absence of spatial and temporal predictions. At the same time,
of course, in the real world, spatial, temporal, and identity-based predictions are often bundled.

Interaction between predictions and perceptual difficulty
In experiment 1 we found a significant interaction between S1 predictiveness and target difficulty (easy or difficult) for both error rates and reaction times. Interestingly, we did not find neural evidence for such an interaction in the identified alpha attenuation or ERPs during the period between S1 and S2. One may have expected that a more difficult target would call for a stronger activation of the perceptual template. However, our data do not speak to this conclusion. On the one hand, we cannot rule out differences in the extent of template pre-activation that could not be detected with our methods. There may be other neural correlates of perceptual identity preparation that do depend on expected target difficulty, which we were unable to measure. On the other hand, the results invite us to consider whether and how similar levels of template activation may result in differential performance benefits. It is possible that the same perceptual templates will be more effective when incoming stimuli are harder to perceive. In this scenario, the consequences of pre-activation of relevant neuronal populations may critically depend on the strength of neuronal activity triggered by incoming stimulation, playing a greater facilitatory role when incoming stimulation is weaker or more ambiguous.

Conclusion

Taken together, our results suggest that proactive preparation for the identity of a target – based on successive associations – impacts perception and is accompanied by the attenuation of alpha oscillations and modulations of ERPs, including the CNV. We here demonstrate this while matching spatial and temporal predictions, as well as target probability and response demands. While isolating identity anticipation has proven instrumental to our aims, we should also not forget that, in natural behavior, memory-based anticipation is often multifaceted – affording concurrent anticipation of the what, where and when of upcoming percepts. In future studies, it will be interesting to consider systematically the dynamic interplay and potential synergies among each of these different dimensions of memory-based perceptual anticipation.
References

Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: a failed theoretical dichotomy. *Trends in Cognitive Sciences, 16*(8), 437–443. https://doi.org/10.1016/j.tics.2012.06.010

Barne, L. C., Lange, F. P. de, & Cravo, A. M. (2020). Prestimulus alpha power is related to the strength of stimulus representation. *BioRxiv*, 2020.02.04.933382. https://doi.org/10.1101/2020.02.04.933382

Barrett, J., & Ehrlichman, H. (1982). Bilateral hemispheric alpha activity during visual imagery. *Neuropsychologia, 20*(6), 703–708. https://doi.org/10.1016/0028-3932(82)90071-9

Benwell, C. S. Y., Tagliabue, C. F., Veniero, D., Cecere, R., Savazzi, S., & Thut, G. (2017). Prestimulus EEG power predicts conscious awareness but not objective visual performance. *ENeuro, 4*(6). https://doi.org/10.1523/ENEURO.0182-17.2017

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10*(4), 433–436. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9176952

Brignani, D., Lepsien, J., Rushworth, M. F. S., & Nobre, A. C. (2009). The timing of neural activity during shifts of spatial attention. *Journal of Cognitive Neuroscience, 21*(12), 2369–2383. https://doi.org/10.1162/jocn.2008.21176

Brincat, S. L., & Miller, E. K. (2015). Frequency-specific hippocampal-prefrontal interactions during associative learning. *Nature Neuroscience, 18*(4), 576–581. https://doi.org/10.1038/nn.3954

Carlisle, N. B., Arita, J. T., Pardo, D., & Woodman, G. F. (2011). Attentional templates in visual working memory. *Journal of Neuroscience, 31*(25), 9315–9322. https://doi.org/10.1523/JNEUROSCI.1097-11.2011

Chelazzi, L., Duncan, J., Miller, E. K., & Desimone, R. (1998). Responses of Neurons in Inferior Temporal Cortex During Memory-Guided Visual Search. *Journal of Neurophysiology, 80*(6), 2918–2940. https://doi.org/10.1152/jn.1998.80.6.2918

Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual search in inferior temporal cortex. *Nature, 363*(6427), 345–347. https://doi.org/10.1038/363345a0

Chun, M. M., & Jiang, Y. (1998). Contextual cueing: implicit learning and memory of visual
context guides spatial attention. *Cognitive Psychology, 36*(1), 28–71. 688
https://doi.org/10.1006/cogp.1998.0681

Coull, J. T., & Nobre, A. C. (1998). Where and when to pay attention: the neural systems for
690
directing attention to spatial locations and to time intervals as revealed by both PET and
691
fMRI. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience,*
692
18(18), 7426–7435. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9736662

Cravo, A. M., Rohenkohl, G., Santos, K. M., & Nobre, A. C. (2017). Temporal Anticipation Based
695
on Memory. *Journal of Cognitive Neuroscience, 29*(12), 2081–2089.
https://doi.org/10.1162/jocn_a_01172

Cravo, A. M., Rohenkohl, G., Wyart, V., & Nobre, A. C. (2011). Endogenous modulation of low
698
frequency oscillations by temporal expectations. *Journal of Neurophysiology, 106*(6), 2964–
699
2972. https://doi.org/10.1152/jn.00157.2011

de Vries, I. E. J., van Driel, J., & Olivers, C. N. L. (2017). Posterior α EEG dynamics dissociate
700
current from future goals in working memory-guided visual search. *Journal of Neuroscience,*
701
37(6), 1591–1603. https://doi.org/10.1523/JNEUROSCI.2945-16.2016

Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual
704
Review of Neuroscience, 18*(1), 193–222.
https://doi.org/10.1146/annurev.ne.18.030195.001205

Donaldson, D. I., & Rugg, M. D. (1999). Event-related potential studies of associative recognition
706
and recall: electrophysiological evidence for context dependent retrieval processes. *Brain
707
Research. Cognitive Brain Research, 8*(1), 1–16. Retrieved from
708
http://www.ncbi.nlm.nih.gov/pubmed/10216269

Donchin, E., Tueting, P., Ritter, W., Kutas, M., & Heffley, E. (1975). On the independence of the
710
CNV and the P300 components of the human averaged evoked potential. *Electroencephalography
711
and Clinical Neurophysiology, 38*(5), 449–461. Retrieved from
712
http://www.ncbi.nlm.nih.gov/pubmed/50170

Draschkow, D., Heikel, E., Vo, M. L.-H., Fiebach, C. J., Sassenhagen, J., Võ, M. L.-H., ...
714
Sassenhagen, J. (2018). No evidence from MVPA for different processes underlying the
715
N300 and N400 incongruity effects in object-scene processing. *Neuropsychologia, 120,* 9–
Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review, 96*(3), 433–458. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2756067

Fukuda, K., & Woodman, G. F. (2017). Visual working memory buffers information retrieved from visual long-term memory. *Proceedings of the National Academy of Sciences of the United States of America, 114*(20), 5306–5311. https://doi.org/10.1073/pnas.1617874114

Gallistel, C. R. (1990). *The organization of learning. The organization of learning.* Cambridge, MA, US: The MIT Press.

Goldfarb, E. V., Chun, M. M., & Phelps, E. A. (2016). Memory-Guided Attention: Independent Contributions of the Hippocampus and Striatum. *Neuron, 89*(2), 317–324. https://doi.org/10.1016/j.neuron.2015.12.014

Gramfort, A., Luessi, M., Larson, E., Engemann, D. A., Strohmeier, D., Brodbeck, C., ... Hämäläinen, M. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in Neuroscience, 7*, 267. https://doi.org/10.3389/fnins.2013.00267

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

Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and Episodic Memory: Addressing the Synchronization/Desynchronization Conundrum. *Trends in Neurosciences, 39*(1), 16–25. https://doi.org/10.1016/j.tins.2015.11.004

Heideman, S. G., Rohenkohl, G., Chauvin, J. J., Palmer, C. E., van Ede, F., & Nobre, A. C. (2018). Anticipatory neural dynamics of spatial-temporal orienting of attention in younger and older adults. *NeuroImage, 178*, 46–56. https://doi.org/10.1016/j.neuroimage.2018.05.002

Higuchi, S., & Miyashita, Y. (1996). Formation of mnemonic neuronal responses to visual paired associates in inferotemporal cortex is impaired by perirhinal and entorhinal lesions.
Horst, J. S., & Hout, M. C. (2016). The Novel Object and Unusual Name (NOUN) Database: A collection of novel images for use in experimental research. Behavior Research Methods, 48(4), 1393–1409. https://doi.org/10.3758/s13428-015-0647-3

Hutchinson, J. B., & Turk-Browne, N. B. (2012). Memory-guided attention: control from multiple memory systems. Trends in Cognitive Sciences, 16(12), 576–579. https://doi.org/10.1016/j.tics.2012.10.003

Jiang, Y. V. (2018). Habitual versus goal-driven attention. Cortex, 102, 107–120. https://doi.org/10.1016/j.cortex.2017.06.018

Johnson, R. (1986). A triarchic model of P300 amplitude. Psychophysiology, 23(4), 367–384. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/3774922

Jung, T. P., Makeig, S., Humphries, C., Lee, T. W., McKeown, M. J., Iragui, V., & Sejnowski, T. J. (2000). Removing electroencephalographic artifacts by blind source separation. Psychophysiology, 37(2), 163–178. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10731767

Kluyver, T., Ragan-Kelley, B., Pérez, F., Granger, B., Bussonnier, M., Frederic, J., ... Development Team, J. (2016). Jupyter Notebooks—a publishing format for reproducible computational workflows. Retrieved from https://nbviewer.jupyter.org/

Kok, P., Failing, M. F., & de Lange, F. P. (2014). Prior expectations evoke stimulus templates in the primary visual cortex. Journal of Cognitive Neuroscience, 26(7), 1546–1554. https://doi.org/10.1162/jocn_a_00562

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

Kok, P., Mostert, P., & De Lange, F. P. (2017). Prior expectations induce prestimulus sensory templates. Proceedings of the National Academy of Sciences of the United States of America, 114(39), 10473–10478. https://doi.org/10.1073/pnas.1705652114

Lawrence, M. (2013). ez: Easy analysis and visualization of factorial experiments. R Package
Lemi, L., Chaumon, M., Crouzet, S. M., & Busch, N. A. (2017). Spontaneous neural oscillations bias perception by modulating baseline excitability. *Journal of Neuroscience, 37*(4), 807–819. https://doi.org/10.1523/JNEUROSCI.1432-16.2016

Los, S. A., & Heslenfeld, D. J. (2005). Intentional and Unintentional Contributions to Nonspecific Preparation: Electrophysiological Evidence. *Journal of Experimental Psychology: General, 134*(1), 52–72. https://doi.org/10.1037/0096-3445.134.1.52

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods, 164*(1), 177–190. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/17517438

Miniussi, C., Wilding, E. L., Coull, J. T., & Nobre, A. C. (1999). Orienting attention in time. *Brain, 122*(8), 1507–1518. https://doi.org/10.1093/brain/122.8.1507

Navarro, D. J. (2015). *Learning statistics with R: a tutorial for psychology students and other beginners.* Adelaide, Australia: University of Adelaide. Retrieved from https://cran.r-project.org/web/packages/lsr/index.html

Nobre, A. C. (2001). Orienting attention to instants in time. *Neuropsychologia, 39*(12), 1299–1313. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11550756

Peelen, M. V., & Kastner, S. (2014). Attention in the real world: toward understanding its neural basis. *Trends Cogn Sci., 18*(5), 242–250.

Pfeuty, M., Ragot, R., & Pouthas, V. (2005). Relationship between CNV and timing of an upcoming event. *Neuroscience Letters, 382*(1–2), 106–111. https://doi.org/10.1016/j.neulet.2005.02.067

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. https://doi.org/10.1016/J.CLINPH.2007.04.019
Posner, M. I. (1980). Orienting of attention. The Quarterly Journal Of Experimental Psychology, 32, 3–25. https://doi.org/10.1080/00335558008248231

Praamstra, P., Kourtis, D., Kwok, H. F., & Oostenveld, R. (2006). Neurophysiology of Implicit Timing in Serial Choice Reaction-Time Performance. Journal of Neuroscience, 26(20), 5448–5455. https://doi.org/10.1523/JNEUROSCI.0440-06.2006

R Core Team. (2018). R: A Language and Environment for Statistical Computing.

Rainer, G., Rao, S. C., & Miller, E. K. (1999). Prospective coding for objects in primate prefrontal cortex. Journal of Neuroscience, 19(13), 5493–5505. https://doi.org/10.1523/jneurosci.19-13-05493.1999

Rohenkohl, G., & Nobre, A. C. (2011). Alpha Oscillations Related to Anticipatory Attention Follow Temporal Expectations. Journal of Neuroscience, 31(40), 14076–14084. https://doi.org/10.1523/JNEUROSCI.3387-11.2011

Romei, V., Brodbeck, V., Michel, C., Amedi, A., Pascual-Leone, A., & Thut, G. (2008). Spontaneous fluctuations in posterior α-band EEG activity reflect variability in excitability of human visual areas. Cerebral Cortex, 18(9), 2010–2018. https://doi.org/10.1093/cercor/bhm229

Romei, V., Gross, J., & Thut, G. (2010). On the role of prestimulus alpha rhythms over occipito-parietal areas in visual input regulation: Correlation or causation? Journal of Neuroscience, 30(25), 8692–8697. https://doi.org/10.1523/JNEUROSCI.0160-10.2010

Rose, M., Verleger, R., & Wascher, E. (2001). ERP correlates of associative learning. Psychophysiology, 38(3), 440–450. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11352132

Salenius, S., Kajola, M., Thompson, W. L., Kosslyn, S., & Hari, R. (1995). Reactivity of magnetic parieto-occipital alpha rhythm during visual imagery. Electroencephalography and Clinical Neurophysiology, 95(6), 453–462. https://doi.org/10.1016/0013-4694(95)00155-7

Samaha, J., Gosseries, O., & Postle, B. R. (2017). Distinct oscillatory frequencies underlie excitability of human occipital and parietal cortex. Journal of Neuroscience, 37(11), 2824–2833. https://doi.org/10.1523/JNEUROSCI.3413-16.2017

Sassenhagen, J., & Draschkow, D. (2019). Cluster-based permutation tests of MEG/EEG data do not establish significance of effect latency or location. Psychophysiology, e13335.
Sauseng, P., Klimesch, W., Stadler, W., Schabus, M., Doppelmayr, M., Hanslmayr, S., ... Birbaumer, N. (2005). A shift of visual spatial attention is selectively associated with human EEG alpha activity. *European Journal of Neuroscience*, 22(11), 2917–2926. https://doi.org/10.1111/j.1460-9568.2005.04482.x

Siegel, M., Donner, T. H., Oostenveld, R., Fries, P., & Engel, A. K. (2008). Neuronal Synchronization along the Dorsal Visual Pathway Reflects the Focus of Spatial Attention. *Neuron*, 60(4), 709–719. https://doi.org/10.1016/j.neuron.2008.09.010

Slatter, K. H. (1960). Alpha rhythms and mental imagery. *Electroencephalography and Clinical Neurophysiology*, 12(4), 851–859. https://doi.org/10.1016/0013-4694(60)90133-4

Snyder, A. C., & Foxe, J. J. (2010). Anticipatory Attentional Suppression of Visual Features Indexed by Oscillatory Alpha-Band Power Increases: A High-Density Electrical Mapping Study. *Journal of Neuroscience*, 30(11), 4024–4032. https://doi.org/10.1523/JNEUROSCI.5684-09.2010

Squires, N. K., Squires, K. C., & Hillyard, S. A. (1975). Two varieties of long-latency positive waves evoked by unpredictable auditory stimuli in man. *Electroencephalography and Clinical Neurophysiology*, 38(4), 387–401. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/46819

Staresina, B. P., Michelmann, S., Bonnefond, M., Jensen, O., Axmacher, N., & Fell, J. (2016). Hippocampal pattern completion is linked to gamma power increases and alpha power decreases during recollection. *Elife*, 5. https://doi.org/10.7554/eLife.17397

Stokes, M. G., Atherton, K., Patai, E. Z., & Nobre, A. C. (2012). Long-term memory prepares neural activity for perception. *Proceedings of the National Academy of Sciences*, 109(6), E360–E367. https://doi.org/10.1073/pnas.1108555108

Stokes, M. G., Kusunoki, M., Sigala, N., Nili, H., Gaffan, D., & Duncan, J. (2013). Dynamic coding for cognitive control in prefrontal cortex. *Neuron*, 78(2), 364–375. https://doi.org/10.1016/j.neuron.2013.01.039

Stokes, M. G., Myers, N. E., Turnbull, J., & Nobre, A. C. (2014). Preferential encoding of behaviorally relevant predictions revealed by EEG. *Frontiers in Human Neuroscience*, 8, 687.
Stokes, M. G., Thompson, R., Nobre, A. C., & Duncan, J. (2009). Shape-specific preparatory activity mediates attention to targets in human visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, 106(46), 19569–19574. https://doi.org/10.1073/pnas.0905306106

Summerfield, C., Trittschuh, E. H., Monti, J. M., Mesulam, M.-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

Summerfield, J. J., Lepsien, J., Gitelman, D. R., Mesulam, M. M., & Nobre, A. C. (2006). Orienting Attention Based on Long-Term Memory Experience. *Neuron*, 49(6), 905–916. https://doi.org/10.1016/j.neuron.2006.01.021

Thut, G., Nietzel, A., Brandt, S. A., & Pascual-Leone, A. (2006). -Band Electroencephalographic Activity over Occipital Cortex Indexes Visuospatial Attention Bias and Predicts Visual Target Detection. *Journal of Neuroscience*, 26(37), 9494–9502. https://doi.org/10.1523/JNEUROSCI.0875-06.2006

Treue, S., & Martinez Trujillo, J. C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature*, 399(6736), 575–579. https://doi.org/10.1038/21176

Turk-Browne, N. B., Isola, P. J., Scholl, B. J., & Treat, T. A. (2008). Multidimensional Visual Statistical Learning. *Journal of Experimental Psychology: Learning Memory and Cognition*, 34(2), 399–407. https://doi.org/10.1037/0278-7393.34.2.399

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

van Driel, J., Gunseli, E., Meeter, M., & Olivers, C. N. L. (2017). Local and interregional alpha EEG dynamics dissociate between memory for search and memory for recognition. *NeuroImage*, 149, 114–128. https://doi.org/10.1016/j.neuroimage.2017.01.031

van Ede, F. (2018). Mnemonic and attentional roles for states of attenuated alpha oscillations in perceptual working memory: a review. *European Journal of Neuroscience*, 48(7), 2509–2515. https://doi.org/10.1111/ejn.13759
van Ede, F., Chekroud, S. R., Stokes, M. G., & Nobre, A. C. (2018). Decoding the influence of anticipatory states on visual perception in the presence of temporal distractors. *Nature Communications*, 9(1), 1449. https://doi.org/10.1038/s41467-018-03960-z

van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting Attention to an Upcoming Tactile Event Involves a Spatially and Temporally Specific Modulation of Sensorimotor Alpha- and Beta-Band Oscillations. *Journal of Neuroscience*, 31(6), 2016–2024. https://doi.org/10.1523/JNEUROSCI.5630-10.2011

van Ede, F., Jensen, O., & Maris, E. (2017). Supramodal Theta, Gamma, and Sustained Fields Predict Modality-specific Modulations of Alpha and Beta Oscillations during Visual and Tactile Working Memory. *Journal of Cognitive Neuroscience*, 29(8), 1455–1472. https://doi.org/10.1162/jocn_a_01129

van Ede, F., Niklaus, M., & Nobre, A. C. (2017). Temporal Expectations Guide Dynamic Prioritization in Visual Working Memory through Attenuated α Oscillations. *Journal of Neuroscience*, 37(2), 437–445. https://doi.org/10.1523/JNEUROSCI.2272-16.2016

Viola, F. C., Thorne, J., Edmonds, B., Schneider, T., Eichele, T., & Debener, S. (2009). Semi-automatic identification of independent components representing EEG artifact. *Clinical Neurophysiology*, 120(5), 868–877. https://doi.org/10.1016/j.clinph.2009.01.015

Waldhauser, G. T., Braun, V., & Hanslmayr, S. (2016). Episodic Memory Retrieval Functionally Relies on Very Rapid Reactivation of Sensory Information. *Journal of Neuroscience*, 36(1), 251–260. https://doi.org/10.1523/JNEUROSCI.2101-15.2016

Walter, W. G., Cooper, R., Aldridge, V. J., McCallum, W. C., & Winter, A. L. (1964). Contingent Negative Variation: An Electric Sign of Sensori-Motor Association and Expectancy in the Human Brain. *Nature*, 203(4943), 380–384. https://doi.org/10.1038/203380a0

Wickham, H. (2009). *Ggplot2: elegant graphics for data analysis*. New York: Springer. https://doi.org/10.1007/978-0-387-98141-3

Wildegger, T., van Ede, F., Woolrich, M., Gillebert, C. R., & Nobre, A. C. (2017). Preparatory α-band oscillations reflect spatial gating independently of predictions regarding target identity. *Journal of Neurophysiology*, 117(3), 1385–1394. https://doi.org/10.1152/jn.00856.2016
Wolfe, J. M. (1994). Guided Search 2.0 A revised model of visual search. *Psychonomic Bulletin & Review*, 1(2), 202–238. https://doi.org/10.3758/BF03200774

Worden, M. S., Foxe, J. J., Wang, N., & Simpson, G. V. (2000). Anticipatory biasing of visuospatial attention indexed by retinotopically specific alpha-band electroencephalography increases over occipital cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 20(6), RC63. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10704517

Zanto, T. P., Pan, P., Liu, H., Bollinger, J., Nobre, A. C., & Gazzaley, A. (2011). Age-Related Changes in Orienting Attention in Time. *Journal of Neuroscience*, 31(35), 12461–12470. https://doi.org/10.1523/JNEUROSCI.1149-11.2011
A) Predictive S1 vs. Non-Predictive S1

Frequency (Hz)

Time (ms)

500-1000ms
8-12 Hz

B) Time Course of Alpha Suppression

Change in Power (%)

Time (ms)

Predictive S1 vs. Non-Predictive S1
A) Predictive S1 vs. Non-Predictive S1

B) Predictive S1 vs. Non-Predictive S1

C) Predictive S1 vs. Non-Predictive S1
