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

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

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4 Sage E.P. Boettcher^{1,2}, Mark G. Stokes¹, Anna C. Nobre^{1,2*}, & Freek van Ede^{2*}

5
6 ¹Department of Experimental Psychology, University of Oxford, Oxford, United Kingdom

7 ²Oxford Centre for Human Brain Activity, Wellcome Centre for Integrative Neuroimaging,
8 Department of Psychiatry, University of Oxford, Oxford, United Kingdom

9 *These authors share senior authorship

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14
15 Corresponding author contact information:

16 Sage E.P. Boettcher
17 University of Oxford
18 Department of Experimental Psychology
19 Brain & Cognition Lab
20 Oxford Center for Human Brain Activity

21
22 Phone: +44 (0) 7783 814670

23 Mail: sage.boettcher@psy.ox.ac.uk

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25
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40

41 **Abstract**

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

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69 **Significance Statement**

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

80

81 **Introduction**

82 Probabilistic associations between stimuli can lead to memory-based templates that impact
83 perceptual performance through anticipation of the location, temporal onset, identity, or
84 features of anticipated sensory events. Early studies relied on relatively simple symbolic cues
85 (e.g., arrows) to demonstrate that attention can be guided in space, time, and across features to
86 facilitate performance (Coull & Nobre, 1998; Posner, 1980; Treue & Martinez Trujillo, 1999).
87 More recently, studies have considered attentional orienting in more naturalistic tasks, in which
88 the contents of long-term memory, often probabilistic in nature, guide the processing of
89 incoming stimuli (Hutchinson & Turk-Browne, 2012). The bulk of the studies investigating
90 memory-guided attention have focused primarily on anticipating spatial location (Awh,
91 Belopolsky, & Theeuwes, 2012; Chun & Jiang, 1998; Goldfarb, Chun, & Phelps, 2016; Jiang, 2018;
92 J. J. Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006) and the expected temporal onset
93 of items (Cravo, Rohenkohl, Santos, & Nobre, 2017; Olson & Chun, 2001). However, in addition,
94 there is mounting interest in investigating mechanisms that support memory-based anticipation
95 of the *identity* of upcoming percepts (Kok, Jehee, & de Lange, 2012; Peelen & Kastner, 2014;
96 Stokes, Myers, Turnbull, & Nobre, 2014; C. Summerfield, Trittschuh, Monti, Mesulam, & Egner,
97 2008; Turk-Browne, Isola, Scholl, & Treat, 2008; Turk-Browne, Scholl, Johnson, & Chun, 2010).

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

110 1999; Turk-Browne et al., 2008, 2010), we here targeted two specific human electrophysiological
111 substrates of associative memory templates during the anticipatory period.

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

119 Alpha attenuation has been associated with both spatial (Haegens, Nacher, Luna, Romo,
120 & Jensen, 2011; Thut, Nietzel, Brandt, & Pascual-Leone, 2006; van Ede, 2018; Worden, Foxe,
121 Wang, & Simpson, 2000) and temporal (Heideman et al., 2018; Rohenkohl & Nobre, 2011; van
122 Ede, Niklaus, & Nobre, 2017; Zanto et al., 2011) orienting of attention, including during long-
123 term-memory-guided anticipation (Stokes, Atherton, Patai, & Nobre, 2012). Likewise, the CNV is
124 an ERP component classically associated with temporal anticipation (Cravo, Rohenkohl, Wyart, &
125 Nobre, 2011; Los & Heslenfeld, 2005; Miniussi, Wilding, Coull, & Nobre, 1999; Nobre, 2001;
126 Pfeuty, Ragot, & Pouthas, 2005; Praamstra, Kourtis, Kwok, & Oostenveld, 2006), also in the
127 context of long-term-memory-guided anticipation (Cravo et al., 2017). Probing the involvement
128 of these electrophysiological signatures during object-identity anticipation is important to inform
129 a relevant and current theoretical debate about the nature of such markers. Alpha and CNV
130 modulations during anticipation in space and time may purely reflect changes in the excitability
131 of underlying neuronal populations (Benwell et al., 2017; Lemi, Chaumon, Crouzet, & Busch,
132 2017; Romei et al., 2008; Romei, Gross, & Thut, 2010; Samaha, Gosseries, & Postle, 2017),
133 independent of “informational content”. In the current work, we isolate identity anticipation and
134 control for general “readiness” or “excitability” by equating spatial and temporal anticipation as
135 well as target and response probabilities. If alpha and CNV modulations nevertheless still occur
136 under these conditions, this would provide evidence that they also play a role in the anticipation
137 of visual content.

138

139 **Methods**

140 **Participants**

141 In both experiments, all participants were right-handed with normal/corrected-to-normal vision
142 had no history of neurological disorders, and were not taking any neurological medication. All
143 participants gave informed written consent, and were compensated £15 per hour for a total of
144 £45. The experiments were approved by the Oxford Central University Research Ethics
145 Committee.

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

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

154

155 **Procedures**

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

162

163 *Experiment 1*

164 The structure of Experiment 1 is shown in Figure 1. Participants were shown a random sequence
165 of objects taken from a set of 14 objects from the Novel Object and Unusual Name database
166 (NOUN) (Horst & Hout, 2016). Among these objects there were four critical objects: *easy S1*,
167 *easy target*, *difficult S1*, and *difficult target*, and ten *neutral objects*. These four objects were

168 randomly allocated to every fourth participant and then counter-balanced for subsequent
169 participants such that for each random allocation of four objects, each object held each of the
170 four critical roles. Participants' task was to press a corresponding key (either "m" or "x" key)
171 whenever they detected a target. The targets switched their association with the keys randomly
172 between blocks, such that each target was associated with the "x" and "m" buttons for half of
173 the blocks.

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

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

190

191 *Experiment 2*

192 The structure of Experiment 2 is shown in Figure 4. The stimuli, experimental set up, and EEG
193 procedures were the same as in Experiment 1. A trial was similar to that of Experiment 1, with a
194 few critical changes. On each trial, participants first saw S1 (250 ms) which again could be a
195 predictive or a non-predictive S1 with equal probability. This was followed by a 750-ms blank
196 and the quick presentation of one of three targets (30 ms) – we will refer to these targets as

197 target A, B, or C. That is, there was a task-relevant item presented on every trial. Critically, two of
198 these items (target A and target B) were predictable based on S1, whereas the other item (target
199 C) was always equally probable after all S1 stimuli. Following the presentation of the target and a
200 mask (100 ms), all three potential targets appeared on the screen and observers used the left,
201 down, and right arrow keys to indicate which object they had just seen. The position of the three
202 targets was randomized across trials such that observers could not prepare their response
203 before the response screen. The stimuli were randomly allocated to each participant. With these
204 changes to the design, every trial and item was task relevant, and participants could not prepare
205 a specific response during the period after S1. Here, therefore, predictive and non-predictive S1s
206 differed only with regard to its ability vs inability to form a specific target template in anticipation
207 of S2.

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

216

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

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

222

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

224 We acquired EEG using Synamps amplifiers and Neuroscan data acquisition software
225 (Compumedics). Sixty-one electrodes were distributed across the scalp using the international

226 10–10 positioning system. The left mastoid was used as the active reference, and we included a
227 right mastoid measurement to derive an average-mastoid reference offline. The ground was
228 placed on the left upper arm. Additionally, vertical and horizontal EOG electrodes were used to
229 monitor for eye blinks and eye movements. During acquisition, data were low-pass filtered by an
230 anti-aliasing filter (250-Hz cutoff), digitized at 1000 Hz, and stored for offline analysis.

231

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

233 The preprocessing and analysis scripts for both experiments can be found as html files and as
234 reproducible scripts (jupyter notebooks; (Kluyver et al., 2016) at
235 <https://github.com/SageBoettcher/identityTemplates>. The preprocessing pipeline is modified
236 from the analysis pipeline used by Draschkow and colleagues (Draschkow et al., 2018). All EEG
237 data analysis was conducted in MNE-Python (Gramfort et al., 2013). The data were down-
238 sampled to 200 Hz, and high-pass filtered at 0.1 Hz. To regress out eye-movement activity, an
239 Independent component analysis (ICA; Jung et al., 2000) was used to decompose the data –
240 which was high-pass filtered at 1 Hz – into sixty temporally independent components. Eye-
241 movement components were detected by first correlating the filtered data with the
242 electrooculography (EOG) and subsequently, when needed, manually selecting a subset of
243 typical component maps and identifying the best group match to them (Viola et al., 2009).
244 Selected components were then removed from the data. Trials were segmented from -200 ms to
245 +750 ms (Experiment 1) or +1000 ms (Experiment 2) relative to the onset of S1. Average activity
246 over the 200 ms preceding the stimulus onset was used as a baseline against which all
247 amplitudes were calculated. Finally, epochs with especially high variance were discarded. These
248 epochs were detected through a generalized extreme studentized deviate (ESD) test for outliers
249 with an alpha value of .05 and discarded from the analysis. On average 34 trials out of 1400 were
250 discarded in the manner.

251

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

253 *Alpha*

254 For the time-frequency analysis, we used epochs from -200 to 1000 ms. Morlet wavelets were
255 convolved with the data between 3 and 40 Hz. For each frequency, we used a fixed 400-ms time
256 window such that the number of cycles changed with the frequency. After the time frequency
257 transformation, activity was averaged over all posterior electrodes (P7, P5, P3, P1, Pz, P2, P4, P6,
258 P8, PO7, PO3, POz, PO4, PO8, O1, Oz, O2) and contrasted between predictive and non-predictive
259 trials (separately for the easy and difficult conditions in Experiment 1). We expressed this as a
260 normalised difference $((\text{predictive} - \text{non-predictive}) / (\text{predictive} + \text{non-predictive})) * 100$.
261

262

263 *ERPs*

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

272

273 *EEG statistical analysis*

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

277

278 **Results**

279 **Experiment 1: Target Templates and Target Difficulty**

280 In Experiment 1 we investigated whether identity templates from associative memory impact
281 perception, as well as the neural markers that may be involved in this template-based
282 anticipation. To evaluate the adaptive utility of the identity template, we additionally asked to

283 what extent these hypothesized effects depend on the anticipated perceptual difficulty of the
284 target.

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

294
295 **Figure 1. Trial schematic and behavioral data from Experiment 1.** (A) an example of the trial sequence
296 from Experiment 1. On each trial, participants saw stimulus 1 (S1) which could either be predictive or
297 non-predictive about the following stimulus 2 (S2) which could be an easy target (150 ms), a difficult
298 target (25 ms), or a foil (25 or 150 ms). S2 was immediately followed by a mask. Participants were
299 instructed to respond to the targets (but not the foils) with the corresponding button as quickly as
300 possible. (B) The probability of a specific S2 target following a predictive S1 was 70%, whereas non-
301 predictive S1s were equally likely to be followed by either of the two potential targets, or either of the
302 4 foils. S1-S2 relationships were made explicit to participants before starting the experiment. (C)
303 Participants responded more quickly and more accurately to targets preceded by a predictive S1 as
304 well as to easy targets. Additionally, there was a significant interaction in both RT and percent error
305 indicating that predictive S1s had a larger benefit in the difficult-target trials.

307 Behavioral Results

308 To assess whether predictive S1s impact performance and whether this effect was modulated by
309 the expected target difficulty, we conducted repeated-measures ANOVAs on RT and error rates
310 with S1 type (predictive and non-predictive) and target difficulty (easy and difficult) as factors.
311 Behavioral results are depicted in Figure 1C. Target difficulty and S1 type interacted significantly
312 in both RT ($F(1,24) = 5.4, p = .03, \eta_G^2 = .002$) as well as error rates ($F(1,24) = 12.0, p = .002, \eta_G^2 =$
313 $.08$). Moreover, we found main effects of S1 type and target difficulty for both RT (S1 effect:
314 $F(1,24) = 87.3, p < .001, \eta_G^2 = .41$; difficulty effect: $F(1,24) = 7.9, p = .009, \eta_G^2 = .01$) and error
315 rates (S1 effect: $F(1,24) = 29.5, p < .001, \eta_G^2 = .21$; difficulty effect: $F(1,24) = 15.4, p < .001, \eta_G^2$
316 $= .28$). Paired samples t-tests (Bonferroni corrected p-values) revealed a significant RT benefit
317 (i.e., faster RTs) of the predictive S1 for both easy and difficult targets (easy: $t(24) = 9.17, p <$

318 .001, $d = 1.83$; difficult: $t(24) = 9.11$, $p < .001$, $d = 1.82$), and that the benefit of the predictive S1
319 was larger for difficult targets ($t(24) = 2.33$, $p = .03$, $d = .47$). The same pattern occurred for error
320 rates, with a significant benefit (i.e., lower errors) following predictive vs. non-predictive S1 items
321 in trials with an easy target ($t(24) = 2.9$, $p = .01$, $d = .59$) as well as trials with a difficult target
322 ($t(24) = 4.93$, $p < .001$, $d = .99$). Once again this benefit of predictive S1s was larger for difficult
323 targets ($t(24) = 3.46$, $p = .002$, $d = .69$). Thus, predictive objects impact performance on the
324 target, and this benefit was particularly pronounced when the targets were difficult to perceive.

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

333

334 EEG Results

335 *Alpha*

336 To assess the effect of a predictive vs. non-predictive S1s on induced brain activity, we first
337 compared time- and frequency-resolved maps of power (collapsed over all posterior electrodes;
338 see insets Figure 2A,B) from the onset of S1 until 250 ms after the onset of the S2 as seen in
339 Figure 2. More specifically, we directly contrasted trials with a predictive and a non-predictive
340 S1. We did so separately for trials with a predictive S1 that predicted an easy target (predictive-
341 easy S1) and trials with a predictive S1 that predicted a difficult target (predictive-difficult S1).
342 The same non-predictive-S1 trials were used for both comparisons. Significant clusters emerged
343 following both the predictive-easy S1 (Fig. 2A, $p < .001$) and following the predictive-difficult S1
344 (Fig. 2B, $p < .001$) in comparison to following the non-predictive S1. The maximal attenuation
345 within these clusters for both the easy and difficult S1 occurred around 11 Hz and 600 ms after
346 S1 onset, i.e. mostly concentrated within the alpha band. A topographic inspection confirmed

347 that these effects had a clear posterior topography in line with a visual preparation effect. There
348 were no significant clusters when directly contrasting easy to difficult S1s (all cluster $ps > .13$).

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

354

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

363

364 *ERPs*

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

370 We first considered the frontal electrode cluster (Fig. 3A). For both the predictive-easy
371 and the predictive-difficult S1 cues, we found a significantly larger negativity in the late S1-S2
372 cue-target interval, compared to the non-predictive S1 cues (easy: $p < .001$, difficult: $p < .001$).
373 These negativities were associated with a frontal topography characteristic of the CNV (Fig. 3C).
374 In the S1-predictive-easy condition we additionally found an early positivity ($p = .004$) that is
375 likely a spillover effect from an earlier more posterior positivity that we return to below (as also
376 confirmed by the time-resolved topographical analysis presented in Figure 3C). There were no
377 significant clusters when contrasting the easy and difficult S1s ($ps > .43$).

378 When comparing effects for predictive vs. non-predictive S1 cues in the predefined
379 posterior electrodes (Fig. 3B) a significant cluster was identified from around 200 to 600 ms for
380 both easy and difficult ($ps < .01$) The effect reflected a late positive potential elicited by

381 predictive cues. Topographical analysis confirmed the potential was centrally distributed over
382 the posterior scalp (Fig. 3C). As with the alpha modulations and the CNV, there were no
383 significant clusters when comparing the easy and difficult predictive S1s (all cluster p s > .43).

384 These effects were confirmed, and also nicely demonstrated, by the time-resolved
385 topographies of predictive vs. non-predictive S1 (separated by the easy and difficult conditions),
386 as depicted in Figure 3C.

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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).

400 Experiment 2: Target Templates While Equating Target and Response Probabilities

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

407 Although neural markers clearly signaled target anticipation, it was not possible to
408 conclude that the neural effects were specifically related to the perceptual identity of the
409 anticipated target. On average, task-relevant items (targets) were also more likely following
410 predictive vs. non-predictive S1s, which may have led to differential motor anticipation, or states
411 of attention. Because responses were only required to the target stimuli, during predictive S1
412 trials observers could not only prepare for a task-relevant visual target, but possibly also for the
413 associated motor response. The neural effects may thus reflect general task readiness (or
414 "excitability"), rather than template-specific anticipation of visual identity. To rule out this
415 potential interpretation, we designed Experiment 2 (Fig. 4).

416 In Experiment 2, we equated these other forms of anticipation by making S2 a task-
417 relevant stimulus on every trial. Specifically, participants were always tasked with discriminating
418 S2, but only a subset of S1 stimuli predicted the identity of S2. Therefore, the only difference
419 between predictive and non-predictive S1s was the likelihood of a *specific* target appearing. As
420 such, differences between the S1 conditions must be attributed to proactive target template
421 activation. Participants once again saw predictive and non-predictive S1s (Fig. 4B) which were
422 equated for their spatial and temporal predictions, as well as motor affordances. Three stimuli
423 served as S2, two of which were predicted by a subset of S1 stimuli and one of which was
424 completely unpredictable. Participants responded to S2 in a 3-alternative forced choice (3AFC)
425 design. To eliminate anticipation of specific motor responses, response mappings were random
426 on every trial. Across the experiment, all three targets were equally probable and potential
427 differences in the preparatory period can no longer be attributed to differences in target
428 probability or response preparation. In Experiment 2, all trials had the same difficulty level,
429 allowing us to focus exclusively on the central question of identity anticipation.

430 **Figure 4. Trial schematic and behavioral data from Experiment 2.** (A) Schematic of an example non-
431 predictive trial in Experiment 2. Participants' task was to always report the second S2 object. The
432 paradigm is very similar to experiment 1 with the exception that participants must respond on every
433 trial (i.e., each S2 is a target). Probabilities of each S2 target given the preceding S1 are shown in
434 panel (B). In (C) we see that there is a significant effect of the predictive S1 on error rates. Because this
435 task was a delayed forced choice, reaction times were no longer informative.
436

437 Behavioral Results

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

443

444 EEG Results

445 *Alpha*

446 To assess the alpha attenuation following predictive vs. non-predictive S1s, we compared the
447 time-frequency maps in the period between the onset of S1 and the onset of S2. As shown in

448 Figure 5A, we observed a significant cluster ($p = .005$), with a qualitatively similar profile (in
 449 terms of time range, frequency-range, sign, and topography) as in Experiment 1. The peak
 450 attenuation in this cluster was found at 11 Hz and 610 ms post S1. As in Experiment 1, this
 451 attenuation was associated with a predominantly posterior topography (Fig. 5A). When focusing
 452 on the predefined 8-12 Hz alpha band (Fig. 5B), we found a significant cluster ($p = .01$), which
 453 spanned a similar time range as in Experiment 1.

454

455

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

462

463 *ERPs*

464 As in Experiment 1, we also investigated ERPs locked to the onset of S1 in the pre-defined frontal
 465 and posterior electrode clusters (Fig. 6). In the frontal electrode cluster (Fig. 6A), we again
 466 observed a CNV – a larger negativity following predictive S1s just before the onset of S2 (cluster
 467 $p = .04$). Like in Experiment 1, we also found a significant positive cluster in the frontal electrodes
 468 between about 300 and 450 ms ($p = .01$), which again likely involved a spillover from a more
 469 posterior effect (Fig. 6C). Indeed, in the posterior cluster (Fig. 6B), predictive S1s again elicited a
 470 larger positive potential from about 300 ms until around 550 ms, yielding a significant cluster (p
 471 $= .001$).

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

475

476 **Figure 6. Posterior positivity and frontal negativity following predictive vs. non-predictive S1 in**
 477 **Experiment 2.** A) ERPs locked to the onset of S1 and averaged across a subset of frontal electrodes.
 478 Predictive S1s show a late frontal negativity relative to non-predictive S1s. B) ERPs locked to the onset
 479 of S1 and averaged across a subset of posterior electrodes. The predictive S1s show a clear positive
 480 deflection from the non-predictive S1s. C) Topographies of the ERP effects (Predictive vs. Non-
 481 predictive) show an early posterior positivity followed by a late frontal negativity. Significant clusters
 482 with a p value $< .05$ are denoted with horizontal lines in panels A and B. Shaded areas represent ± 1
 483 SEM (68% confidence intervals).

484

485 The tightly controlled identity-expectation manipulation in Experiment 2 also enabled us to
486 investigate whether the proactive deployment of probabilistic associative-memory templates
487 based on S1 improved neural processing of S2 during perceptual analysis (i.e., post S2 target
488 onset). Unlike in Experiment 1, the S1 items were all followed by target items, thus equating
489 motor demands and degree of preparation. Presentation duration of S2 was also equated. To
490 test for qualitative changes in sensory processing, we applied linear discriminant analysis to
491 decode the content of the two predictable targets in posterior electrodes when they were
492 preceded either by a predictive or a non-predictive S1 (Fig. 7). Cluster-based permutations that
493 considered the first 300 ms of target processing showed a single cluster of better decoding for
494 predictable compared to unpredictable targets, though this did not survive cluster-correction (p
495 = .09). When we considered only the peak decoding period of all targets (at 145ms; Fig. 7B) we
496 found better decoding for predicted vs. unpredicted targets ($t(29) = 2.89$, $p = .007$). However,
497 because this effect was not particularly strong (Fig. 7), we would like to present this as a
498 tentative result in the hope that it will motivate further investigation, without further
499 elaboration in the discussion.

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Figure 7. (A) LDA classification accuracy of S2 target A vs. S2 target B (in Experiment 2) when preceded either by a predictive (blue line) or non-predictive (gray line) S1. (B) Classifier accuracy at the peak classification time for the group average (145 ms) for both predicted and not predicted targets. To avoid circularity, the peak time was found based on the average of the predicted and not predicted data. LDA was performed in a time-resolved fashion on the baseline-corrected time series, using the topographical distribution across all posterior electrodes (as indicated in the inset) as the multi-variate data features.

509 Discussion

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

514 Our behavioral and EEG results build on and extend earlier work on memory-guided
515 attentional orienting and perceptual identity templates in several ways. When considering
516 memory-guided anticipation, we have focused here on perceptual consequences and the
517 electrophysiological signatures of memory-guided predictions based on identity, as opposed to

518 anticipation in space and time (Awh et al., 2012; Chun & Jiang, 1998; Cravo et al., 2017; Goldfarb
519 et al., 2016; Jiang, 2018; Olson & Chun, 2001; J. J. Summerfield et al., 2006). We have studied
520 this in a context where the templates must be retrieved from complex probabilistic associations
521 in memory templates (Higuchi & Miyashita, 1996; Kok et al., 2014, 2012, 2017; Rainer et al.,
522 1999; Stokes, Thompson, Nobre, & Duncan, 2009; Turk-Browne et al., 2008, 2010) – rather than
523 being explicitly provided (Carlisle et al., 2011; Chelazzi et al., 1993; van Driel et al., 2017) – and
524 have focused specifically on the anticipatory electrophysiological substrates associated with such
525 templates.

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

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

537

538 **Alpha attenuation**

539 In previous work, alpha attenuation has been noted during anticipatory periods for both spatially
540 and temporally predictable targets (Heideman et al., 2018; Rohenkohl & Nobre, 2011; Sauseng
541 et al., 2005; Siegel, Donner, Oostenveld, Fries, & Engel, 2008; Thut et al., 2006; van Ede, de
542 Lange, Jensen, & Maris, 2011; Worden et al., 2000; Zanto et al., 2011). In this context, alpha
543 attenuation has been theorized to reflect engagement of sensory processing areas in
544 preparation for a task-relevant event, in line also with the notion that alpha is inversely related
545 to firing-rates (Haegens et al., 2011) and/or processing capacity (Hanslmayr, Staresina, &
546 Bowman, 2016) of the underlying populations. In our results, we have shown alpha attenuation

547 when S1 specifically predicts the identity of an upcoming target over and above its location and
548 temporal onset. Accordingly, we propose that the alpha attenuation also reflects engagement
549 with visual processing areas to prepare a specific target template. As such, the alpha
550 modulations reported here complement recent work showing that lower alpha power is
551 associated with higher fidelity of stimulus-specific information (Barne, Lange, & Cravo, 2020;
552 Griffiths et al., 2019; van Ede, Chekroud, Stokes, & Nobre, 2018). In this light, it is interesting to
553 note that alpha-band oscillations were not significantly modulated by the anticipated perceptual
554 difficulty in identifying the target, as might be expected from a pure “excitability” account (e.g.
555 Benwell et al., 2017; Lemi et al., 2017; Romei et al., 2008, 2010; Samaha et al., 2017). Rather, at
556 least in our task, the observed alpha attenuation appears to reflect anticipation of specific visual
557 content related to target identity, though we note that visual content in our task entailed
558 different shapes across objects, and thus included some spatial attributes.

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

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

574 Interestingly, a previous study in which participants could prepare for a specific defining
575 feature of a forthcoming target grating (Wildegger, van Ede, Woolrich, Gillebert, & Nobre, 2017)

576 found no evidence for modulations within the alpha-band. The apparent discrepancy with the
577 current finding could be due to statistical variability (i.e. a false negative in previous work), or
578 reflect crucial task dependencies. For example, our task utilised complex stimuli, memory
579 associations, and targets that were always presented centrally whereas the previous work used
580 simple orientations, symbolic cues, and uncertainty about target location.

581 In the current work, we focused on the process of template-guided attention. The
582 instantiation of the target template putatively involves a process of retrieval from long-term
583 memory, possibly followed by storage in visual working memory and accompanied by visual
584 imagery. Retrieval from long-term memory (Fukuda & Woodman, 2017; Hanslmayr et al., 2016;
585 Staresina et al., 2016; Waldhauser, Braun, & Hanslmayr, 2016); storage, and prioritization of
586 perceptual representations in working memory (Fukuda & Woodman, 2017; van Ede, 2018; van
587 Ede, Jensen, & Maris, 2017); and visual imagery (Barrett & Ehrlichman, 1982; Salenius, Kajola,
588 Thompson, Kosslyn, & Hari, 1995; Slatter, 1960), have all previously been associated with
589 attenuation of alpha oscillations. Our findings are thus in line with this large body of prior work.
590 In contrast to this work, in the current study, these individual processes were never explicitly
591 tasked to the participants. Rather, here, these processes may constitute the natural chain of
592 events that support adaptive memory-guided perceptual anticipation.

593

594 ERPs

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

602 The CNV is a classic signature of temporal and response anticipation (Donchin, Tueting,
603 Ritter, Kutas, & Heffley, 1975; Walter, Cooper, Aldridge, McCallum, & Winter, 1964), and is likely

604 to reflect the anticipation of the target – here shown to be strengthened by foreknowledge of
605 the identity of the ensuing target.

606 Our late posterior positive potential may relate to the processing of S1 when it predicts a
607 specific target, or serve as a link between the S1 and the S2 item. The exact functional
608 contribution of the late positive potential in our task is difficult to pinpoint. Its posterior
609 topography and time course are compatible with a few different possibilities. Identification of
610 the S1 as a relevant, predictive stimulus may have triggered a P300, which has a long history as a
611 marker of stimulus relevance or meaning (Johnson, 1986; Polich, 2007; Squires, Squires, &
612 Hillyard, 1975). Alternatively, it may have reflected the process of recalling the associated target
613 (Donaldson & Rugg, 1999), therefore providing a link between S1 and S2. A similar potential has
614 also been noted during the orienting of spatial attention (Brignani, Lepsien, Rushworth, & Nobre,
615 2009), raising the possibility of an analogous mechanism for orienting attention to identity-
616 defining stimulus attributes.

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

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

631

632 **Interaction between predictions and perceptual difficulty**

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

647

648 **Conclusion**

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

658

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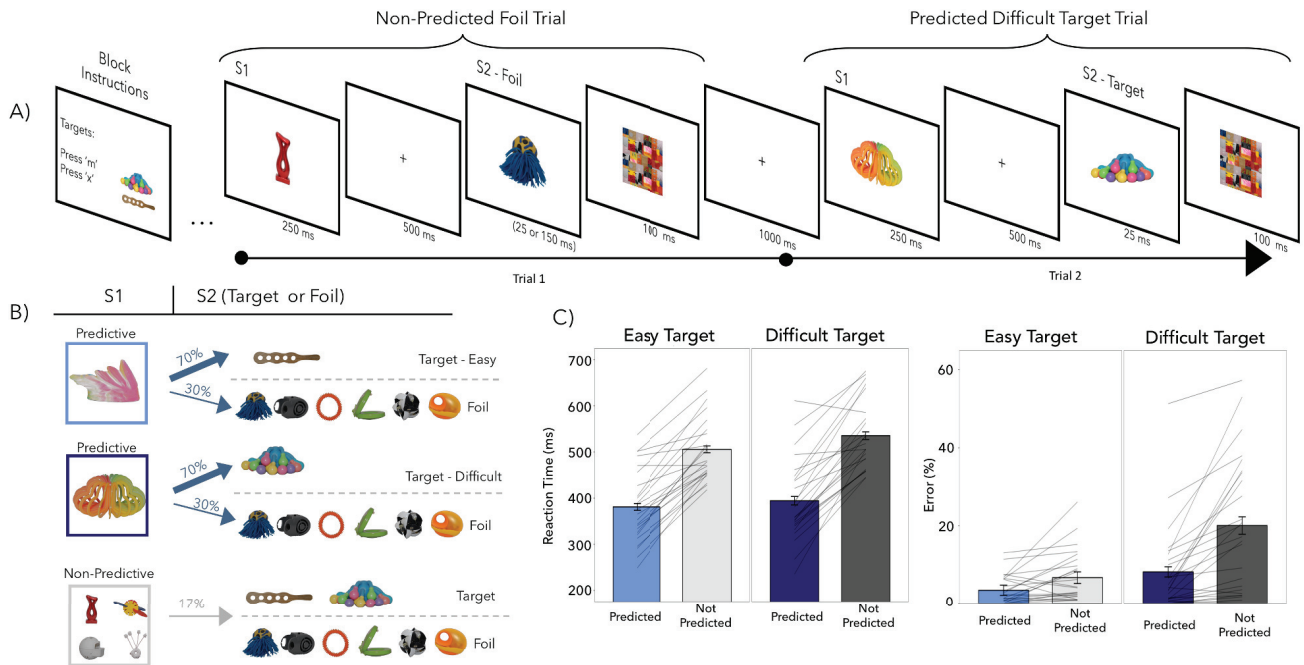
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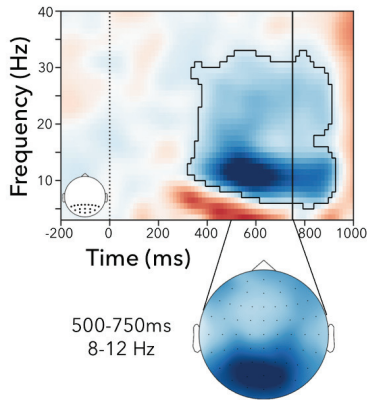
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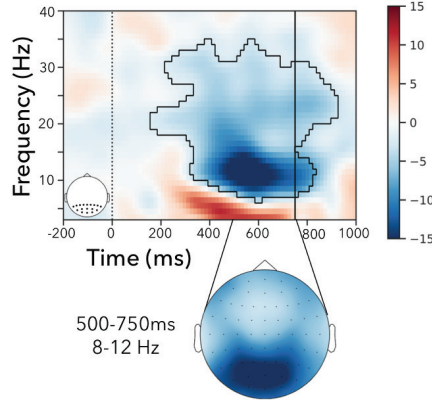
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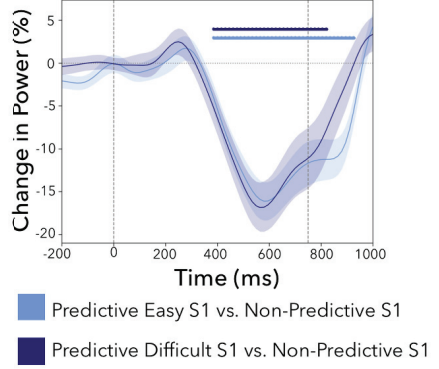
A) Predictive Easy S1 vs. Non-Predictive S1

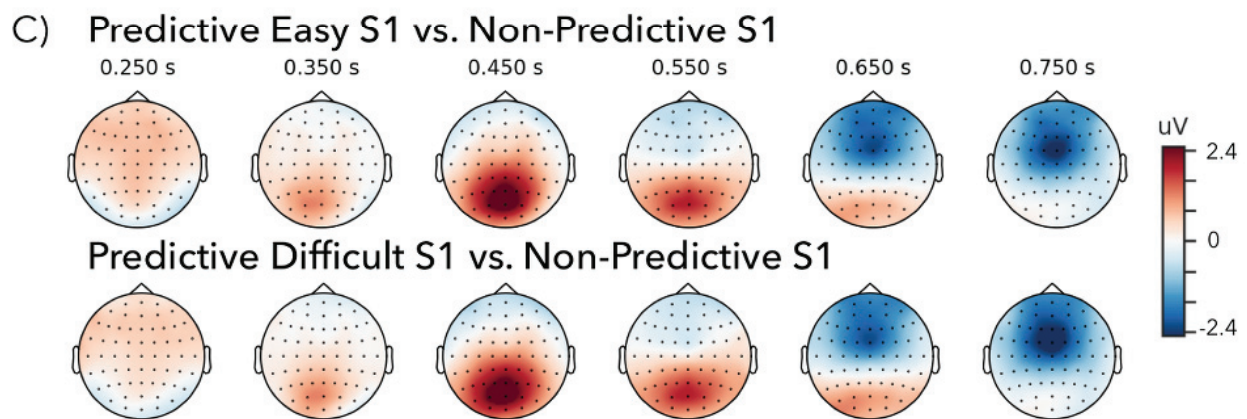
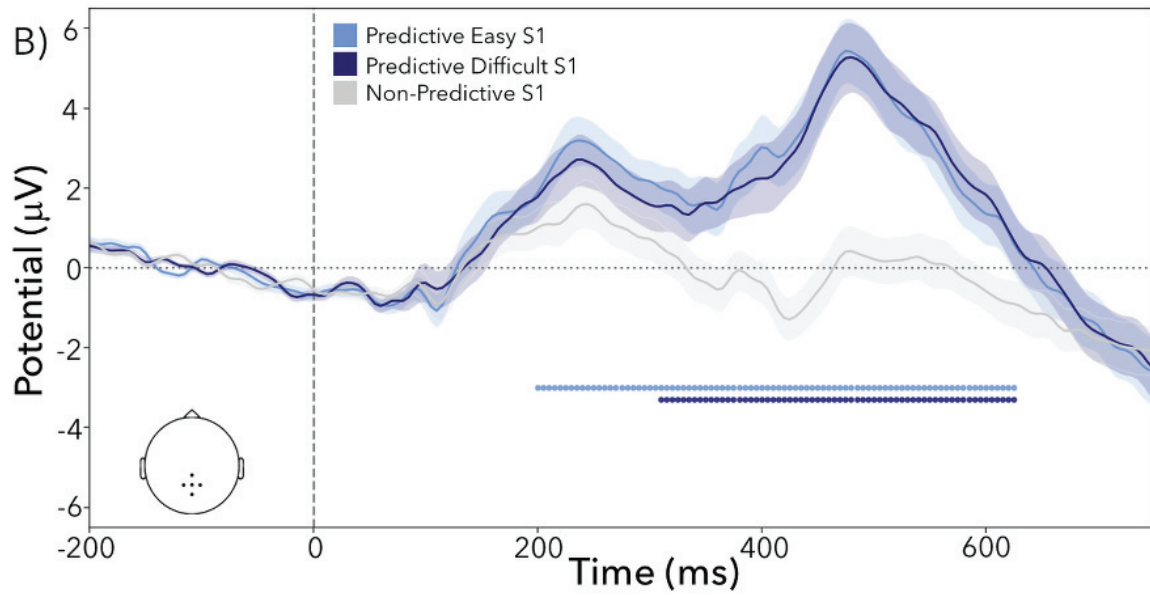
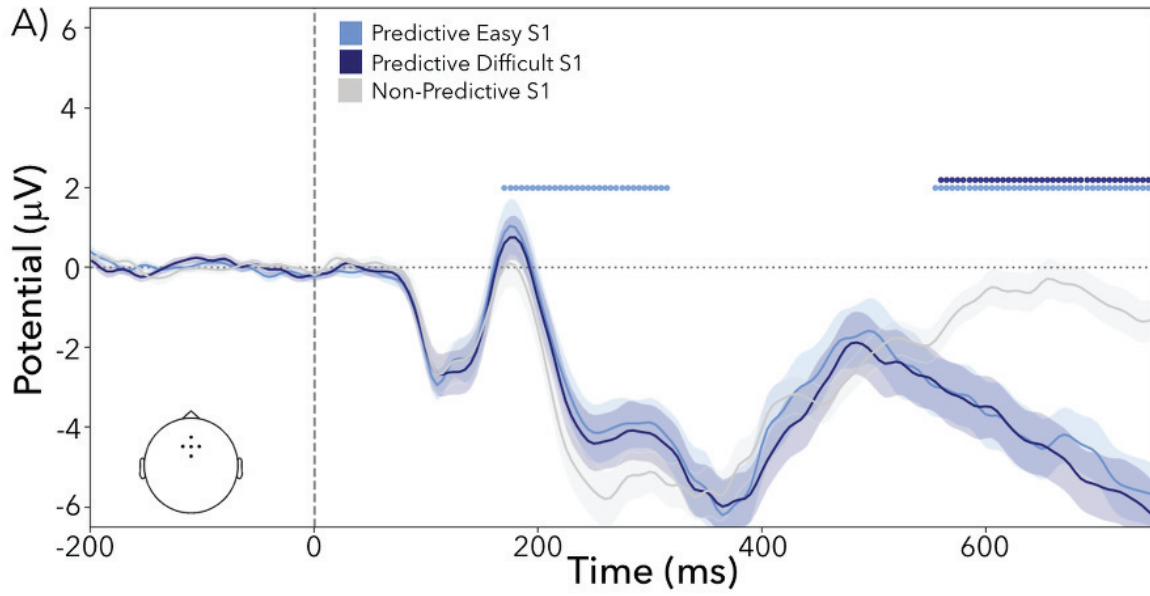


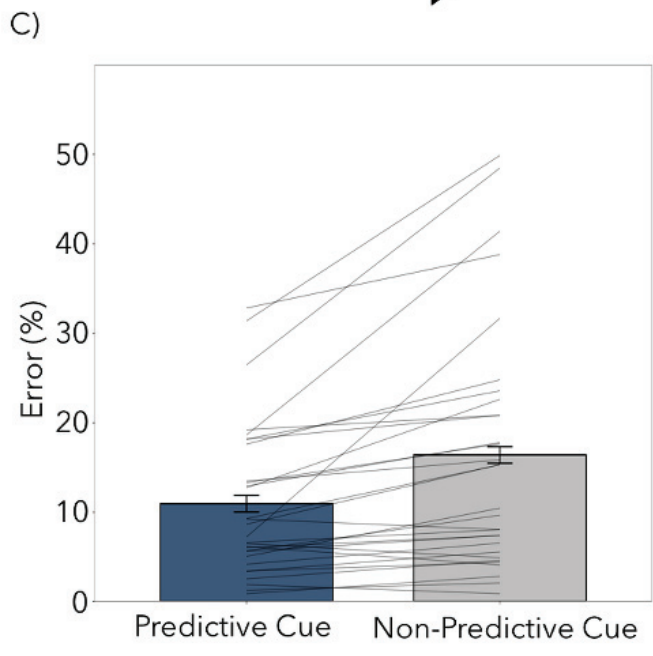
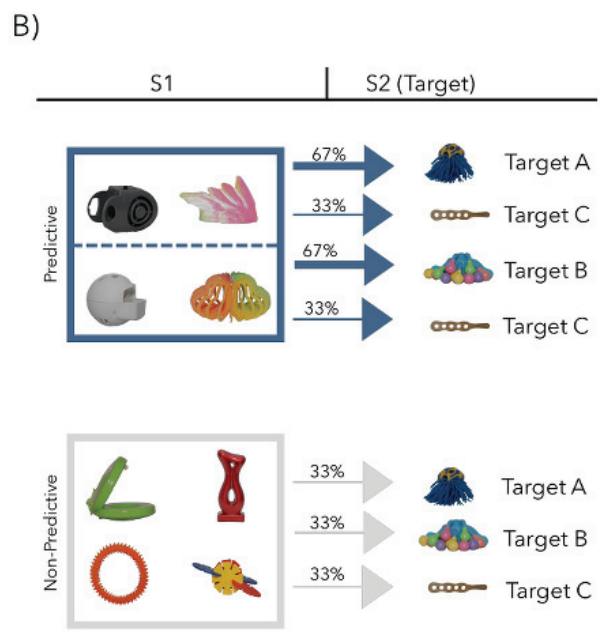
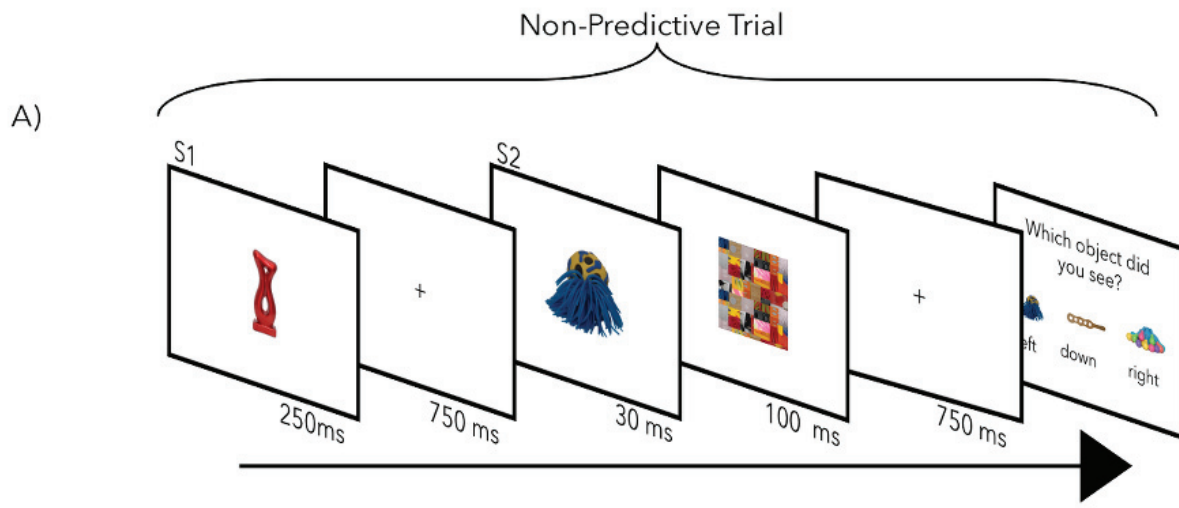
B) Predictive Difficult S1 vs. Non-Predictive S1



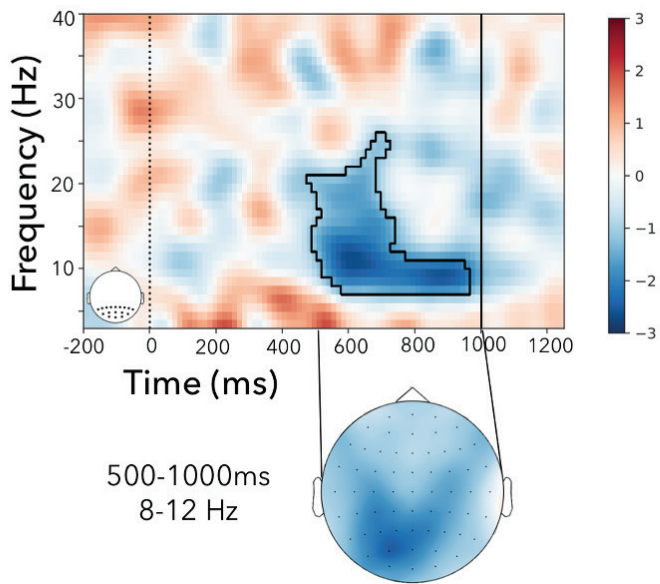
C) Time Course of Alpha Suppression







A) Predictive S1 vs. Non-Predictive S1



B) Time Course of Alpha Suppression

