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Research Articles: Behavioral/Cognitive

Hippocampal and prefrontal theta-band mechanisms underpin implicit spatial context learning

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2 **underpin implicit spatial context learning**

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9 Running title: Neural mechanisms for implicit context learning

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Abstract

Humans can rapidly and seemingly implicitly learn to predict typical locations of relevant items when those items are encountered in familiar spatial contexts. Two important questions remain, however, concerning this type of learning: (1) which neural structures and mechanisms are involved in acquiring and exploiting such contextual knowledge?; and (2) is this type of learning truly implicit and unconscious? We now answer both these questions after closely examining behaviour and recording neural activity using magneto-encephalography (MEG) while observers (male and female) were acquiring and exploiting statistical regularities. Computational modelling of behavioural data suggested that after repeated exposures to a spatial context, participants' behaviour was marked by an abrupt switch to an exploitation strategy of the learnt regularities. MEG recordings showed that hippocampus and prefrontal cortex were involved in the task; and furthermore revealed a striking dissociation: only the initial learning phase was associated with hippocampal theta band activity, while the subsequent exploitation phase showed a shift in theta band activity to the prefrontal cortex. Intriguingly, the behavioural benefit of repeated exposures to certain scenes was inversely related to explicit awareness of such repeats, demonstrating the implicit nature of the expectations acquired. Taken together, these findings demonstrate (1a) that hippocampus and prefrontal cortex play complementary roles in the implicit, unconscious learning and exploitation of spatial statistical regularities; (1b) that these mechanisms are implemented in the theta frequency band; and (2) that contextual knowledge can indeed be acquired unconsciously, and that awareness of such knowledge can even interfere with the exploitation thereof.

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Significance statement

Human visual perception is determined not just by the light that strikes our eyes, but also strongly by our prior knowledge and expectations. Such expectations, particularly about where to expect certain objects given scene context, might be learned implicitly and unconsciously--although this is hotly debated. Furthermore, it is unknown which brain mechanisms underpin this type of learning. We now show that, indeed, spatial prior expectations can be learned without awareness; in fact, strikingly, awareness seems to hinder the exploitation of the relevant knowledge. Furthermore, we demonstrate that one brain mechanism (hippocampal theta-band activity) is responsible for learning in these settings, while another mechanism (prefrontal theta-band activity) is involved in exploiting the learned associations.

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Introduction

Objects are rarely encountered in isolation, but typically within certain spatial contexts. The encountered context, or scene, in which objects appear often induces clear expectations about where particular objects are likely to be located; e.g. we expect (and would more rapidly locate) a computer mouse next to the keyboard and not on top of the monitor. Such scene-based contextual expectations can greatly facilitate perception of individual elements of the scene (Biederman, 1972; Bar, 2004; Oliva and Torralba, 2007; De Lange et al., 2018). Humans are able to automatically and rapidly learn these spatial expectations through repeated exposure to the same or similar scenes, as demonstrated most forcefully by the experimental paradigm known as *contextual cueing* (Chun and Jiang, 1998; Chun, 2000; Goujon et al., 2015).

Contextual cueing is the effect robustly reported that observers engaged in visual search tasks become considerably faster in identifying target items in search displays that they have encountered before. Importantly, this effect becomes evident after only a few exposures to the same scene, and it appears to be fully implicit and automatic, happening outside of conscious awareness (Chun and Jiang, 1998). The robust nature and rapid establishment of the contextual cueing effect makes it ideally suited to study the neural and computational mechanisms involved in the acquisition of scene-based spatial expectations (Goujon et al., 2015).

Some work has been done on elucidating the neural mechanisms underlying this rapid learning and exploitation of statistical regularities, yet much remains unknown. Evidence from neuropsychology indicates that damage to the hippocampus and/or associated medial temporal lobe structures results in deficits in contextual cueing (Chun and Phelps, 1999; Manns and Squire, 2001), a finding which was later corroborated by

83   functional magnetic resonance imaging (fMRI) (Greene et al., 2007; Giesbrecht et al.,

84   2013). Additionally, fMRI studies have demonstrated the involvement in contextual

85   cueing of parietal and frontal cortical structures associated with the top-down guidance

86   of attention (Pollmann and Manginelli, 2009; Giesbrecht et al., 2013), lending support

87   to the hypothesis that contextual cueing likely involves top-down guided attention based

88   on a learned associative link. If, how, and when the hippocampal and parieto-frontal

89   systems interact during learning and exploitation of regularities remains, however,

90   unknown.

91   So far, little work has been done in understanding the role of neural oscillations in the

92   acquisition and exploitation of the associative link underlying contextual cueing. This is

93   surprising, considering the proposed role of especially low-frequency oscillations

94   (theta/alpha/beta) in communicating predictive and top-down information within and

95   across brain regions (Lisman and Jensen, 2013; Jensen et al., 2014; Kerkoerle et al.,

96   2014; Bastos et al., 2015; Michalareas et al., 2016; Spaak et al., 2016; Chao et al.,

97   2018). Given this proposed (and reported) role of neural oscillations, we used the

98   contextual cueing paradigm to examine the neural oscillatory mechanisms involved in

99   the acquisition and exploitation of spatial predictions.

100   The learning of an associative link (especially involving the hippocampus, which is

101   crucial for declarative memory) and the top-down guidance of attention are often

102   thought to be associated with deliberate, conscious thought (Eichenbaum, 2000;

103   Dehaene et al., 2006; Cohen et al., 2012). Interestingly, the spatial predictions learnt in

104   contextual cueing, possibly depending on the same mechanisms, are typically thought to

105   be fully implicit and automatic. Many studies have made such a claim, based on an

106   explicit recognition task following the main visual search task (e.g. (Chun and Jiang,

107   1998)) or more elaborate target-generation tasks (Chun and Jiang, 2003). However, it

108   has been demonstrated that the statistical power to detect conscious awareness in these

109   paradigms was limited, and a more powerful meta-analysis has shown that participants

110   were likely aware of the contextual repeats to some extent (Vadillo et al., 2016). We

111   therefore additionally set out to quantify to what extent the benefit derived from

112   previous exposures to a scene depends on conscious awareness of these exposures or

113   not.

114   To answer these questions, we recorded magnetoencephalography (MEG) data while

115   participants were performing a variant of the classical contextual cueing search task. To

116   preview our results: during the first few blocks, as participants were becoming familiar

117   with the repeated scenes, we observed stronger hippocampal theta activity for familiar

118   (old) compared to unfamiliar (new) scenes. During these blocks, however, there was no

119   behavioural advantage yet for repeated scenes. After the first few blocks, there was a

120   marked shift in both neural processing and behavioural performance. Now frontal cortex

121   (but not hippocampus) showed elevated theta activity for old compared to new scenes,

122   and participants showed a marked behavioural benefit for these familiar scenes. This

123   benefit clearly occurred outside of conscious awareness of scene familiarity; in fact,

124   larger awareness was associated with a smaller benefit. These findings thus shed light

125   on how the brain rapidly extracts statistical regularities from our environment and can

126   use them to guide goal-directed behaviour, even without conscious awareness.

127

Materials and Methods

Participants

We recruited 36 healthy right-handed participants (23 female; 13 male; age 24 ± 5 years (mean $\pm$ standard deviation), range 17–45 years) from the Radboud University participant pool. The sample size was chosen to obtain ≥ 80 % power for detecting a medium effect size (d = 0.5) with a two-sided paired t-test at an alpha level of 0.05. All participants had normal or corrected-to-normal vision. Participants received € 12 compensation for their participation in the main MEG experiment, and an additional € 5 in case they returned for an anatomical magnetic resonance imaging (MRI) scan (i.e., if no such scan was available yet from participation in other experiments). The study was approved by the local ethics committee (CMO Arnhem-Nijmegen, Radboud University Medical Center) under the general ethical approval for the Donders Centre for Cognitive Neuroimaging ("Imaging Human Cognition", CMO 2014/288). Participants provided written informed consent prior to the experiment.

Stimuli, task, and experimental design

Throughout the experiment, a fixation dot (outer white diameter 8 pixels; inner black diameter 4 pixels) was presented in the center of the screen. Participants were asked to blink as little as possible and keep looking at the central fixation dot. Participants were instructed to search for a single T-shaped target stimulus amongst 9 L-shaped distractors (all stimuli measured 1.5×1.5 ° of visual angle and were coloured white, presented on a grey background). Distractor L shapes were rotated a random multiple of 90 °. The target T could be rotated 90 ° to the left or right, and participants made a left or right handed index finger button press to indicate the orientation of the T. Each trial

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152 started with a 1 s fixation period, and search displays were presented for 1.5 s or until

153 the response button press. After the button press, participants were informed whether

154 their response was correct or not by the white part of the fixation dot turning green

155 (correct) or red (incorrect) for 0.5 s (Figure 1A). Search stimuli were arranged

156 pseudorandomly on an 8 × 6 regular grid spanning −9 to +9 ° horizontal and −6 to +6 °

157 vertical from the center of the screen, with an added amount of random jitter ± 0.4 ° per

158 stimulus to prevent exact collinearities (Chun and Jiang, 1998). The target was

159 constrained to always appear between 6 ° and 8 ° of excentricity, and the mean distance

160 between the target and all distractors was constrained to be between 9 ° and 11 °.

161 The main search task consisted of 22 blocks of 40 trials each. Participants were given

162 the option to take a short break (while remaining seated in the MEG chair) every second

163 block. We embedded repeats of search displays in each block to establish the classical

164 contextual cueing effect, i.e. the 'Old' displays. The search configuration of an Old trial

165 was exactly the same across blocks, i.e. the location and rotation of all distractors was

166 maintained, as well as the location of the target. Importantly, the orientation of the

167 target was always randomly chosen and not repeated, so participants could not learn

168 associations between a given display and the appropriate response, only between the

169 display and the target location. All search blocks contained 20 'New' trials, i.e., newly

170 randomly generated search displays. The first 8 blocks contained 20 Old trials.

171 Blocks 9–22 contained 10 Old displays included as-is, with the remaining 10 Old

172 displays modified to yield the 'Target violation' and 'Distractor violation' conditions (5

173 trials per violation condition per block each). To generate a Target violation display, the

174 target was swapped with a randomly chosen distractor, while leaving all other

175 parameters (i.e., distractor location and rotation) untouched. To generate a Distractor

176 violation display, the target location remained the same, but each individual distractor

177   was rotated a random multiple of 90 ° (Figure 1B). Within each block, different Old

178   displays were selected to be converted into a violation display, and trials were presented

179   in random order.

180   After the main search task, participants were asked "Did you have the feeling that some

181   of the search displays occurred multiple times over the course of the experiment?" and

182   indicated their answer with a left ('yes') or right ('no') button press. Next, they were

183   asked: "How sure are you about your answer to the previous question?" and again

184   pressed the left ('very sure') or right ('not very sure') button. 24/36 (75 %) of

185   participants indicated 'not very sure' to this confidence question, so we did not

186   investigate this confidence rating in further detail and instead pooled responses across

187   confidence levels.

188   Finally, participants performed a recognition block, consisting of the 20 Old trials and

189   20 newly generated New trials, randomly intermixed, and were instructed to indicate

190   whether they thought they had seen the display during the main search task. Responses

191   were now self-paced (unspeeded), and participants could freely move their eyes. No

192   feedback was presented during the recognition block.

193

194   **Apparatus**

195   Stimuli were presented using Matlab (The Mathworks, Inc., Natick, Massachussetts,

196   United States) and custom-written scripts using the Psychophysics Toolbox (Brainard,

197   1997), and back-projected onto a translucent screen (48 × 27 cm) using a ProPixx

198   projector (VPixx Technologies, Saint-Bruno, Québec, Canada) at a resolution of 1920 ×

199   1080 pixels and a refresh rate of 120 Hz. Participants were seated at a distance of 85 cm

200   from the screen.

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201   Brain activity was recorded using a 275-channel axial gradiometer MEG system

202   (VSM/CTF Systems, Coquitlam, British Columbia, Canada) in a magnetically shielded

203   room. 5 faulty channels were disabled during the recording, leaving 270 recorded MEG

204   channels. During the experiment, head position was monitored using three fiducial coils

205   (nasion/left ear/right ear). Whenever participants' head movement exceeded ~5mm, the

206   experiment was manually paused and the head position was shown to the participant,

207   who would subsequently reposition (Stolk et al., 2013). Eye position and blinks were

208   recorded using an Eyelink 1000 eye tracker (SR Research Ltd., Mississuaga, Ontario,

209   Canada). All data were on-line low-pass filtered at 300 Hz and digitized at a sampling

210   rate of 1200 Hz. Immediately prior to the MEG session, participants' headshape and the

211   location of the three fiducial coils were digitized using a Polhemus 3D tracking device

212   (Polhemus, Colchester, Vermont, United States) in order to facilitate subsequent source

213   analysis.

214   Anatomical MRI scans were acquired using a 3T MRI system (Siemens, Erlangen,

215   Germany) and a T1-weighted MP-RAGE sequence with a GRAPPA acceleration factor

216   of 2 (TR = 2.3 s, TE = 3.03 ms, voxel size 1 mm isotropic, 192 transversal slices, 8 °

217   flip angle).

218

219   **Behavioural data analysis**

220   The main behavioural variable of interest for the main search task was reaction time

221   (RT), with accuracy being of secondary interest. The evolution of RT and accuracy over

222   the time course of the experiment (Figure 1C) were smoothed $\pm$ 1 blocks (i.e., the data

223   plotted at block n represents the mean of blocks $n-1$, n, and $n+1$). Statistical assessment

224   of the RT data was done for the *a priori* defined window of interest of blocks 9–22

225 (unsmoothed). RT data for trials with incorrect responses was discarded. Since RT

226 distributions are typically heavily skewed, the RT data was log-transformed prior to any

227 analysis to improve normality. Furthermore, since performance improved substantially

228 over the course of the experiment (see Figure 1C), a linear trend over experiment time

229 was fitted and removed from the (condition-pooled) log-transformed RT data per

230 participant before performing group-wise analyses (Figures 1D, 2, 3B, 3C, 4A, 5).

231 Although these preprocessing steps improved the sensitivity of our analyses

232 considerably, we note that our conclusions do not depend on them and also hold when

233 analyzing raw RT.

234 The detrending is crucial for the behavioural modelling only (see below), as the typical

235 time-on-task effect will bias model comparisons. However, care must also be taken to

236 prevent imbalances in trial numbers across the experiment to bias the detrending and

237 hence the results. There are equal numbers of New trials in all blocks (20 per block),

238 and 20 Old trials in blocks 1−8, but only 10 Old (non-violation) trials in blocks 9−22.

239 To rule out that this difference in trial numbers per condition across the experiment

240 influenced the model comparisons, we performed the following control analysis. Instead

241 of estimating the linear trend on the raw log(RT) values as a function of trial index, we

242 first computed mean log(RT) values per condition, per block, and then averaged the two

243 condition-wise means together to form the condition-agnostic block mean (i.e. block

244 mean = mean(mean(RT_{Old}), mean(RT_{New})). Then, we estimated the linear trend on these

245 blockwise means, and subtracted this estimated trend from the raw log(RT) values. If

246 any condition bias is present in the detrending we originally used, this approach will

247 remove it. All model comparison results were unaltered by this change.

248

Behavioural data modelling

We performed Bayesian model comparison in order to determine whether the reaction time difference between Old and New trials exhibited a switchpoint or not. Detrended, log-transformed reaction times (no smoothing across blocks applied) were modelled as drawn from a normal distribution with a given standard deviation σ, and mean μ that could be determined by one of six models (Figure 2B): No effect (no difference in mean between conditions), No switchpoint (constant difference in mean between conditions), Switchpoint (no difference in mean between conditions until a particular point in time in the experiment and a constant difference afterwards), Linear (linearly changing difference in mean, trialwise across the experiment time), Blockwise linear (linearly changing difference in mean, blockwise across the experiment time), and Quadratic (both linearly and quadratically changing difference in mean, trialwise across the experiment time). Specifically, the detrended log-RT for an individual Old or New trial y with index k was modelled according to the following prior and likelihood structure:

$$y_{\text{New}}(k) \sim \text{Normal}(\mu_{\text{New}}, \sigma^2)$$

$$y_{\text{Old}}(k) \sim \text{Normal}(\mu_{\text{Old}}(k), \sigma^2)$$

$$\sigma \sim \text{HalfNormal}(2 \cdot s_{\text{Obs}})$$

$$\mu_{\text{New}} \sim \text{Normal}(\bar{x}_{\text{Obs}}, 2 \cdot s_{\text{Obs}})$$

$$\mu_{\text{Old}}(k) = \mu_{\text{New}} - \Delta\mu(k)$$

where s_{Obs} and $\bar{x}_{\text{Obs}}$ are the sample standard deviation and sample mean of the condition-pooled RT data, respectively. The No effect model was defined by $\Delta\mu = 0$. The No switchpoint model was defined by:

$$\Delta\mu \sim \text{Normal}(\bar{x}_{\text{Obs}}, 2 \cdot s_{\text{Obs}})$$

The Switchpoint model included an extra switchpoint parameter γ and was defined by:

$$\Delta\mu(k) \simeq \begin{cases} \text{Normal}(\bar{x}_{\text{Obs}}, 2 \cdot s_{\text{Obs}}), & k > \gamma \\ 0, & k \leq \gamma \end{cases}$$

$$\gamma \sim \text{DiscreteUniform}(0, 22)$$

267   The Linear model included an extra parameter λ for the trialwise linearly changing

268   reaction time benefit and was defined by:

$$\Delta\mu(k) = \Delta\mu_{\text{Const}} + \lambda k$$

$$\Delta\mu_{\text{Const}} \sim \text{Normal}(\bar{x}_{\text{Obs}}, 2 \cdot s_{\text{Obs}})$$

$$\lambda \sim \text{Normal}(\bar{x}_{\text{Obs}}, 2 \cdot s_{\text{Obs}})$$

269   Analogously, the Blockwise linear model incorporated a blockwise linear change:

$$\Delta\mu(k) = \Delta\mu_{\text{Const}} + \lambda \left\lfloor \frac{k}{40} \right\rfloor$$

270   with $\left\lfloor \frac{k}{40} \right\rfloor$ representing zero-based block index, and the other quantities as above for the

271   Linear model. Lastly, the Quadratic model included all parameters of the Linear model

272   plus an additional quadratic term ν:

$$\Delta\mu(k) = \Delta\mu_{\text{Const}} + \lambda k + \nu k^2$$

$$\nu \sim \text{Normal}(\bar{x}_{\text{Obs}}, 2 \cdot s_{\text{Obs}})$$

273   Posterior probability distributions for the model parameters given the data were

274   obtained per participant using Markov Chain Monte Carlo (MCMC) with a Metropolis-

275   Hastings sampling scheme. Four chains were sampled for each model, with 40,000

276   samples per chain. We discarded the first 20,000 samples (burn-in), and used every 5th

277   sample of the remaining samples (i.e., thinning factor of 5). Convergence of the chains

278   was checked by visual inspection. We computed the Watanabe-Akaike Information

279   Criterion (WAIC) (Watanabe, 2010; Gelman et al., 2014) for each model, given the

280   resulting MCMC posterior probability distribution. In order to compare the different

281   models across the sample of participants, we z-scored the resulting WAIC scores across

282   models per participant before testing. Relative WAIC scores reported in the text are

283   expressed relative to the model with highest WAIC (i.e., the worst fitting model) per

284   participant. Models and sampling scheme were implemented using the PyMC3 library

285   for Python (Salvatier et al., 2016), along with Numpy (van der Walt et al., 2011) and

286   SciPy (Jones et al., 2001).

287   To assess the relationship between the model-based switchpoint and the time courses of

288   neural effects over the experiment (Figure 4B), we aligned these time courses to

289   individual samples from the MCMC approximation of the posterior distribution over

290   switchpoints. Only the center 90% of samples were used (i.e., the 90% credible

291   interval), to reduce the effects of outliers. We computed the mean of the neural time

292   courses over all these samples per participant and proceeded to compute across-

293   participant statistics. Note that not all participants might have a clear switchpoint, but

294   we chose not to restrict this analysis to those that do in order to avoid biasing the

295   results. The resulting time courses will therefore likely be smoother and more gradual

296   than if we had a clear point estimate for the switchpoints for all participants.

297

298   **MEG data preprocessing and trial selection**

299   All MEG data analyses were performed using custom-written scripts and the FieldTrip

300   toolbox (Oostenveld et al., 2011). MEG data were segmented from −1 to +1.5 s around

301   each search display onset. The CTF MEG system records noise in separate reference

302   sensors, concomitantly with brain activity. As a first preprocessing step, the signals

303   from these reference sensors were used to denoise the recorded MEG data. Next, the

304   per-trial and per-channel mean across time was subtracted from the data. Data were

305   screened for outliers including eye blinks or eye movements, MEG SQUID jumps, and

306   muscle artifacts, using a semi-automatic routine (FieldTrip's ft_rejectvisual), rejecting

307   artifactual segments and/or excessively noisy MEG channels. This resulted in 268.9 ±

308   1.4 (mean ± standard deviation) MEG channels retained of the total 270 recorded, and

309   795.9 ± 34.5 trials per participant retained out of a total of 880. After artifact rejection,

310   data were downsampled to 400 Hz (after applying an anti-aliasing filter) to speed up

311   subsequent analyses. Infomax Independent Component Analysis (ICA; (Bell and

312   Sejnowski, 1995)) was then used to clean the data of artifacts caused by ongoing cardiac

313   activity and any residual eye movements.

314

315   **Time-frequency analysis of power**

316   To obtain time-frequency representations of the evolution of oscillatory power over trial

317   time (Figure 3A), we first computed an approximation of the MEG planar gradient to

318   facilitate the interpretation of the resulting topography (Hari and Salmelin, 1997;

319   Bastiaansen and Knösche, 2000). Power was estimated using a 500 ms sliding Hann

320   window, centered from −0.5 to +1 s around search array onset, in steps of 50 ms, with

321   frequency steps of 1 Hz from 1 Hz to 30 Hz. To attenuate edge artifacts, trials were

322   zero-padded to a length of 3 s before spectral estimation. After estimating single-trial

323   power, the two orientations of the planar gradient were combined by summing.

324   Subsequently, we regressed out a linear trend across the experiment time from the

325   power data to remove very slow drifts. For all key results, we verified that these were

326   not driven by the removal of this linear drift. We finally normalized the single-trial data

327   by z-scoring (Grandchamp and Delorme, 2011). Power data was averaged per condition,

328   using only those trials for which the participant responded correctly. For visualization

15

329   purposes only, the time-frequency representation of the power contrast (Figure 3A) was

330   smoothed and interpolated using a 512 × 512 grid.

331

MRI preprocessing and source analysis

333   Anatomical MRI images were realigned to individuals' CTF space by using the three

334   fiducial coil locations and the recorded headshape information, using an automatic

335   procedure followed by manual inspection and optional correction. A source model was

336   created by non-linearly warping a regular 8 mm isotropic grid defined in Montreal

337   Neurological Institute (MNI) space to the individual participants' CTF space. For each

338   grid point, the lead field was computed using a realistic single-shell volume conduction

339   model (Nolte, 2003).

340   The cross-spectral density required for source analysis was estimated on the condition-

341   pooled axial gradiometer data at the frequency of interest, as identified in the sensor-

342   level statistical contrast (specifically: center frequency of interest 4 Hz, ± 3 Hz

343   smoothing by using multitapers, resulting in frequency window 1–7 Hz). Beamformer

344   spatial filters were computed from the lead field and cross-spectral density using

345   Dynamic Imaging of Coherent Sources (DICS) (Gross et al., 2001).

346   We multiplied the resulting filters with the single-trial time-resolved channel-level

347   Fourier spectra, converting the result to power values, to obtain source level estimates

348   of time-resolved power. The source-level estimates were normalized analogously to the

349   sensor level data, i.e. a slow linear trend across the experiment was fitted and removed

350   and single-trial z-scoring was applied (Grandchamp and Delorme, 2011). We averaged

351   the resulting values in the time window of interest, as identified in the sensor-level

352   statistical contrast (0–500 ms post-stimulus), as well as per condition, and computed t-

353 contrasts between Old and New trials across the participants. These were interpolated

354 onto and visualized on the average MNI brain template, with scores below 65 % of the

355 peak masked as fully transparent, everything above 80 % fully opaque, and values in

356 between ramping up sigmoidally (Figure 3B). Note that the t-scores were computed for

357 localization purposes only; we did not repeat the statistical test here, to avoid "double-

358 dipping" concerns (since the effect was already deemed significant at the sensor level).

359 For the analysis of the evolution of the power effect over the time course of the

360 experiment (Figure 3C), we averaged the normalized source-level data in the same 0–

361 500 ms time window per condition, per block. For the observed hippocampus effect, the

362 power was averaged for this single grid point of interest; while for the frontal effect, the

363 power was averaged across the three identified peak grid points of interest (see Results

364 for details). Analogous to the reaction time data, we increased the signal-to-noise ratio

365 of the resulting power time courses by smoothing with ± 1 block.

366

367

368 **Statistical inference**

369 For all pairwise comparisons, we report Student's t statistics along with two-tailed p

370 values, unless otherwise indicated. We furthermore report Bayes factors quantifying

371 how much more likely the data are under the alternative hypothesis than under the null

372 hypothesis (BF_{10}). Bayes factors were estimated analytically using noninformative

373 priors: a Cauchy prior on effect size and a Jeffreys prior on variance, using the default

374 Cauchy scale parameter of $r = 0.707$, resulting in a quantity known in the literature as

375 the "JZS Bayes factor" (Zellner and Siow, 1980; Jeffreys, 1998; Rouder et al., 2009).

17

376   The sensor-level mass univariate contrast (Figure 4A) was assessed using a cluster-

377   based permutation test, which leverages the inherent correlation between the data at

378   neighbouring time points, frequencies, and channels, to correct for multiple

379   comparisons (Maris and Oostenveld, 2007). We used 1,000 permutations, the default

380   maximum-sum cluster statistic, a cluster-forming threshold of 0.05 (also the default),

381   and a minimum channel neighbour count of 2.

382   Error shading in figures (Figures 1C, 3C) reflects the unbiased within-participant

383   corrected standard error of the mean (Cousineau, 2005; Morey, 2008). For visualization

384   purposes, we furthermore highlight uncorrected $p < 0.05$ using thick over- or underlying

385   bars in the same plots.

386

387   **Data and code availability**

388   All data analyzed in the present paper (in anonymized form) are available from the

389   Donders   Repository   (https://data.donders.ru.nl/)   under   persistent   identifier

390   https://hdl.handle.net/11633/aacstiks . All analysis code is available from GitHub

391   (https://github.com/Spaak/contextual-cueing-meg).

392

393   **Results**

394   Human volunteers (N = 36) participated in a variant of the classical contextual cueing

395   task. Participants were instructed to locate a target T stimulus amongst L-shaped

396   distractors, and report the orientation of the T (tilted clockwise/counterclockwise) with a

397   button press (Figure 1A). The experiment consisted of 22 blocks, and in each block the

398   same 20 familiar displays were presented ('Old' trials) in random order, randomly

399   intermixed with 20 unfamiliar displays ('New' trials). In later blocks, we additionally

400   included a small amount of violation trials to be able to study the effects of different

401   types of violations of the established contextual predictions. From block 9 onwards, 5

402   trials per block were changed from an Old trial into a 'Target violation' trial by

403   exchanging the target location with a randomly chosen distractor (thus disrupting the

404   context–target association), and 5 trials per block were changed from an Old trial into a

405   'Distractor violation' trial by randomly rotating each distractor a random multiple of

406   90° (yet preserving the global context–target association) (Figure 1B).

407

Search task behaviour demonstrates robust contextual cueing

409   Over the course of the experiment, responses became faster and accuracy increased

410   (Figure 1C). During the later part of the experiment (*a priori* defined as blocks 9–22),

411   participants showed a clear reaction time benefit for Old displays (678 ± 91 ms; mean ±

412   s.d. across participants), compared to New ones (727 ± 82 ms; $t_{35} = 6.59$, $p = 1.2 \times 10^{-7}$,

413    $BF_{10} = 1.1 \times 10^5$), as well as a higher accuracy (Old: 89 ± 7 %; New: 86 ± 8 %; $t_{35} =$

414   5.30, $p = 6.4 \times 10^{-6}$, $BF_{10} = 3.1 \times 10^3$) (Figure 1D). We thus replicate the classical

415   contextual cueing benefit for visual search in repeated displays.

416   Responses on Distractor violation trials were slower (710 ± 100 ms) than on Old trials

417   ($t_{35} = 5.61$, $p = 2.5 \times 10^{-6}$, $BF_{10} = 7.4 \times 10^3$), and slightly less accurate (87 ± 8 %; $t_{35} =$

418   2.32, $p = 0.03$, $BF_{10} = 1.9$); but faster than on New trials ($t_{35} = 3.01$, $p = 0.0048$, $BF_{10} =$

419   7.9), with no difference in accuracy ($t_{35} = 1.18$, $p = 0.3$, $BF_{10} = 0.34$) (Figure 1D). This

420   indicates that the contextual cueing effect is, at least partly, due to the global

421   configuration of the display, and not exclusively to its local features.

422   Reaction times on Target violation trials (735 ± 105 ms) were slower than on Old trials

423   (t_{35} = 5.86, p = 1.2 × 10^{-6}, BF_{10} = 1.5 × 10^5), slower than on Distractor violation trials (t

424   = 3.05, p = 0.004, BF_{10} = 8.6), and not distinguishable from New trials (t_{35} = 0.678, p =

425   0.50, BF_{10} = 0.22). Accuracy on Target violation trials (84 ± 7 %) was substantially

426   lower than on Old trials (t_{35} = 6.22, p = 3.9 × 10^{-7}, BF_{10} = 4.1 × 10^5), and also

427   somewhat lower than on New (t_{35} = 2.55, p = 0.015, BF_{10} = 3.0) and Distractor violation

428   (t_{35} = 2.54, p = 0.016, BF_{10} = 2.9) trials (Figure 1D). This indicates a contextual cost

429   when the spatial prediction learned from repeated exposures is violated.

430

431   **The contextual cueing benefit appears suddenly and not gradually**

432   The curves of reaction time for Old and New trials over the course of the experiment

433   (Figure 1C) appear to diverge from about block 5 onwards, after which the difference

434   between them appears to remain stable. We sought to quantify the evidence for this

435   potentially interesting descriptive observation through Bayesian model comparison.

436   Specifically, per participant, we fitted six models to the condition-specific reaction time

437   data: No effect (no difference between conditions), No switchpoint (constant difference

438   between conditions), Switchpoint (no difference between conditions until a particular

439   point in time in the experiment and a constant difference afterwards), Linear (linearly

440   changing difference, trialwise across the experiment time), Blockwise linear (linearly

441   changing difference, blockwise across the experiment time), and Quadratic (with both a

442   linearly and quadratically changing difference, trialwise across the experiment time)

443   (Figure 2B).

444   Across our experimental sample, we observed the strongest evidence (quantified by

445   Watanabe-Akaike Information Criterion, WAIC) for the Switchpoint model (relative

446   WAIC = −307.40), followed by the No switchpoint (WAIC = −247.24), Quadratic

447   (WAIC = −231.84), Blockwise linear (WAIC = −226.91), Linear (WAIC = −225.70),

448   and No effect (WAIC = −56.35) models. The pairwise differences between Switchpoint

449   and all the other models were significant and substantial (versus No switchpoint: t_{35} =

450   2.89, p = 0.0066, BF_{10} = 6.1; versus Quadratic: t_{35} = 5.11, p = 1.1 × 10^{-5}; BF_{10} = 1.8 ×

451   10^3; versus Blockwise linear: t_{35} = 5.63, p = 2.4 × 10^{-6}, BF_{10} = 7.8 × 10^3; versus Linear:

452   t_{35} = 6.01, p = 7.6 × 10^{-7}, BF_{10} = 2.2 × 10^4; versus No effect: t_{35} = 5.32, p = 6.1 × 10^{-6},

453   BF_{10} = 3.3 × 10^3) (Figure 2C). This indicates that, indeed, observers first acquire the

454   contextual knowledge (implicitly), and then switch to a strategy in which they start

455   benefitting from repeated exposures to the same display.

456

457   **Learning a predictive context is associated with hippocampal theta activity**

458   During the experiment, we continuously recorded magnetoencephalography (MEG)

459   data from our participants, allowing us to characterize the neural dynamics during the

460   learning and exploitation of the associative link between scene context and target

461   location. We were specifically interested in the role of low-frequency neuronal

462   oscillations in contextual cueing, with repeated versus novel spatial contexts (i.e., Old

463   versus New trials) as the main contrast of interest. We computed time-frequency

464   representations of oscillatory power, averaged over all trials per condition in the

465   experiment, and contrasted these values between conditions. The data were significantly

466   different between Old and New (cluster-based permutation test p = 0.004), with a

467   prominent difference during the first 500 ms of stimulus processing in the theta

468   frequency band (1–7 Hz). The MEG sensor topography of this difference was rather

469   diffuse, with local left frontal/central and right anterior temporal peaks (Figure 3A). We

470   observed no significant difference between conditions in this time-frequency window

471   when we contrasted evoked power, rather than total power (p = 0.11), indicating that the

472   theta frequency effect may be induced, rather than phase-locked, in nature.

473   To get a clearer view of the neural origin of these effects, we performed beamformer

474   source analysis of the theta activity (1–7 Hz) in the time window 0–500 ms post

475   stimulus onset, and again computed condition contrasts. The strongest source of this

476   effect was located in the right hippocampus (peak at 43, −31, −9 mm in Montreal

477   Neurological Institute (MNI) space; Figure 3B, left panel).

478   We next investigated the evolution over the course of the experiment of the difference

479   in stimulus-related hippocampal theta activity between Old and New trials.

480   Interestingly, this difference was primarily evident during blocks 3–6, but not during the

481   later part of the experiment (Figure 3C, left panel). For the majority of this time period,

482   a behavioural contextual cueing effect was not yet evident (Figures 1C, 4A). This

483   suggests that the hippocampal theta rhythm is specifically associated with the *learning*

484   of the predictive link between spatial context and target location, and that, once learned,

485   hippocampal theta activity returns to baseline levels.

486

Exploiting a predictive context is associated with frontal theta activity

488   In addition to the peak in right hippocampus, several sources in frontal cortex also

489   contributed to the difference in theta power between Old and New trials. The strongest

490   frontal contribution was from the left superior frontal cortex (MNI x, y, z = −12, 24, 64

491   mm; Figure 3B, right panel), with additional, weaker, local maxima in right middle

492   frontal gyrus (44, 24, 48 mm) and left precentral gyrus (−44, 0, 40 mm).

493   Interestingly, the evolution of this frontal effect over the time course of the experiment

494   was markedly different from that observed in the hippocampus. Theta power for Old

495   and New trials started to diverge significantly from block 7 onwards, and remained

496   distinct throughout the experiment (Figure 3C, right panel). The frontal theta effect thus

497   emerged as the hippocampal effect was ramping down, and closely mirrored the

498   behavioural benefit for reaction times (Figure 4A). This relationship is also evident

499   when aligning the data to the model-based switchpoints for each participant (Figure

500   4B): around the switchpoint, the hippocampal theta effect is prominent (cluster-based

501   permutation test p = 0.044), whereas the blocks after the switchpoint are dominated by

502   the frontal theta effect (p = 0.0099). Note that the time courses in Figure 4B show more

503   gradual gradients than Figure 4A due to averaging over many samples from the

504   posterior distribution over switchpoints (see Methods for details).

505   Although frontal theta was clearly different between Old and New trials, there were no

506   significant pairwise differences between either of the violation conditions (Distractor

507   violation or Target violation) and Old or New (all p > 0.05), with evidence for the null

508   hypothesis of no difference ranging from moderate to inconclusive ($0.19 < BF_{10} < 0.88$).

509   We therefore cannot exclude the possibility that the absence of an effect here is due to

510   the substantially lower trial count for the violation conditions (65 per condition for each

511   violation condition, versus 355 for Old).

512   The time courses in Figure 4A suggest that the reaction time benefit evident during the

513   post-switchpoint phase is primarily driven by theta activity in the frontal cortex,

514   presumably reflecting top-down driven guidance of attention based on context-induced

515   predictions about target location. If this is the case, then theta power should correlate

516   with the reaction time benefit specifically on Old trials (and not on New, since no

517   predictive link was learned for these), and specifically in the frontal cortex (and not the

518   hippocampus). This is indeed what we found: frontal theta power on Old trials was

519   significantly correlated across participants with the contextual cueing effect (r = 0.34,

520   t_{34} = 2.13, p = 0.041), but there was no such relationship for the hippocampus or for

521   New trials (all p > 0.10, 0.18 < BF_{10} < 0.45) (Figure 4C). However, we note that the

522   evidence for the correlation between frontal theta and the contextual cueing effect,

523   although significant, was inconclusive (BF_{10} = 1.3), and should thus be interpreted with

524   caution.

525   We also assessed whether the hippocampal or frontal theta effects were predictive of

526   reaction time benefit on a per-item basis within individual participants. There was no

527   reliable relationship across items between the magnitude of contextual cueing and

528   frontal power (correlation between power and difference between median RT in first 5

529   blocks and median RT in last 5 blocks; t_{35} = −0.221, p = 0.83, BF_{10} = 0.18) nor for

530   hippocampal power (t_{35} = 0.980, p = 0.34, BF_{10} = 0.28). We note that this analysis was

531   exploratory, and furthermore that these correlations were computed across only 20

532   observations (i.e. the number of repeated displays), thus interpretation should again be

533   done with caution.

534

535   **Explicit recognition is inversely related to implicit behavioural benefit**

536   After completion of the main search task, participants were asked whether they had the

537   "feeling that some of the search displays occurred multiple times over the course of the

538   experiment" and responded with a button press to indicate 'Yes' or' 'No'. Subsequently,

539   participants completed a final (unspeeded) block of 20 New and 20 Old search displays,

540   where the task was to indicate whether they had seen that particular display before

541   during the main task. This allowed us to assess participants' subjective feeling of

542 recognition (question), their objective explicit memory for the search arrays

543 (recognition task), and their relationship to each other and the contextual cueing effect.

544 Results for these analyses are depicted in Figure 5. We used percentage correct as a

545 measure of memory performance, which is an unbiased measure taking into account

546 both hit rate and false alarm rate.

547 As commonly reported in studies of contextual cueing in visual search, the experimental

548 sample as a whole was at chance (50 %) in distinguishing Old from New displays

549 during the recognition task (52 ± 8 %; t-test versus chance level t_{35} = 1.46, p = 0.15),

550 though the data were only ~2 times more likely under the null hypothesis of chance

551 level than under the alternative hypothesis (BF_{10} = 0.47). 16/36 participants (44 %)

552 reported having the feeling that some displays were repeated, while 20/36 (56 %)

553 reported having no such feeling. Interestingly, participants who felt that some of the

554 displays were repeated were on average also slightly above chance level in recognizing

555 displays as Old during the recognition task (55 ± 7 %; t_{15} = 3.03, p = 0.0084, BF_{10} =

556 6.33). In contrast, participants who did not have the impression that displays had been

557 repeated were at chance level in recognizing the displays (49 ± 7 %; t_{19} = -0.538, p =

558 0.60, BF_{10} = 0.27) (Figure 5A). There was thus substantial variability in objective

559 explicit recognition performance among participants, which furthermore appears

560 directly related to the subjective feeling of having encountered displays before.

561 Of considerable interest is the relationship we observed between the subjective feeling

562 of having observed repeats and the strength of the contextual cueing effect during the

563 main search task (Figure 5B). There was a clear reaction time benefit for Old versus

564 New displays in both the Recognizing group (i.e., those who answered 'Yes' to the

565 feeling-of-repeats question; t_{15} = 3.02, p = 0.0087, BF_{10} = 6.1) and the Non-recognizing

566 group (i.e., those who answered 'No'; t_{19} = 6.58, p = 2.7×10^{-6}, BF_{10} = 7.3×10^{3}). If the

25

567   contextual cueing effect were based on explicit knowledge of the repeated displays, one

568   would expect the Recognizing group to show a larger reaction time benefit than the

569   Non-recognizing group. This was clearly not the case ($t_{34} = -1.95$, one-tailed $p = 0.97$),

570   with the data ~8 times more likely under the null hypothesis of equal group means or an

571   effect in the opposite direction than the alternative ($BF_{10} = 0.13$). In fact, the Non-

572   recognizing group showed a numerically larger effect than the Recognizing group ($t_{34} =$

573   1.95, two-tailed $p = 0.060$, $BF_{10} = 1.4$) (Figure 5B), suggesting that search benefits were

574   larger when participants were not aware of the regularities. Further supporting this

575   notion, individual participants' objective performance on the recognition task was

576   negatively correlated with the contextual cueing reaction time effect during the main

577   task ($r = -0.36$, $t_{34} = -2.09$, $p = 0.044$), although the evidence for this relationship was

578   anecdotal ($BF_{10} = 1.3$) (Figure 5C).

579   Reaction time benefit was the main behavioural dependent variable of interest here, as is

580   typical in studies of the contextual cueing effect. However, given the paradoxical

581   relationship we observed between explicit recognition and reaction time benefit, we

582   additionally analyzed search task accuracy as a function of recognition performance,

583   and found similar effects. Both groups show a contextual cueing effect in accuracy

584   (Recognizers: $t_{15} = 2.09$, $p = 0.054$, $BF_{10} = 1.42$; Non-recognizers: $t_{19} = 5.88$, $p = 1.2 \times$

585   10^{-5}, $BF_{19} = 1.9 \times 10^{3}$). Contextual cueing in search task accuracy was not stronger for

586   the Recognizing than for the Non-recognizing group ($t_{34} = -1.69$, one-tailed $p = 0.95$),

587   with substantial evidence in favour of the null hypothesis ($BF_{10} = 0.14$) and a numerical,

588   non-significant, difference in the opposite direction ($t_{34} = 1.69$, two-tailed $p = 0.10$, BF_{10}

589     $= 0.96$). Recognition accuracy was also negatively, non-significantly, correlated with

590   contextual cueing in search task accuracy across participants ($r = -0.255$, $t_{34} = -1.54$, p

591     $= 0.13$, $BF_{10} = 0.53$).

592   To increase sensitivity, we combined the two performance metrics (reaction time and

593   accuracy) in an Inverse Efficiency Score (IES $= \frac{RT_{Correct}}{Acc}$; (Vandierendonck, 2017)). The

594   difference between the Recognizers and Non-recognizers is more strongly apparent in

595   contextual cueing expressed as IES differences (t_{34} = 2.44, p = 0.020, BF_{10} = 2.99;

596   Figure 5D), and the same holds for the negative correlation between recognition

597   accuracy and contextual cueing (r = −0.433, t_{34} = −2.80, p = 0.0084, BF_{10} = 5.0; Figure

598   5E). This relationship between both the objective explicit recognition performance and

599   the subjective feeling-of-repeats on the one hand, and the contextual cueing benefit

600   during the main search task on the other, is rather striking: individuals with *less* explicit

601   knowledge of context-target associations show a *greater* behavioural benefit when

602   exploiting such associations.

603   The inverse relationship between contextual cueing benefit and explicit recognition

604   performance at the level of individuals was not apparent at the level of individual items.

605   Per participant, we assessed whether the learned reaction time speedup during the

606   search task (median RT in first 5 blocks minus median RT in last 5 blocks) for each of

607   the 20 repeated displays was predictive of subsequent recognition performance for that

608   display through logistic regression. We observed no such relationship (t-test of

609   regression coefficients across the sample, t_{35} = 0.858, p = 0.40, BF_{10} = 0.25). The

610   inverse relationship between search task benefit and recognition accuracy thus appears

611   related to individual differences.

612   We finally note that there were no overall (i.e., condition-independent) reaction time (t_{34}

613   = −1.33, p = 0.20, BF_{10} = 0.64) or search task accuracy (t_{34} = −0.765, p = 0.46, BF_{10} =

614   0.41) differences between the Recognizers and the Non-recognizers.

615

Neither hippocampal nor frontal theta is associated with explicit recognition

As mentioned, we observed increased hippocampal theta power for Old displays during the early (learning) phase of the experiment, and increased frontal theta power for Old displays during the later (exploitation) phase. An interesting possibility might be that either the hippocampal or the frontal theta effect dissociates between Recognizers and Non-recognizers, as identified in the previous section. However, we found neither to be the case. We found no evidence that frontal theta in blocks 9–22 was different between the Recognizing and Non-recognizing groups ($t_{34} = 1.69$, $p = 0.10$, $BF_{10} = 0.97$), and frontal theta was not correlated with recognition performance ($r = 0.11$, $t_{34} = 0.65$, $p = 0.52$, $BF_{10} = 0.22$). We also found no evidence that hippocampal theta in blocks 3–6 was different between the Recognizing and Non-recognizing groups ($t_{34} = 1.47$, $p = 0.15$, $BF_{10} = 0.75$), or that it was correlated with recognition performance ($r = 0.29$, $t_{34} = 1.79$, $p = 0.08$, $BF_{10} = 0.76$). The theta band effects described above are thus specifically related to the implicit learning and behavioural exploitation of scene-based spatial predictions, and are unlikely to be explained by either the Recognizers or the Non-recognizers showing the effects, and not the other.

Discussion

We set out to elucidate the neural oscillatory mechanisms underlying the acquisition and exploitation of predictive links between global scene context and search target location. Repeated displays were associated with elevated hippocampal theta power early in the experiment, while there was no behavioural benefit yet. Strikingly, as the hippocampal activity difference receded, stronger frontal theta activity became apparent for repeated scenes, concomitantly with a clear reaction time benefit. This reaction time

640 benefit was furthermore positively correlated with frontal theta power for repeated

641 scenes, and negatively related to participants' explicit recognition of repeated search

642 displays. A hippocampal-prefrontal interplay in the theta band thus underlies the

643 acquisition and exploitation of unconscious scene-based spatial predictions,

644 demonstrating a potential mechanism through which perception can be facilitated by

645 prior expectations (Biederman, 1972; Bar, 2004; Oliva and Torralba, 2007;

646 Summerfield and de Lange, 2014; de Lange et al., 2018).

647 It has been claimed that scene-based expectations are generated based on a rapid

648 extraction of low spatial frequency information from an encountered scene, which can

649 subsequently guide more fine-grained explorations (Bar, 2004). The Distractor violation

650 condition allowed us to investigate to what extent the contextual cueing effect depends

651 on local or global aspects of the search displays. Rotating individual distractors

652 preserves the low spatial frequency distribution of the display, but perturbs the location

653 of individual high spatial frequency edges. If global features, and thus low spatial

654 frequency content, are indeed exclusively responsible for contextual cueing, then

655 Distractor violations should be processed as efficiently as Old displays. We found that

656 Distractor violations are instead processed less efficiently than Old displays (slower RT,

657 slightly lower accuracy), yet still considerably more efficient (faster and more accurate)

658 than New displays. Overall configuration thus indeed seems critical for the contextual

659 cueing effect, though not exclusively responsible for it. This is in line with previous

660 findings (Chun and Jiang, 1998; Jiang and Wagner, 2004).

661 Our experimental sample of participants was at chance level in recognizing individual

662 displays as Old or New after the main search task. This is a common finding in

663 contextual cueing studies, and is interpreted as evidence that the familiarity after

664 repeated search displays is a form of fully implicit knowledge (Chun and Jiang, 2003;

29

665   Goujon et al., 2015). The implicit nature of this effect has been called into question,

666   however, because individual studies have lacked the statistical power to detect above-

667   chance performance (Vadillo et al., 2016). Also in our case, the evidence for the null

668   hypothesis of chance level was only anecdotal across the whole sample, as indexed by

669   Bayesian analysis. A more powerful meta-analysis has instead demonstrated evidence

670   for a weakly *above*-chance recognition of search displays (Vadillo et al., 2016). In our

671   experiment, we included a subjective 'sense of repeated exposure' question after the

672   main search task, only after which the participants performed the recognition task. Some

673   participants appeared to exhibit some awareness of the repeats (as indicated by the

674   group answering that they felt that there were repeats indeed being above-chance at

675   recognition performance), while some had no such awareness (substantial evidence for

676   at-chance performance, no feeling of repeats). We found a *larger* contextual cueing

677   effect in the group *without* awareness, and a *negative* correlation of behavioural benefit

678   with recognition performance. This demonstrates that the behavioural contextual cueing

679   effect is, indeed, likely implicit in nature. Nonetheless, observers might additionally

680   acquire explicit recognition knowledge of the search displays (thus explaining the

681   above-chance result found in the meta-analysis by Vadillo et al.).

682   A straightforward explanation for explicit awareness in only some participants might

683   have been that these 'aware' participants tended to simply look longer at the displays.

684   Since explicit encoding might potentially only be triggered with longer looking times,

685   therefore these longer-looking individuals acquire explicit awareness, and others do not.

686   However, we found no evidence for a difference in overall reaction (and thus looking)

687   times between participants with and without explicit knowledge, so simple differences

688   in looking time cannot explain the differences in awareness. Pinning down *why* certain

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689 individuals do, and others do not, acquire some explicit awareness, is an interesting

690 avenue for future research.

691 The inverse relationship between awareness of the regularities and the performance

692 benefit derived from the regularities is in line with the idea that statistical learning

693 biases sensory and decision processing in an automatic and non-deliberate fashion.

694 Indeed, the benefits of statistical learning in visual search have previously been reported

695 particularly when participants were instructed to "be as receptive as possible and let the

696 [target] 'pop' into [their] mind", but not when participants were instructed to "actively

697 search for the target" (Mühlenen and Lleras, 2004). This corroborates the notion that

698 contextual cueing appears grounded in automatic, unconscious, perception; or, in

699 Kahneman's terms, "System 1" thought (Kahneman, 2013); with any involvement of

700 System 2 (deliberate, conscious thought) abolishing, or at least reducing, the effect.

701 A final result we observed in our behavioural data is that the contextual cueing effect

702 likely emerges suddenly, and not gradually. To our knowledge, this has not been

703 reported (or explicitly tested) before. This suggests that contextual cueing is a form of

704 all-or-none learning (Jones, 1962; Estes, 1964), which has also been shown to underpin

705 simple paired associate learning (Brainerd and Howe, 1978). The all-or-none nature of

706 the phenomenon under study here ties nicely to the fact that synaptic long-term

707 potentiation (LTP) is thought to be discrete and not continuous (Murthy, 1998).

708 Synapses between hippocampal CA3 and CA1 subregions, specifically, are

709 strengthened or weakened in an all-or-none manner (Petersen et al., 1998), which is

710 especially interesting given the hippocampal effects we report in this study. Our

711 conclusion of a sudden, rather than gradual, switch, was based on Bayesian analysis of

712 reaction time data, after visual inspection of the progression of the effect (Figure 1C)

713 suggested the possibility of a switchpoint. The Bayesian modelling clearly designated

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714 the switchpoint model as the winner. Nevertheless, there was substantial inter- and

715 intra-subject variability in the evolution of the contextual cueing effect (see Figure 2A),

716 which potentially could have limited the sensitivity of the analysis. It would be

717 interesting to see future hypothesis-driven work assess the validity of the switchpoint

718 model in more detail.

719 A wide body of evidence has linked the hippocampal theta rhythm to the encoding of

720 memories, both spatial and non-spatial in nature (O'Keefe and Nadel, 1978; O'Keefe

721 and Recce, 1993; Hasselmo, 2005; Buzsaki and Moser, 2013; Colgin, 2013, 2016;

722 Lisman and Jensen, 2013; Staudigl and Hanslmayr, 2013; Backus et al., 2016;

723 Bellmund et al., 2018). We now demonstrate, for the first time, that specifically the

724 acquisition, and not the retrieval, of memories for spatial context in a visual search task

725 involves the hippocampal theta rhythm. Although the involvement of the theta rhythm

726 in contextual cueing has not been reported before, the hippocampus *per se* has been

727 linked to contextual cueing through several strands of evidence. First, lesions to the

728 hippocampus and/or associated medial temporal lobe structures result in severe deficits

729 in the contextual cueing effect (Chun and Phelps, 1999; Manns and Squire, 2001).

730 Second, BOLD activity in the right hippocampus is reduced for Old displays compared

731 to New ones during the learning phase of a contextual cueing task (Giesbrecht et al.,

732 2013). We observed an *increase* in hippocampal theta power for Old versus New

733 displays, whereas Giesbrecht et al. reported a *decrease* in BOLD for Old versus New.

734 This apparent discrepancy can be reconciled by noting that hippocampal theta and

735 BOLD activity tend to be anti-correlated, specifically during memory encoding (Fellner

736 et al., 2016). Our observation of theta activity specifically in the right, and not the left,

737 hippocampus, is in line with the fact that the right, and not the left, hippocampus

738 appears specifically involved in spatial memory (Burgess et al., 2002).

739   It has been debated whether MEG is sensitive enough to measure signals from deep

740   brain structures, such as the hippocampus. In recent years, however, a consensus has

741   emerged that, given proper source reconstruction techniques, MEG is indeed able to

742   measure signals from the hippocampus (Dalal et al., 2013; Pu et al., 2018; Pizzo et al.,

743   2019). We furthermore note that we did not start with an anatomical hippocampus-

744   based region of interest and test the signals coming from that region, but instead used a

745   data-driven approach which subsequently yielded the hippocampus as a strong and

746   significant source of sensor-level effects. Considering these facts, together with the

747   well-established role of the hippocampal theta rhythm in (spatial) memories (thus

748   rendering the effect a priori plausible), we consider the hippocampus to be indeed a

749   likely source of the observed sensor-level effects. We also note here that the identified

750   effects (1–7 Hz) show overlap with the delta frequency range. However, given the

751   limited spectral resolution of the time window we are dealing with here, and the

752   abundant prior literature on the involvement of theta activity in learning, memory, and

753   executive function, we believe that the interpretation of the effect as theta activity is

754   justified.

755   The exploitation of the learned link between spatial context and target location was

756   associated with a clear theta frequency band effect in prefrontal cortex. The peak source

757   of this effect was located in *superior* prefrontal cortex, which is known to be associated

758   with the top-down guided orienting of (spatial) attention (Corbetta and Shulman, 2002).

759   We believe attentional orienting to be the most likely explanation for the frontal theta

760   effect reported here, since it has been shown that participants locate the target more

761   efficiently in repeated displays due to rapid orienting of spatial attention (Zhao et al.,

762   2012, 2013). Frontal theta activity is also commonly linked to the retrieval of memories

763   (Kahana et al., 2001; Osipova et al., 2006; Addante et al., 2011), which might

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764   additionally partly explain the involvement of this rhythm in our experiment. Finally, it

765   is interesting to note that several authors have suggested that these two phenomena (i.e.,

766   memory retrieval and attentional orienting) should be considered two sides of the same

767   coin, (partly) dependent on the same neural mechanisms (Chun and Turk-Browne,

768   2007; Awh et al., 2012; Hutchinson and Turk-Browne, 2012).

769   Intriguingly, the two neural systems identified here (hippocampus during learning;

770   frontal cortex during exploitation) to underlie clearly *implicit* memory are typically

771   associated with *explicit* processes. The hippocampus is crucial for declarative memories,

772   which are by definition amenable to conscious access (Eichenbaum, 2000). The top-

773   down guided (i.e., endogenous) orienting of attention by frontal cortex is often thought

774   to be intimately related to deliberate, conscious thought (Dehaene et al., 2006; Cohen et

775   al., 2012) (although this relationship is fiercely debated, see Koch and Tsuchiya

776   (2007)). We now demonstrate that learning and exploitation of fully implicit knowledge

777   is associated with these two brain structures, and explicit awareness of the same

778   knowledge is not. An interesting corollary is thus that activity in these regions is not

779   necessarily associated with conscious awareness of what is being learned.

780   Recent years have seen considerable interest in and support for the idea that the brain is

781   essentially a prediction machine, continuously trying to minimize the mismatch between

782   expectations and sensory inputs (Clark, 2013). The ubiquitous context effects in

783   perception (Bar, 2004; Oliva and Torralba, 2007; de Lange et al., 2018), established

784   through statistical learning (Turk-Browne et al., 2010), are thus explained by noting that

785   perception depends strongly on prior expectations and not solely on sensory input.

786   These prior expectations, in turn, are continuously fine-tuned in order to optimally

787   process future input, and so on. We demonstrate that the acquisition and exploitation of

788   scene-based expectations involve theta-band dynamics in an interplay between the

789 hippocampus and the prefrontal cortex, which happens outside of conscious awareness.

790 These results shed light on how humans are able to rapidly adapt their prior

791 expectations in order to optimally guide perception and behaviour.

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Figure legends

Figure 1: Experimental design and search task behavioural results. (A) Schematic of an individual search task trial. **(B)** Different trial types: 'New' trials are unfamiliar; 'Old' trials are repeated every block; on 'Target violation' trials the target on an Old display swaps place with a random distractor; 'Distractor violation' trials maintain the spatial configuration of an Old display, but every distractor is rotated a random multiple of 90°. **(C)** Reaction time and accuracy time courses over the experiment for Old and New trials (error shading indicates within-participant corrected standard error of the mean). Black bars on the x-axis indicate pointwise t-tests $p < 0.05$ for illustration. **(D)** Reaction time and accuracy for the four conditions, averaged over blocks 9–22 (well after learning has occurred). Coloured dots are individual participants. Inside the violin plot, the white dot reflects the median, thick box indicates quartiles, thin line indicates quartiles $\pm 1.5 \times$ inter-quartile range.

Figure 2: Reaction time modelling results. (A) Contextual cueing effect over the time course of the experiment, both for the whole experimental sample and for the individual participants. **(B)** Illustration of the six different models that were fit to the reaction time data for Old and New trials. Grey dashed line indicates zero in each subpanel; black solid line indicates the predicted evolution of the contextual cueing effect ($RT_{New} - RT_{Old}$) over the course of the experiment. **(C)** Watanabe-Akaike Information Criterion scores (z-scored across models per participant) for each of the models. Significance bars and violin plot details as in Figure 1.

1100 **Figure 3: Theta band activity differences between Old and New trials. (A)** Time-

1101 frequency representation of sensor-level power difference between Old and New trials

1102 across the whole experiment. Opacity mask indicates cluster-corrected significant

1103 differences ($p < 0.05$) for illustration. Inset shows the sensor topography of the effect;

1104 significantly contributing sensors are highlighted with a dot. **(B)** Source-level contrast

1105 of the time-frequency window of interest identified in (A), projected on the average

1106 Montreal Neurological Institute (MNI) template brain. MNI coordinates given are of

1107 two local maxima; anatomical labels are from the Automated Anatomical Labeling

1108 (AAL) atlas. **(C)** Source-level power values for Old and New trials separately, for the

1109 two identified regions in (B), as a function of experiment time.

1110

1111 **Figure 4: Relationship between neural and behavioural modulation. (A)** Evolution

1112 of theta power differences (Old − New) over the course of the experiment in the right

1113 hippocampus and frontal cortex clusters identified in Figure 4, as well as the contextual

1114 cueing reaction time effect (New − Old). Shading indicates standard error of the mean.

1115 **(B)** Same as in (A), but expressed as relative to the model-based switchpoint (see

1116 Methods for details). **(C)** Scatter plots of the behavioural contextual cueing effect versus

1117 theta power in the two identified clusters, separately for Old and New trials. Each dot is

1118 a participant; black lines are the best-fitting linear regression, with grey shading

1119 indicating the 95% confidence interval.

1120

1121 **Figure 5: Recognition task behavioural results. (A)** Accuracy in recognizing search

1122 displays as Old or New during the recognition task; for the whole sample (left, grey),

1123 and split by whether participants indicated a feeling of repeated displays during the

1124   main task (middle, green) or not (right, blue). **(B)** Contextual cueing effect during the

1125   main search task (defined as RT difference between Old and New trials), for the same

1126   groups as in (A). **(C)** Contextual cueing effect during the main task as a function of

1127   recognition performance. Dots are individual participants, coloured by their response to

1128   the feeling-of-recognition question. **(D,E)** As in panels B and C, but with contextual

1129   cueing effect expressed as difference in Inverse Efficiency Score (IES). * p < 0.05, ** p

1130   < 0.01, *** p < 0.001. Significance bars and violin plot details as in Figure 1. Dashed

1131   line in (B): p = 0.060.

1132

A Fixation (1 s)

Search array (max. 1.5 s)

Button press (Tilt ⊢ or ⊣ ?)

Feedback (0.5 s)

Time

B 'New' trial   'Old' trial

'Old' trial   'Target violation'   'Distractor violation'

C

Reaction time (s)

Old
New

Accuracy (%)

Block

D

Reaction time (log$_{10}$ (RT/s))

Old   New   Distractor violation   Target violation

$p < 0.05$
$p < 0.01$
$p < 0.001$

Accuracy (%)

A

B

C

A

Power Old vs New (t-score)

-2　0　+2

Frequency (Hz)

30

20

10

-0.5　0　0.5　1

Time (s)

B

43, -31, -9 mm
Hippocampus

-12, 24, 60 mm
Superior Frontal

Power Old vs New (t-score)

-4　+4

C

×10⁻²

Hippocampus

15

9

3

Normalized power

1　5　10　15　20　22

×10⁻²

Frontal

6

3

0

-3

1　5　10　15　20　22

Block

Old
New

A

B

C

D

E