1 **The vulnerability of working memory to distraction is rhythmic**

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12 **Keywords**: working memory, distraction, oscillation, attention, suppression, rhythm

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Abstract

Recent research posits that the cognitive system samples target stimuli in a rhythmic fashion, characterized by target detection fluctuating at frequencies of ~3–8 Hz. Besides prioritized encoding of targets, a key cognitive function is the protection of working memory from distractor intrusion. Here, we test to which degree the vulnerability of working memory to distraction is rhythmic. In an Irrelevant-Speech Task, $N = 23$ human participants had to retain the serial order of nine numbers in working memory while being distracted by task-irrelevant speech with variable temporal onsets. The magnitude of the distractor-evoked N1 component in the event-related potential as well as behavioural recall accuracy, both measures of memory distraction, were periodically modulated by distractor onset time in approximately 2–4 cycles per second (Hz). Critically, an underlying 2.5-Hz rhythm explained variation in both measures of distraction such that stronger phasic distractor encoding mediated lower phasic memory recall accuracy. In a behavioural follow-up experiment, we tested whether these results would replicate in a task design without rhythmic presentation of target items. Participants ($N = 6$ with on average >2,500 trials, each) retained two line-figures in memory while being distracted by acoustic noise of varying onset across trials. In agreement with the main experiment, the temporal onset of the distractor periodically modulated memory performance. Together, these results suggest that during working memory retention, the human cognitive system implements distractor suppression in a temporally dynamic fashion, reflected in ~400-ms long cycles of high versus low distractibility.

38 **Introduction**

39 Since our environments are rich in sensory stimuli, our attentional system faces two closely

40 intertwined, yet conceptually dissociable tasks: First, relevant target stimuli need to be

41 prioritized by attention in order to encode them into working memory. Second, irrelevant

42 distractors need to be suppressed to avoid working memory interference. The cognitive

43 system has to orchestrate these two processes dynamically in time (for review, see Nobre &

44 van Ede, 2018), in order to prioritize targets and to suppress distractors from the ongoing

45 stream of sensory inputs. While recent research suggests that the attentional sampling of

46 target stimuli is not constant throughout time but periodically modulated at frequencies in

47 the range of 3–8 Hz (for review, see Fiebelkorn & Kastner, 2019), it is at present unclear

48 whether the vulnerability to distraction is rhythmic as well.

49   It is long known that rhythmic sensory stimulation has the potency to entrain so-called

50 "attending rhythms" (Large & Jones, 1999), which eventually results in enhanced target

51 stimulus detection at time points in-phase versus out-of-phase with the entrained rhythm

52 (in vision: de Graaf et al., 2013; in audition: M. R. Jones, Johnston, & Puente, 2006). Studies

53 have also revealed the neural basis of this phenomenon: Entrainment of brain oscillations

54 by rhythmic stimulation relates to phasic modulation of target detection (Henry & Obleser,

55 2012; Spaak, de Lange, & Jensen, 2014). Furthermore, there is some evidence that direct

56 entrainment of neural oscillations by transcranial alternating current stimulation (tACS)

57 induces phasic modulation of target stimulus detection (Gundlach, Muller, Nierhaus,

58 Villringer, & Sehm, 2016; Helfrich et al., 2014). An important interim summary of this research

59 is that the sensory gain for processing to-be-attended target stimuli fluctuates periodically,

60 likely so as a result of neural entrainment (for recent review articles, see Lakatos, Gross, &

61 Thut, 2019; Obleser & Kayser, 2019).

62   Interestingly, several studies have demonstrated that target detection fluctuates

63 rhythmically even in the absence of entraining sensory input or rhythmic brain stimulation

64 (e.g. Fiebelkorn, Saalmann, & Kastner, 2013; Landau & Fries, 2012). In essence, these studies

65 found that the time interval between an alerting stimulus and subsequent target

66 presentation periodically modulated target detection at frequencies in the theta range of

67 3–8 Hz. On the neural level, rhythmic attentional sampling was accompanied by theta-

68 rhythmic modulation of gamma responses (Landau, Schreyer, van Pelt, & Fries, 2015) and

69 frontoparietal theta activity in humans (Helfrich et al., 2018) and non-human primates

70 (Fiebelkorn, Pinsk, & Kastner, 2018). These results suggest that attention samples target

71 stimuli at a theta rhythm.

72   Attention and working memory are tightly coupled neuro-cognitive faculties (Awh,

73 Vogel, & Oh, 2006). This is evidenced also by retro-cueing paradigms that require the flexible

74 allocation of attention to items in memory (e.g. Lim, Wöstmann, & Obleser, 2015; Oberauer

75 & Hein, 2012; Schneider, Mertes, & Wascher, 2016). It is thus straight-forward to assume that

76 sampling of target objects in memory might be theta-rhythmic as well. Speaking directly to

77 this, Peters and colleagues (2018) varied the time-interval between a retro-cue (which cued

78 one of two spatially separated visual objects in memory) and a subsequent memory probe.

79 They found rhythmic modulation of response times to the probe at a frequency of 6 Hz.

80 Interestingly, rhythmic trajectories of response times across probe times for the cued versus

81 non-cued object were in anti-phase, suggesting that target items in working memory were

82 sampled in alternation. From a more general perspective, theta oscillations have been

83 implicated in working memory function as they increase during temporal order

84 maintenance (Hsieh, Ekstrom, & Ranganath, 2011) and induce increased working memory

85 performance (for a recent review, see Hanslmayr, Axmacher, & Inman, 2019) if entrained by

86 rhythmic transcranial magnetic stimulation (Albouy, Weiss, Baillet, & Zatorre, 2017) or by

87 rhythmic visual stimulation (Köster, Martens, & Gruber, 2019).

88   Here, we test whether the temporal onset of task-irrelevant auditory stimuli would prove

89 disruptive in a slow oscillatory fashion. During working memory retention, distractor onset

90 periodically modulated both, the distractor-evoked N1 component in the event-related

91 potential (at ~3.5 Hz) and memory recall accuracy (at ~2 Hz). Critically, these two measures

92 of distraction were co-modulated by an underlying ~2.5-Hz rhythm. In a behavioural follow-

93 up experiment, we conceptually replicated the rhythmic vulnerability of working memory

94 to distraction in a visual match-to-sample paradigm.

95   **Materials and methods**

96   The main study poses a re-analysis of a previously published dataset. Below, we describe

97   essential methodological aspects but we refer to the original article for details (Wöstmann,

98   Lim, & Obleser, 2017).

99

100   **Participants**. In the main study and in the follow-up experiment, we tested N = 23 (12

101   females & 11 males; mean age: 24.5 years) and N = 6 (5 females & 1 male; mean age: 22 years)

102   participants, respectively. Participants provided informed consent and were compensated

103   financially or by course credit. Experimental procedures were approved by the ethics

104   committee of the University of Lübeck.

105

106   **Task design and stimuli in the main study**. For the main study, to-be-remembered

107   auditory materials were the German numbers from 1 to 9, spoken by a female voice (average

108   number duration 0.6 s). To-be-ignored distractors were short German sentences (5–8 words,

109   average duration: 2.1 s), taken from a German version of speech-in-noise sentences (Erb,

110   Henry, Eisner, & Obleser, 2012), spoken by the same female voice as the numbers.

111   We used an adapted version of the Irrelevant-Speech Task (Colle & Welsh, 1976; D. M.

112   Jones & Morris, 1992). On each trial, participants had to retain nine target numbers in

113   memory, which were presented in random order with onset-to-onset delay of 0.75 s

114   (presentation rate of 1.33 Hz). The most important manipulation for the present study was

115   the temporal onset of the speech distractor. During the ensuing 5-s memory retention

116   period, a task-irrelevant distractor sentence was presented, which had to be ignored. On

117   each trial, the distractor onset was drawn from a uniform distribution including all

118   millisecond values between 1.035 and 1.835 s relative to the offset of the last target number.

119   On average, the distractor sentence was centred in the middle of the retention period, which

120   corresponded to a distractor onset of 1.435 s.

121   At the end of each trial, participants were presented with a number pad on a computer

122   screen. They had to select the numbers in their order of presentation using a computer

123   mouse. In order to prevent participants' motor preparation for a particular behavioural

124   response, the number pad was randomly arranged on each trial.

125   The experiment was implemented in Presentation software (Neurobehavioral Systems).

126   All auditory materials were presented via Sennheiser HD-25 headphones at a comfortable

127   level of ~65 dB A.

128

129   **Additional manipulations of no interest in the main study.** Two additional

130   manipulations of the speech distractor were implemented in the main study but these have

131   been analysed previously (Wöstmann et al., 2017) and were thus not of primary interest here.

132   First, acoustic detail of distractor sentences was manipulated using noise-vocoding. In brief,

133   noise-vocoding parametrically degrades the spectral content of the speech signal but leaves

134   the temporal information largely intact (Shannon, Zeng, Kamath, Wygonski, & Ekelid, 1995).

135   The fewer spectral bands are used for noise-vocoding, the stronger the degradation and the

136   lower the resulting intelligibility of speech materials. In the present study, 1, 4, and 32

137   spectral bands were used for vocoding. As we know from previous studies that a logarithmic

138   increase in spectral bands of noise-vocoded distractors linearly increases the degree of

139   distraction (Wöstmann et al., 2017; Wöstmann & Obleser, 2016), we regressed out noise-

140   vocoding (coded 1, 2, and 3 for 1, 4, and 32 spectral bands, respectively) in the statistical

141   analysis (see below).

142   Second, half of the distractor sentences ended in a final word that was highly predictable

143   (e.g. "She covers the bed with fresh sheets"; translated from German), whereas the final word

144   was unpredictable in the other half (e.g. "We are very happy about the sheets"). Since we

145   found in a previous study (Wöstmann & Obleser, 2016) and in the current dataset

146   (Wöstmann et al., 2017) that final word predictability of distractor sentences had no effect

147   on performance in the Irrelevant-Speech Task, predictability was not further considered in

148   the present study.

149

150   **EEG recording and preprocessing in the main study**. The EEG was recorded at 64 active

151   scalp electrodes (Ag/Ag-Cl; ActiChamp, Brain Products, München, Germany) at a sampling

152   rate of 1,000 Hz, with a DC–280 Hz bandwidth, against a left-mastoid reference (channel

153   TP9). All electrode impedances were kept below 5 kOhm. Offline, the continuous EEG data

154   were filtered (0.3-Hz high-pass; 180-Hz low-pass) and segmented into epochs relative to the

155   onset of the first target number (–2 to +16 s). As described in detail in (Wöstmann et al.,

156   2017), an independent component analysis (ICA) and subsequent automatic artefact

157   rejection were used to clean the EEG data.

158   For the purpose of the present study, the single-trial epoched EEG data were aligned to

159   the onset of the task-irrelevant speech distractor (–2 to +4 s), re-referenced to the average

160   of all electrodes, low-pass filtered at 10 Hz in order to obtain robust single-trial distractor-

161 evoked ERPs, and baseline corrected by subtraction of mean voltage in the time window

162 –0.1 to 0 s relative to distractor onset. For the EEG data analyses we used the Fieldtrip

163 toolbox (version 2018-06-14; Oostenveld, Fries, Maris, & Schoffelen, 2011) for Matlab

164 (R2018a) and customized Matlab scripts.

165

166 **Analysis of periodic modulation of recall behaviour and distractor-evoked N1**

167 **amplitude in the main study.** Each participant performed 180 experimental trials. After

168 removal of artefactual EEG epochs, an average of 153 trials (SD = 23.4) per participant

169 remained for the analyses of behavioural and EEG data.

170   The two major outcome variables of interest were memory recall accuracy and neural

171 distractor encoding. The former was quantified as the proportion of numbers recalled at

172 their respective positions of presentation; the latter was quantified as the mean EEG

173 amplitude at electrode Cz in the time interval 0.09–0.13 s relative to distractor onset. This

174 time interval was determined by inspection of the grand-average ERP waveform (see Fig.

175 1D). To quantify and visualize memory recall and N1 amplitude as a function of distractor

176 onset time, both of these single-trial measures were averaged for a 0.1-s long sliding

177 window, which was moved in 0.01-s steps over distractor onset time for each participant

178 (resulting in 71 time bins; see Fig. 1D).

179   To quantify rhythmic modulation of memory recall and distractor-evoked N1 across

180 distractor onset time, linear mixed-effects models were used to regress single-trial outcome

181 measures on circular sine and cosine predictors (a method that also proved superior in a

182 recent article that compared different approaches to analyse phasic modulation of neural

183 and behavioural responses; Zoefel, Davis, Valente, & Riecke, 2019).

184   Before the analysis of rhythmic memory recall modulation, single-trial accuracy (ranging

185 from 0 to 9 out of 9 correctly recalled numbers) was logit transformed. Since the logit for

186 proportions 0 and 1 is undefined, the following adjusted equation was used to logit-

187 transform single-trial proportion correct (PC) values (Fox & Weisberg, 2019):

188

189 $$logit_{adj}(PC) = ln\left(\frac{0.5 + 0.95 \cdot (PC - 0.5)}{1 - (0.5 + 0.95 \cdot (PC - 0.5))}\right) \quad \text{(Eq. 1)}$$

190

191   Prior to mixed-effects model analyses, predictor and outcome variables were z-

192 transformed.

193   We first regressed out potential effects of auditory distractor vocoding, by regression of

194   single-trial accuracy and N1 amplitude on vocoding level plus random subject intercept,

195   using the *fitlme* function in Matlab and the model formulae 'Accuracy ~ Vocoding +

196   (1|Subject ID)' and 'N1 amplitude ~ Vocoding + (1|Subject ID)', respectively. Next, we

197   regressed the residuals of these regression models on sine- and cosine transformed

198   distractor onset times, using the model formulae 'Accuracy residuals ~ Sine predictor +

199   Cosine predictor + (1|Subject ID)' and 'N1 residuals ~ Sine predictor + Cosine predictor +

200   (1|Subject ID)'. Sine- and cosine-transformed distractor onsets for a given frequency *freq*

201   were determined using the formulae:

202

203               $Sine\ predictor = \sin(2 \cdot \pi \cdot freq \cdot Distractor\ onset)$ (Eq. 2)

204               $Cosine\ predictor = \cos(2 \cdot \pi \cdot freq \cdot Distractor\ onset)$ (Eq. 3)

205

206   This step was iteratively repeated for frequencies 0.5 to 8 Hz in steps of 0.25 Hz. For each

207   frequency, spectral magnitude was computed from the resulting coefficients (coef) for the

208   Sine and Cosine predictor using the formula:

209

210               $Spectral\ Magnitude = \sqrt{Sine\ coef^2 + Cosine\ coef^2}$ (Eq. 4)

211

212   Significance of rhythmic modulation of measures of distraction (accuracy & N1

213   amplitude) was derived using a permutation approach. For each frequency, we compared

214   the empirical value of spectral magnitude to 5,000 permutations of the data, generated by

215   randomly shuffling single-trial sine- and cosine-transformed distractor onset time within

216   individual participants. Spectral magnitude was considered significantly larger than

217   expected under the null hypothesis if the empirical value of spectral magnitude for a given

218   frequency exceeded the 95th percentile of permuted data (i.e. one-sided testing).

219

220   **Analysis of joint modulation of behaviour and N1 amplitude in the main study.** We

221   computed the cross-correlation (using the *xcorr* function in Matlab) of average binned

222   accuracy and N1 amplitude as a function of distractor onset time. We also calculated the

223   cross power spectral density of these two measures (using the *cpsd* function in Matlab;

224   rectangular window length = 0.3 s, window overlap = 0.1 s). Empirical cross-correlation and

225   cross power spectral density were compared to surrogate data, generated by 5,000

226 permutations of single-trial distractor onset time within single participants before binning

227 the data.

228 In order to test whether a joint 2.5-Hz rhythm, which turned out most prominent in the

229 cross power spectral density analysis, modulates memory recall accuracy directly or

230 indirectly (mediated via N1 amplitude), we performed a mediation analysis. To this end, we

231 extracted the 2.5-Hz phase ($\varphi_{2.5\,Hz}$) of the mixed-effects model to regress single trial accuracy

232 on sine-and cosine-transformed distractor onset time (using the *atan* function in Matlab to

233 calculate the inverse tangent) using the formula:

234

235 $$\varphi_{2.5Hz} = \text{atan} \left(\frac{Cosine\ coef}{Sine\ coef} \right) \ \text{(Eq. 5)}$$

236

237 To estimate individual path coefficients between the 2.5-Hz rhythm, average accuracy,

238 and N1 amplitude binned for distractor onset time, linear regression analyses were used

239 (using the *fitlm* function in Matlab). Significance of the *indirect path*, which would link the

240 2.5-Hz rhythm and memory recall accuracy via the mediator distractor-evoked N1

241 amplitude, was calculated in the *medmod* package in Jamovi (version 1.1.9).

242

243 **Task design, stimuli and statistical analysis in the follow-up experiment**. In order to test

244 whether the results of the main experiment would conceptually replicate in a task that does

245 not contain rhythmic presentation of to-be-remembered target stimuli, we used a visual

246 match-to-sample task in a behavioural follow-up experiment. On each trial, participants

247 were presented with a central black fixation cross on a screen with grey background, flanked

248 by two line-figures, each one of which was generated by connecting 20 randomly drawn

249 points with black lines. Edge length of line-figures was ~4.05 * 4.05 cm and each line figure

250 was displaced from the central fixation cross by ~0.405 cm. In order that the entire visual

251 display did not exceed 5° visual angle, participants were seated at a distance of ~102 cm

252 from the screen.

253 Participants had the task to encode both line-figures into visual working memory while

254 remaining central fixation. Line-figures were presented for a duration of 0.3 s. In order to

255 reset the phase of a potential rhythm that samples the two line-figures in memory, the

256 corners of one of the two line-figures were highlighted in white within the last 0.05 s of the

257 encoding period. Note that such a "flash event" was also used in previous studies that tested

258 the rhythmic attentional sampling of visual target objects (e.g., Fiebelkorn et al., 2013;
259 Landau & Fries, 2012).

260   During the ensuing 3-s retention period, participants kept the line-figures in memory
261 while being distracted by a broad-band noise distractor (0.1–5 kHz) of 1-s duration, with
262 0.01-s linear onset and offset ramps. The distractor onset varied across 24 linearly spaced
263 time points in the time interval 0.5–1.5 s relative to the end of the encoding period. In the
264 end of a trial, one line-figure was presented on the left or right side of the fixation cross.
265 Participants had to indicate via button press whether the line-figure matched the one
266 presented on the same side during encoding. Note that the follow-up experiment also
267 contained trials without a distractor stimulus, as well as trials with the flash event on the side
268 opposite to the probed line-figure. These trials were excluded from the present analysis. The
269 experiment was implemented in Psychtoolbox (Brainard, 1997) for Matlab. Auditory
270 materials were presented via Sennheiser HD-280 Pro headphones.

271   The follow-up experiment was designed to increase the signal-to-noise ratio in the data
272 by testing relatively few participants on a huge number of experimental trials. Participants
273 ($N = 6$) were tested in two data recording sessions of ~3.5–4 h duration, each (on two
274 different days). For one participant, data of the first session were excluded due to a
275 misunderstanding of task instructions. One other participant did not finish the experiment,
276 so that 77 trials were missing. On average, 2,537 trials (SD: 566) of each participant were
277 included in the present analysis, corresponding to an average of 105.7 trials per participant
278 and distractor onset time. Note that the approach to collect rich behavioural data of few
279 individuals has been adopted also in previous studies that investigated rhythmic sampling
280 of target stimuli in monkeys (Fiebelkorn et al., 2018) and in humans (Tomassini, Spinelli,
281 Jacono, Sandini, & Morrone, 2015).

282   For the statistical analysis, we used the same procedure as for the main study with the
283 following exceptions. First, no factors were regressed out prior to regression of accuracy on
284 sine- and cosine- transformed distractor onset time. Second, since single-trial accuracy was
285 binary (1 = correct response; 0 = incorrect response), we used logistic regression (using the
286 *fitglme* function in Matlab for a *binomial* distribution of the response variable and a *logit* link
287 function).

288   For visualization purposes, average accuracy was calculated for each participant and
289 distractor onset time, followed by smoothing via replacement of accuracy for bin_b by: 0.25 *

290   accuracy bin$_{b-1}$ + 0.25 * accuracy bin$_{b+1}$ + 0.5 * accuracy bin$_b$. Then, smoothed accuracy data

291   were averaged across participants, detrended, and z-transformed.

292 **Results and Discussion**

293 In the main study, participants (N = 23) retained the serial order of nine numbers in working

294 memory, while being distracted by a task-irrelevant spoken sentence of varying temporal

295 onset across trials (Fig. 1A&B). As it is typical for an Irrelevant-Speech Task (e.g. D. M. Jones,

296 Macken, & Murray, 1993; Kreitewolf, Wöstmann, Tune, Plöchl, & Obleser, 2019; Wöstmann &

297 Obleser, 2016), primacy and recency effects in working memory (Henson, 1998) were

298 reflected in relatively high recall accuracy for early number positions (1–4) and for the last
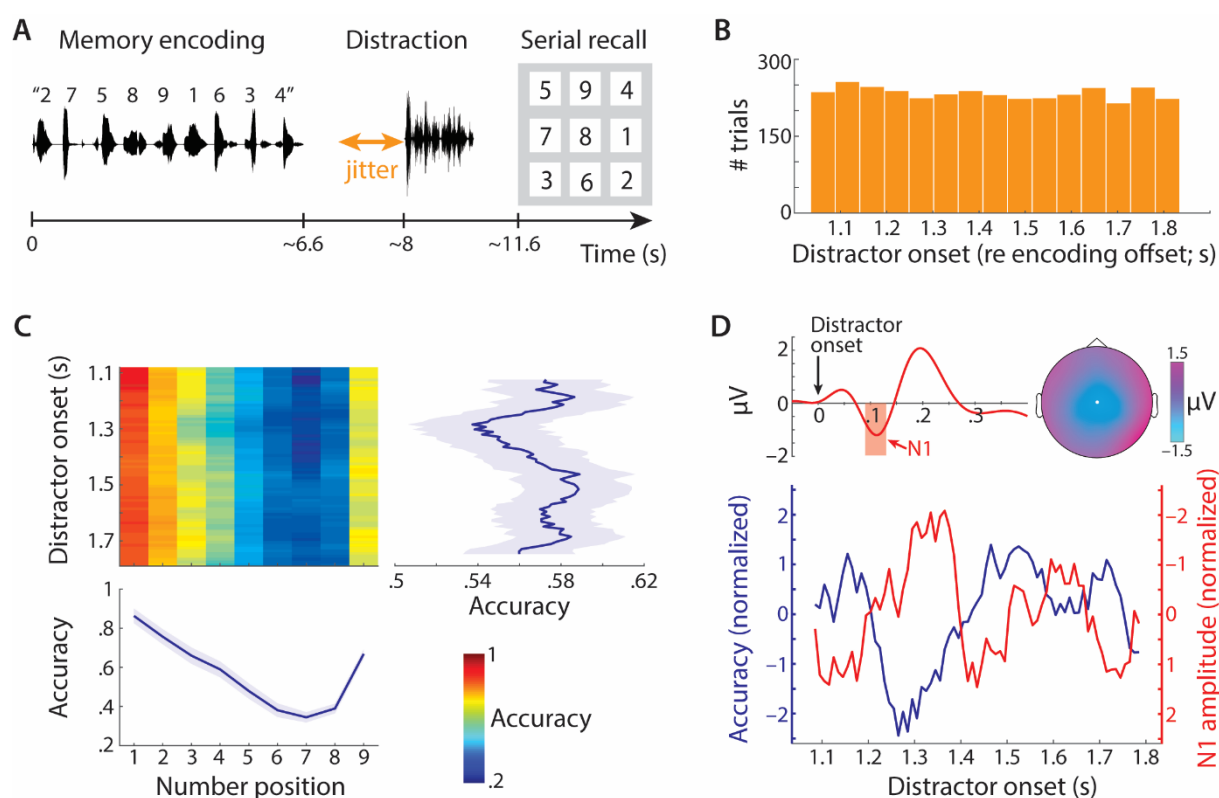
299 number position, respectively (Fig. 1C).

300

301

302
303 **Figure 1.** (**A**) Irrelevant-Speech Task. During retention of numbers in memory, participants were distracted by
304 a task-irrelevant spoken sentence. At the end of each trial, participants had the task to select the numbers from
305 a visual display in the order of presentation. (**B**) Histogram of distractor onset times across all (N = 23)
306 participants. (**C**) Heatmap shows average recall accuracy as a function of number position (x-axis) and binned
307 distractor onset time (y-axis). Blue lines show marginal means. Shaded areas show ±1 between-subject
308 standard error of the mean (SEM). (**D**) Top: Grand-average distractor-evoked event-related potential (ERP) at
309 electrode Cz. The topographic map shows the N1 component in the time window .09–.13 s after distractor
310 onset (red shaded area). Bottom: Lines show z-transformed grand-average proportion correct (blue) and N1
311 amplitude (red) as a function of binned distractor onset time. Note that negative N1 amplitude values
312 (referring to stronger distractor encoding) are plotted upwards.

313

314 **Distractor onset periodically modulates target recall and distractor encoding.** In order

315 to test whether the vulnerability of working memory to distraction is rhythmic, we

316 investigated two outcome measures of interest. First, on the behavioural level, serial recall

317 accuracy averaged across number positions was thought to be inversely related to the
318 degree of distraction. That is, the more a participant is distracted by irrelevant speech, the
319 lower the recall accuracy on an individual trial. Second, on the neural level, the amplitude of
320 the N1 component of the distractor-evoked ERP was utilized as a measure of neural
321 distractor encoding.

322 Both average recall accuracy and N1 amplitude fluctuated periodically across distractor
323 onset times (Fig. 1D), with such distractor onsets associated with stronger distractor
324 encoding (more negative N1 amplitude) coinciding with lower recall accuracy. As to be
325 expected for two measures of the same underlying construct (i.e. distraction), average serial
326 recall accuracy and N1 amplitude binned for distractor onset time were significantly
327 correlated ($r = 0.536$; $p < 0.001$).

328 To statistically analyse the periodic modulation of both measures of distraction, we used
329 linear mixed-effects models to regress single-trial accuracy and N1 amplitude on sine- and
330 cosine-transformed distractor onset time (Fig. 2A–C; see Materials and Methods for details).
331 Empirical spectra from mixed-effects models were contrasted against surrogate spectra,
332 derived from 5,000 permutations of single-subject distractor onset time. We found
333 significant periodic modulation of both measures by distractor onset time, for memory recall
334 accuracy at frequencies ~1.25–2.5 Hz and for N1 amplitude at frequencies ~3–3.75 Hz (Fig.
335 2D&E).

336 While previous research has shown that the attentional sampling of exogenous target
337 stimuli (Fiebelkorn et al., 2013; Landau & Fries, 2012) and target stimuli retained in working
338 memory is rhythmic (Peters et al., 2018), we demonstrate here that the vulnerability of
339 working memory to distraction is rhythmic as well. Mechanistically, a straight-forward
340 interpretation of the present results is that the suppression of distractors fluctuates
341 rhythmically, which results in alternating periods of higher versus lower vulnerability to
342 distraction. If the onset of a distractor stimulus falls into a period of high distractibility (i.e.
343 low distractor suppression), neural encoding of the distractor is enhanced, resulting in
344 stronger memory disruption. Such an interpretation implies that distractor encoding and
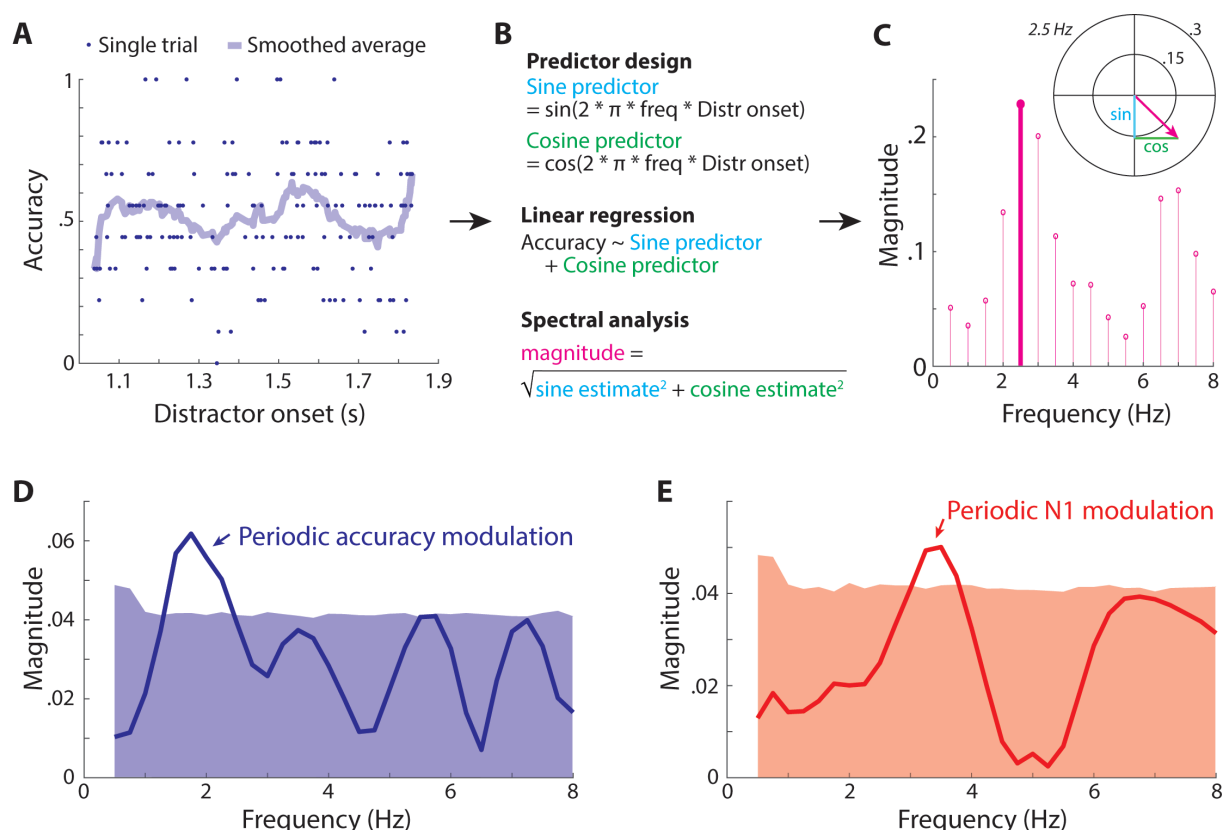345 memory recall are co-modulated by a joint rhythm, which we tested next.

346

347

Figure 2. (**A–C**) Schematic depiction of the analysis procedure for periodic modulation of single-trial measures of distraction. (**A**) Dots show single-trial accuracy as function of distractor onset for one exemplary participant. For visualization, the shaded line shows accuracy averaged across twenty neighbouring distractor onsets. (**B**) For statistical analysis, sine- and cosine-transforms of distractor onset time were used as predictors in a linear regression to model single-trial accuracy. Spectral magnitude was calculated as the square root of the sum of squared sine and cosine estimates. Variables with uppercase names denote vectors that contain multiple entries; lowercase variables contain a single entry. (**C**) Spectral magnitudes derived from multiple linear models for frequencies 0.5–8 Hz. The unit circle shows sine/cosine estimates and spectral magnitude (length of pink arrow) for a frequency of 2.5 Hz. (**D**) Solid line shows spectral magnitude of periodic modulation of single-trial accuracy by distractor onset (derived from linear mixed-effects models). Shaded area shows the 95th percentile of surrogate spectra (derived from 5,000 permutations of single-trial distractor onset time within single participants). (**E**) Same as D but for periodic modulation of N1 amplitude.

A joint rhythm modulates distractor encoding and memory recall. We tested to what degree memory recall accuracy and the distractor-evoked N1 amplitude were periodically modulated by a joint underlying rhythm. To this end, we employed average accuracy and N1 amplitude binned for distractor onset time (shown in Fig. 1D) and computed their cross-correlation and cross power spectral density, which significantly exceeded surrogate data (derived from 5,000 permutations of single-subject distractor onset time) at frequencies of ~1.5–4 Hz and peaking at 2.5 Hz (Fig. 3). These results are in line with the notion that a common slow-oscillatory rhythm (here, 2.5 Hz) modulates memory recall accuracy and the distractor-evoked N1 amplitude.
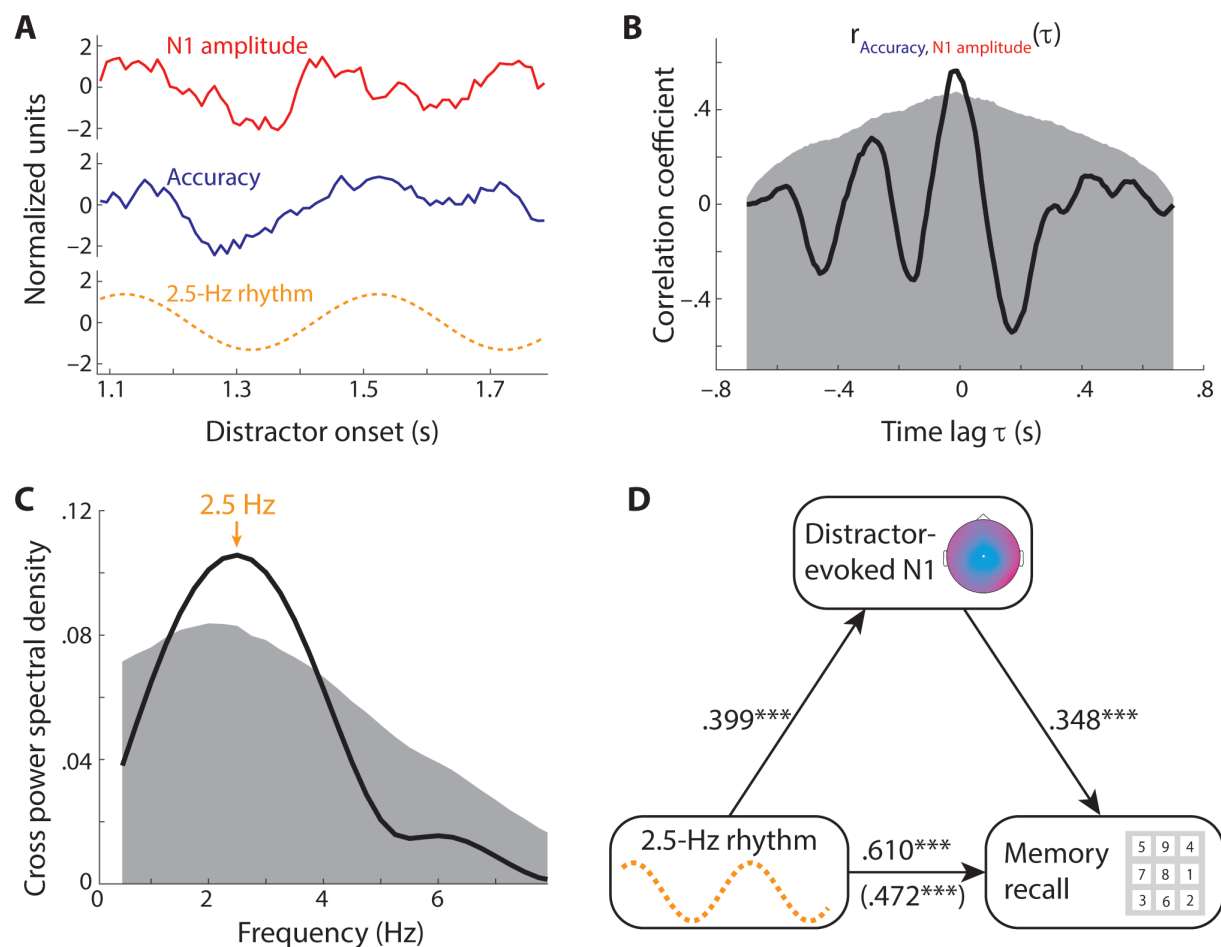
Figure 3. (**A**) Lines show average N1 amplitude (red), accuracy (blue), and the 2.5-Hz rhythm (orange) extracted from the mixed-effects model to regress single-trial accuracy on 2.5-Hz sine- and cosine-transformed distractor onset time. (**B**) Line shows cross-correlation of average recall accuracy and N1 amplitude binned for distractor onset time. Shaded area shows 95th percentile of surrogate cross-correlations, computed on surrogate data (derived from 5,000 permutations of single-subject distractor onset times). (**C**) Line shows cross power spectral density of average recall accuracy and N1 amplitude binned for distractor onset time. Shaded area shows the 95th percentile of surrogate data (computed for the same permutations as in B). (**D**) Depiction of mediation analysis. Numbers at arrows show beta-coefficients of linear regression models. The total effect of the 2.5-Hz rhythm on memory recall accuracy ($\beta = 0.610$) was weakened when N1 amplitude was controlled for (*direct effect*; $\beta = 0.472$), resulting in a significant partial mediation via N1 amplitude (*indirect effect*; $\beta = 0.139$). *** $p < 0.001$.

If the rhythmic modulation of distractor encoding drives synchronized modulation of memory recall accuracy, the 2.5-Hz periodic modulation of memory recall should be mediated by the distractor-evoked N1 amplitude. To test this, we performed a mediation analysis. We extracted the phase of 2.5-Hz rhythm from the mixed-effects model to regress single-trial accuracy on 2.5-Hz sine- and cosine-transformed distractor onset time ($\varphi_{2.5\,Hz} = 2.79$). The 2.5-Hz rhythm significantly predicted N1 amplitude ($\beta = 0.399$; $p < 0.001$) and memory recall (*total effect*; $\beta = 0.610$; $p < 0.001$). Importantly, the latter effect was significantly reduced when the regression model included N1 amplitude as an additional predictor (*direct effect*; $\beta = 0.472$; $p < 0.001$). A significant indirect effect (*total effect – direct*

394   *effect;* β = 0.139; *p* = 0.009) revealed that the 2.5-Hz rhythmic modulation of memory recall

395   accuracy was partially mediated by the distractor-evoked N1 amplitude (22.7 % mediation).

396   This supports the view that periodic fluctuation of distractibility induces synchronized states

397   of increased versus decreased neural distractor encoding, which in turn result in increased

398   versus decreased working memory disruption, respectively.

399   These results provide converging behavioural and neural evidence that a 2.5-Hz rhythm

400   governs the degree to which task-irrelevant stimuli disrupt working memory (see also next

401   section). Notably, however, rhythmic vulnerability to memory distraction found in the

402   present study appears to be somewhat slower than rhythmic sampling of target stimuli,

403   which is typically observed in the theta range of 3–8 Hz (Fiebelkorn & Kastner, 2019). Why

404   would that be?

405   Recent neuroscience work suggests that distractor suppression is not the mere inverse of

406   target enhancement, but an independent neuro-cognitive mechanism that operates on

407   distractors in the sensory environment (Noonan et al., 2016; Wöstmann, Alavash, & Obleser,

408   2019), as well as on distractors in working memory (Schneider, Goddertz, Haase, Hickey, &

409   Wascher, 2019). In this view, it is well conceivable that rhythms of different frequency

410   orchestrate the dynamic sampling of target stimuli (at 3–8 Hz) versus suppression of

411   distractors (at ~2.5 Hz).

412   Alternatively, it might be that the nature of the present experimental paradigm induced

413   rhythmic distractibility at 2.5 Hz. In contrast to previous studies that investigated rhythmic

414   sampling of visual targets, the present study used a serial recall working memory task in the

415   auditory modality. Furthermore, the rhythmic presentation of target stimuli in the present

416   study might have entrained distractibility to a certain extent. To test whether these

417   alternative explanations can be ruled out, we next analysed the data of a behavioural follow-

418   up experiment.

419

420   **The origin of rhythmic distractibility.** An obvious question is whether the observed

421   rhythmic modulation of memory distractibility is entrained by external sensory stimulation

422   or whether it reflects a spontaneous internal rhythm underlying memory function.

423   Although the present study cannot provide a definite answer to this question, we address

424   both options below.

425   In theory, it is possible that the rhythmic presentation of target numbers entrained an

426   attending rhythm at 1.33 Hz, which periodically modulated also the distractibility during

427 memory retention. Consistent with this notion, distractor onset time modulated recall

428 accuracy at frequencies including this attending rhythm (~1.25–2.5 Hz). Furthermore, the

429 time point of highest memory distractibility (at ~1.26 s following target offset; see Fig. 1D)

430 falls precisely in-between two peaks of the hypothetical 1.33-Hz attending rhythm (i.e., in-

431 between the onsets of putative number positions 11 and 12). However, the joint periodic

432 modulation of accuracy and distractor-evoked N1 amplitude was strongest at a frequency

433 of 2.5 Hz rather than 1.33 Hz, which speaks against the view of entrained distractibility.

434 Alternatively, the observed ~2.5-Hz rhythm might be a spontaneous internal rhythm

435 underlying memory function (see Fig 3D). If this is the case, a similar rhythm should be

436 observed also in the absence of a potentially entraining stimulus sequence. In a behavioural

437 follow-up experiment, we used a visual match-to-sample task to test this hypothesis. While

438 participants retained two line-figures in working memory, they were distracted by an

439 auditory noise distractor of varying onset time (Fig. 4). Distractor onset time periodically

440 modulated task accuracy at a frequency of 2.75 Hz, which supports the claim that memory

441 distractibility fluctuates rhythmically even when no rhythmic sensory stimulation precedes

442 working memory retention. Note that in addition to a frequency of 2.75 Hz, accuracy in the

443 follow-up experiment was modulated at lower frequencies (< 1 Hz), most likely because

444 distractor onset time linearly modulated task accuracy. Later distractors were more

445 detrimental to accuracy (linear effect of absolute distractor onset time; $\beta = -.062$; $p = 0.001$

446 in a logistic regression of single-trial accuracy).

447 The results of this follow-up experiment constitute an analogy of distractor suppression

448 to what has previously been shown for the attentional sampling of target stimuli (Fiebelkorn

449 et al., 2013; Landau & Fries, 2012): there is an inherent (~2.5-Hz) rhythm that regulates the

450 temporally dynamic suppression of task-irrelevant distraction during working memory

451 maintenance. Relatively slow oscillatory effects in the delta frequency band (< 4 Hz) have

452 also been related to the sequential prioritization in working memory (de Vries, van Driel, &

453 Olivers, 2019). One candidate neural structure where the inherent rhythm that modulates

454 distractibility might originate is the hippocampus, where endogenous delta oscillations

455 have been found to orchestrate synchronized states of working memory activation

456 (Leszczynski, Fell, & Axmacher, 2015). In this sense, the ~2.5-Hz rhythm of distractor

457 suppression might be a temporally dynamic mechanism specific to working memory. That

458 is, during memory retention of target items, suppression of distraction is not a constant

459 process but instead modulated at ~2.5 Hz, which allows for (partial) memory intrusion of

460 currently task-irrelevant stimuli approximately every 400 ms.

461   The fact that the present study found periodic modulation of distractor suppression at a

462 frequency of ~2.5-Hz does not preclude that the rate of distractor suppression might adapt

463 to task demands. For instance, we found rhythmic modulation of neural indices of

464 attentional filtering during stimulus encoding (i.e. target selection and distractor

465 suppression) in previous studies at 0.67 Hz (Wöstmann, Herrmann, Maess, & Obleser, 2016)

466 and 0.375 Hz (Wöstmann, Schmitt, & Obleser, 2020), corresponding to the respective rates

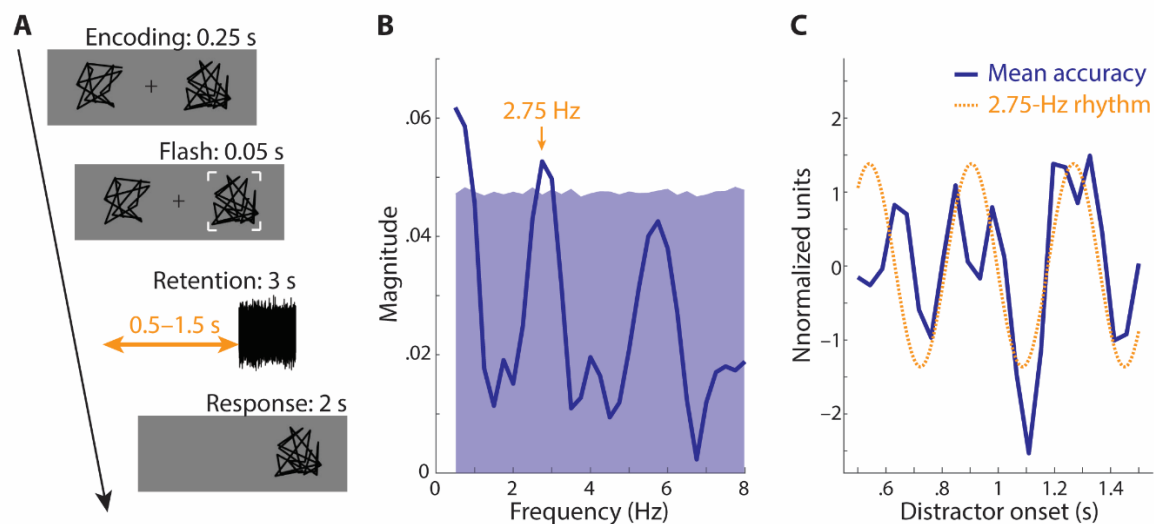467 of stimulus presentation.

468

469

470 **Figure 4. (A)** Design of behavioural follow-up experiment. Participants (N = 6) encoded two line-figures, before
471 one of them was highlighted by a flash event. During the ensuing 3-s memory retention period, an auditory
472 distractor was presented at one of 24 linearly spaced delays between 0.5 and 1.5 s. In the end of a trial,
473 participants had to indicate whether the probe figure matched the one presented on the same side during
474 encoding (response timeout: 2 s). **(B)** Line shows spectral magnitude of periodic modulation of single-trial
475 accuracy by distractor onset. Shaded area shows the 95th percentile of surrogate spectra (derived from 5,000
476 permutations of single-trial distractor onset time within single participants). **(C)** The blue line shows average
477 accuracy (which was temporally smoothed, detrended, and z-transformed for purpose of visualization). The
478 orange line shows the 2.75-Hz rhythm derived from the mixed model to regress accuracy on sine- and cosine-
479 transformed distractor onset time.

480

481 **Limitations.** The concept of rhythmicity implies that the mechanism of interest, e.g.

482 attentional sampling of targets or vulnerability to distraction, is rhythmically modulated

483 over an extended period of time. However, for practical reasons, the present study varied

484 the distractor onset within relatively short time windows of 0.8 s in the main study and 1 s

485 in the follow-up experiment. In fact, short time windows of investigation are a common

486 limitation also for studies exploring the rhythmic attentional sampling of targets (1.3 s in

487 Fiebelkorn et al., 2018; 0.8 s in Fiebelkorn et al., 2013; 1.2 s in Helfrich et al., 2018; 1 s in Landau

488   & Fries, 2012; 0.8 s in Peters et al., 2018). Thus, although the present results suggest memory

489   distractibility to be a rhythmic process, it is at present an open question to what extent this

490   rhythmicity extends over longer time intervals.

491   Furthermore, it must be noted that the present results suggest the effect of rhythmic

492   working memory distraction to be relatively small. In the main experiment, the maximum

493   and minimum of average proportion correct as a function of distractor onset differed only

494   by 0.052 (0.069 in the follow-up experiment). For comparison, the range of average recall

495   accuracy as a function of number position, which is known to be a large effect in the

496   Irrelevant-Speech Task, was 0.518. While we consider it likely that the former effect could be

497   increased in future studies that employ task-irrelevant stimuli of higher distractibility, it must

498   also be considered that the rhythmic modulation of vulnerability to distraction might be a

499   small effect of limited practical significance.

500

501   **Conclusion**. The primary goal the present study was to enhance our understanding of how

502   the human neuro-cognitive system orchestrates the suppression of task-irrelevant

503   distraction dynamically in time. Convergingly, the results of two experiments indicate that

504   during retention of target information in working memory, the suppression of distractors

505   fluctuates at a rate of ~2.5 Hz. Neurally, this effect was in part mediated by the strength of

506   distractor encoding, which occurred in sync with behavioural indices of distraction.

507   The present study sets the stage for future work to test (i) whether the observed rhythmic

508   distractor suppression can be entrained by external stimulation, (ii) whether top-down

509   executive control has the potency to modulate rhythmic distractor suppression to optimise

510   task goals, and (iii) to what degree rhythmic distractor suppression is independent of

511   rhythmic target sampling and how these two interact.

References

512

513   Albouy, P., Weiss, A., Baillet, S., & Zatorre, R. J. (2017). Selective Entrainment of Theta
514   Oscillations in the Dorsal Stream Causally Enhances Auditory Working Memory
515   Performance. *Neuron, 94*(1), 193-206 e195. doi:10.1016/j.neuron.2017.03.015

516   Awh, E., Vogel, E. K., & Oh, S. H. (2006). Interactions between attention and working memory.
517   *Neuroscience, 139*(1), 201-208. doi:10.1016/j.neuroscience.2005.08.023

518   Brainard, D. H. (1997). The Psychophysics Toolbox. *Spat Vis, 10*(4), 433-436.

519   Colle, H. A., & Welsh, A. (1976). Acoustic Masking in Primary Memory. *Journal of Verbal*
520   *Learning and Verbal Behavior, 15*(1), 17-31.

521   de Graaf, T. A., Gross, J., Paterson, G., Rusch, T., Sack, A. T., & Thut, G. (2013). Alpha-band
522   rhythms in visual task performance: phase-locking by rhythmic sensory stimulation.
523   *PLoS One, 8*(3), e60035. doi:10.1371/journal.pone.0060035

524   de Vries, I. E. J., van Driel, J., & Olivers, C. N. L. (2019). Decoding the status of working memory
525   representations in preparation of visual selection. *Neuroimage, 191*, 549-559.
526   doi:10.1016/j.neuroimage.2019.02.069

527   Erb, J., Henry, M. J., Eisner, F., & Obleser, J. (2012). Auditory skills and brain morphology
528   predict individual differences in adaptation to degraded speech. *Neuropsychologia,*
529   *50*(9), 2154-2164. doi:10.1016/j.neuropsychologia.2012.05.013

530   Fiebelkorn, I. C., & Kastner, S. (2019). A Rhythmic Theory of Attention. *Trends Cogn Sci, 23*(2),
531   87-101. doi:10.1016/j.tics.2018.11.009

532   Fiebelkorn, I. C., Pinsk, M. A., & Kastner, S. (2018). A Dynamic Interplay within the
533   Frontoparietal Network Underlies Rhythmic Spatial Attention. *Neuron, 99*(4), 842-853
534   e848. doi:10.1016/j.neuron.2018.07.038

535   Fiebelkorn, I. C., Saalmann, Y. B., & Kastner, S. (2013). Rhythmic sampling within and between
536   objects despite sustained attention at a cued location. *Curr Biol, 23*(24), 2553-2558.
537   doi:10.1016/j.cub.2013.10.063

538   Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression* (3rd Edition ed.): Sage.

539   Gundlach, C., Muller, M. M., Nierhaus, T., Villringer, A., & Sehm, B. (2016). Phasic Modulation
540   of Human Somatosensory Perception by Transcranially Applied Oscillating Currents.
541   *Brain Stimul, 9*(5), 712-719. doi:10.1016/j.brs.2016.04.014

542   Hanslmayr, S., Axmacher, N., & Inman, C. S. (2019). Modulating Human Memory via
543   Entrainment   of   Brain   Oscillations.   *Trends   Neurosci,   42*(7),   485-499.
544   doi:10.1016/j.tins.2019.04.004

Helfrich, R. F., Fiebelkorn, I. C., Szczepanski, S. M., Lin, J. J., Parvizi, J., Knight, R. T., & Kastner, S. (2018). Neural Mechanisms of Sustained Attention Are Rhythmic. *Neuron, 99*(4), 854-865 e855. doi:10.1016/j.neuron.2018.07.032

Helfrich, R. F., Schneider, T. R., Rach, S., Trautmann-Lengsfeld, S. A., Engel, A. K., & Herrmann, C. S. (2014). Entrainment of brain oscillations by transcranial alternating current stimulation. *Curr Biol, 24*(3), 333-339. doi:10.1016/j.cub.2013.12.041

Henry, M. J., & Obleser, J. (2012). Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proc Natl Acad Sci U S A, 109*(49), 20095-20100. doi:10.1073/pnas.1213390109

Henson, R. N. (1998). Short-term memory for serial order: the Start-End Model. *Cogn Psychol, 36*(2), 73-137. doi:10.1006/cogp.1998.0685

Hsieh, L. T., Ekstrom, A. D., & Ranganath, C. (2011). Neural oscillations associated with item and temporal order maintenance in working memory. *J Neurosci, 31*(30), 10803-10810. doi:10.1523/JNEUROSCI.0828-11.2011

Jones, D. M., Macken, W. J., & Murray, A. C. (1993). Disruption of visual short-term memory by changing-state auditory stimuli: the role of segmentation. *Mem Cognit, 21*(3), 318-328.

Jones, D. M., & Morris, N. (1992). Irrelevant speech and serial recall: implications for theories of attention and working memory. *Scand J Psychol, 33*(3), 212-229.

Jones, M. R., Johnston, H. M., & Puente, J. (2006). Effects of auditory pattern structure on anticipatory and reactive attending. *Cogn Psychol, 53*(1), 59-96. doi:10.1016/j.cogpsych.2006.01.003

Kreitewolf, J., Wöstmann, M., Tune, S., Plöchl, M., & Obleser, J. (2019). Working-memory disruption by task-irrelevant talkers depends on degree of talker familiarity. *Atten Percept Psychophys, 81*(4), 1108-1118. doi:10.3758/s13414-019-01727-2

Köster, M., Martens, U., & Gruber, T. (2019). Memory entrainment by visually evoked theta-gamma coupling. *Neuroimage, 188*, 181-187. doi:10.1016/j.neuroimage.2018.12.002

Lakatos, P., Gross, J., & Thut, G. (2019). A New Unifying Account of the Roles of Neuronal Entrainment. *Curr Biol, 29*(18), R890-R905. doi:10.1016/j.cub.2019.07.075

Landau, A. N., & Fries, P. (2012). Attention samples stimuli rhythmically. *Curr Biol, 22*(11), 1000-1004. doi:10.1016/j.cub.2012.03.054

576   Landau, A. N., Schreyer, H. M., van Pelt, S., & Fries, P. (2015). Distributed Attention Is
577   Implemented through Theta-Rhythmic Gamma Modulation. *Curr Biol, 25*(17), 2332-
578   2337. doi:10.1016/j.cub.2015.07.048

579   Large, E. W., & Jones, M. R. (1999). The dynamics of attending: How people track time-varying
580   events. *Psychological Review, 106*, 119-159.

581   Leszczynski, M., Fell, J., & Axmacher, N. (2015). Rhythmic Working Memory Activation in the
582   Human Hippocampus. *Cell Rep, 13*(6), 1272-1282. doi:10.1016/j.celrep.2015.09.081

583   Lim, S. J., Wöstmann, M., & Obleser, J. (2015). Selective Attention to Auditory Memory
584   Neurally Enhances Perceptual Precision. *J Neurosci, 35*(49), 16094-16104.
585   doi:10.1523/JNEUROSCI.2674-15.2015

586   Nobre, A. C., & van Ede, F. (2018). Anticipated moments: temporal structure in attention. *Nat
587   Rev Neurosci, 19*(1), 34-48. doi:10.1038/nrn.2017.141

588   Noonan, M. P., Adamian, N., Pike, A., Printzlau, F., Crittenden, B. M., & Stokes, M. G. (2016).
589   Distinct Mechanisms for Distractor Suppression and Target Facilitation. *J Neurosci,
590   36*(6), 1797-1807. doi:10.1523/JNEUROSCI.2133-15.2016

591   Oberauer, K., & Hein, L. (2012). Attention to Information in Working Memory. *Current
592   Directions in Psychological Science, 21*(3), 164-169. doi:10.1177/0963721412444727

593   Obleser, J., & Kayser, C. (2019). Neural Entrainment and Attentional Selection in the Listening
594   Brain. *Trends Cogn Sci, 23*(11), 913-926. doi:10.1016/j.tics.2019.08.004

595   Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J. M. (2011). FieldTrip: Open source software
596   for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput
597   Intell Neurosci, 2011*, 156869. doi:10.1155/2011/156869

598   Peters, B., Rahm, B., Kaiser, J., & Bledowski, C. (2018). Attention fluctuates rhythmically
599   between objects in working memory. *Journal of Vision, 18*(186).
600   doi:https://doi.org/10.1167/18.10.186

601   Schneider, D., Goddertz, A., Haase, H., Hickey, C., & Wascher, E. (2019). Hemispheric
602   asymmetries in EEG alpha oscillations indicate active inhibition during attentional
603   orienting within working memory. *Behav Brain Res, 359*, 38-46.
604   doi:10.1016/j.bbr.2018.10.020

605   Schneider, D., Mertes, C., & Wascher, E. (2016). The time course of visuo-spatial working
606   memory updating revealed by a retro-cuing paradigm. *Sci Rep, 6*, 21442.
607   doi:10.1038/srep21442

608   Shannon, R. V., Zeng, F. G., Kamath, V., Wygonski, J., & Ekelid, M. (1995). Speech recognition
609   with primarily temporal cues. *Science, 270*(5234), 303-304.

610   Spaak, E., de Lange, F. P., & Jensen, O. (2014). Local entrainment of alpha oscillations by visual
611   stimuli causes cyclic modulation of perception. *J Neurosci, 34*(10), 3536-3544.
612   doi:10.1523/JNEUROSCI.4385-13.2014

613   Tomassini, A., Spinelli, D., Jacono, M., Sandini, G., & Morrone, M. C. (2015). Rhythmic
614   oscillations of visual contrast sensitivity synchronized with action. *J Neurosci, 35*(18),
615   7019-7029. doi:10.1523/JNEUROSCI.4568-14.2015

616   Wöstmann, M., Alavash, M., & Obleser, J. (2019). Alpha oscillations in the human brain
617   implement distractor suppression independent of target selection. *J Neurosci, 39*(49),
618   9797-9805. doi:10.1523/JNEUROSCI.1954-19.2019

619   Wöstmann, M., Herrmann, B., Maess, B., & Obleser, J. (2016). Spatiotemporal dynamics of
620   auditory attention synchronize with speech. *Proc Natl Acad Sci U S A, 113*(14), 3873-
621   3878. doi:10.1073/pnas.1523357113

622   Wöstmann, M., Lim, S. J., & Obleser, J. (2017). The Human Neural Alpha Response to Speech
623   is a Proxy of Attentional Control. *Cereb Cortex, 27*(6), 3307-3317.
624   doi:10.1093/cercor/bhx074

625   Wöstmann, M., & Obleser, J. (2016). Acoustic detail but not predictability of task-irrelevant
626   speech disrupts working memory. *Front Hum Neurosci, 10*(538).
627   doi:10.3389/fnhum.2016.00538

628   Wöstmann, M., Schmitt, L. M., & Obleser, J. (2020). Does Closing the Eyes Enhance Auditory
629   Attention? Eye Closure Increases Attentional Alpha-Power Modulation but Not
630   Listening Performance. *J Cogn Neurosci, 32*(2), 212-225. doi:10.1162/jocn_a_01403

631   Zoefel, B., Davis, M. H., Valente, G., & Riecke, L. (2019). How to test for phasic modulation of
632   neural and behavioural responses. *Neuroimage, 202*, 116175.
633   doi:10.1016/j.neuroimage.2019.116175

634