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1 Category-based attention facilitates memory search

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20 Abstract

21 We often need to decide whether the object we look at is also the object we look for. When we
22 look for one specific object, this process can be facilitated by feature-based attention. However,
23 when we look for many objects at the same time (e.g., the products on our shopping list) such
24 a strategy may no longer be possible, as research has shown that we can actively prepare to
25 detect only one or two objects at a time. Therefore, looking for multiple objects additionally
26 requires long-term memory search, slowing down decision making. Interestingly, however,
27 previous research has shown that distractor objects can be efficiently rejected during memory
28 search when they are from a different category than the items in the memory set. Here, using
29 EEG, we show that this efficiency is supported by top-down attention at the category level. In
30 Experiment 1, human participants (both sexes) performed a memory search task on individually
31 presented objects from different categories, most of which were distractors. We observed
32 category-level attentional modulation of distractor processing from ~150 ms after stimulus
33 onset, expressed both as an evoked response modulation and as an increase in decoding
34 accuracy of same-category distractors. In Experiment 2, memory search was performed on two
35 concurrently presented objects. When both objects were distractors, spatial attention (indexed
36 by the N2pc component) was directed to the object that was of the same category as the objects
37 in the memory set. Together, these results demonstrate how top-down attention can facilitate
38 memory search.

39 *Keywords:* memory search, categorical similarity, top-down modulation, attentional template,
40 object perception

41

42 **Significance statement**

43 When we are in the supermarket, we repeatedly decide whether a product we look at (e.g., a
44 banana) is on our memorized shopping list (e.g., apples, oranges, kiwis). This requires
45 searching our memory, which takes time. However, when the product is of an entirely
46 different category (e.g., dairy instead of fruit), the decision can be made quickly. Here, we
47 used EEG to show that this between-category advantage in memory search tasks is supported
48 by top-down attentional modulation of visual processing: The visual response evoked by
49 distractor objects was modulated by category membership, and spatial attention was quickly
50 directed to the location of within-category (vs. between-category) distractors. These results
51 demonstrate a close link between attention and memory.

52

53 **Introduction**

54 Visual object processing is modulated by top-down goals. For example, the same object
55 evokes a stronger neural response in visual cortex when the object is a target as compared to
56 when it is a distractor (e.g., Chelazzi et al., 1993; Bansal et al., 2014). These modulations have
57 typically been studied in the context of attention, with a top-down attentional set (or
58 “template”) modulating visual processing (Desimone & Duncan, 1995). Such templates can
59 operate at different levels of the visual hierarchy, from simple visual features to high-level
60 object categories (Battistoni et al., 2017).

61 While the mechanisms behind single-target detection have been extensively studied, much
62 less is known about multiple-target detection (Ort & Olivers 2020), even though this task is
63 common in daily life. For example, when we are in the supermarket, we must decide whether
64 the product we look at is one of the (possibly many) products on our memorized shopping list.

65 This task is typically referred to as a memory search task (Sternberg, 1966), as it involves
66 searching memory for the currently fixated item. Indeed, as memory set size (MSS) increases,
67 responses systematically slow down, reflecting the memory search process (Wolfe, 2012).

68 An important difference between single-target and multiple-target detection is that observers
69 can no longer use an attentional template-based strategy when looking for multiple targets.

70 This is because only one or two attentional templates can be activated at a given time
71 (Houtkamp & Roelfsema, 2006; Olivers et al., 2011; Ort & Olivers 2020; van Moorselaar et
72 al., 2014; Wolfe 2021). Accordingly, the attentional template-based modulation of visual
73 object processing, as observed for single-target detection, may be absent for multiple-target
74 detection (i.e., memory search). This is in line with findings from memory research, showing
75 relatively late (~300-500 msec) electroencephalography (EEG) responses over mid-frontal
76 and parietal electrodes reflecting recognition memory (see Rugg & Curran, 2007 for a

77 review), rather than the earlier (150-200 ms) attentional modulation observed in single-target
78 detection tasks (VanRullen & Thorpe, 2001; Kaiser et al., 2016).

79 Interestingly, however, memory search efficiency depends on the categorical relationship
80 between the objects in the memory set and the probe (Cunningham & Wolfe, 2012, 2014;
81 Drew & Wolfe, 2014). If the probe (e.g., a banana) is of the same category as the items in the

82 memory set (e.g., apple, pear, orange), search is inefficient, such that RT increases strongly

83 with increasing MSS. However, when the probe is of a different category (e.g., an animal),

84 search is highly efficient, such that RT increases only weakly with increasing MSS

85 (Cunningham & Wolfe, 2012, 2014; Drew & Wolfe, 2014). Previous work has proposed that

86 the between-category advantage in memory search is mediated by visual selective attention,

87 with between-category distractors rejected as possible targets before entering the memory

88 search stage (Cunningham & Wolfe, 2014). Indeed, participants may have spontaneously used

89 the shared category of the memory items to form a category-level attentional template,

90 thereby obviating the need to search long-term memory (Figure 1A). An alternative

91 explanation is that between-category distractors are rejected efficiently because they are

92 represented distinctly in long-term memory (Figure 1B). Behavioral results alone cannot

93 distinguish between these explanations. However, the category-based attention explanation

94 (Figure 1A) makes specific predictions about the neural time course of processing within- vs

95 between-category distractors, which we tested in the current study.

96 Here, in two experiments, we used EEG to test if, and when, visual object processing is

97 modulated by category similarity in a memory search task. In Experiment 1, we found that the

98 visually evoked N1 ERP component differentiated between distractors that were of the same

99 vs a different category as the memorized items, in line with the selective attention account. In

100 Experiment 2, we used two-object displays to show that this modulation is followed by the

101 allocation of spatial attention towards within-category distractors. Altogether, our results

102 show that the between-category advantage in memory search can be explained by category-
103 level attentional selection.

104

105 **Materials and Methods**

106 ***Participants***

107 *Experiment 1a.*

108 Experiment 1a was run online. Forty-one participants (15 females; mean age, 23.81 years; age
109 range, 20-35 years) were recruited from the online platform Prolific to arrive at a final sample
110 size of 40. Twenty participants (8 females; mean age, 22.95 years; age range, 20-28 years)
111 were assigned to the animate-category group, while 21 participants (7 females; mean age,
112 24.94 years; age range, 20-35 years) were assigned to the inanimate-category group. One
113 participant in this group had to be excluded because of low accuracy (ACC) for set size 16
114 (<65%). All participants signed an online informed consent form and received 6 euro per hour
115 for their participation in the experiment, which was approved by the Ethics Committee of the
116 Faculty of Social Sciences, Radboud University Nijmegen.

117

118 *Experiment 1b.*

119 We employed pwr [R] package to compute the sample size at the significance level of 0.05
120 with Cohen's $d = 0.5$ (corresponding to a medium effect size) and power = 0.8. Thirty-four
121 participants were needed. We included 32 participants (23 females; age range, 18-30 years
122 with $Mean = 22.031$ years and $SD = 3.036$) in Experiment 1b because of the Latin square
123 design (see Experimental Design and Procedure). All participants had normal or corrected-to-
124 normal vision. The participants gave written informed consent and received a gift card of 10
125 euro per hour for their participation. The study was approved by the Ethics Committee of the
126 Faculty of Social Sciences, Radboud University Nijmegen.

127

128 Experiment 2.

129 To arrive at 32 participants, as in Experiment 1b, 35 right-handed participants (11 females;
130 age ranges from 18 to 35 years with *Mean* = 22.51 years and *SD* = 3.61) were recruited. Three
131 participants were excluded due to missing more than 20% of trials after incorrect responses
132 exclusion and artifact rejection. All participants had normal or corrected-to-normal vision.
133 The participants gave written informed consent and received a gift card of 10 euro per hour
134 for their participation. The study was approved by the Ethics Committee of the Faculty of
135 Social Sciences, Radboud University Nijmegen.

136

137 **Stimuli**

138 Experiment 1a.

139 Stimuli consisted of full-color photographs of isolated animals (from Google Images) and
140 inanimate objects (from Brady et al., 2008). Both categories had 30 subcategories (e.g., horse,
141 cat, binoculars, bowl), and each subcategory consisted of 17 exemplar images, for a total of
142 1020 unique images. Stimulus size was 500 × 500 pixels. The experiment was programmed
143 with PsychoPy v2020.2.3 (Peirce et al., 2019) and was hosted on Pavlovia.

144

145 Experiment 1b.

146 The stimuli were the same as in Experiment 1a. The experiment was programmed with
147 PsychoPy v2022.2.4 (Peirce et al., 2019) and ran on a 24-inch monitor (BenQ XL2420Z) with
148 a refresh rate of 120 Hz and a resolution of 1920×1080. Participants were required to keep a
149 distance of approximately 57 cm from the screen, and the stimuli subtended a visual angle of
150 4.9°.

151

152 Experiment 2.

153 The stimuli were a subset of those used in Experiment 1, removing one subcategory of each
154 superordinate category for a total of 986 full-color images of unique isolated objects. Stimuli
155 were presented on a white background with a visual angle of 4°. The experiment was
156 programmed with PsychoPy v2022.2.5 (Peirce et al., 2019) and was presented on a 24-inch
157 monitor (BenQ XL2420Z) with a refresh rate of 120 Hz and a resolution of 1920×1080.

158

159 ***Experimental Design and Procedure***

160 Experiment 1a.

161 The experimental design followed a 2 (animate/inanimate category group; between-subjects)
162 × 2 (within/between category; within-subjects) × 5 (MSS 1/2/4/8/16; within-subjects) mixed
163 factorial design. Category group was manipulated between subjects, such that each participant
164 remembered either animate or inanimate objects in all blocks of the experiment. MSS was
165 blocked, with one block for each MSS, for a total of 5 blocks per participant. Block order was
166 randomized. Each block consisted of the following three phases (Figure 2):

167 (1) In the first phase (memorization), participants memorized the objects belonging to the
168 memory set in that block. Object images were randomly assigned to the memory set, with the
169 constraint that each image in the set came from a different subordinate category (e.g., horse,
170 cat). All images in the memory set were new to the participant. In each trial, a central fixation
171 cross appeared for 800 msec as a prompt, followed by an object presented in the center of the
172 screen on a white background, one at a time, for 3000 msec with an inter-stimulus interval
173 (ISI) of 950 msec. Participants were instructed to memorize the objects without giving a
174 response.

175 (2) In the second phase (memory test), participants again viewed the objects but now had to
176 indicate, with a button press, whether the object belonged to the memory set (press “z”) or not

177 (press “m”). This task was self-paced. Non-target objects were randomly drawn from the same
178 sub-ordinate categories as the target objects (e.g., a different cat). Half of the objects were
179 targets and half were not, presented in random order without repetition. Participants had to be
180 at least 80% correct on two subsequent tests to be able to proceed to the next phase of the
181 experiment. If they did not meet this criterion, they would repeat Phase 1.

182 (3) In the third and main phase (memory search) of each block, participants performed a
183 speeded old/new recognition task, deciding for each object whether or not it was part of the
184 memory set. This phase consisted of 60 trials, presented in random order. Twenty percent of
185 the trials (12 trials) showed an image selected from the memory set, while the remaining 48
186 trials were target-absent trials. Of these target-absent trials, 24 belonged to the animate
187 category and 24 belonged to the inanimate category. Therefore, depending on the category
188 group the participant was assigned to, these could be either within- or between-category
189 distractors (relative to the memory set). In each trial, a central fixation cross appeared for 800
190 msec as a prompt, followed by an object presented in the center of the screen on a white
191 background for 200 msec with an ISI of 1800 msec. Participants had to indicate whether the
192 object belonged to the memory set within 2000 msec. The target images were randomly
193 drawn from the memory set, such that these could repeat within a block. However, all the non-
194 target images were unique across the whole experiment.

195

196 Experiment 1b.

197 **Memory Search.** The memory search design generally followed the design of Experiment 1a
198 with minor adjustments. To simplify the experimental procedure, set size 16 was removed.
199 Furthermore, unlike Experiment 1a, the category (animate or inanimate) was manipulated
200 within participants (i.e., participants memorized the targets from both animate and inanimate
201 categories). As in Experiment 1a, each MSS was designed as a block; there were therefore 8

202 blocks in total in the memory task. A Latin square design was used to order the four MSS
203 blocks, with category order within MSS randomly determined. Unlike Experiment 1a, the
204 fixation cross was always presented except during the stimulus presentation, and the ISI in the
205 memory search phase was jittered between 1800 and 2300 msec. Other procedures were
206 identical to Experiment 1a (Figure 2).

207 **Visual Oddball Task.** A visual oddball task was included to measure visually evoked response
208 patterns to animate and inanimate objects without a memory search task. These data were
209 used to train an animate/inanimate classifier, ensuring that classifier training was done on
210 independent data. In each run, 50 animate and 50 inanimate objects were shown for 200 msec,
211 one by one, with an ISI of 1800-2300 msec, in random order. The 100 objects were randomly
212 selected from the same stimulus pool as used for the memory search task. Objects that were
213 selected for the oddball task were not selected for the memory search task. In addition to the
214 objects, there were ten two-digit numbers that were randomly interspersed. Participants
215 pressed a button when seeing one of these numbers. In total, participants performed the
216 oddball task three times. These runs were preceded and followed by two memory search
217 blocks.

218 **EEG Acquisition and Pre-Processing.** Scalp EEG signals were recorded with a customized
219 64-channel active electrode actiCAP system with 500 Hz sampling rate. AFz served as ground
220 electrode, and TP9 placed on left mastoid as a reference electrode. FT9/FT10 and Fp1/Fp2
221 were reset to left/right and up/down eye movement recorder. Impedance of all the electrodes
222 was kept below 20 k Ω . The EEG data were pre-processed in Python 3.10 using custom code
223 adapted from MNE toolbox (Gramfort, 2013). All the data were bandpass filtered (0.1 and 40
224 Hz) and resampled to 250 Hz. Each trial epoch was segmented from -200 to 800 msec relative
225 to the onset of the object. Only epochs with correct responses were included in further
226 analyses. Then, independent component analysis (ICA) was performed for each subject to

227 remove components of eye movements and blinks. Finally, the ICA-corrected data were re-
228 referenced to the average of all channels, and were baseline corrected by subtracting the mean
229 activity from -200 to 0 msec.

230

231 Experiment 2.

232 As in Experiment 1b, Experiment 2 manipulated category (animate/inanimate) and MSS
233 (1,2,4,8) within subjects, resulting in 8 blocks per participant. Block order was randomized.
234 Each block again consisted of three phases (Figure 3).

235 Unlike Experiment 1b, the third phase now consisted of a memory search task in which
236 participants were presented with a pair of object images. Participants decided, as quickly as
237 possible, whether the image pair included one of the memorized objects. Each block included
238 a total of 120 trials, presented in random order. In target-present trials (50%), the target was
239 presented together with a within- or a between-category distractor (Figure 3). In target-absent
240 trials (50%), three combinations of two distractors (two within-category distractors, two
241 between-category distractors, one within- and one between-category distractors) were
242 presented with equal probability (Figure 3). Category (animate/inanimate) and target location
243 (left/right visual field) were counterbalanced for each combination. At the beginning of each
244 trial, a black fixation cross appeared for 500 msec, followed by one of the five combinations
245 randomly presented for 200 msec, with a jittered inter-trial interval between 1800 and 2200
246 msec, during which participants needed to press up arrow key or down arrow key to indicate
247 whether the image pair contained a target or not. Participants were instructed to blink only
248 after making a response.

249 **EEG Acquisition and Pre-Processing.** The EEG acquisition system and the pre-processing
250 were exactly the same as Experiment 1b. However, trials with correct responses were
251 segmented from -200 to 500 msec relative to the onset of the image pair. Eye movements and

252 other artifacts (e.g., blinks) were removed based on visual inspection (Yeh & Peelen, 2022)
253 rather than using ICA, considering the cortical overlap and functional relationship between
254 saccades and spatial attention shifts (Kowler et al., 1995), which could lead to distortion of the
255 N2pc signal. After that, the clean data were re-referenced to the average of all channels.
256 Baseline correction was from -200 to the stimulus onset. All the pre-processing above was
257 completed in Python 3.11 using the MNE toolbox (Gramfort, 2013).

258

259 ***Statistical Analyses***

260 **Experiment 1a.**

261 All analyses focused on reaction time (RT) to target-absent trials (80% of trials) in the
262 memory search task, for which each image was presented only once. Only correct responses
263 and RTs above 200 msec were included in further analyses. Furthermore, for each participant,
264 RTs beyond 3 standard deviations (SD) from the condition mean were excluded. Under this
265 criterion, a total of 0.260% data points were excluded from further analyses. RT was analyzed
266 in a three-way mixed-design analysis of variance (ANOVA) with one between- (animate-
267 /inanimate-category group) and two within-subjects factors (within-/between-category
268 condition; MSS 1/2/4/8/16). The Greenhouse-Geisser correction was applied to adjust for lack
269 of sphericity (Jennings & Wood, 1976), and only corrected degrees of freedom and *p*-values
270 are reported. Because the three-way interaction was not significant, $F_{(4, 152)} = 1.228, p = 0.277$,
271 $\eta_P^2 = 0.033$, we collapsed the data across animate and inanimate groups in all subsequent
272 analyses. Accuracy was >92% in all conditions. The result pattern of accuracy across
273 conditions were in line with the RT results (data not shown).

274

275 **Experiment 1b.**

276 The exclusion criteria of behavioral data were identical to those of Experiment 1a. In total,
277 1.139% of data points were removed. Only correct responses in target-absent trials were
278 included for both behavioral and EEG analysis. Accuracy was >98% in all conditions and the
279 pattern of accuracy across conditions supported the RT results (data not shown).

280 **ERP Analyses.** The ERP analysis focused on P1, N1, and P2 components over posterior
281 electrodes. We first visually inspected the visually-evoked ERP waveform, both at the group
282 level and for each individual participant. Averaging across participants and conditions, the
283 following twelve posterior electrodes showed a strong visually-evoked ERP consisting of P1,
284 N1, and P2 components: P5/P6, P7/P8, PO3/PO4, PO7/PO8, PO9/PO10, and O1/O2. These
285 components were also visible in each individual participant. The time window for each
286 component was defined based on the peak range among the participants (Robinson et al.,
287 2015). P1 peak was observed between 100 to 160 msec after stimulus onset. N1 and P2 peaks
288 were from 160 to 200 msec and from 200 to 300 msec, respectively.

289 Two-way repeated-measures ANOVA (MSS 1/2/4/8 × within-/between-category conditions)
290 was employed to test for differences in the mean amplitudes of the twelve posterior electrodes
291 across MSS and category conditions, separately for the P1, N1, and P2 components. The
292 Greenhouse-Geisser correction was applied for adjusting for lack of sphericity (Jennings &
293 Wood, 1976), and only corrected degrees of freedom and *p*-value are reported. Then, cluster-
294 based nonparametric permutation tests (Maris & Oostenveld, 2007) were employed to further
295 examine the time courses of the main effects and interaction with 1-ms resolution from 100-
296 300 msec; the range that included the three ERP components.

297 **Decoding analyses.** Based on the pattern across the twelve electrodes, a linear support vector
298 machine (SVM) was employed to conduct cross-task decoding analysis. The visual oddball
299 task data was used to train an animacy decoder, which was used to decode the object
300 categories in the memory search task between 0 and 600 msec, separately for each participant.

301 Temporal resolution was down-sampled to 100 Hz. The area under the receiver-operator-
302 characteristic curve (AUC) was employed to evaluate the performance on classification,
303 which referred to the probability to distinguish positive and negative classes. As classification
304 metric, it is independent from the classifier threshold, and more robust for imbalanced classes
305 than classification accuracy (Treder, 2020).

306

307 Experiment 2.

308 The exclusion criteria for removing trials based on behavioral responses were identical to
309 those of Experiment 1. In total, 1.471% of data points were excluded from further analysis.
310 Accuracy was >91% in all conditions and the pattern of accuracy across conditions supported
311 the RT results (data not shown).

312 **ERP Analyses.** ERP analyses focused on the amplitude of the N2pc component, which was
313 defined by the time window of 200 to 299 msec (Luck & Hillyard, 1994b; Yeh & Peelen,
314 2022) at two electrode sites PO7/8 (Burra & Kerzel, 2013; Eimer & Kiss, 2008; Kiss et al.,
315 2008; Mazza et al., 2007; Stoletniy et al., 2022). For target-present trials, differences in the
316 N2pc (contra-ipsilateral responses) were tested in a two-way repeated-measures ANOVA
317 (MSS 1/2/4/8 × T-Dw/T-Db category). Finally, cluster-based nonparametric permutation test
318 (Maris & Oostenveld, 2007) was adopted to test the time courses of the main effects and
319 interaction with 1-ms resolution from 100-400 msec.

320

321 **Results**

322 Experiment 1a.

323 Experiment 1a was a behavioral study aimed at replicating previous findings of category
324 effects in memory search (e.g., Drew & Wolfe, 2014) but now using a paradigm that would be
325 suitable to use with EEG (Experiment 1b). To avoid differential repetition effects across

326 conditions (Nosofsky, Cao, et al., 2014), we measured behavioral responses to individually
327 presented distractor objects, with distractor objects making up 80% of trials. Each distractor
328 image was only shown once. We asked: 1) whether search efficiency was modulated by the
329 categorical similarity between the distractors and the objects in the memory set, and 2)
330 whether reaction times for distractors under these conditions would follow the typical log-
331 linear relationship with set size (e.g., Drew & Wolfe, 2014; Wolfe, 2012).

332 **Set Size and Category Effects.** A two-way repeated-measures ANOVA with RT as dependent
333 variable and memory set size (MSS; 1/2/4/8/16) and category (within-/between-category
334 conditions) as independent variables revealed significant main effects of MSS, $F_{(3.41, 133)} =$
335 35.521, $p < 0.001$, $\eta_P^2 = 0.477$, and category, $F_{(1, 39)} = 320.039$, $p < 0.001$, $\eta_P^2 = 0.891$.
336 Furthermore, the interaction between MSS and category was significant, $F_{(4, 156)} = 24.230$, $p <$
337 0.001 , $\eta_P^2 = 0.383$. As can be observed in Figure 4A, MSS had a stronger effect (i.e., memory
338 search was less efficient) for within-category than between-category distractors. The simple
339 main effect of set size was significant for both within-, $F_{(4, 156)} = 54.442$, $p < 0.001$, $\eta_P^2 =$
340 0.583, and between-category conditions, $F_{(4, 156)} = 10.873$, $p < 0.001$, $\eta_P^2 = 0.218$.

341 **Linear vs Loglinear models.** The increase with MSS visibly displayed a non-linear increase,
342 in line with previous work (Drew & Wolfe, 2014; Wolfe, 2012). To confirm these results
343 statistically, the RTs from set size 1 to 8 were used to predict the performance on set size 16
344 (Figure 4C), following previous studies (e.g., Drew & Wolfe, 2014). For both category
345 conditions, no significant difference was observed between the observed data and the
346 predicted data based on the log2 model, $t_{(78)} = 1.406$, $p = 0.164$, $d = 0.314$ in within-category
347 condition and $t_{(78)} = 0.898$, $p = 0.372$, $d = 0.201$ in between-category condition. By contrast,
348 the predicted data based on a linear model was significantly higher than the observed data in
349 both within-category condition, $t_{(78)} = 4.997$, $p < 0.001$, $d = 1.117$, and between-category
350 condition, $t_{(78)} = 2.434$, $p = 0.018$, $d = 0.544$.

351 Finally, we fitted the log-linear model to the observed data using all five set sizes. Confirming
352 the category \times MSS interaction observed in the ANOVA, the log-linear slope coefficients for
353 the two category conditions differed significantly, $t_{(39)} = 9.604, p < 0.001, d = 1.519$, with a
354 steeper slope for within- than between-category distractors.

355 **Summary.** In this behavioral experiment, we replicated previous findings of a log-linear
356 increase of RT with MSS (e.g., Drew & Wolfe, 2014; Wolfe, 2012). Interestingly, this was
357 observed for distractor objects, which made up 80% of trials. Furthermore, each of these
358 objects was presented only once, excluding the possibility that the set size effect reflected the
359 influence of differential repetition (e.g., items repeating more often in low than high set size
360 conditions; Nosofsky, Cao, et al., 2014; Nosofsky, Cox, et al., 2014). Most importantly for the
361 present purpose, we found a strong category effect on search efficiency: memory search was
362 much more efficient for distractors that were categorically dissimilar to the items in the
363 memory set than for distractors that were of the same category as the items in the memory set
364 (Cunningham & Wolfe, 2012, 2014; Drew & Wolfe, 2014).

365

366 Experiment 1b.

367 Experiment 1b adopted EEG to test when categorical similarity modulates the processing of
368 the distractor objects. We reasoned that if the between-category advantage is driven by the
369 (proactive) use of categorical attentional templates, this would be observed as a modulation of
370 visual processing (150-200 ms). By contrast, if the between-category advantage is due to a
371 more efficient search in memory (post visual processing), no such early modulation would be
372 observed. Accordingly, we focused our analysis on two visually evoked event-related
373 potential (ERP) components that emerge within the first 200 ms after stimulus onset: P1 and
374 N1. While the P1 is only modulated by spatial attention, the N1 is modulated by feature-based
375 attention (Hopf et al., 2004; Motter, 1994; but see Zhang & Luck, 2009). Similar to feature-

376 based attention, category-based attention was shown to modulate processing from 150-200 ms
377 after stimulus onset (VanRullen & Thorpe, 2001), with better decoding of attended than
378 unattended categories at this latency (Kaiser et al., 2016). Based on these findings, we
379 expected that a category-based attention mechanism during memory search would similarly
380 modulate the N1 component and increase the accuracy of object category decoding at that
381 latency. Finally, the P2 component was also included in our analyses, based on previous
382 studies implicating the P2 in matching perceptual inputs to memory templates (Dunn et al.,
383 1998; Freunberger et al., 2007; Lefebvre et al., 2005; Luck & Hillyard, 1994a).

384 **Behavioral Results.** Figure 4B shows the behavioral results of Experiment 1b. These results
385 replicated the findings of Experiment 1a. There were significant main effects of MSS, $F_{(3, 93)} =$
386 31.591, $p < 0.001$, $\eta_P^2 = 0.505$, and category, $F_{(1, 31)} = 91.205$, $p < 0.001$, $\eta_P^2 = 0.746$. As in
387 Experiment 1a, the interaction between MSS and category was significant, $F_{(2.34, 72.61)} = 6.798$,
388 $p = 0.003$, $\eta_P^2 = 0.180$. Simple effects of MSS were significant in both within-category
389 condition, $F_{(3, 93)} = 42.176$, $p < 0.001$, $\eta_P^2 = 0.576$, and between-category condition, $F_{(3, 93)} =$
390 14.41, $p < 0.001$, $\eta_P^2 = 0.317$. Pairwise comparisons showed significant category effects for
391 all MSSs ($p < 0.001$), except for set size 1 ($p = 0.175$).

392 The linear/log 2 prediction based on set sizes 1 to 4 demonstrated that the log-linear model
393 was a better fit for both within-category and between-category conditions (Figure 4D): Within
394 category: log-linear vs observed: $t_{(62)} = -0.121$, $p = 0.904$, $d = 0.030$, while linear vs observed:
395 $t_{(62)} = 2.116$, $p = 0.019$, $d = 0.529$ (1-tailed; greater); between category: log-linear vs observed:
396 $t_{(62)} = 0.575$, $p = 0.568$, $d = 0.144$ while linear vs observed: $t_{(62)} = 1.798$, $p = 0.039$, $d = 0.449$
397 (1-tailed; greater). The slope coefficients between these two conditions (fitting the model on
398 all set sizes) were also significantly different, $t_{(31)} = 3.488$, $p = 0.001$, $d = 0.617$.

399 **ERP Results.** Separate ANOVAs were run for the three components of interest (P1, N1, P2).
400 There were no significant effects for the P1, MSS effect: $F_{(3, 93)} = 0.629$, $p = 0.598$, $\eta_P^2 =$

401 0.020, category effect: $F_{(1, 31)} = 1.593, p = 0.216, \eta_P^2 = 0.049$, and interaction: $F_{(3, 93)} = 0.034,$
402 $p = 0.992, \eta_P^2 = 0.001$ (Figure 5B). Importantly, confirming our hypothesis, the N1 showed a
403 significant main effect of category, $F_{(1, 31)} = 9.185, p = 0.005, \eta_P^2 = 0.229$ (Figure 5C). The
404 main effect of MSS, $F_{(3, 93)} = 2.272, p = 0.085, \eta_P^2 = 0.068$, and the interaction between
405 category and MSS, $F_{(3, 93)} = 0.285, p = 0.836, \eta_P^2 = 0.009$, were not significant. Finally, the P2
406 showed main effects of MSS, $F_{(3, 93)} = 9.233, p < 0.001, \eta_P^2 = 0.229$, and category, $F_{(1, 31)} =$
407 $18.195, p < 0.001, \eta_P^2 = 0.370$ (Figure 5D). The interaction between category and MSS was
408 not significant, $F_{(3, 93)} = 0.650, p = 0.585, \eta_P^2 = 0.021$.
409 The ERP results were confirmed by a cluster permutation test (Figure 6), showing significant
410 category effects from 152 to 260 msec (cluster-based $p = 0.001$) and significant MSS effects
411 from 188 to 292 msec (cluster-based $p = 0.002$). No interaction effects were found in this
412 analysis.

413 **Decoding Results.** To test whether attention modulated information about object category, we
414 decoded the category of the distractor objects using a classifier trained on data from a separate
415 experiment that did not involve memory search (see Materials and Methods), following the
416 cross-decoding approach of a previous attention study (Kaiser et al., 2016). Decoding
417 accuracy reflects the representational strength of the distractor objects, rather than the
418 amplitude of the evoked responses. Results showed that AUC scores in all eight conditions
419 reached significance (cluster-based $p < 0.05$) from around 130-150 to 400-580 msec (Figure
420 7A, 7B), with the first peak at around 170 msec, in line with previous decoding studies
421 (Carlson et al., 2013; Cichy et al., 2014; Kaiser et al., 2016).

422 Next, we averaged decoding accuracy across the time window of each ERP component and
423 tested these using repeated-measures ANOVAs. In line with the ERP results, no significant
424 effects were observed for the P1 time window ($p > 0.335$, for all tests; Figure 7C).

425 Interestingly, the N1 showed a significant main effect of category, $F_{(1, 31)} = 4.516, p = 0.042,$

426 $\eta_P^2 = 0.127$, with better decoding for within- than between-category distractors (Figure 7D). It
427 should be noted, however, that this analysis was not corrected for multiple comparisons. The
428 main effect of MSS, and the interaction between MSS and category, were not significant ($p >$
429 0.678, for all tests). Finally, no significant effects were observed for the P2 time window ($p >$
430 0.109, for all tests; Figure 7E).

431 **Summary.** The behavioral results of Experiment 1b replicated those of Experiment 1a, again
432 showing that memory search was more efficient for between- than within-category distractors.
433 The ERP results showed that category membership modulated the visually evoked N1
434 component (160-200 ms) as well as the subsequent P2 component (200-300 ms), while set
435 size only modulated the P2 component. The cluster permutation test confirmed these results,
436 showing a relatively early category effect, from 152 to 260 msec, while set size effects
437 emerged from 188 to 292 msec. Finally, the decoding results of the N1 window showed that
438 object category decoding was higher for within-category distractors than between-category
439 distractors. Altogether, these results provide evidence for category-level attentional
440 modulation during a memory search task. Distractor objects matching the category of the
441 memory set received more processing than non-matching distractor objects, demonstrated
442 both by a differential evoked responses (VanRullen & Thorpe, 2001) and more accurate
443 categorical representation (Kaiser et al., 2016) around 160-200 ms after onset.

444

445 Experiment 2.

446 In Experiment 2, we followed up on the findings of Experiment 1b, testing whether category-
447 matching distractors attract spatial attention. Spatial attention shifts were expected to occur
448 later than the category-based modulation of visual processing observed in Experiment 1b,
449 with category-based modulation guiding spatial attention (Battistoni et al., 2020). For
450 example, in a categorical visual search task, category-based modulation of visual object

451 processing (as also observed in Experiment 1b) occurred from 180 ms after image onset
452 (Kaiser et al., 2016) while spatial attention shifts to the target occurred at 240 ms after image
453 onset (Battistoni et al., 2020). By having participants search for targets in two-object displays
454 (Figure 3), here we could measure the allocation of spatial attention using the lateralized N2pc
455 EEG component, occurring 200-300 ms after image onset: previous studies showed that
456 template-matching objects (e.g., targets) during visual search attract spatial attention, eliciting
457 an N2pc (Eimer, 1996; Luck et al., 2000). This target-elicited N2pc is reduced when a target
458 appears together with a distractor that partially matches the template (Nako et al., 2016; Wu et
459 al., 2016; Yeh et al., 2019; Yeh & Peelen, 2022). Therefore, if participants adopted a
460 category-level attentional template in our memory search task, we expected the N2pc to be
461 reduced when a target appeared next to a within-category (“T-Dw”) as compared to a
462 between-category (“T-Db”) distractor. For the same reason, we expected to observe an N2pc
463 in response to a within-category distractor (“Dw”) when shown together with a between-
464 category (“Db”) distractor.

465 **Behavioral Results.** Figure 8A shows the RT results for target-present trials. A two-way
466 repeated-measures ANOVA (MSS; 1/2/4/8 × category; T-Dw/T-Db) showed a main effect of
467 MSS, $F_{(2.03, 62.88)} = 104.097, p < 0.001, \eta_P^2 = 0.771$, a main effect of category, $F_{(1, 31)} = 32.212,$
468 $p < 0.001, \eta_P^2 = 0.510$, and an interaction between MSS and category, $F_{(3, 93)} = 4.568, p <$
469 $0.001, \eta_P^2 = 0.128$. Simple main effects of MSS were also significant within both the T-Dw
470 condition, $F_{(2.23, 69.1)} = 88.3, p < 0.001, \eta_P^2 = 0.576$, and the T-Db condition, $F_{(1.93, 59.9)} = 92.5,$
471 $p < 0.001, \eta_P^2 = 0.749$. Simple main effects of category were observed in MSS 4 and 8, $F_{(1, 31)}$
472 $= 20.4, p < 0.001, \eta_P^2 = 0.397$ and $F_{(1, 31)} = 11.5, p = 0.002, \eta_P^2 = 0.271$, but not in MSS 1 and
473 2, $F_{(1, 31)} = 0.65, p = 0.426, \eta_P^2 = 0.021$ and $F_{(1, 31)} = 1.55, p = 0.222, \eta_P^2 = 0.048$.
474 For target-absent trials (Figure 8B), a two-way repeated-measures ANOVA (MSS 1/2/4/8 ×
475 Dw-Db/Dw-Dw/Db-Db category) showed a main effect of MSS, $F_{(3, 93)} = 99.905, p < 0.001,$

476 $\eta_P^2 = 0.763$, a main effect of category, $F_{(1.61,50.05)} = 88.455$, $p < 0.001$, $\eta_P^2 = 0.740$, and an
477 interaction between set size and category, $F_{(3.7,114.82)} = 12.108$, $p < 0.001$, $\eta_P^2 = 0.281$.
478 Significant main effects of MSS were observed in all three category conditions (Dw-Db: $F_{(3, 93)} = 95.57$, $p < 0.001$, $\eta_P^2 = 0.755$; Dw-Dw: $F_{(3, 93)} = 75.906$, $p < 0.001$, $\eta_P^2 = 0.710$; Db-Db:
480 $F_{(3, 93)} = 34.368$, $p < 0.001$, $\eta_P^2 = 0.526$).

481 **ERP Results.** *N2pc induced by targets.* In a first analysis, we wanted to verify that the targets
482 in our experiment evoked a reliable N2pc. Averaged across conditions, we observed a strong
483 N2pc, with a more negative response contralateral vs ipsilateral to the target from around 200
484 ms after stimulus onset (Figure 9A). Next, we averaged the amplitude of the evoked response
485 in the N2pc time window (200-299 ms after onset) and tested the N2pc effect for each set size
486 (Figure 9B). This analysis revealed a significant N2pc for each set size ($p < 0.005$, for all
487 tests).

488 Having established a reliable target-related N2pc, we then tested how this effect was
489 modulated by MSS and category through a two-way repeated-measures ANOVA with the
490 N2pc as dependent variable (contra-ipsi, averaged across 200-299 ms) and MSS (1/2/4/8) and
491 category (T-Dw/T-Db) as independent variables. Results are shown in Figure 10A. The main
492 effects of MSS and category were significant, MSS: $F_{(3, 93)} = 8.672$, $p < 0.001$, $\eta_P^2 = 0.219$,
493 category: $F_{(1, 31)} = 49.580$, $p < 0.001$, $\eta_P^2 = 0.615$. The interaction between MSS and category
494 was also significant, $F_{(3, 93)} = 4.822$, $p = 0.004$, $\eta_P^2 = 0.135$. Following up on the interaction,
495 we found that the simple main effect of MSS was significant in the T-Dw condition, $F_{(3, 93)} =$
496 11.4 , $p < 0.001$, $\eta_P^2 = 0.268$, but not in the T-Db condition, $F_{(3, 93)} = 1.87$, $p = 0.14$, $\eta_P^2 =$
497 0.057 . Furthermore, the effect of category was significant for MSS 4 and 8, $F_{(1, 31)} = 20.1$, $p <$
498 0.001 , $\eta_P^2 = 0.394$ and $F_{(1, 31)} = 19.1$, $p < 0.001$, $\eta_P^2 = 0.381$, but not for MSS 1 and 2, $F_{(1, 31)} =$
499 0.64 , $p = 0.43$, $\eta_P^2 = 0.02$ and $F_{(1, 31)} = 1.81$, $p = 0.188$, $\eta_P^2 = 0.055$.

500 These results were confirmed by cluster permutation tests (Figures 10B and 10C), which
501 showed significant MSS effects from 220 to 284 msec and 308 to 392 msec (both cluster-
502 based $p = 0.001$) and significant category effects from 168 to 300 msec (cluster-based $p =$
503 0.001). The interaction of the two effects was significant from 264 to 328 msec (cluster-based
504 $p = 0.013$).

505 Together, these results confirm our first hypothesis, that the target-induced N2pc is reduced in
506 the presence of a within-category distractor. Mirroring the behavioral results, this reduction
507 was stronger for larger set size.

508 *N2pc induced by distractors.* Next, we tested our second hypothesis, that of an N2pc induced
509 by within-category (“Dw”) versus between-category (“Db”) distractors. Dw-Dw and Db-Db
510 trials were not included in the analysis because there was, by definition, no lateralized
511 attentional bias in these two conditions. Results confirmed our hypothesis: we observed a
512 significant difference between contra- and ipsi-lateral responses from around 200 ms after
513 stimulus onset (Figure 11A). Averaging responses across the N2pc time window (200 and 299
514 msec) revealed a significant N2pc, $F_{(1, 31)} = 121.917, p < 0.001, \eta_P^2 = 0.797$. The N2pc did not
515 differ significantly across set size, $F_{(3, 93)} = 1.474, p = 0.227, \eta_P^2 = 0.045$ (Figure 11B).

516 **Summary.** The results of Experiment 2 showed that the target-elicited N2pc was reduced
517 when the target was shown next to a same-category distractor. Furthermore, spatial attention
518 (indexed by the N2pc component) was directed towards distractors that matched the category
519 of the memory set. Altogether, these results provide evidence that participants formed a
520 categorical attentional template, with spatial attention being directed to distractor objects
521 belonging to the category of the memory set.

522

523 **Discussion**

524 In three experiments, we investigated the role of attention in memory search. In an online
525 behavioral experiment (Experiment 1a), participants memorized target objects; then, during a
526 memory search phase, they viewed one object at a time and decided whether the object was
527 part of the memorized set of objects. The memory set always consisted of objects from a
528 single category (animate or inanimate objects), while the distractor objects could be from this
529 or another category. Our analyses focused on responses to these distractor objects (80% of
530 trials) as a function of memory set size (1, 2, 4, 8, 16) and category (same or different
531 category as the memory set). Results showed that memory search was much more efficient for
532 between-category than within-category distractors, replicating earlier work (Cunningham &
533 Wolfe, 2012, 2014; Drew & Wolfe, 2014). Using EEG (Experiment 1b), we tested whether
534 this increased efficiency could be explained by attentional modulation at the level of object
535 category. Results confirmed this hypothesis, showing that early visual object processing was
536 modulated by the category membership of the distractor: We found a larger N1 in response to
537 distractors from the target category compared to distractors from a different category.
538 Furthermore, decoding analyses showed that within-category distractors were more strongly
539 represented than between-category distractors at this latency. The results of Experiment 1 are
540 in line with the attentional modulation of visual processing observed in single-target detection
541 tasks (Kaiser et al., 2016; VanRullen & Thorpe, 2001). This modulation is much earlier than
542 the typical time window of memory retrieval, which usually starts after ~300 msec (Curran &
543 Hancock, 2007; Noh et al., 2018; Rugg et al., 1998; Rugg & Curran, 2007). In Experiment 2,
544 we presented two objects simultaneously to test whether spatial attention (indexed by the
545 N2pc component) was guided to the location of template-matching objects (Battistoni et al.,
546 2020; Eimer, 2014; Hopf et al., 2004; Wolfe, 2021). We found that spatial attention was
547 directed towards distractor objects that were of the same category as the items in the memory
548 set. Together, the results provide evidence that participants spontaneously use the shared

549 category of the memory items to form a category-level attentional template. By allocating
550 more attentional resources to the features (N1) and location (N2pc) of the target category, they
551 were able to efficiently reject between-category distractors before commencing search in
552 long-term memory.

553 The behavioral results of all experiments (Figure 4; Figure 8) and the target related
554 N2pc results of Experiment 2 (Figure 10A) revealed that category interacted with memory set
555 size, such that the categorical modulation became stronger with increasing set size. This result
556 can be explained in at least two ways. First, it is possible that participants only started to use
557 an attentional template-based strategy when memory search became effortful (i.e., with high
558 set size). Alternatively, participants may have adopted an attentional template-based strategy
559 for all set sizes, but the specificity of the template varied with the memory set size. For a set
560 size of two, the template may have been specific to the subcategories of the two targets (e.g., a
561 cat and a horse). In that case, distractor objects from other subcategories (e.g., reptile, bird)
562 may not have provided a strong match to the template. Instead, for higher set sizes, a larger
563 number of subcategories made up the memory set. In that case, the features that the
564 subcategories had in common were more likely to generalize to the distractor objects from the
565 same superordinate category (e.g., animals). Future studies could systematically manipulate
566 the similarity of the subcategories within the memory set to distinguish between these
567 accounts.

568 The interaction between set size and category also shows that set size more strongly
569 affected the rejection of within-category than between-category distractors. This suggests that
570 within-category distractors activated a memory search process, while between-category
571 distractors did so only weakly. Of note, the effect of set size was still significant for between-
572 category distractors in all behavioral analyses, suggesting that categorical attention was not
573 fully preventing between-category distractors from entering the memory search process.

574 Interestingly, not all analyses showed an interaction between set size and category.

575 Specifically, the modulation of visual distractor processing in Experiment 1b (Figure 5C; 7D)

576 and the distractor evoked N2pc in Experiment 2 (Figure 11B) only showed a main effect of

577 category. It is possible that the absence of an interaction in these analyses reflected a lack of

578 power (e.g., see the weak trend towards an interaction in Figure 11B). Alternatively, the

579 interaction may reflect a true dissociation between these measures. For example, in

580 Experiment 2, if we assume that the within-category distractor only weakly matched the

581 template when set size was low (e.g., because the template was specific to the subcategories in

582 the memory set) these distractors would not have provided strong competition when shown

583 next to a target, resulting in the category x set size interaction observed for the target-related

584 N2pc. However, when the same within-category distractor is shown next to a between-

585 category distractor, it would still provide a relatively better match to the template than the

586 between-category distractor, and thus attract spatial attention even in the low set size

587 conditions.

588 Our findings raise the question of what features the categorical template consists of, and

589 whether categorical templates are specific to the categories used here. Animate and inanimate

590 objects differ in terms of mid-, and high-level visual features (e.g., Jozwik et al., 2022; Long

591 et al., 2018; Proklova et al., 2016; Thorat et al., 2019) and it has been proposed that the human

592 visual system is particularly sensitive to these category-diagnostic features (New et al., 2007),

593 as also reflected in the animate-inanimate organization of the ventral visual cortex (Chao et

594 al., 1999; Grill-Spector & Weiner, 2014; Kriegeskorte et al., 2008; Thorat et al., 2019). This

595 raises the possibility that categorical attention in memory search, as revealed here, is specific

596 to the distinction between animate and inanimate objects. Future studies will need to test

597 whether our results generalize to other categorical distinctions (e.g., fruit vs non-fruit). We

598 anticipate that results are most likely to generalize to categories that, like animals, are highly
599 familiar and that are characterized by diagnostic visual features (Battistoni et al., 2017).
600 To conclude, our study reveals a crucial role of attention in memory search. When observers
601 look for multiple objects at the same time, they can use the objects' shared categorical
602 features to direct attention at that level, leading to the efficient rejection of distractor objects
603 belonging to other categories (Figure 1A).

604

605

606 **References**

- 607 Bansal, A. K., Madhavan, R., Agam, Y., Golby, A., Madsen, J. R., & Kreiman, G. (2014).
608 Neural Dynamics Underlying Target Detection in the Human Brain. *Journal of
609 Neuroscience*, 34(8), 3042–3055. <https://doi.org/10.1523/JNEUROSCI.3781-13.2014>
- 610 Battistoni, E., Kaiser, D., Hickey, C., & Peelen, M. V. (2020). The time course of spatial
611 attention during naturalistic visual search. *Cortex*, 122, 225–234.
612 <https://doi.org/10.1016/j.cortex.2018.11.018>
- 613 Battistoni, E., Stein, T., & Peelen, M. V. (2017). Preparatory attention in visual cortex:
614 Preparatory attention in visual cortex. *Annals of the New York Academy of Sciences*,
615 1396(1), 92–107. <https://doi.org/10.1111/nyas.13320>
- 616 Brady, T. F., Konkle, T., Alvarez, G. A., & Oliva, A. (2008). Visual long-term memory has a
617 massive storage capacity for object details. *Proceedings of the National Academy of
618 Sciences of the United States of America*, 105(38), 14325–14329.
619 <https://doi.org/10.1073/pnas.0803390105>
- 620 Burra, N., & Kerzel, D. (2013). Attentional capture during visual search is attenuated by
621 target predictability: Evidence from the N2pc, Pd, and topographic segmentation:

- 622 Saliency and target predictability. *Psychophysiology*, 50(5), 422–430.
- 623 <https://doi.org/10.1111/psyp.12019>
- 624 Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal
625 cortex for perceiving and knowing about objects. *Nature neuroscience*, 2(10), 913–
626 919.
- 627 Chelazzi, L., Miller, E. K., Duncan, J., & Desimone, R. (1993). A neural basis for visual
628 search in inferior temporal cortex. *Nature*, 363(6427), 345–347.
629 <https://doi.org/10.1038/363345a0>
- 630 Cunningham, C. A., & Wolfe, J. M. (2012). Lions or tigers or bears: Oh my! Hybrid visual
631 and memory search for categorical targets. *Visual Cognition*, 20(9), 1024–1027.
632 <https://doi.org/10.1080/13506285.2012.726455>
- 633 Cunningham, C. A., & Wolfe, J. M. (2014). The role of object categories in hybrid visual and
634 memory search. *Journal of Experimental Psychology: General*, 143(4), 1585–1599.
635 <https://doi.org/10.1037/a0036313>
- 636 Curran, T., & Hancock, J. (2007). The FN400 indexes familiarity-based recognition of faces.
637 *NeuroImage*, 36(2), 464–471. <https://doi.org/10.1016/j.neuroimage.2006.12.016>
- 638 Desimone, R., & Duncan, J. (1995). Neural Mechanisms of Selective Visual Attention.
639 *Annual Review of Neuroscience*, 18(1), 193–222.
640 <https://doi.org/10.1146/annurev.ne.18.030195.001205>
- 641 Drew, T., & Wolfe, J. M. (2014). Hybrid search in the temporal domain: Evidence for rapid,
642 serial logarithmic search through memory. *Attention, Perception, & Psychophysics*,
643 76(2), 296–303. <https://doi.org/10.3758/s13414-013-0606-y>
- 644 Dunn, B. R., Dunn, D. A., Languis, M., & Andrews, D. (1998). The Relation of ERP
645 Components to Complex Memory Processing. *Brain and Cognition*, 36(3), 355–376.
646 <https://doi.org/10.1006/brcg.1998.0998>

- 647 Eimer, M. (1996). The N2pc component as an indicator of attentional selectivity.
- 648 *Electroencephalography and Clinical Neurophysiology*, 99(3), 225–234.
- 649 [https://doi.org/10.1016/0013-4694\(96\)95711-9](https://doi.org/10.1016/0013-4694(96)95711-9)
- 650 Eimer, M., & Kiss, M. (2008). Involuntary Attentional Capture is Determined by Task Set:
- 651 Evidence from Event-related Brain Potentials. *Journal of Cognitive Neuroscience*,
- 652 20(8), 1423–1433. <https://doi.org/10.1162/jocn.2008.20099>
- 653 Freunberger, R., Klimesch, W., Doppelmayr, M., & Höller, Y. (2007). Visual P2 component
- 654 is related to theta phase-locking. *Neuroscience Letters*, 426(3), 181–186.
- 655 <https://doi.org/10.1016/j.neulet.2007.08.062>
- 656 Gramfort, A. (2013). MEG and EEG data analysis with MNE-Python. *Frontiers in*
- 657 *Neuroscience*, 7. <https://doi.org/10.3389/fnins.2013.00267>
- 658 Grill-Spector, K., & Weiner, K. S. (2014). The functional architecture of the ventral temporal
- 659 cortex and its role in categorization. *Nature Reviews Neuroscience*, 15(8), 536–548.
- 660 Hopf, J.-M., Boelmans, K., Schoenfeld, M. A., Luck, S. J., & Heinze, H.-J. (2004). Attention
- 661 to Features Precedes Attention to Locations in Visual Search: Evidence from
- 662 Electromagnetic Brain Responses in Humans. *The Journal of Neuroscience*, 24(8),
- 663 1822–1832. <https://doi.org/10.1523/JNEUROSCI.3564-03.2004>
- 664 Houtkamp, R., & Roelfsema, P. R. (2006). The effect of items in working memory on the
- 665 deployment of attention and the eyes during visual search. *Journal of Experimental*
- 666 *Psychology: Human Perception and Performance*, 32(2), 423–442.
- 667 <https://doi.org/10.1037/0096-1523.32.2.423>
- 668 Jennings, J., & Wood, C. C. (1976). The epsilon-Adjustment Procedure for Repeated-
- 669 Measures Analyses of Variance. *Psychophysiology*, 13(3), 277–278.
- 670 <https://doi.org/10.1111/j.1469-8986.1976.tb00116.x>

- 671 Jozwik, K. M., Najarro, E., Van Den Bosch, J. J., Charest, I., Cichy, R. M., & Kriegeskorte,
672 N. (2022). Disentangling five dimensions of animacy in human brain and
673 behaviour. *Communications Biology*, 5(1), 1247.
- 674 Kaiser, D., Oosterhof, N. N., & Peelen, M. V. (2016). The Neural Dynamics of Attentional
675 Selection in Natural Scenes. *Journal of Neuroscience*, 36(41), 10522–10528.
676 <https://doi.org/10.1523/JNEUROSCI.1385-16.2016>
- 677 Kiss, M., Van Velzen, J., & Eimer, M. (2008). The N2pc component and its links to attention
678 shifts and spatially selective visual processing. *Psychophysiology*, 45(2), 240–249.
679 <https://doi.org/10.1111/j.1469-8986.2007.00611.x>
- 680 Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the
681 programming of saccades. *Vision Research*, 35(13), 1897–1916.
682 [https://doi.org/10.1016/0042-6989\(94\)00279-U](https://doi.org/10.1016/0042-6989(94)00279-U)
- 683 Kriegeskorte, N., Mur, M., Ruff, D. A., Kiani, R., Bodurka, J., Esteky, H., ... & Bandettini, P.
684 A. (2008). Matching categorical object representations in inferior temporal cortex of
685 man and monkey. *Neuron*, 60(6), 1126-1141.
- 686 Lefebvre, C. D., Marchand, Y., Eskes, G. A., & Connolly, J. F. (2005). Assessment of
687 working memory abilities using an event-related brain potential (ERP)-compatible
688 digit span backward task. *Clinical Neurophysiology*, 116(7), 1665–1680.
689 <https://doi.org/10.1016/j.clinph.2005.03.015>
- 690 Long, B., Yu, C. P., & Konkle, T. (2018). Mid-level visual features underlie the high-level
691 categorical organization of the ventral stream. *Proceedings of the National Academy of
692 Sciences*, 115(38), E9015-E9024.
- 693 Luck, S. J., & Hillyard, S. A. (1994a). Electrophysiological correlates of feature analysis
694 during visual search. *Psychophysiology*, 31(3), 291–308.
695 <https://doi.org/10.1111/j.1469-8986.1994.tb02218.x>

- 696 Luck, S. J., & Hillyard, S. A. (1994b). Spatial filtering during visual search: Evidence from
697 human electrophysiology. *Journal of Experimental Psychology: Human Perception
698 and Performance*, 20(5), 1000–1014. <https://doi.org/10.1037/0096-1523.20.5.1000>
- 699 Luck, S. J., Woodman, G. F., & Vogel, E. K. (2000). Event-related potential studies of
700 attention. *Trends in Cognitive Sciences*, 4(11), 432–440.
701 [https://doi.org/10.1016/S1364-6613\(00\)01545-X](https://doi.org/10.1016/S1364-6613(00)01545-X)
- 702 Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data.
703 *Journal of Neuroscience Methods*, 164(1), 177–190.
704 <https://doi.org/10.1016/j.jneumeth.2007.03.024>
- 705 Mazza, V., Turatto, M., Umiltà, C., & Eimer, M. (2007). Attentional selection and
706 identification of visual objects are reflected by distinct electrophysiological responses.
707 *Experimental Brain Research*, 181(3), 531–536. [https://doi.org/10.1007/s00221-007-1002-4](https://doi.org/10.1007/s00221-007-
708 1002-4)
- 709 Motter, B. (1994). Neural correlates of attentive selection for color or luminance in
710 extrastriate area V4. *The Journal of Neuroscience*, 14(4), 2178–2189.
711 <https://doi.org/10.1523/JNEUROSCI.14-04-02178.1994>
- 712 Nako, R., Grubert, A., & Eimer, M. (2016). Category-based guidance of spatial attention
713 during visual search for feature conjunctions. *Journal of Experimental Psychology:
714 Human Perception and Performance*, 42(10), 1571–1586.
715 <https://doi.org/10.1037/xhp0000244>
- 716 New, J., Cosmides, L., & Tooby, J. (2007). Category-specific attention for animals reflects
717 ancestral priorities, not expertise. *Proceedings of the National Academy of
718 Sciences*, 104(42), 16598–16603.

- 719 Noh, E., Liao, K., Mollison, M. V., Curran, T., & Sa, V. R. de. (2018). Single-Trial EEG
720 Analysis Predicts Memory Retrieval and Reveals Source-Dependent Differences.
721 *Frontiers in Human Neuroscience*, 12, 258. <https://doi.org/10.3389/fnhum.2018.00258>
- 722 Nosofsky, R. M., Cao, R., Cox, G. E., & Shiffrin, R. M. (2014). Familiarity and categorization
723 processes in memory search. *Cognitive Psychology*, 75, 97–129.
724 <https://doi.org/10.1016/j.cogpsych.2014.08.003>
- 725 Nosofsky, R. M., Cox, G. E., Cao, R., & Shiffrin, R. M. (2014). An exemplar-familiarity
726 model predicts short-term and long-term probe recognition across diverse forms of
727 memory search. *Journal of Experimental Psychology: Learning, Memory, and*
728 *Cognition*, 40(6), 1524–1539. <https://doi.org/10.1037/xlm0000015>
- 729 Olivers, C. N. L., Peters, J., Houtkamp, R., & Roelfsema, P. R. (2011). Different states in
730 visual working memory: When it guides attention and when it does not. In *Trends in*
731 *Cognitive Sciences* (Vol. 15). <https://doi.org/10.1016/j.tics.2011.05.004>
- 732 Ort, E., & Olivers, C. N. (2020). The capacity of multiple-target search. *Visual*
733 *Cognition*, 28(5-8), 330-355
- 734 Peirce, J., Gray, J. R., Simpson, S., MacAskill, M., Höchenberger, R., Sogo, H., Kastman, E.,
735 & Lindeløv, J. K. (2019). PsychoPy2: Experiments in behavior made easy. *Behavior*
736 *Research Methods*, 51(1), 195–203. <https://doi.org/10.3758/s13428-018-01193-y>
- 737 Proklova, D., Kaiser, D., & Peelen, M. V. (2016). Disentangling representations of object
738 shape and object category in human visual cortex: The animate–inanimate
739 distinction. *Journal of cognitive neuroscience*, 28(5), 680-692.
- 740 Robinson, A. K., Reinhard, J., & Mattingley, J. B. (2015). Olfaction Modulates Early Neural
741 Responses to Matching Visual Objects. *Journal of Cognitive Neuroscience*, 27(4),
742 832–841. https://doi.org/10.1162/jocn_a_00732

- 743 Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends*
744 in *Cognitive Sciences*, 11(6), 251–257. <https://doi.org/10.1016/j.tics.2007.04.004>
- 745 Rugg, M. D., Mark, R. E., Walla, P., Schloerscheidt, A. M., Birch, C. S., & Allan, K. (1998).
746 Dissociation of the neural correlates of implicit and explicit memory. *Nature*,
747 392(6676), 595–598. <https://doi.org/10.1038/33396>
- 748 Sternberg, S. (1966). High-Speed Scanning in Human Memory. *Science*, 153(3736), 652–654.
749 <https://doi.org/10.1126/science.153.3736.652>
- 750 Stoletniy, A. S., Alekseeva, D. S., Babenko, V. V., Anokhina, P. V., & Yavna, D. V. (2022).
751 The N2pc Component in Studies of Visual Attention. *Neuroscience and Behavioral*
752 *Physiology*, 52(8), 1299–1309. <https://doi.org/10.1007/s11055-023-01359-y>
- 753 Thorat, S., Proklova, D., & Peelen, M. V. (2019). The nature of the animacy organization in
754 human ventral temporal cortex. *Elife*, 8, e47142.
- 755 Treder, M. S. (2020). MVPA-Light: A Classification and Regression Toolbox for Multi-
756 Dimensional Data. *Frontiers in Neuroscience*, 14, 289.
757 <https://doi.org/10.3389/fnins.2020.00289>
- 758 van Moorselaar, D., Theeuwes, J., & Olivers, C. N. L. (2014). In competition for the
759 attentional template: Can multiple items within visual working memory guide
760 attention? *Journal of Experimental Psychology: Human Perception and Performance*,
761 40(4), 1450–1464. <https://doi.org/10.1037/a0036229>
- 762 VanRullen, R., & Thorpe, S. J. (2001). The Time Course of Visual Processing: From Early
763 Perception to Decision-Making. *Journal of Cognitive Neuroscience*, 13(4), 454–461.
764 <https://doi.org/10.1162/08989290152001880>
- 765 Wolfe, J. M. (2012). Saved by a Log: How Do Humans Perform Hybrid Visual and Memory
766 Search? *Psychological Science*, 23(7), 698–703.
767 <https://doi.org/10.1177/0956797612443968>

- 768 Wolfe, J. M. (2021). Guided Search 6.0: An updated model of visual search. *Psychonomic
769 Bulletin & Review*, 28(4), 1060-1092.
- 770 Wu, R., Pruitt, Z., Runkle, M., Scerif, G., & Aslin, R. N. (2016). A neural signature of rapid
771 category-based target selection as a function of intra-item perceptual similarity, despite
772 inter-item dissimilarity. *Attention, Perception, & Psychophysics*, 78(3), 749–760.
773 <https://doi.org/10.3758/s13414-015-1039-6>
- 774 Yeh, L.-C., & Peelen, M. V. (2022). The time course of categorical and perceptual similarity
775 effects in visual search. *Journal of Experimental Psychology: Human Perception and
776 Performance*, 48(10), 1069–1082. <https://doi.org/10.1037/xhp0001034>
- 777 Yeh, L.-C., Yeh, Y.-Y., & Kuo, B.-C. (2019). Spatially Specific Attention Mechanisms Are
778 Sensitive to Competition during Visual Search. *Journal of Cognitive Neuroscience*,
779 31(8), 1248–1259. https://doi.org/10.1162/jocn_a_01418
- 780 Zhang, W., & Luck, S. J. (2009). Feature-based attention modulates feedforward visual
781 processing. *Nature Neuroscience*, 12(1), 24–25. <https://doi.org/10.1038/nn.2223>
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- 783

784 **Figure Legends**

785

786 **Figure 1.** Schematic illustration of two accounts explaining category effects in memory
787 search. The memory set in this example consists of four animals. The current study was aimed
788 at providing evidence for category-level attentional selection in a memory search task, as
789 illustrated in panel A. On this attentional selection account, participants spontaneously attend
790 to the category of the items in the memory set, modulating visual processing and resulting in
791 the quick rejection of between-category distractors, largely avoiding memory search for these
792 items. An alternative account (illustrated in panel B) holds that all objects enter the memory
793 search phase after visual object processing is completed. On this account, faster RTs for
794 between-category than within-category distractors are explained by differences in the
795 efficiency of the memory search process.

796

797 **Figure 2.** Illustration of the three phases in each block of Experiments 1a and b. The example
798 presents an animate block with two targets (i.e., MSS 2).

799

800 **Figure 3.** Illustration of the procedure of Experiment 2. The example presents an animate
801 block with two targets (i.e., MSS 2). For target-present trials, a target shown with a within-
802 category distractor condition was abbreviated as T-Dw, a target with a between-category
803 distractor as T-Db; for target-absent trials, trials showing one distractor of the target (i.e.,
804 within) category together with one distractor of the other (i.e., between) category was
805 abbreviated as Dw-Db, trials where both distractors were within category as Dw-Dw. Finally,
806 trials where both distractors were between category were abbreviated as Db-Db. Our main
807 analyses focused on T-Dw, T-Db, and Dw-Db conditions, as we hypothesized lateralized
808 responses in these conditions.

809

810 **Figure 4.** Mean RT (in sec) and fitted models in Experiment 1a and b. (A) and (B) show the
811 mean RTs in Experiment 1a and b, respectively. (C) and (D) show the fitted models in
812 Experiment 1a and b, respectively. The light grey dots and dark grey crosses refer to the
813 observed data in within-category and between-category conditions. The dashed lines represent
814 linear models, while the solid lines represent log-linear models. For all the figures, the error
815 bars represent the standard error of the mean; the light blue represents within-category
816 conditions while the dark blue represents between-category conditions.

817

818 **Figure 5.** EEG results of Experiment 1b. (A) The mean amplitude based on 12 electrodes
819 (P5/P6, P7/P8, PO3/PO4, PO7/PO8, PO9/PO10, and O1/O2) averaged across all conditions,
820 illustrating the three ERP components of interest. (B), (C), and (D) compare the mean
821 amplitude of the 12 electrodes in the two category and four MSS conditions.

822

823 **Figure 6.** Cluster-based analyses of Experiment 1b. (A) Main effect of category. The light
824 blue solid line represents within-category condition while the dark blue dashed line represents
825 between-category condition. (B) Main effect of MSS. The blue color from dark to light refers
826 to set size 1, 2, 4 and 8, respectively. The grey bars indicate the time windows of significant
827 main effects based on a cluster permutation test.

828

829 **Figure 7.** Cross-task decoding in Experiment 1b. (A) AUC as a function of category
830 condition. The light blue solid line represents within-category condition while the dark blue
831 dashed line represents between-category condition. (B) AUC as a function of MSS. The blue
832 color from dark to light refers to set size 1, 2, 4 and 8, respectively. (C), (D), and (E) compare
833 the mean AUC in the two categories and four MSS conditions, averaged across the time
834 points of each component (P1, N1, P2). The main effect of category was significant for the N1
835 time window (panel D).

836

837 **Figure 8.** Mean RT (in sec) in Experiment 2. (A) RTs in target-present trials. The red bars
838 represent the within-category condition (T-Dw; target shown next to a within-category
839 distractor) while the blue bars represent the between-category condition (T-Db; target shown
840 next to a between-category distractor). (B) RTs in target-absent trials. The grey, yellow, and
841 green bars represent Dw-Db, Dw-Dw, and Db-Db trials.

842

843 **Figure 9.** Main effect of visual field location, showing a target related N2pc. (A) Main effect
844 of contra/ipsi-lateral visual field. (B) Comparison of the contra/ipsi-lateral amplitude averaged
845 across the N2pc time window (200-299 msec).

846

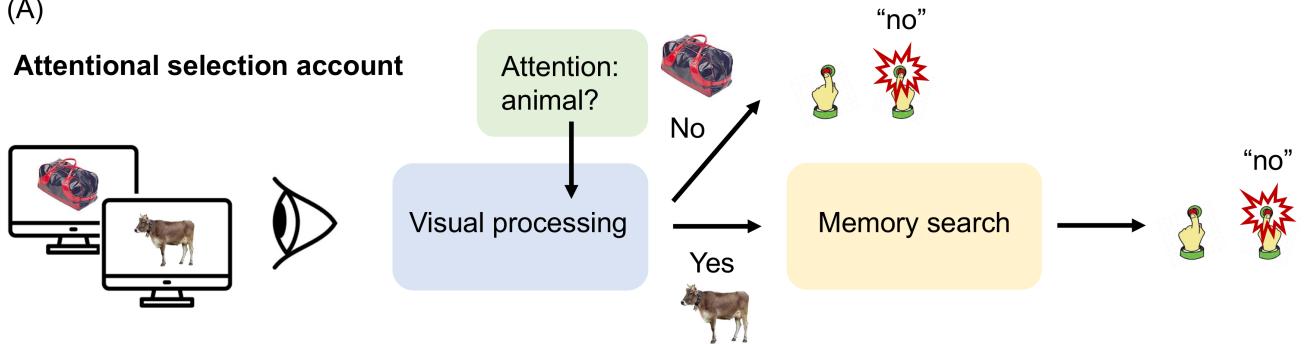
847 **Figure 10.** ERP results of Experiment 2. (A) Comparison of the mean N2pc amplitude in the
848 two categories and four MSS conditions. (B) Main effect of MSS in a cluster analysis. (C)
849 Main effect of category in a cluster analysis. (D) Interaction of MSS and category in a cluster
850 analysis. Different colors from dark to light refer to MSS 1 to 8. T-Dw = a target shown next
851 to a within-category distractor, T-Db = a target shown next to a between-category distractor.

852

853 **Figure 11.** Main effect of visual field location for the Dw-Db condition (target-absent trials).
854 In this analysis, contralateral is relative to the location of the within-category distractor (Dw).
855 (A) Main effect of contra/ipsi-lateral visual field based on a cluster permutation test (cluster-
856 based $p = 0.001$). (B) Comparison of the contra/ipsi-lateral amplitude averaged across the
857 N2pc time window (200-299 msec).

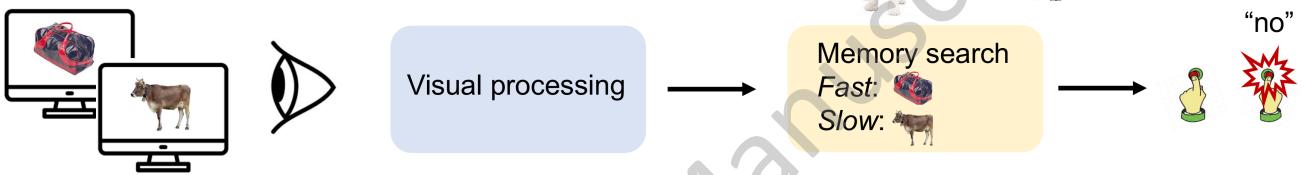
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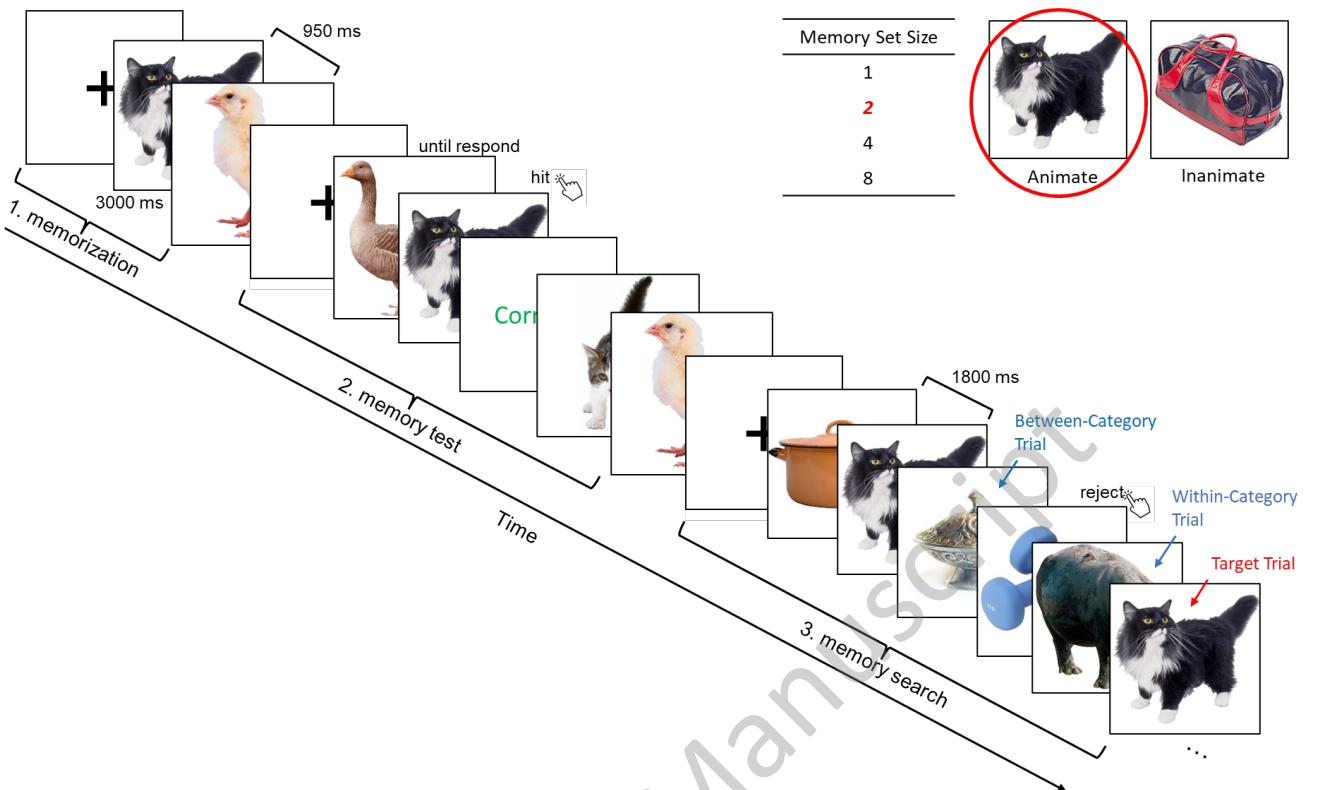
Attentional selection account

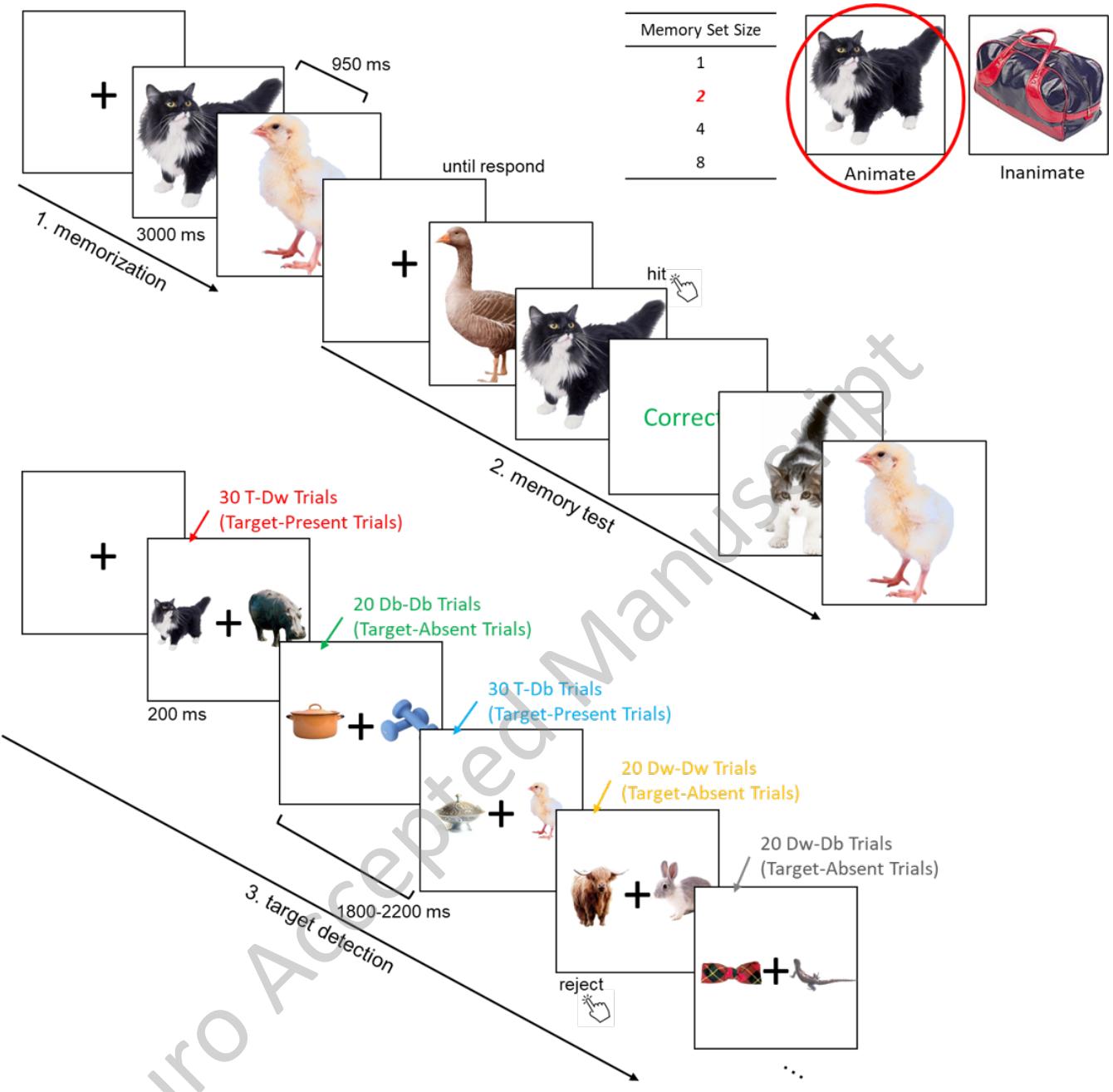


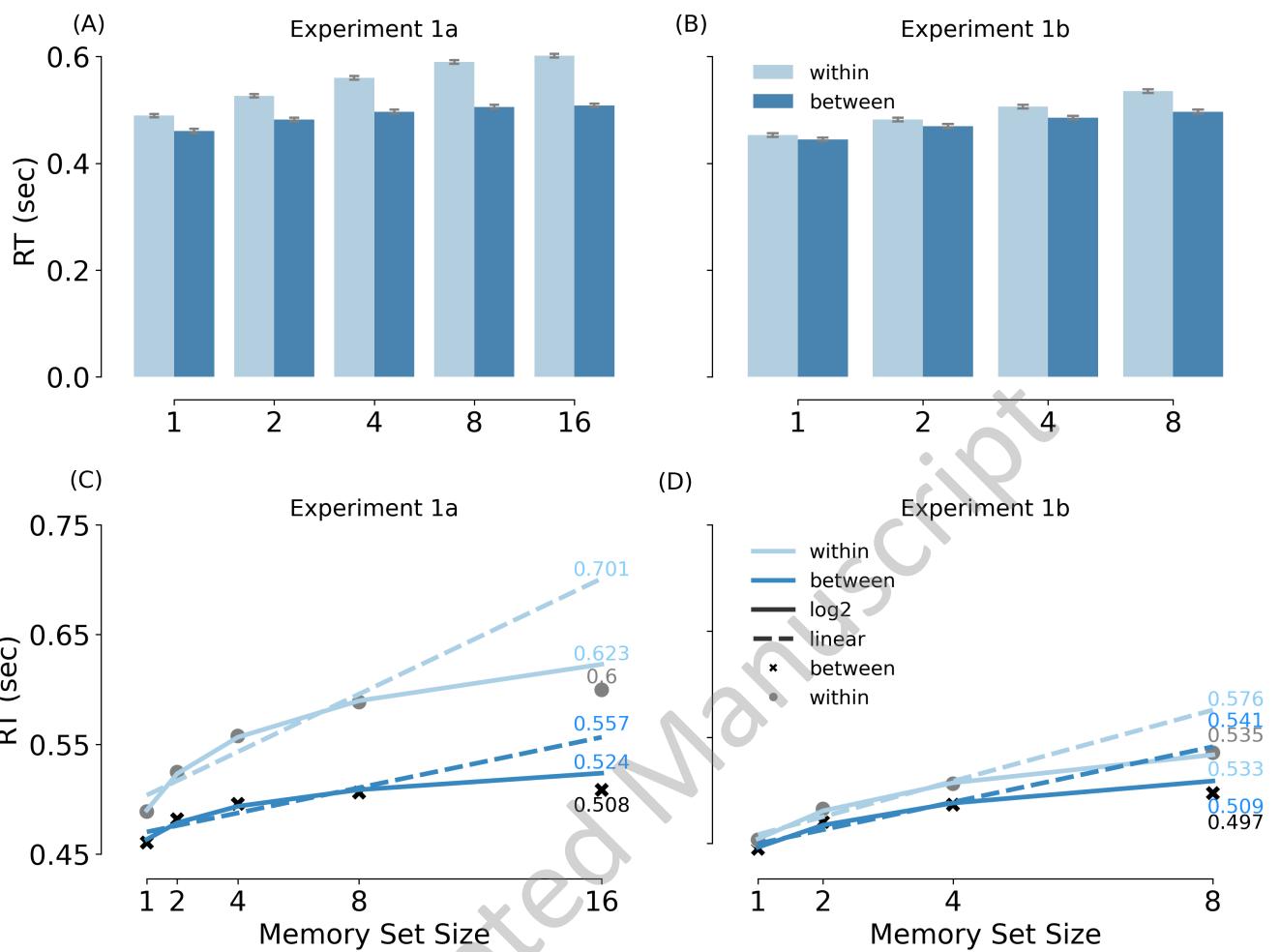
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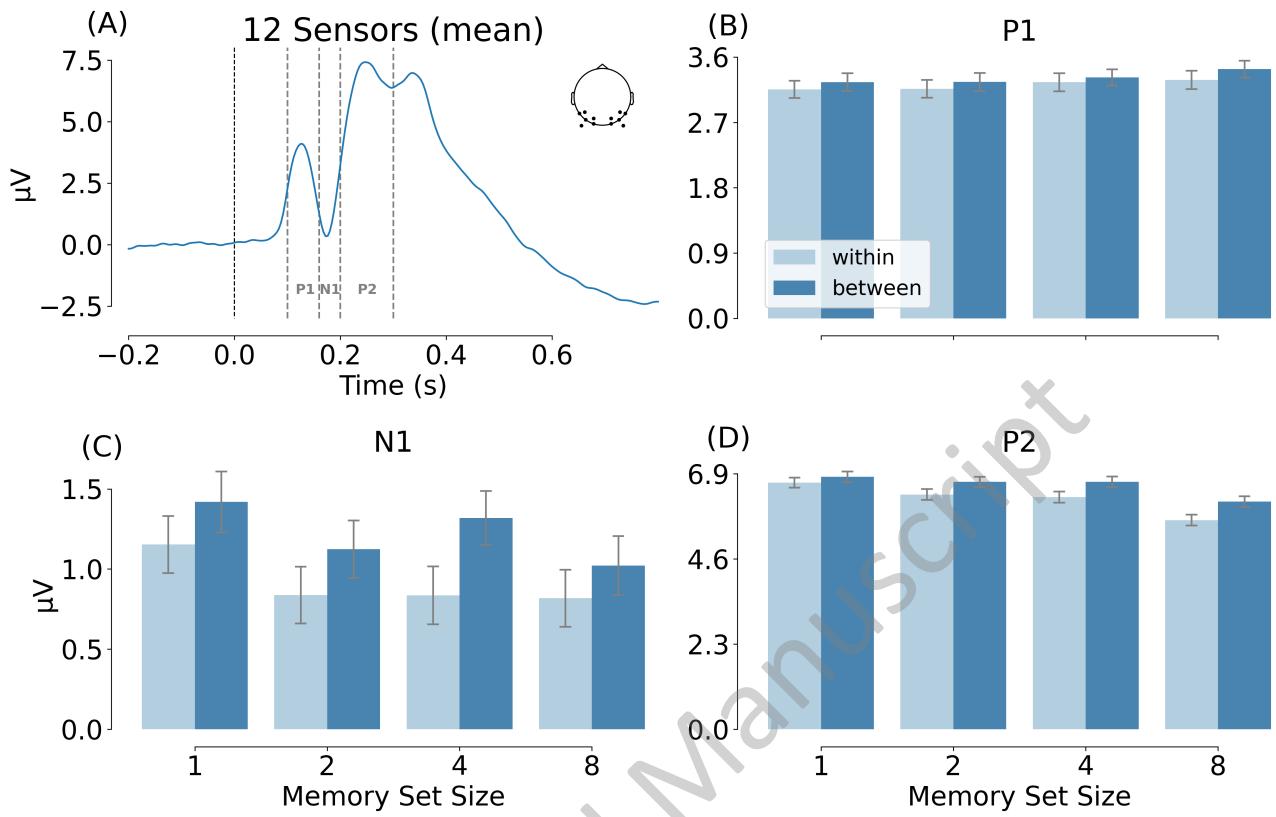
Efficient memory search account

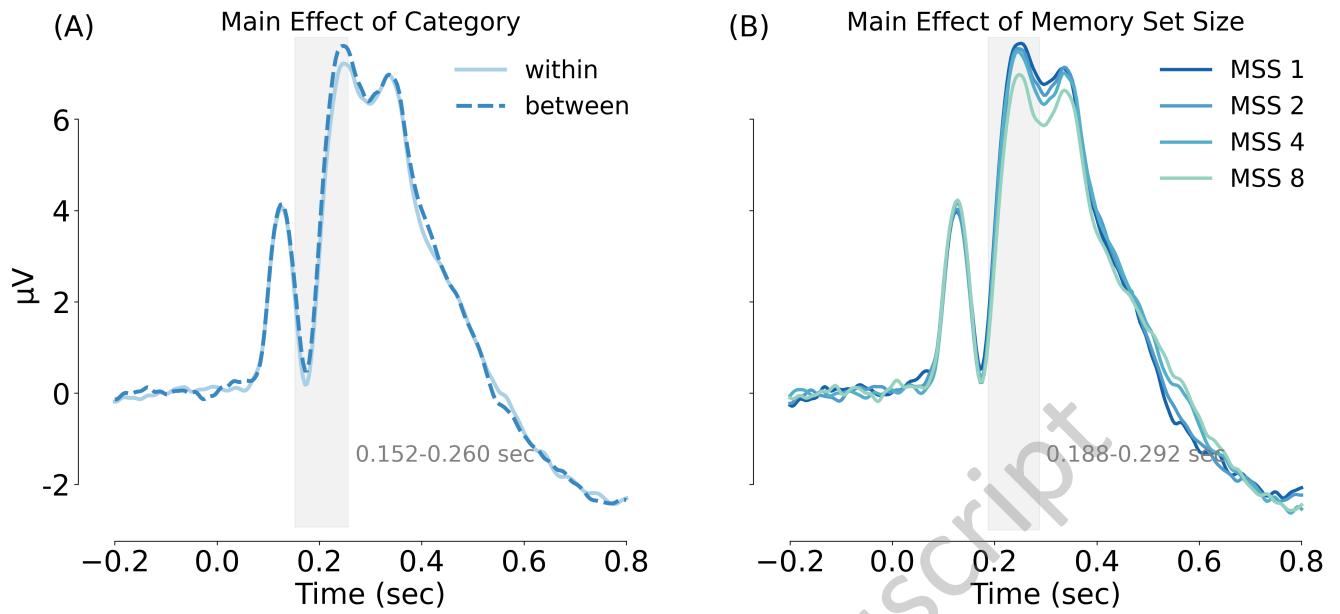


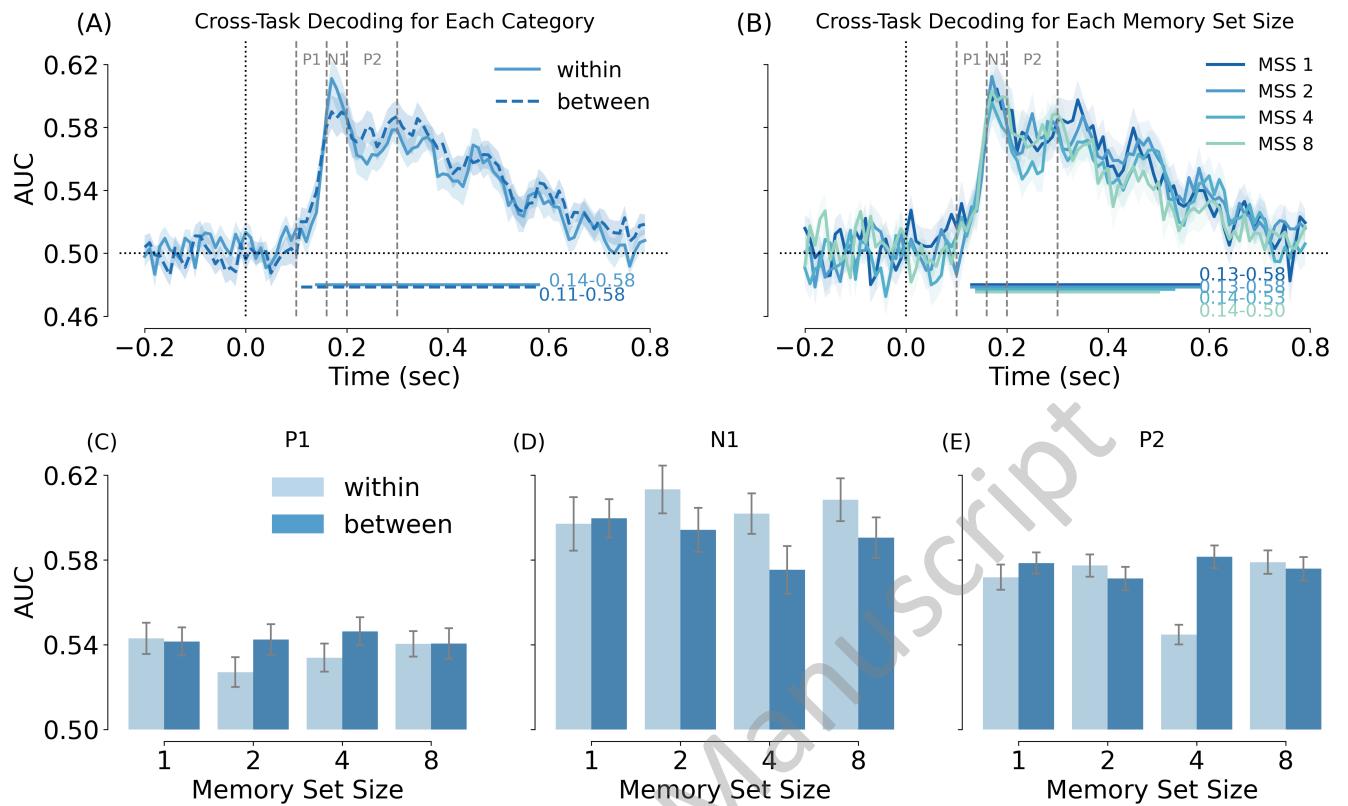


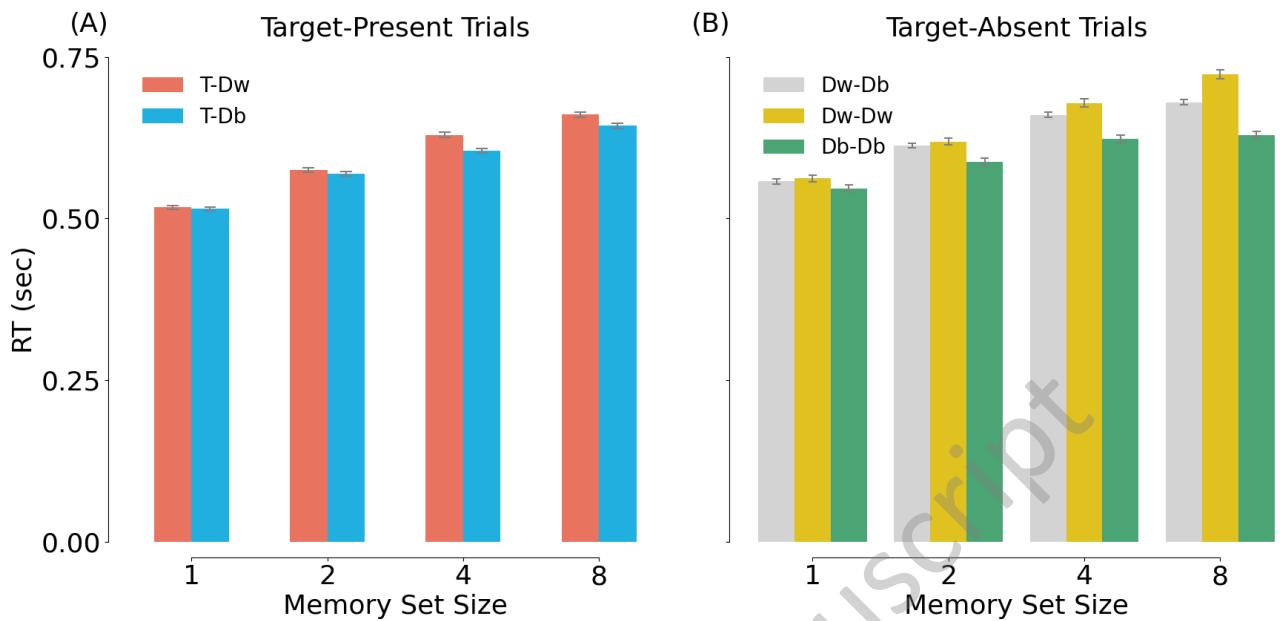




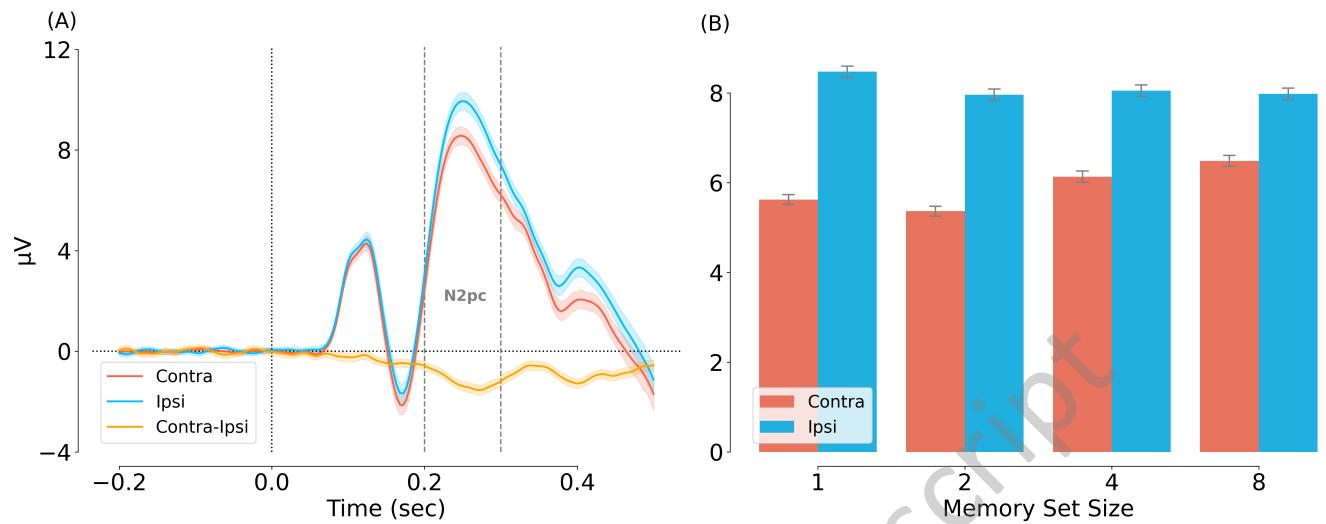


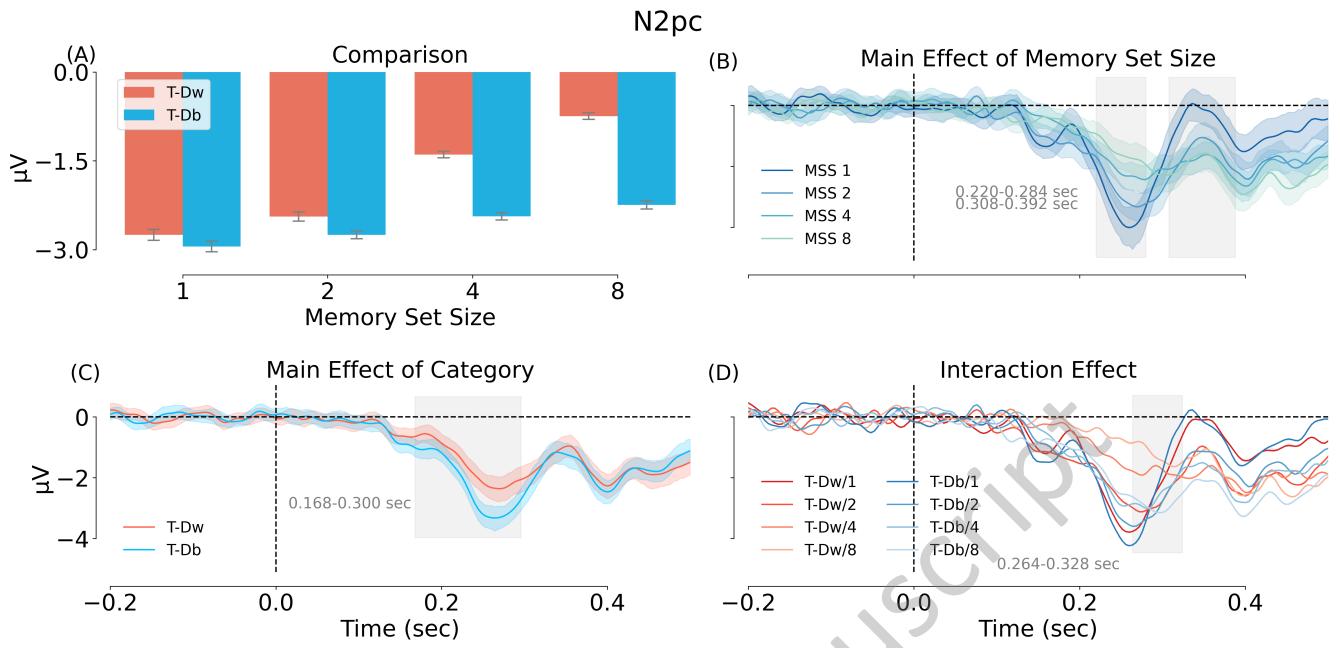






Target-Present Trials





Target-Absent Trials

