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## Hippocampus guides adaptive learning during dynamic social interactions

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1 Hippocampus guides adaptive learning during dynamic social interactions

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3 Running Title: Hippocampus and adaptive social decision-making

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37

38 **Abstract**

39 How do we evaluate whether someone will make a good friend or collaborative peer? A hallmark of  
40 human cognition is the ability to make adaptive decisions based on information garnered from limited  
41 prior experiences. Using an interactive social task measuring adaptive choice (deciding who to re-engage  
42 or avoid) in male and female participants, we find the hippocampus supports value-based social choices  
43 following single shot learning. These adaptive choices elicited a suppression signal in the hippocampus,  
44 revealing sensitivity for the subjective perception of a person and how well they treat you during choice.  
45 The extent to which the hippocampus was suppressed was associated with flexibly interacting with prior  
46 generous individuals and avoiding selfish individuals. Further, we found that hippocampal signals during  
47 decision-making were related to subsequent memory for a person and the offer they made before.  
48 Consistent with the hippocampus leveraging previously executed choices to solidify a reliable neural  
49 signature for future adaptive behavior, we also observed a later hippocampal enhancement. These  
50 findings highlight the hippocampus playing a multifaceted role in socially adaptive learning.

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53 **Significance Statement**

54 Adaptively navigating social interactions requires an integration of prior experiences with information  
55 gleaned from the current environment. While most research has focused on striatal-based feedback  
56 learning, open questions remain regarding the role of hippocampal-based episodic memory systems.  
57 Here, we show that during social decisions based on prior experience, hippocampal suppression signals  
58 were sensitive to adaptive choice, while hippocampal enhancements was related to subsequent  
59 memory for the original social interaction. These findings highlight the hippocampus playing a  
60 multifaceted role in socially adaptive learning.

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67 **Introduction**

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70 Humans expertly navigate through dynamic social worlds despite the sheer amount of  
71 information they are bombarded with. Even though another's motivations are largely hidden to us, we  
72 can make socially adaptive<sup>1</sup> decisions, such as who to cooperate with or trust (FeldmanHall & Shenhav,  
73 2019). Such success requires an efficient integration of prior experiences with information gleaned from  
74 the current environment. Classic models of decision-making suggest that through repeated experience,  
75 humans incrementally fine-tune their behavior using prediction errors (Glascher, Daw, Dayan, &  
76 O'Doherty, 2010; Glascher, Hampton, & O'Doherty, 2009; King-Casas et al., 2008; Montague & Berns,  
77 2002), which enables us to learn who to approach and who to avoid. However, we can also learn and  
78 make adaptive decisions from relatively limited experience. Indeed, a hallmark of human cognition is  
79 that complex concepts can be learned from a single experience (Lake, Salakhutdinov, & Tenenbaum,  
2015).

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A growing body of research shows that individuals routinely make judgements based on limited  
prior experience. Even briefly glancing at a person's face can provide enough information to judge  
whether that person can be trusted (Engell, Haxby, & Todorov, 2007; Mende-Siedlecki, Said, & Todorov,  
2013; Todorov & Mende-Siedlecki, 2013). Thus, even when information is dynamic, multi-dimensional,  
and involves moral qualities, humans are highly adept at encoding relevant information from a single  
brief exposure. Less is known, however, about how people retrieve this information to adaptively decide  
whether to re-engage or avoid a particular individual. Our group showed that intact detailed, episodic  
memories of the prior exchange may be a necessary requirement (Murty, FeldmanHall, Hunter, Phelps,  
& Davachi, 2016; Schaper, Mieth, & Bell, 2019). This suggests that making flexibly adaptive choices from  
limited experience necessitates the recollection of contextual details from the original social encounter.

Despite this behavioral evidence, the neural mechanisms that instantiate socially adaptive single  
shot learning remain unknown. There are two competing theories (Ghiglieri, Sgobio, Costa, Picconi, &  
Calabresi, 2011; Woolley et al., 2013). On the one hand, value-based learning is canonically considered  
to be in the domain of the striatum, for both multi-trial non-social learning (Bornstein & Norman, 2017a;  
Diederer, Spencer, Vestergaard, Fletcher, & Schultz, 2016; Hare, O'Doherty, Camerer, Schultz, & Rangel,  
2008; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003) and social learning (Hackel, Doll, & Amodio,  
2015). On the other hand, the hippocampus, a region known for its central role in long-term episodic  
memory (Davachi, 2006; Eichenbaum, Yonelinas, & Ranganath, 2007) may instead be recruited, which

98 would mirror the functional role of this region in memory retrieval, spatial learning, and cognitive maps  
99 (Kaplan, King, et al., 2017; Kaplan, Schuck, & Doeller, 2017; Nau, Julian, & Doeller, 2018; Omer, Maimon,  
100 Las, & Ulanovsky, 2018; Schapiro, Rogers, Cordova, Turk-Browne, & Botvinick, 2013; Schapiro, Turk-  
101 Browne, Norman, & Botvinick, 2016). Indeed, prior research shows that the hippocampus prioritizes the  
102 encoding of valuable everyday items and the contexts in which they are encountered (Adcock,  
103 Thangavel, Whitfield-Gabrieli, Knutson, & Gabrieli, 2006; Murty & Adcock, 2014; Wittmann et al., 2005).

104 By focusing on the hippocampus and striatum, we can identify the role of these distinct learning  
105 systems during the instantiation of an adaptive social choice informed by a single prior social  
106 interaction. We hypothesized that the hippocampus would play an outsized role in supporting socially  
107 adaptive choices from just one learning episode. We collected fMRI data during a social decision-making  
108 task (Murty et al., 2016), in which participants first played an interactive game where a series of people  
109 either offered fair or unfair monetary splits in a Dictator Game (Figure 1A). After a delay, subjects  
110 indicated which of these people they would prefer to interact with in a subsequent Dictator Game.  
111 Finally, participants completed a surprise memory test to probe whether individuals' episodic memory  
112 for the initial exposure was intact. This design allowed us to test whether such adaptive decisions to re-  
113 engage with fair individuals and avoid unfair individuals recruits a hippocampal-dependent learning  
114 system rather than a striatal-dependent learning system.

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## 117 **Methods**

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119 **Subjects.** We scanned 28 healthy, right-handed participants to yield a sample of at least 20 participants  
120 after removing participants for lack of behavioral variance. Sample size was determined by existing work  
121 using the same paradigm and behavioral analysis pipeline (Murty et al., 2016). Eight participants were  
122 excluded from analyses due to: computer malfunctions during retrieval (N=2); failure to show any  
123 variability in choice behavior (same choice selected throughout the task; N=5); and failure to believe  
124 that they were playing with other real partners during the task (N=1). This led to a final sample of 20  
125 participants (median age = 23, age range = 18-34; 10 female). Participants provided written consent and  
126 the experiment was approved by the New York University Committee on Activities Involving Human  
127 Subjects. All subjects were paid \$25/h and could make up to an additional \$10 based on their decisions  
128 during the task.

129

130 **Stimuli Set.** The stimuli used in the Dictator Game (DG) and subsequent Decision Task, were taken from  
131 pictures of white male faces approximately between the ages of 18-24  
132 (<http://iilab.utep.edu/stimuli.htm>). Each stimulus featured a unique, emotionally neutral face. To  
133 determine if the stimuli were matched in attractiveness, dominance, and trustworthiness, an  
134 independent group (N=30) rated each stimulus on Amazon Mechanical Turk. This task consisted of 179  
135 faces and were rated along the dimensions of “Attractiveness,” “Approachability,” and “Overall Positive  
136 or Negative Feeling”. From this task, we selected 120 faces that were the most neutral of these three  
137 dimensions.

138

139 **Tasks.** As detailed in previous work (Murty et al., 2016), subjects completed four tasks (Fig. 1). While in  
140 the scanner, participants first played as the recipient in a Dictator Game (DG), receiving varied monetary  
141 splits of \$10 from trial-unique Dictators. The Dictator could divide the \$10 however he saw fit and  
142 subjects were required to accept the split. Monetary splits ranged from highly unfair (\$0.10-\$1.50 out of  
143 \$10) to relatively fair (\$3.6-\$5 out of \$10). Following the offer, participants were then asked how they  
144 felt about the split (on a 3-point scale; 1=good to 3=bad). Subjects interacted with 60 unique color  
145 images of Dictators (30 fair offers, 30 unfair offers).

146         After the DG, subjects completed a distractor task, a 6-minute task comprised of easily, solvable  
147 math problems. After this short delay, subjects completed the Decision Task in which they could select a  
148 partner for a subsequent DG. On each trial, a face and a schematic gray face were presented side by side  
149 (Fig 1A). Subjects were tasked with deciding whether they would like to play with that person or a new  
150 person who would be chosen at random (indicated by selecting the schematic gray face). Every trial  
151 contained a trial-unique face such that either the face was previously seen during the first DG, or it was  
152 an entirely novel face. Faces were selected randomly without replacement from the 60 faces presented  
153 during the first DG and 30 never before seen faces. Each trial was presented for 4 seconds, during which  
154 participants could make decisions any time while the face was visible. Once a decision was made,  
155 subjects did not play with the target player or receive additional feedback about that player’s behavior.  
156 Each trial was followed by the presentation of a jittered fixation cross lasting between 2-6 seconds  
157 (average = 4 seconds). Trial order was pseudo-randomized across participants such that no more than 3  
158 trials of the same condition (fair, unfair, novel) would appear in a row.

159         Outside of the scanner, subjects were given a surprise memory test in which we measured item  
160 memory (whether subjects recognized each face) and associative memory (memory for both the face  
161 and how much money the Dictator offered). We only tested memory for faces appearing in the Dictator

162 Phase, not novel faces from the Decision Phase. Each trial consisted of a face either presented during  
163 the initial DG or an entirely new face, alongside a Likert scale of how confident they were that they had  
164 seen the face before during encoding (face memory: 1=high confidence old, 2=low confidence old, 3=  
165 not sure, 4=low confidence new, or 5=high confidence new). To probe episodic memory for the offers  
166 previously made by each player, if subjects responded with a 1-3 for item memory, they had to indicate  
167 the monetary split associated with that person using a 5-point Likert scale (\$0 –\$5, with \$1 increments).  
168 After the experiment, subjects were funnel debriefed in a manner that effectively probes true  
169 believability of the task. Subjects answered on a 6-point Likert scale whether they had any doubt as to  
170 the veracity of the paradigm (1=completely believed, 6=did not believe). This allowed us to exclude  
171 subjects (N=1) who indicated any disbelief that they were playing with real players.

172

173 **fMRI acquisition and preprocessing.** Functional imaging was performed using a Siemens Allegra 3T  
174 head-only scanner located at the Center for Brain Imaging at New York University. Functional data were  
175 collected using an echo-planar (EPI) pulse sequence (36 interleaved slices; TR = 2000ms; TE = 30ms; flip  
176 angle = 78°; FOV 192 mm, voxel size = 3 mm isotropic). Slices were positioned ventrally to provide full  
177 coverage of the anterior temporal lobes and prefrontal cortex; this resulted in omission of the most  
178 dorsal parts of the superior parietal cortex. A high resolution T1-weighted anatomical scan  
179 (magnetization-prepared rapid-acquisition gradient echo sequence, 1 mm isotropic) was also obtained  
180 for each subject after the Decision Task.

181 Functional MRI data were preprocessed using a pipeline designed to minimize the effects of  
182 head motion (Hallquist, Hwang, & Luna, 2013). This included simultaneous 4d slice-timing and head  
183 motion correction, skull stripping, intensity thresholding, co-registration to the MPRAGE, nonlinear  
184 warping to MNI space, spatial smoothing with a 6mm FWHM kernel, nuisance regression based on head  
185 motion (translation/rotation and their first derivative) and non-gray matter signal, and high-pass  
186 filtering (100s). To account for magnetic equilibrium, the first four volumes of the functional scan were  
187 discarded.

188

189 Experimental Design and Statistical Analyses

190

191 **Behavioral analysis.** We first tested whether players showed subjective responses that were congruent  
192 with the Dictator's offer during the DG. For each participant, we ran a regression with individual self-  
193 reported feelings of the offer as the dependent variable and offer value as the independent variable. To

194 test for significance, we submitted r-to-z transformed scores to one-sample t-tests. Next, we tested  
195 whether individuals were more likely to approach Dictators that offered them more or less money  
196 during the DG. For each participant, we ran a Generalized Linear Model (GLM), as implemented by  
197 MATLAB's 'glmfit' function with participants' choice behavior during the Decision Task as the dependent  
198 variable, and offer amounts as the independent variable. To investigate the influence of different types  
199 of memory on choice behavior during the Decision task, we ran an analysis of variance (ANOVA) where  
200 the dependent variable was choice, and within-subject predictors were value outcome and memory  
201 (Face and Offer memory). Outcome was split into binary categories of high/fair (\$3.6-\$5.00) offers and  
202 low/unfair offers (\$0.10-\$1.50) offers. We note that in social situations low values are often yoked to  
203 unfair offers (e.g., \$.10 out of \$10) and high values to fair offers, such that it is difficult to dissociate high  
204 reward from fair or equitable outcomes. Memory was split into three categories: no memory, face  
205 memory, face+offer memory. Evidence of a significant ANOVA effect was followed by post-hoc t-tests to  
206 specify the nature of the interaction. Trials in which participants had the opportunity of selecting the  
207 novel face stimuli were not included in these behavioral analyses.

208

209 **fMRI first-level and group analysis.** Imaging analysis focused on the data from the Decision Task. Data  
210 was modeled using three regressors of interest: Adaptive choice, Maladaptive choice, and Novel choice.  
211 The adaptive choice regressor modeled trials in which participants either decided to re-engage with  
212 players who made fair offers or avoid engaging with players who made unfair offers in the DG. The  
213 maladaptive choice regressor modeled trials in which participants either decided to re-engage players  
214 who made unfair offers or avoid engaging with players who made fair offers in the DG. The novel choice  
215 regressor modeled all trials in which participants made choices about novel players either by selecting to  
216 play or avoid them.

217         Given that prior research regarding the nature of the hemodynamic response function in the  
218 hippocampus does not always follow a canonical shape during memory retrieval, we opted to estimate  
219 voxel-specific responses for each condition. This was performed by implementing the 3dDeconvolve  
220 function as implemented in AFNI, modeling each regressor over a 20 TR time period using 10 parameter  
221 sine series expansion. In addition to our regressors of interest described above, each individual's first-  
222 level model also included a 7<sup>th</sup> order Legendre polynomial basis set to account for low-frequency drifts  
223 in the data. Preliminary analyses using a traditional temporal window of 13 TRs revealed that responses  
224 in the hippocampus failed to reach baseline at 26s, despite other regional responses—for example in the  
225 visual cortex—reaching baseline in the same time frame. Thus, to fully characterize the hemodynamic



226 response in the hippocampus and provide a more complete and accurate representation of our data, we  
227 used an extended time period of 20 TRs.

228 We additionally performed a separate GLM to look at whether responses during the Decision  
229 Task represent individual performance during a later memory test. We implemented three regressors of  
230 interest representing (1) trials in which participants subsequently had memory for the Dictator and the  
231 offer made, (2) trials in which participants either had memory only for the Dictator but not the offer, or,  
232 no memory at all, and (3) trials in which decisions were made about Novel players. The same modelling  
233 procedures and inclusion of nuisance regressors were used as detailed in the GLM described above. We  
234 should note that for this analysis we were somewhat under-powered, as the mean number of trials in  
235 which participants had memory for the Dictator and their offer was 7.7 with a range of 1 to 19 trials.

236 Group-level analyses were conducted using a multi-level model implemented in AFNI's 3dMVM  
237 with each individual's voxel-specific HRF as an input, which tested for interactions between condition  
238 (i.e., Adaptive, Maladaptive) and time (i.e., each TR). We used 3dClustSim to identify significant clusters  
239 with the option to simulate noise using the spatial auto-correlation function given by a mixed model run  
240 on noise estimates on 1<sup>st</sup> level data. Height extant thresholds were set at a height level of  $p < 0.001$  and a  
241 corrected alpha level of  $p = 0.01$  (two-tailed; using third-nearest neighbor clustering). We first estimated  
242 significance within a regions-of-interest mask, which included bilateral hippocampus (defined in the  
243 Automated Anatomical Labeling Atlas), as well as the regions within the striatum known to participate in  
244 affective and cognitive processes (defined by the Oxford-GSK-Imanova structural striatal atlas). This  
245 yielded a cluster of 7 voxels, thus any clusters consisting of 7 or more voxels within our ROIs were  
246 deemed significant. Notably, the definitions of the striatum include the entire ventral striatum and  
247 anterior and middle portions of the caudate. Additionally, we ran a whole-brain analysis which yielded a  
248 minimum cluster of 21 voxels.

249 Investigating differences in brain activation using a TR\*condition interaction with a multi-level  
250 model cannot specify the direction of the effect. To characterize the direction of this interaction, post-  
251 hoc analyses were run to unpack the nature of the clusters showing significant interactions at or above  
252 threshold within our region-of-interest. First, we plotted the entire estimated hemodynamic response  
253 function for the adaptive and maladaptive regressors, and identified time-points where there were  
254 significant differences by running a t-test on each individual TR. These post-hoc tests were corrected for  
255 multiple-comparisons using a False-Discovery Rate reported at  $q < 0.1$ .

256 To further unpack the behavioral relevance of these differences while controlling for multiple  
257 comparisons, we isolated TRs that revealed peak differences between adaptive and maladaptive trials in

258 both the positive (Adaptive > Maladaptive) and negative (Maladaptive > Adaptive) directions. We then  
259 independently compared activation at these TRs against the Novel hemodynamic response to gain  
260 better traction of the hippocampal signal. Critically, novel stimuli were not included in the original  
261 analysis when identifying the significant clusters and could thus serve as independent comparison  
262 stimuli to decipher the nature of the interactions (i.e., these t-tests are statistically independent from  
263 prior analyses). Finally, we computed a neural difference score of adaptive versus maladaptive from  
264 these two time points in an across-subject analyses in order to measure the effect on adaptive choice  
265 behavior (i.e., an independent statistical analysis).

266

## 267 **RESULTS**

268

### 269 ***Behavioral Findings***

270         Confirming that participants were sensitive to the offers made by Dictators, a linear regression  
271 revealed that subjects reported feeling more positive about fair versus unfair offers from Dictators in  
272 the DG ( $\beta=0.83(.01)$ ;  $t=24.63$ ;  $p<0.001$ ). During the Decision Phase, there were no significant differences  
273 in reaction time (RT) when individuals were making decisions in response to a Fair Dictator (mean(se) =  
274  $1.71(0.12)$ ), Unfair Dictator (mean(se)= $1.70(1.11)$ ), or Novel Dictator (mean(se)= $1.73(0.11)$ ;  $P_s>.40$ ). A  
275 linear regression revealed, however, that participants were more likely to re-engage with Dictators that  
276 gave them fair versus unfair offers during the previous DG ( $\beta=.24(.08)$ ;  $t=3.17$ ;  $p=0.005$ ), indicating that,  
277 on the whole, subjects were making decisions that were adaptive and likely to benefit them in the  
278 future. Participants also made these adaptive decisions more slowly (i.e., selecting Fair Dictators,  
279 avoiding Unfair Dictators;  $1.85(.10)$ ) than maladaptive decisions (i.e., select Unfair Dictators, avoid Fair  
280 Dictators;  $1.78(0.10)$ :  $t(19)=3.84$ ,  $p<0.001$ )—which dovetails with recent work revealing that the  
281 hippocampus is involved in deliberating over valued options (Bakkour et al., 2019). Table 1 provides  
282 descriptive statistics of our item memory test. While there was significant item memory for faces  
283 encountered during the original dictator game ( $p<0.001$ ), there were no significant differences in item  
284 memory across Fair and Unfair (Fair: mean(se)= $0.63(.04)$ ; Unfair: mean(se)= $0.62(.04)$ ;  $t(19)=0.78$ ,  
285  $p=0.44$ ). For associative memory, there was evidence of significantly greater associative memory for  
286 Unfair versus Fair Dictators (Fair: mean(se)= $0.10(.02)$ ; Unfair: mean(se)= $0.33(.03)$ ;  $t(19)=5.43$ ,  $p<0.001$ ).

287

288         An ANOVA testing for interactions between memory and choice revealed that adaptive choices  
289 were dependent on an individual's memory of their prior experience with each Dictator ( $p<0.001$ ; Fig.  
289 1B, Table 2). Post-hoc t-tests revealed that subjects did not show any differences in their tendency to  
290 approach fair and unfair Dictators when they did not have memory for the Dictator (no memory;  $t(19)=$

291 0.14;p=0.99) or when they only had memory for the Dictator but not how much the Dictator offered  
292 (face memory;  $t(19)=0.58;p=0.57$ ). However, when individuals had intact memory for the Dictator and  
293 how much they previously offered, they decided to re-engage with fair players far more often than  
294 unfair players (face+offer memory;  $t(19)=4.05; p=0.001$ ). This finding was driven by exhibiting stronger  
295 associative memories for unfair (lower) offers compared to fair (higher) offers ( $t(19)=-5.13, p<0.001$ ).

296

297

### 298 ***Neuroimaging Results***

299

300 We first identified regions showing significant differences when individuals made adaptive  
301 versus maladaptive choices when encountering dictators. Significant differences were found in the right  
302 hippocampus ( $p<0.01$ , small-volume corrected;  $[X,Y,Z] = [33, -30, -9]$ ,  $k=16$ , Fig. 2A) as well as a network  
303 of regions including the middle frontal gyrus, insula and fusiform gyrus ( $p<0.01$ , whole-brain corrected).  
304 Full time-courses for regions showing significant differences outside of the hippocampus are depicted in  
305 Figure 3. Critically, we observed no significant activations within our striatal ROI using the same time-  
306 course analysis that identified the hippocampal cluster—even when using a very liberal threshold of  
307  $p<0.01$  uncorrected. Similarly, no clusters were identified using a canonical HRF (i.e., a double gamma  
308 HRF) at a liberal threshold of  $p<0.01$ .

309 Post-hoc analyses of the right hippocampus cluster revealed a complex time course in which  
310 there were three discrete phases comprised of six TRs (time course series broken into three phases of  
311 equal TR length: Fig 2B). In the early phase (TR0-5), hippocampal activation did not differ across  
312 conditions. During the middle phase (TR6-11), hippocampal activation for adaptive choice was  
313 suppressed compared to maladaptive choices (i.e., adaptive suppression). During the late phase (TR12-  
314 17), hippocampal activation for adaptive choice was enhanced compared to maladaptive choices (i.e.,  
315 hippocampal enhancement during adaptive choice). These findings suggest that there are two putative  
316 neural signals—a hippocampal suppression (maladaptive>adaptive) followed by a hippocampal  
317 enhancement (adaptive>maladaptive)—that support adaptive choice. Notably, the suppression signals  
318 were unique to the hippocampus and were not apparent in any regions identified in the comparison of  
319 adaptive versus maladaptive trials (Figure 3). Notably, post-hoc analysis did not reveal any differences in  
320 the hippocampus as a function of the condition (fair, unfair) on the concurrent or previous trial,  
321 suggesting that our late signals were not a function of the content of the subsequent trial.

322 To gain more traction on the nature of these adaptive suppression and enhancement signals  
323 evoked in the hippocampus, we conducted additional post-hoc analyses on TRs showing peak

324 hippocampal suppression for adaptive choices (i.e., TR = 10, maladaptive > adaptive Fig. 2B) and peak  
325 hippocampal enhancement for adaptive choices (i.e., TR = 12, adaptive > maladaptive, Fig. 2B). We first  
326 tested whether these adaptive suppression and enhancement signals predicted individual differences in  
327 adaptive decision-making. Adaptive choice was defined as the beta-value in a regression between  
328 participants' propensity to approach players depending on how fair or unfair their offers were during  
329 the Dictator Game. We found that attenuated hippocampal BOLD response during the middle  
330 suppression phase correlated with a greater likelihood of making adaptive choices (TR=10;  $r(19)=-0.51$ ,  
331  $p=0.02$ , Fig. 3, Left Panel). There was no significant relationship between the later hippocampal  
332 enhancements and adaptive choice (TR=12,  $r(19)=-0.19$ ,  $p=0.61$ , Fig 4A, Right Panel). However, the  
333 direct comparison between suppression and enhancement phases was not significant ( $P>.2$ ). A similar  
334 coupling between hippocampal responses and adaptive behavior was observed at other timepoints as  
335 well, revealing a significant enhancement and suppression signal in the hippocampus (Table 3).

336 To test whether the adaptive suppression and enhancement signals showed properties  
337 reflecting more general memory retrieval, we compared these responses to when participants  
338 responded to novel players they had never seen before (i.e., Novel choice), which allowed us to uniquely  
339 identify signals specifically linked to memory (previously encountered players) versus encoding for  
340 future adaptive choice (novel players). During the adaptive enhancement phase, there was a significant  
341 increase in hippocampal activation during adaptive choice compared to novel choice (TR=12; estimated  
342 timeseries of the HRF:  $t(19)=3.71$ ,  $p=0.002$ , Figure 5a), and no differences comparing maladaptive choice  
343 and novel choice ( $t(19)=-1.14$ ,  $p=0.27$ ), suggesting that memory-like responses only emerged when  
344 individuals made adaptive choices. In contrast, during the adaptive suppression phase, there were no  
345 significant systematic differences in hippocampal activation during either adaptive or maladaptive  
346 choice compared to novel choice (TR=10,  $P>0.15$ ). A similar trending pattern between hippocampal  
347 responses to adaptive versus maladaptive behavior was also observed at other time points, revealing a  
348 significant suppression in the hippocampus, while all TRs showing enhancements were un-related to  
349 adaptive behavior (Table 3).

350 While these findings suggest that memory-related processes are important when enacting a  
351 choice that benefits oneself, documenting an early hippocampal signal would provide converging  
352 evidence that the relationship between the hippocampus and adaptive choice is robust. Accordingly, we  
353 explored hippocampal signals during choice when individuals had memory for Dictators and their offers  
354 versus trials in which a Dictator might be remembered but their offer was not, or when there was no  
355 memory for the Dictator at all. This analysis of subsequent memory during the choice period revealed a

356 significant cluster in the right hippocampus ( $p < 0.01$ , small-volume corrected;  $[X, Y, Z] = [36, -18, -15]$ ,  
357  $k = 21$ , Figure 6a), the Left Middle Frontal Gyrus ( $p < 0.01$ , whole-brain corrected;  $[X, Y, Z] = [-47, 19, 37]$ ,  
358  $k = 21$ , Figure 6b) and Right Middle Occipital Gyrus ( $p < 0.01$ , whole-brain corrected;  $[X, Y, Z] = [25, -97, 10]$ ,  
359  $k = 236$ , Figure 6b). Within the hippocampal cluster, peak differences occurred at  $TR = 5$ , revealing  
360 greater activation when individuals had intact memory for Dictators and their offers compared to  
361 memory for the Dictator alone or no memory at all. We should note, however, that this analysis should  
362 be interpreted with caution, as there were relatively few trials in which participants had memory for the  
363 Dictator and their offer (mean number of trials [range] =  $7.7[1-19]$ ).

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#### 365 Discussion

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367 Based on recent work showing that episodic memory supports adaptive choice during single  
368 shot learning (Murty et al., 2016), we tested the hypothesis that the hippocampus plays a critical role in  
369 guiding choice when decisions are based on limited previous social exposure. We observed that adaptive  
370 choices, selecting partners who treated you well in the past and avoiding those who treated you poorly,  
371 relies on a trace signal in the hippocampus evocative of repetition suppression seen during episodic  
372 memory (Chen, Olsen, Preston, Glover, & Wagner, 2011; Howard, Kumaran, Olafsdottir, & Spiers, 2011;  
373 Kohler, Danckert, Gati, & Menon, 2005; Kumaran & Maguire, 2007). Since there was no evidence of  
374 striatal involvement during either adaptive or maladaptive choice, this provides evidence that  
375 hippocampal, rather than striatal, signals are associated with socially adaptive value-based learning.

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377 Our results indicate that while early hippocampal responses ( $TRs$  0-5) do not discriminate  
378 between adaptive and maladaptive choices, they do index subsequent memory. In contrast, middle ( $TRs$   
379 6-11) and later hippocampal responses ( $TRs$  12-17) are sensitive to adaptive versus maladaptive choices.  
380 Specifically, we observed a suppression signal across subjects during the middle phase of the  
381 hippocampal timeseries response, which was associated with an individual's capacity to make socially  
382 adaptive choices during single-shot learning. In other words, deciding to re-engage with someone who  
383 treated you well and avoid someone that treated you poorly was linked to the degree to which the  
384 hippocampus was suppressed. Prior research illustrates that repetition suppression in the hippocampus  
385 scales with memory strength (Gonsalves, Kahn, Curran, Norman, & Wagner, 2005), which may be  
386 especially sensitive to memories for associations between discrete elements of an episode (Howard et  
387 al., 2011; Kohler et al., 2005)—such as players who made generous or selfish offers in our paradigm.  
388 Notably, the hippocampus did not distinguish between adaptive and novel trials during  $TR = 10$ , which  
challenges our interpretation that this suppression response reflects associative memory retrieval.

389 However, our task structure cannot tease apart whether subjects are employing retrieval strategies (i.e.,  
390 recall to reject, generalization) or are newly encoding novel faces.

391         Accordingly, our findings that adaptive choices first show a repetition suppression signal,  
392 suggests that hippocampal sensitivity for the subjective perception of a person and how well they treat  
393 you may also be invoked during the choice itself (Desimone, 1996). The adaptive decision to play with  
394 good people and avoid bad people seems to be supported by the hippocampus indexing the relationship  
395 between the previous person encountered and the outcome of that particular exchange, which parallels  
396 prior work that intact episodic memory is needed to make these adaptive choices (Murty et al., 2016). In  
397 line with this, we also found that the right hippocampus was more active during decision-making trials  
398 when there was intact memory for the Dictators and their offers. Thus, when deciding, it is likely that  
399 the hippocampus exhibits both a signal supporting the current adaptive choice, as well as a detailed  
400 episodic memory of the original social exchange. However, it is impossible to explicitly probe episodic  
401 memory during decision-making, which leaves open the possibility that the hippocampus is not only  
402 representing consciously accessible memories, but implicit memories as well. If this were the case, the  
403 hippocampus' ability to distinguish between individuals who should be approached versus avoided may  
404 be due in part to the absence of any conscious memory, which may help explain the fact that subjects  
405 reported intact episodic memory for a fraction of the dictators, and yet still managed to behave in an  
406 adaptive manner.

407         Together, these findings add to a literature illustrating that the hippocampus plays a larger role  
408 than just encoding episodic memory per se (Davidow, Foerde, Galvan, & Shohamy, 2016; Gerraty,  
409 Davidow, Wimmer, Kahn, & Shohamy, 2014; Shohamy & Turk-Browne, 2013). Prior work has elegantly  
410 demonstrated that by implicitly spreading value to never before experienced choice options (Wimmer &  
411 Shohamy, 2012), and by reactivating prior feedback-based learning experiences (Bakkour et al., 2019;  
412 Bornstein, Khaw, Shohamy, & Daw, 2017; Bornstein & Norman, 2017b), the hippocampus interacts with  
413 the striatum to encode value. Here, we extend these findings by revealing that the ability to make  
414 socially adaptive choices with limited prior experience also relies on the hippocampus rather than the  
415 striatum. We interpret our hippocampal findings at TR=10 to reflect processes directly related to  
416 decision-making as this signal was related to adaptive behavior both within- and across-participants, and  
417 did not directly relate to subsequent source memory. However, given the lack of ability to assess  
418 causality in neuroimaging data and the late emergence of this signal, we cannot discredit that this signal  
419 may reflect post-encoding processes that we did not capture in our behavioral measures.

420           After this initial suppression of the hippocampus, we further observed a late enhancement  
421 signal within the hippocampus, a signal exhibited well after the decision was executed ( $TR > 11$ ). In this  
422 stage of the timeseries, the responses to adaptive decisions was not associated with individual  
423 differences in decision-making across subjects, suggesting that this signal did not directly contribute to  
424 choice. However, we did find that this hippocampal enhancement signal, unlike the suppression signal,  
425 differentiated between subjects making adaptive choices for a previously encountered person versus  
426 making choices about a never before seen stranger, signifying the existence of a discrete memory-  
427 related signal. Together, our data suggests that the hippocampus is likely involved in multiple aspects of  
428 the memory and decision-making process. This is best evidenced by the observation that at TR 5 the  
429 hippocampus predicts subsequent retrieval of source memory—which could theoretically reflect  
430 reconsolidation—but at TR 10 there is no observed effect directly related to memory (i.e., no  
431 differentiation between old and new faces or relationships to subsequent memory).

432           Although speculative, it is possible that a late onset enhancement signal may not directly relate  
433 to the current choice, but may instead represent a post-choice strengthening of memory traces for  
434 future choices. This would allow the hippocampus to play a critical role in actively reinforcing the  
435 memory of the person (and whether that person was associated with good or bad outcomes) so that  
436 subsequent decisions made in similar contexts are easier to deploy. This would fit with research  
437 illustrating that enhanced activity in the hippocampus occurs when individuals successfully encode,  
438 integrate, or update associative memories (Bridge & Voss, 2014; Spaniol et al., 2009). Moreover, prior  
439 evidence demonstrates that the simple act of choosing strengthens the associative memories relating to  
440 the choice (Murty, DuBrow, & Davachi, 2015, 2019) and can even enhance the value of the selected  
441 option when the choice is inconsequential (Sharot, Velasquez, & Dolan, 2010)—which would indicate  
442 that the hippocampus plays a dynamic role during social learning. Future work can help elucidate how  
443 current adaptive choices and their associated memories influences subsequent choice, and identify  
444 whether the hippocampus is indexing an increase in value for the selected partner or a de-valuing of the  
445 unselected partner (or perhaps a combination of both).

446           Together, our findings reveal that hippocampal responses exhibit a suppression signal that both  
447 differentiated between adaptive and maladaptive decisions on a trial-by-trial basis, while also being  
448 associated with the propensity to implement adaptive behavior across participants. If we consider these  
449 findings alongside theoretical work implicating the hippocampus in episodic simulation (Gaesser,  
450 Spreng, McLelland, Addis, & Schacter, 2013; Schacter, Addis, & Buckner, 2008; Schacter, Benoit, &  
451 Szpunar, 2017) and model-based choice (Chersi & Pezzulo, 2012; Doll, Simon, & Daw, 2012), it is possible

452 that retrieving a trace memory of past experiences is akin to processes that also evoke cognitive maps of  
453 the decision space. For example, episodic simulation enables individuals to use past events to construct  
454 plausible future events (e.g., I probably will meet this person again), which in turn can help a person  
455 decide what is the best option to take (e.g., I should trust him next time).

456         Within the framework of model-based decision-making, it has also been proposed that the  
457 hippocampus generates representations of the contingencies of a task—cognitive maps that include rich  
458 information about previous experiences—which can then be used to make adaptive choices (Doll,  
459 Shohamy, & Daw, 2015). Dovetailing with this, recent work illustrates that lesioning the hippocampus  
460 leads to a decrease in model-based choices (Vikbladh et al., 2019). Although model-based learning is  
461 mostly probed using trial-by-trial learning paradigms, the reliance on a rich, cognitive map of the  
462 decision space need not be unique to multi-shot learning and may actually be more prominent when  
463 decisions are informed by limited prior experience. Indeed, our findings that the hippocampus supports  
464 episodic memory retrieval and value based choice hints that single shot learning likely also leverages the  
465 retrieval of episodic memories to bolster a rich cognitive map of the future decision space, a finding that  
466 would be consistent with the view that computations in the hippocampus support multiple types of  
467 learning and decision-making (Doll et al., 2015; Shohamy & Turk-Browne, 2013). Future work can help  
468 bridge the current findings with the broader literature on both statistical and single shot learning to  
469 explicitly probe the role of the hippocampus during model-based choice.

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471 **References**

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652 **Figure Legends**

653

654 **FIGURE 1 | Task structure and behavioral results. A)** All subjects completed three tasks. The first two  
655 tasks (Encoding and Decision Phases) occurred in the scanner, while the surprise memory task happened  
656 outside of the scanner. In the Decision Task pictured here, subjects could select who they would like to  
657 play with in a subsequent Dictator Game. **B)** Proportion of decisions to select a partner in the Dictator  
658 game are broken down by no memory, memory for only the face, or memory for both the face and  
659 associated offer. Here adaptive behavior is defined as the ability to re-approach fair players more often  
660 than unfair players, independent of their baseline propensity. Bars in green indicate fair offers while  
661 orange bars indicate unfair offers. \*\*\* $p < 0.001$

662

663 **FIGURE 2 | The hippocampus indexes adaptive decisions. A)** Right hippocampus activity supports  
664 adaptive, compared to maladaptive social decisions. **B)** Time course series of BOLD signal in the right  
665 hippocampus, plotted separately for adaptive and maladaptive choices. **C)** As a control region, we  
666 plotted time course series of BOLD signals in bilateral calcarine sulcus, separately for adaptive and  
667 maladaptive choices. \* $q < 0.10$ , \*\* $q < 0.05$

668

669 **FIGURE 3 | Regions outside of the hippocampus indexing adaptive decisions** Hemodynamic response  
670 functions of regions outside of the hippocampus showing differences between Adaptive versus  
671 Maladaptive trials. Data plots are for visualization purposes only, and do not include post-hoc tests

672

673 **FIGURE 4 | Brain-Behavior Correlations reveal hippocampal suppression leads to adaptive choice.** Only  
674 during adaptive suppression did we observe a relationship between hippocampal BOLD activity and the  
675 likelihood of making an adaptive choice: dampened hippocampal responses correlated with increasing  
676 adaptive behavior. \* $p < 0.05$

677

678 **FIGURE 5 | Memory sensitivity in the hippocampus. A)** During the time period when the hippocampus  
679 showed enhancement ( $TR=12$ ) we observed an increase in hippocampal BOLD activation in response to  
680 adaptive versus novel choices, with no significant difference when the hippocampus showed suppression  
681 ( $TR=10$ ). This revealed a discrete memory signal associated with late onset enhanced hippocampal  
682 activity. Data from the Novel condition are presented in both graphs and were plotted separately to  
683 avoid circular analyses: comparisons are only made for each condition contrasted against novel trials,  
684 rather than comparisons between Adaptive and Maladaptive trials. **B)** Visualization of the entire HRF in  
685 the Hippocampus for Novel, Adaptive, and Maladaptive trials. \*\* $p < 0.01$

686

687 **FIGURE 6 | The hippocampus indexes successful subsequent memory. A)** Right hippocampus activity  
688 differentiates between decisions in which individuals exhibit successful memory for Dictators and their  
689 offers, compared to trials in which only the Dictator was remembered or participants reported having no  
690 memory at all. BOLD time course series in the hippocampus, plotted by performance during the  
691 subsequent memory test (right). **B)** Hemodynamic response functions of regions outside of the  
692 hippocampus showing differences between subsequent memory for visualization purposes only.  
693 \* $q < 0.10$ , \*\* $q < 0.05$ .

694

695

696 **Table 1** | *Item memory performance for faces appearing in the Dictator Game.*  
697

Condition	Proportion indicated remembered
Fair	Mean (SE)=.63 (.04)
Unfair	Mean (SE)=.62 (.04)
Novel Foils (false alarms)	Mean (SE)=.41 (.05)

698

699 **Table 2** | Tests for differences between selecting fair or unfair Dictators as a function of having intact  
 700 episodic memory, item memory, or no memory.

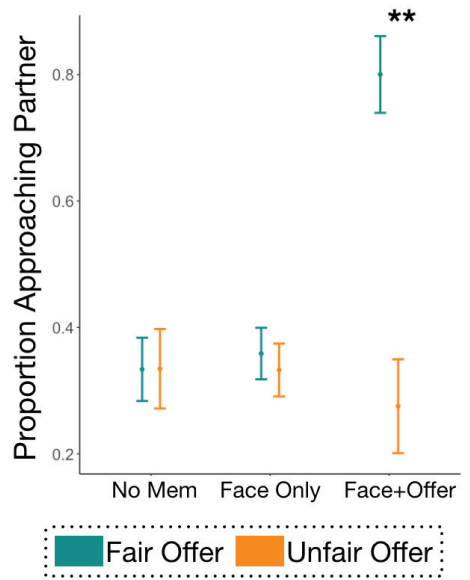
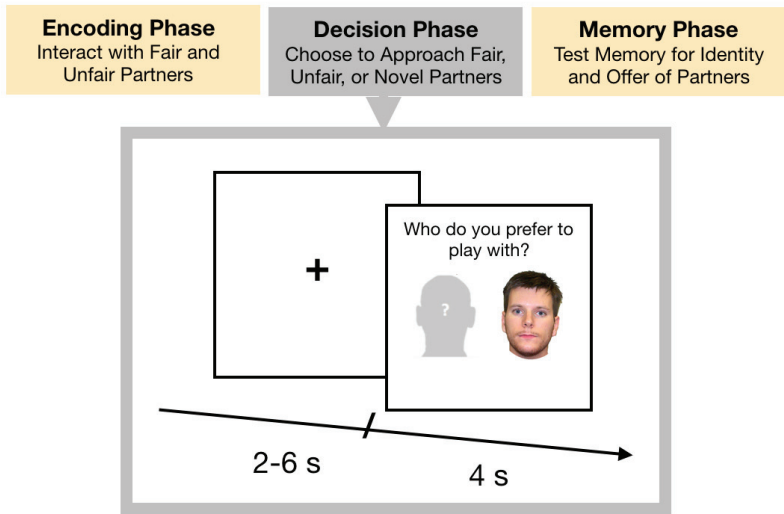
	t	df	Sig. (2-tailed)
Select fair dictator w/ source memory > select fair dictator w/out memory	3.817	15	.002
Select unfair dictator w/ source memory > select unfair dictator w/out memory	-.702	19	.491
Select fair dictator w/ item memory > select fair dictator w/out memory	.616	19	.545
Select unfair dictator w/ item memory > select unfair dictator w/out memory	-.035	19	.973
Select fair dictator w/ source memory > select fair dictator w/ item memory	3.956	15	.001
Select unfair dictator w/ source memory > select unfair dictator w/ item memory	-.718	19	.481

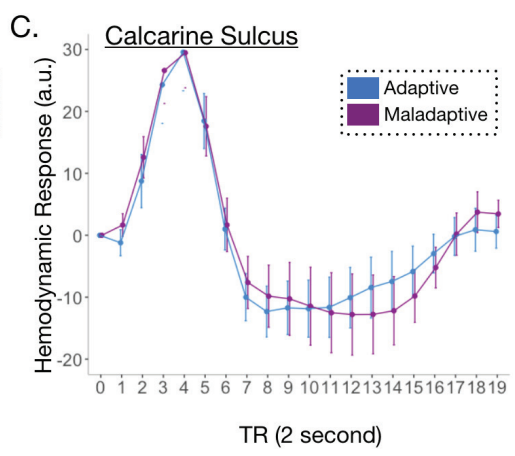
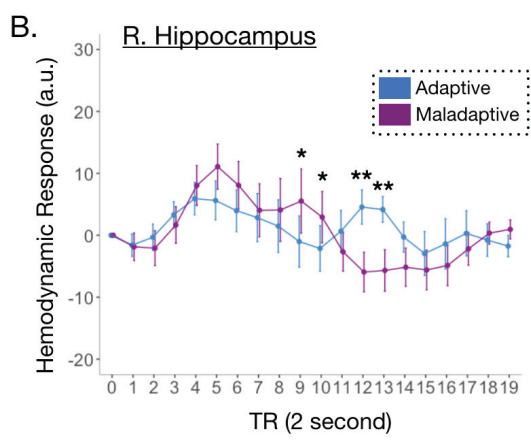
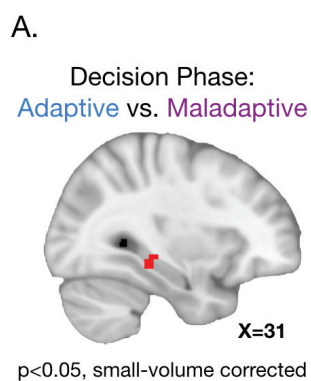


713 **Table 3** | Post-hoc analyses for all TRs showing significant differences in the hippocampus for Adaptive  
 714 versus Maladaptive trials. Reported values include mean beta-parameters for each condition against  
 715 baseline, t-tests between adaptive and maladaptive trials, t-tests between adaptive/maladaptive versus  
 716 novel trials, and regressions between beta-parameters of adaptive>maladaptive and adaptive behavioral  
 717 responses. For t-tests, positive values represent relative enhancement signals and negative values  
 718 represent relative suppression signals.  
 719

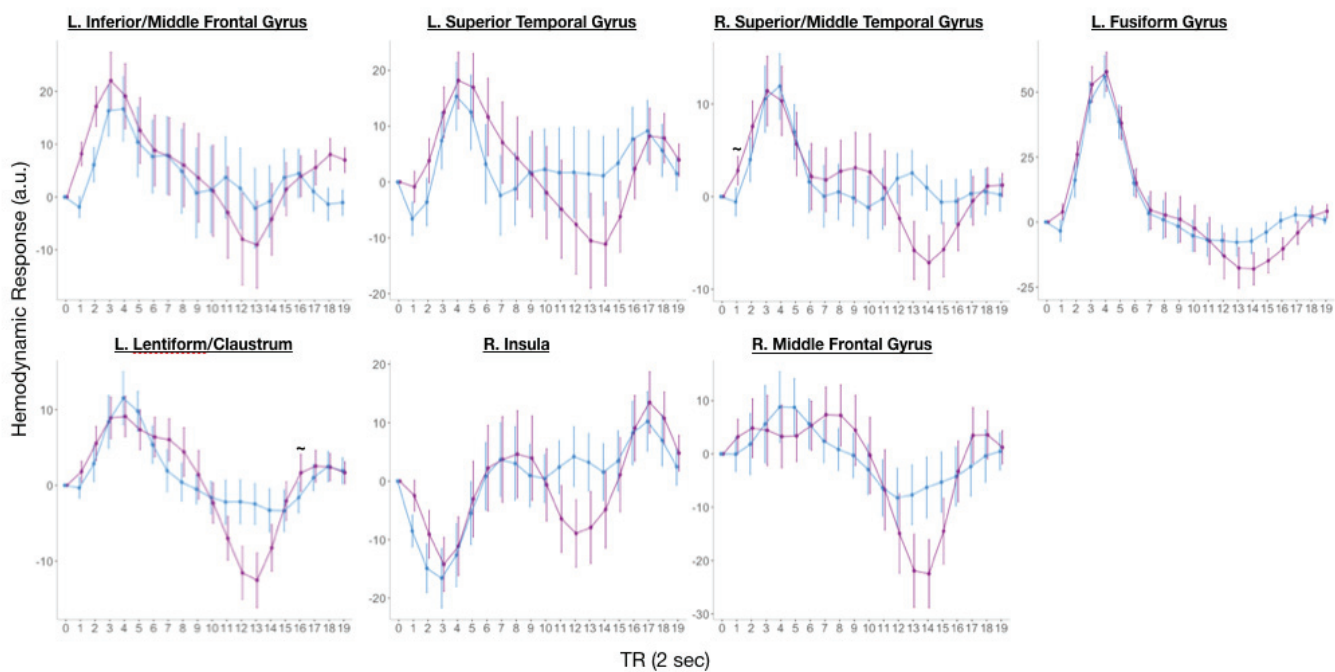
Contrast	TR				
	9	10	12	13	14
Adaptive > Baseline: Mean (SE)	-1.0 (4.1)	-2.1 (3.7)	4.6 (2.8)	4.2 (2.1)	-0.3 (2.4)
Maladaptive > Baseline: Mean (SE)	5.5 (5.2)	2.9 (4.1)	-5.9 (3.2)	-5.7 (3.3)	-5.2 (3.1)
Adaptive vs. Maladaptive t-test (p-value)	-2.5 (0.02)	-2.6 (0.02)	4.1 (0.001)	3.5 (0.002)	2.5 (0.02)
Adaptive vs Novel: t-test (p-value)	-1.9 (0.06)	-1.3 (0.19)	3.7 (0.002)	3.1 (0.006)	1.0 (0.34)
Maladaptive vs Novel: t-test (p-value)	1.15 (0.26)	1.48 (0.15)	-1.14 (0.26)	-1.09 (0.29)	-1.28 (0.22)
[Adapt > Maladapt] ~ Adaptive Behavior r-value (p-value)	-0.39 (0.09)	-0.5 (0.02)	-0.12 (0.61)	-0.1 (0.68)	-0.14 (0.54)

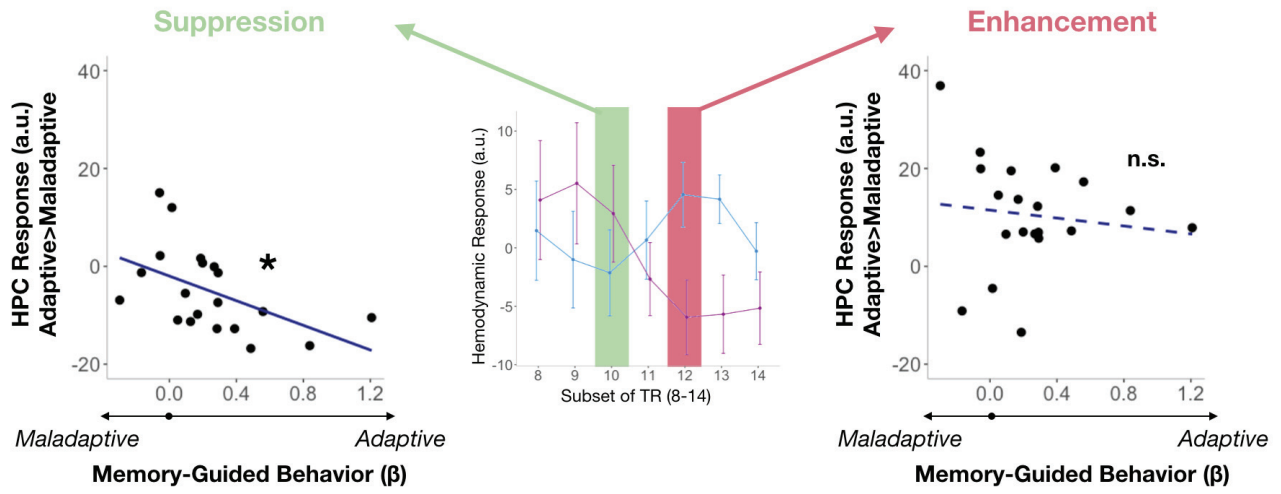
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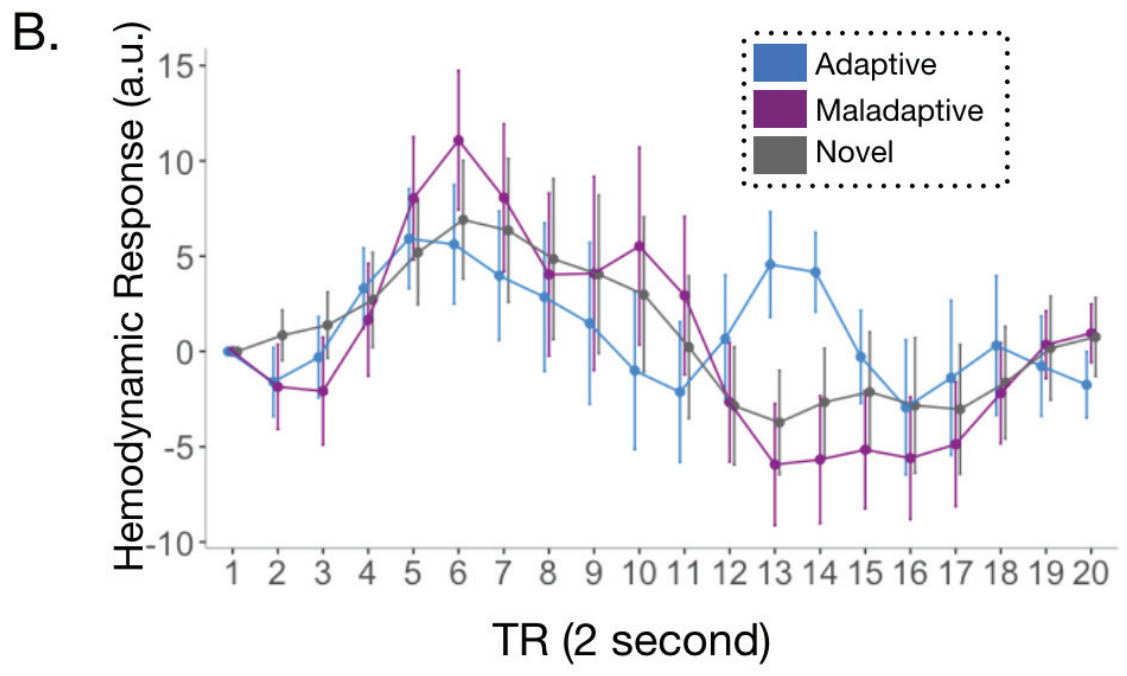
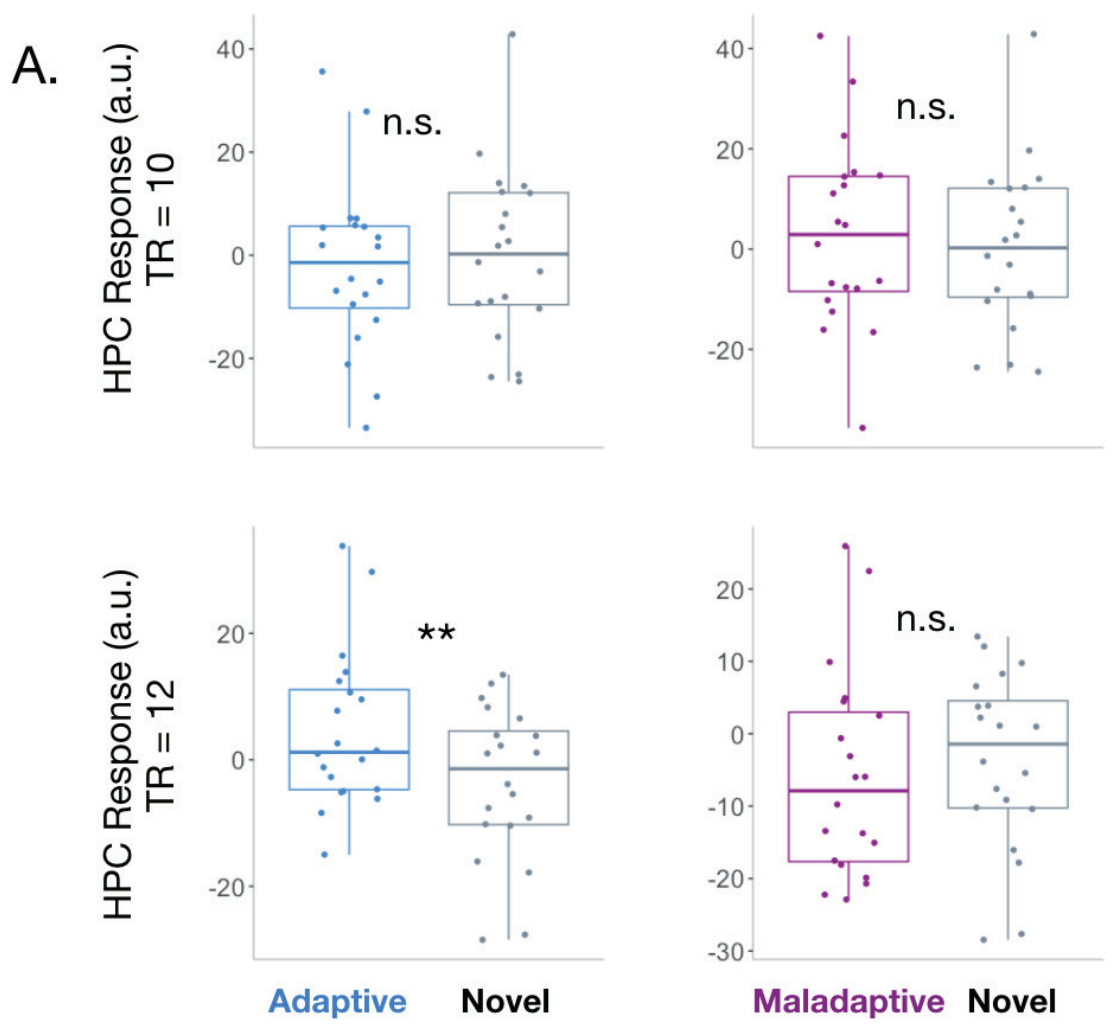




Decision Phase: Adaptive vs. Maladaptive

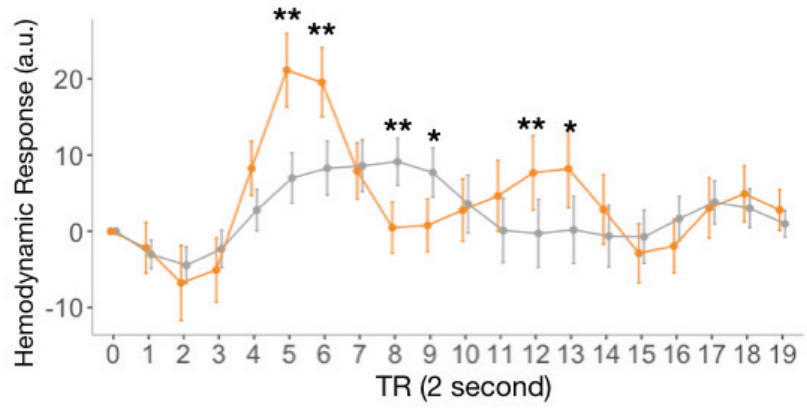
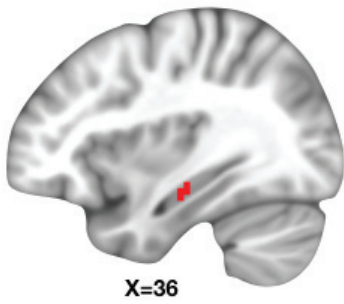






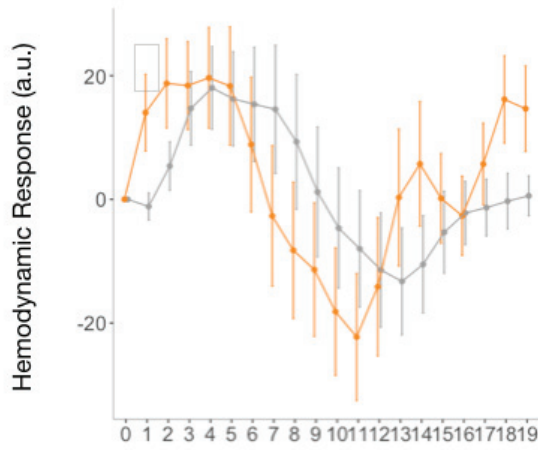
**A**

Decision Phase: **Source Memory** vs. Item/No Memory

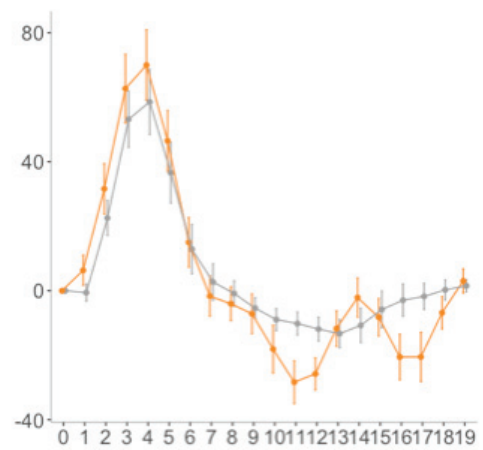


**B**

**L. Middle Frontal Gyrus**



**R. Middle Occipital Gyrus**



TR (2 second)