

Research Articles: Behavioral/Cognitive

Hippocampus guides adaptive learning during dynamic social interactions

<https://doi.org/10.1523/JNEUROSCI.0873-20.2020>

Cite as: J. Neurosci 2020; 10.1523/JNEUROSCI.0873-20.2020

Received: 16 April 2020

Revised: 2 December 2020

Accepted: 7 December 2020

This Early Release article has been peer-reviewed and accepted, but has not been through the composition and copyediting processes. The final version may differ slightly in style or formatting and will contain links to any extended data.

Alerts: Sign up at www.jneurosci.org/alerts to receive customized email alerts when the fully formatted version of this article is published.

1 Hippocampus guides adaptive learning during dynamic social interactions

2
3 Running Title: Hippocampus and adaptive social decision-making

4 Oriel FeldmanHall^{1,2}, David F. Montez³, Elizabeth A. Phelps⁴, Lila Davachi⁵, Vishnu P. Murty⁶

- 5
6
7 1. Department of Cognitive, Linguistic, & Psychological Sciences, Brown University, Providence, RI,
8 02912, USA
9 2. Carney Institute of Brain Science, Brown University, Providence, RI 02912, USA
10 3. Department of Neurology, Washington University of St. Louis, St. Louis, MO, 63110, USA
11 4. Department of Psychology, Harvard University, Cambridge, MA, 02138, USA
12 5. Department of Psychology, Columbia University, New York City, NY, 10027, USA
13 6. Department of Psychology, Temple University, Philadelphia, PA, 19122, USA
14

15 Corresponding Authors:

16 Oriel FeldmanHall

17 Brown University

18 Department of Cognitive, Linguistic, & Psychological Science

19 e: oriel.feldmanhall@brown.edu

20
21 Vishnu Murty

22 Temple University

23 Department of Psychology

24 e: vishnu.murty@temple.edu

25
26 Introduction Word Count: 650

27 Discussion Word Count: 1495

28 Figures: 6

29 Table: 3

30
31 Acknowledgements: The research was funded by internal grants from New York University's

32 neuroimaging center. This work was also funded in part by a NARSAD Young Investigator Award and P20

33 GM103645 to OFH and a NARSAD Young Investigator Award, K01 MH111991, and R21 DA043568 to

34 VPM.

35 Conflicts of Interest: The authors declare no competing financial interests.

36

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.

51

52

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.

61

67 **Introduction**

68

69 Humans expertly navigate through dynamic social worlds despite the sheer amount of
70 information they are bombarded with. Even though another's motivations are largely hidden to us, we
71 can make socially adaptive¹ decisions, such as who to cooperate with or trust (FeldmanHall & Shenhav,
72 2019). Such success requires an efficient integration of prior experiences with information gleaned from
73 the current environment. Classic models of decision-making suggest that through repeated experience,
74 humans incrementally fine-tune their behavior using prediction errors (Glascher, Daw, Dayan, &
75 O'Doherty, 2010; Glascher, Hampton, & O'Doherty, 2009; King-Casas et al., 2008; Montague & Berns,
76 2002), which enables us to learn who to approach and who to avoid. However, we can also learn and
77 make adaptive decisions from relatively limited experience. Indeed, a hallmark of human cognition is
78 that complex concepts can be learned from a single experience (Lake, Salakhutdinov, & Tenenbaum,
79 2015).

80 A growing body of research shows that individuals routinely make judgements based on limited
81 prior experience. Even briefly glancing at a person's face can provide enough information to judge
82 whether that person can be trusted (Engell, Haxby, & Todorov, 2007; Mende-Siedlecki, Said, & Todorov,
83 2013; Todorov & Mende-Siedlecki, 2013). Thus, even when information is dynamic, multi-dimensional,
84 and involves moral qualities, humans are highly adept at encoding relevant information from a single
85 brief exposure. Less is known, however, about how people retrieve this information to adaptively decide
86 whether to re-engage or avoid a particular individual. Our group showed that intact detailed, episodic
87 memories of the prior exchange may be a necessary requirement (Murty, FeldmanHall, Hunter, Phelps,
88 & Davachi, 2016; Schaper, Mieth, & Bell, 2019). This suggests that making flexibly adaptive choices from
89 limited experience necessitates the recollection of contextual details from the original social encounter.

90 Despite this behavioral evidence, the neural mechanisms that instantiate socially adaptive single
91 shot learning remain unknown. There are two competing theories (Ghiglieri, Sgobio, Costa, Picconi, &
92 Calabresi, 2011; Woolley et al., 2013). On the one hand, value-based learning is canonically considered
93 to be in the domain of the striatum, for both multi-trial non-social learning (Bornstein & Norman, 2017a;
94 Diederer, Spencer, Vestergaard, Fletcher, & Schultz, 2016; Hare, O'Doherty, Camerer, Schultz, & Rangel,
95 2008; O'Doherty, Dayan, Friston, Critchley, & Dolan, 2003) and social learning (Hackel, Doll, & Amodio,
96 2015). On the other hand, the hippocampus, a region known for its central role in long-term episodic
97 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.

115

116

117 **Methods**

118

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 7th 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 1st 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

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

288

289 An ANOVA testing for interactions between memory and choice revealed that adaptive choices
290 were dependent on an individual's memory of their prior experience with each Dictator ($p<0.001$; Fig.
1B, Table 2). Post-hoc t-tests revealed that subjects did not show any differences in their tendency to
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] = $7.7[1-19]$).

364
365
366
367

Discussion

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.

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

470

471 **References**

472

473 Adcock, R. A., Thangavel, A., Whitfield-Gabrieli, S., Knutson, B., & Gabrieli, J. D. E. (2006).

474 Reward-motivated learning: Mesolimbic activation precedes memory formation.

475 *Neuron*, *50*(3), 507-517. doi:10.1016/j.neuron.2006.03.036

476 Bakkour, A., Palombo, D. J., Zylberberg, A., Kang, Y. H. R., Reid, A., Verfaellie, M., . . . Shohamy,

477 D. (2019). The hippocampus supports deliberation during value-based decisions. *Elife*, *8*.

478 doi:ARTN e46080

479 10.7554/eLife.46080

480 Bornstein, A. M., & Daw, N. D. (2012). Dissociating hippocampal and striatal contributions to

481 sequential prediction learning. *European Journal of Neuroscience*, *35*(7), 1011-1023.

482 doi:10.1111/j.1460-9568.2011.07920.x

483 Bornstein, A. M., Khaw, M. W., Shohamy, D., & Daw, N. D. (2017). Reminders of past choices

484 bias decisions for reward in humans. *Nature Communications*, *8*. doi:ARTN 15958

485 10.1038/ncomms15958

486 Bornstein, A. M., & Norman, K. A. (2017a). Reinstated episodic context guides sampling-based

487 decisions for reward. *Nature Neuroscience*, *20*(7), 997-1003. doi:10.1038/nn.4573

488 Bornstein, A. M., & Norman, K. A. (2017b). Reinstated episodic context guides sampling-based

489 decisions for reward. *Nature Neuroscience*, *20*(7), 997-+. doi:10.1038/nn.4573

490 Bridge, D. J., & Voss, J. L. (2014). Hippocampal Binding of Novel Information with Dominant

491 Memory Traces Can Support Both Memory Stability and Change. *Journal of*492 *Neuroscience*, *34*(6), 2203-2213. doi:10.1523/Jneurosci.3819-13.2014

493 Chen, J., Olsen, R. K., Preston, A. R., Glover, G. H., & Wagner, A. D. (2011). Associative retrieval

494 processes in the human medial temporal lobe: Hippocampal retrieval success and CA1

495 mismatch detection. *Learning & Memory*, *18*(8), 523-528. doi:10.1101/lm.2135211

496 Chersi, F., & Pezzulo, G. (2012). Using hippocampal-striatal loops for spatial navigation and goal-

497 directed decision making. *Cognitive Processing*, *13*, S56-S57.498 Davachi, L. (2006). Item, context and relational episodic encoding in humans. *Curr Opin*499 *Neurobiol*, *16*(6), 693-700. doi:10.1016/j.conb.2006.10.012

500 Davidow, J. Y., Foerde, K., Galvan, A., & Shohamy, D. (2016). An Upside to Reward Sensitivity:

501 The Hippocampus Supports Enhanced Reinforcement Learning in Adolescence. *Neuron*,502 *92*(1), 93-99. doi:10.1016/j.neuron.2016.08.031503 Desimone, R. (1996). Neural mechanisms for visual memory and their role in attention. *Proc*504 *Natl Acad Sci U S A*, *93*(24), 13494-13499. doi:DOI 10.1073/pnas.93.24.13494

505 Diederer, K. M. J., Spencer, T., Vestergaard, M. D., Fletcher, P. C., & Schultz, W. (2016).

506 Adaptive Prediction Error Coding in the Human Midbrain and Striatum Facilitates

507 Behavioral Adaptation and Learning Efficiency. *Neuron*, *90*(5), 1127-1138.

508 doi:10.1016/j.neuron.2016.04.019

509 Doeller, C. F., King, J. A., & Burgess, N. (2008). Parallel striatal and hippocampal systems for

510 landmarks and boundaries in spatial memory. *Proc Natl Acad Sci U S A*, *105*(15), 5915-

511 5920. doi:10.1073/pnas.0801489105

512 Doll, B. B., Shohamy, D., & Daw, N. D. (2015). Multiple memory systems as substrates for

513 multiple decision systems. *Neurobiology of Learning and Memory*, *117*, 4-13.

514 doi:10.1016/j.nlm.2014.04.014

- 515 Doll, B. B., Simon, D. A., & Daw, N. D. (2012). The ubiquity of model-based reinforcement
 516 learning. *Curr Opin Neurobiol*, *22*(6), 1075-1081. doi:10.1016/j.conb.2012.08.003
- 517 Duncan, K., Doll, B. B., Daw, N. D., & Shohamy, D. (2018). More Than the Sum of Its Parts: A
 518 Role for the Hippocampus in Configural Reinforcement Learning. *Neuron*, *98*(3), 645-+.
 519 doi:10.1016/j.neuron.2018.03.042
- 520 Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and
 521 recognition memory. *Annual review of neuroscience*, *30*, 123-152.
 522 doi:10.1146/annurev.neuro.30.051606.094328
- 523 Engell, A. D., Haxby, J. V., & Todorov, A. (2007). Implicit trustworthiness decisions: Automatic
 524 coding of face properties in the human amygdala. *J Cogn Neurosci*, *19*(9), 1508-1519.
 525 doi:DOI 10.1162/jocn.2007.19.9.1508
- 526 FeldmanHall, O., & Shenhav, A. (2019). Resolving uncertainty in a social world. *Nat Hum Behav*.
 527 doi:10.1038/s41562-019-0590-x
- 528 Gaesser, B., Spreng, R. N., McLelland, V. C., Addis, D. R., & Schacter, D. L. (2013). Imagining the
 529 Future: Evidence for a Hippocampal Contribution to Constructive Processing.
 530 *Hippocampus*, *23*(12), 1150-1161. doi:10.1002/hipo.22152
- 531 Gerraty, R. T., Davidow, J. Y., Wimmer, G. E., Kahn, I., & Shohamy, D. (2014). Transfer of
 532 Learning Relates to Intrinsic Connectivity between Hippocampus, Ventromedial
 533 Prefrontal Cortex, and Large-Scale Networks. *Journal of Neuroscience*, *34*(34), 11297-
 534 11303. doi:10.1523/Jneurosci.0185-14.2014
- 535 Ghiglieri, V., Sgobio, C., Costa, C., Picconi, B., & Calabresi, P. (2011). Striatum-hippocampus
 536 balance: From physiological behavior to interneuronal pathology. *Prog Neurobiol*, *94*(2),
 537 102-114. doi:10.1016/j.pneurobio.2011.04.005
- 538 Glascher, J., Daw, N., Dayan, P., & O'Doherty, J. P. (2010). States versus rewards: dissociable
 539 neural prediction error signals underlying model-based and model-free reinforcement
 540 learning. *Neuron*, *66*(4), 585-595. doi:10.1016/j.neuron.2010.04.016
- 541 Glascher, J., Hampton, A. N., & O'Doherty, J. P. (2009). Determining a role for ventromedial
 542 prefrontal cortex in encoding action-based value signals during reward-related decision
 543 making. *Cerebral cortex*, *19*(2), 483-495. doi:10.1093/cercor/bhn098
- 544 Gonsalves, B. D., Kahn, I., Curran, T., Norman, K. A., & Wagner, A. D. (2005). Memory strength
 545 and repetition suppression: Multimodal imaging of medial temporal cortical
 546 contributions to recognition. *Neuron*, *47*(5), 751-761. doi:10.1016/j.neuron.2005.07.013
- 547 Hackel, L. M., Doll, B. B., & Amodio, D. M. (2015). Instrumental learning of traits versus rewards:
 548 dissociable neural correlates and effects on choice. *Nature Neuroscience*, *18*(9), 1233-+.
 549 doi:10.1038/nn.4080
- 550 Hallquist, M. N., Hwang, K., & Luna, B. (2013). The nuisance of nuisance regression: Spectral
 551 misspecification in a common approach to resting-state fMRI preprocessing
 552 reintroduces noise and obscures functional connectivity. *Neuroimage*, *82*, 208-225.
 553 doi:10.1016/j.neuroimage.2013.05.116
- 554 Hare, T. A., O'Doherty, J., Camerer, C. F., Schultz, W., & Rangel, A. (2008). Dissociating the role
 555 of the orbitofrontal cortex and the striatum in the computation of goal values and
 556 prediction errors. *J Neurosci*, *28*(22), 5623-5630. doi:10.1523/JNEUROSCI.1309-08.2008
- 557 Howard, L. R., Kumaran, D., Olafsdottir, H. F., & Spiers, H. J. (2011). Double Dissociation
 558 between Hippocampal and Parahippocampal Responses to Object-Background Context

- 559 and Scene Novelty. *Journal of Neuroscience*, *31*(14), 5253-5261.
 560 doi:10.1523/Jneurosci.6055-10.2011
- 561 Kaplan, R., King, J., Koster, R., Penny, W. D., Burgess, N., & Friston, K. J. (2017). The Neural
 562 Representation of Prospective Choice during Spatial Planning and Decisions. *PLoS Biol*,
 563 *15*(1). doi:ARTN e1002588
 564 10.1371/journal.pbio.1002588
- 565 Kaplan, R., Schuck, N. W., & Doeller, C. F. (2017). The Role of Mental Maps in Decision-Making.
 566 *Trends in neurosciences*, *40*(5), 256-259. doi:10.1016/j.tins.2017.03.002
- 567 King-Casas, B., Sharp, C., Lomax-Bream, L., Lohrenz, T., Fonagy, P., & Montague, P. R. (2008).
 568 The rupture and repair of cooperation in borderline personality disorder. *Science*,
 569 *321*(5890), 806-810. doi:10.1126/science.1156902
- 570 Kohler, S., Danckert, S., Gati, J. S., & Menon, R. S. (2005). Novelty responses to relational and
 571 non-relational information in the hippocampus and the parahippocampal region: A
 572 comparison based on event-related fMRI. *Hippocampus*, *15*(6), 763-774.
 573 doi:10.1002/hipo.20098
- 574 Kumaran, D., & Maguire, E. A. (2007). Match-mismatch processes underlie human hippocampal
 575 responses to associative novelty. *Journal of Neuroscience*, *27*(32), 8517-8524.
 576 doi:10.1523/Jneurosci.1677-07.2007
- 577 Lake, B. M., Salakhutdinov, R., & Tenenbaum, J. B. (2015). Human-level concept learning
 578 through probabilistic program induction. *Science*, *350*(6266), 1332-1338.
- 579 Liljeholm, M., & O'Doherty, J. P. (2012). Contributions of the striatum to learning, motivation,
 580 and performance: an associative account. *Trends in Cognitive Sciences*, *16*(9), 467-475.
 581 doi:10.1016/j.tics.2012.07.007
- 582 McClure, S. M., Berns, G. S., & Montague, P. R. (2003). Temporal prediction errors in a passive
 583 learning task activate human striatum. *Neuron*, *38*(2), 339-346. doi:Doi 10.1016/S0896-
 584 6273(03)00154-5
- 585 Mende-Siedlecki, P., Said, C. P., & Todorov, A. (2013). The social evaluation of faces: a meta-
 586 analysis of functional neuroimaging studies. *Soc Cogn Affect Neurosci*, *8*(3), 285-299.
 587 doi:10.1093/scan/nsr090
- 588 Montague, P. R., & Berns, G. S. (2002). Neural economics and the biological substrates of
 589 valuation. *Neuron*, *36*(2), 265-284.
- 590 Murty, V. P., & Adcock, R. A. (2014). Enriched Encoding: Reward Motivation Organizes Cortical
 591 Networks for Hippocampal Detection of Unexpected Events. *Cerebral cortex*, *24*(8),
 592 2160-2168. doi:10.1093/cercor/bht063
- 593 Murty, V. P., DuBrow, S., & Davachi, L. (2015). The Simple Act of Choosing Influences
 594 Declarative Memory. *Journal of Neuroscience*, *35*(16), 6255-6264.
 595 doi:10.1523/Jneurosci.4181-14.2015
- 596 Murty, V. P., DuBrow, S., & Davachi, L. (2019). Decision-making Increases Episodic Memory via
 597 Postencoding Consolidation. *J Cogn Neurosci*, *31*(9), 1308-1317.
 598 doi:10.1162/jocn_a_01321
- 599 Murty, V. P., FeldmanHall, O., Hunter, L. E., Phelps, E. A., & Davachi, L. (2016). Episodic
 600 memories predict adaptive value-based decision-making. *Journal of Experimental*
 601 *Psychology-General*, *145*(5), 548-558. doi:10.1037/xge0000158

- 602 Nau, M., Julian, J. B., & Doeller, C. F. (2018). How the Brain's Navigation System Shapes Our
603 Visual Experience. *Trends in Cognitive Sciences*, 22(9), 810-825.
604 doi:10.1016/j.tics.2018.06.008
- 605 O'Doherty, J. P., Dayan, P., Friston, K., Critchley, H., & Dolan, R. J. (2003). Temporal difference
606 models and reward-related learning in the human brain. *Neuron*, 38(2), 329-337.
- 607 Omer, D. B., Maimon, S. R., Las, L., & Ulanovsky, N. (2018). Social place-cells in the bat
608 hippocampus. *Science*, 359(6372), 218+. doi:10.1126/science.aao3474
- 609 Schacter, D. L., Addis, D. R., & Buckner, R. L. (2008). Episodic simulation of future events -
610 Concepts, data, and applications. *Year in Cognitive Neuroscience 2008*, 1124, 39-60.
611 doi:10.1196/annals.1440.001
- 612 Schacter, D. L., Benoit, R. G., & Szpunar, K. K. (2017). Episodic future thinking: mechanisms and
613 functions. *Current Opinion in Behavioral Sciences*, 17, 41-50.
614 doi:10.1016/j.cobeha.2017.06.002
- 615 Schaper, M. L., Mieth, L., & Bell, R. (2019). Adaptive memory: Source memory is positively
616 associated with adaptive social decision making. *Cognition*, 186, 7-14.
617 doi:10.1016/j.cognition.2019.01.014
- 618 Schapiro, A. C., Rogers, T. T., Cordova, N. I., Turk-Browne, N. B., & Botvinick, M. M. (2013).
619 Neural representations of events arise from temporal community structure. *Nature*
620 *Neuroscience*, 16(4), 486-U161. doi:10.1038/nn.3331
- 621 Schapiro, A. C., Turk-Browne, N. B., Norman, K. A., & Botvinick, M. M. (2016). Statistical learning
622 of temporal community structure in the hippocampus. *Hippocampus*, 26(1), 3-8.
623 doi:10.1002/hipo.22523
- 624 Sharot, T., Velasquez, C. M., & Dolan, R. J. (2010). Do Decisions Shape Preference? Evidence
625 From Blind Choice. *Psychol Sci*, 21(9), 1231-1235. doi:10.1177/0956797610379235
- 626 Shohamy, D., & Turk-Browne, N. B. (2013). Mechanisms for Widespread Hippocampal
627 Involvement in Cognition. *Journal of Experimental Psychology-General*, 142(4), 1159-
628 1170. doi:10.1037/a0034461
- 629 Spaniol, J., Davidson, P. S. R., Kim, A. S. N., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-
630 related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation
631 likelihood estimation. *Neuropsychologia*, 47(8-9), 1765-1779.
632 doi:10.1016/j.neuropsychologia.2009.02.028
- 633 Todorov, A., & Mende-Siedlecki, P. (2013). The cognitive and neural basis of impression
634 formation. . In K. O. S. Kosslyn (Ed.), *The Oxford Handbook of Cognitive Neuroscience*
635 . New York: Oxford University Press.
- 636 Vikbladh, O. M., Meager, M. R., King, J., Blackmon, K., Devinsky, O., Shohamy, D., . . . Daw, N. D.
637 (2019). Hippocampal Contributions to Model-Based Planning and Spatial Memory.
638 *Neuron*. doi:10.1016/j.neuron.2019.02.014
- 639 Wimmer, G. E., & Shohamy, D. (2012). Preference by Association: How Memory Mechanisms in
640 the Hippocampus Bias Decisions. *Science*, 338(6104), 270-273.
641 doi:10.1126/science.1223252
- 642 Wittmann, B. C., Schott, B. H., Guderian, S., Frey, J. U., Heinze, H. J., & Duzel, E. (2005). Reward-
643 related fMRI activation of dopaminergic midbrain is associated with enhanced
644 hippocampus-dependent long-term memory formation. *Neuron*, 45(3), 459-467.
645 doi:10.1016/j.neuron.2005.01.010

646 Woolley, D. G., Laeremans, A., Gantois, I., Mantini, D., Vermaercke, B., Op de Beeck, H. P., . . .
647 D'Hooge, R. (2013). Homologous involvement of striatum and prefrontal cortex in
648 rodent and human water maze learning. *Proc Natl Acad Sci U S A*, *110*(8), 3131-3136.
649 doi:10.1073/pnas.1217832110
650
651

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

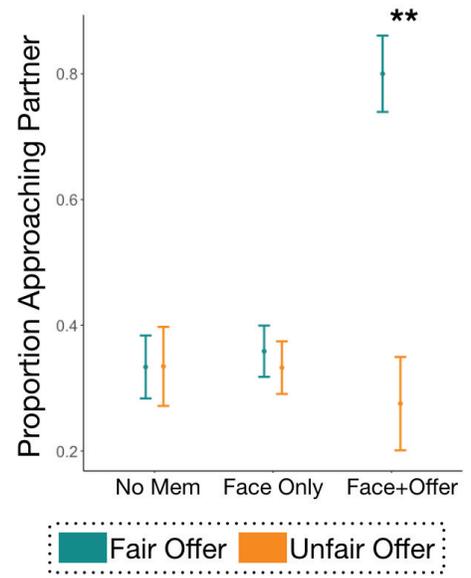
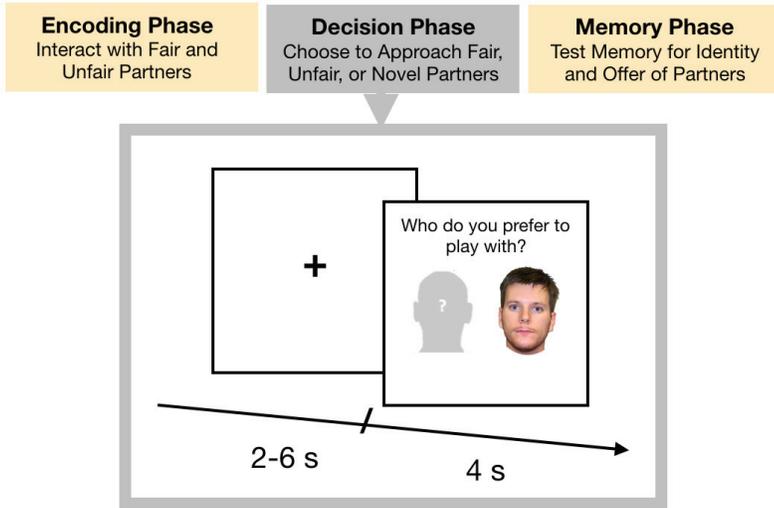
699 **Table 2** | Tests for differences between selecting fair or unfair Dictators as a function of having intact
 700 episodic memory, item memory, or no memory.

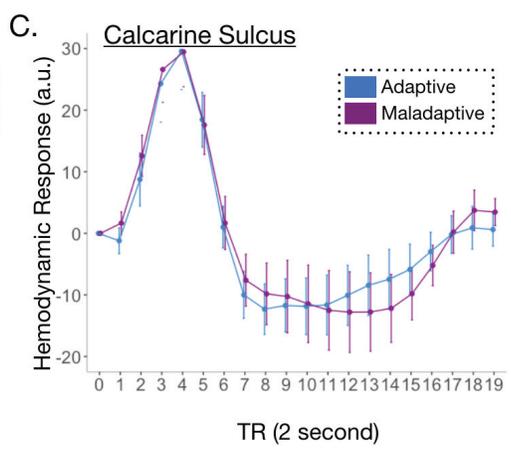
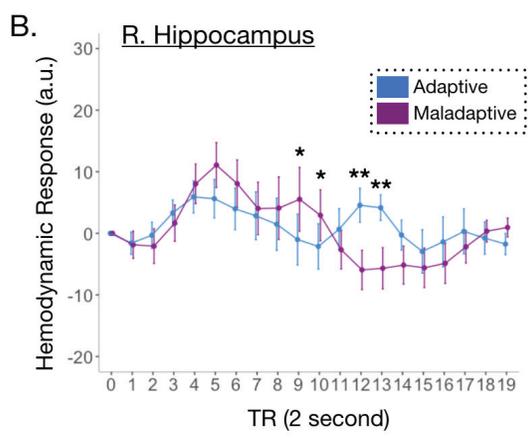
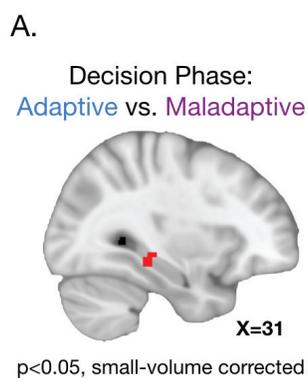
	t	df	Sig. (2-tailed)
Select fair dictator w/ source memory > select fair dictator w/out memory	3.817	15	.002
Select unfair dictator w/ source memory > select unfair dictator w/out memory	-.702	19	.491
Select fair dictator w/ item memory > select fair dictator w/out memory	.616	19	.545
Select unfair dictator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

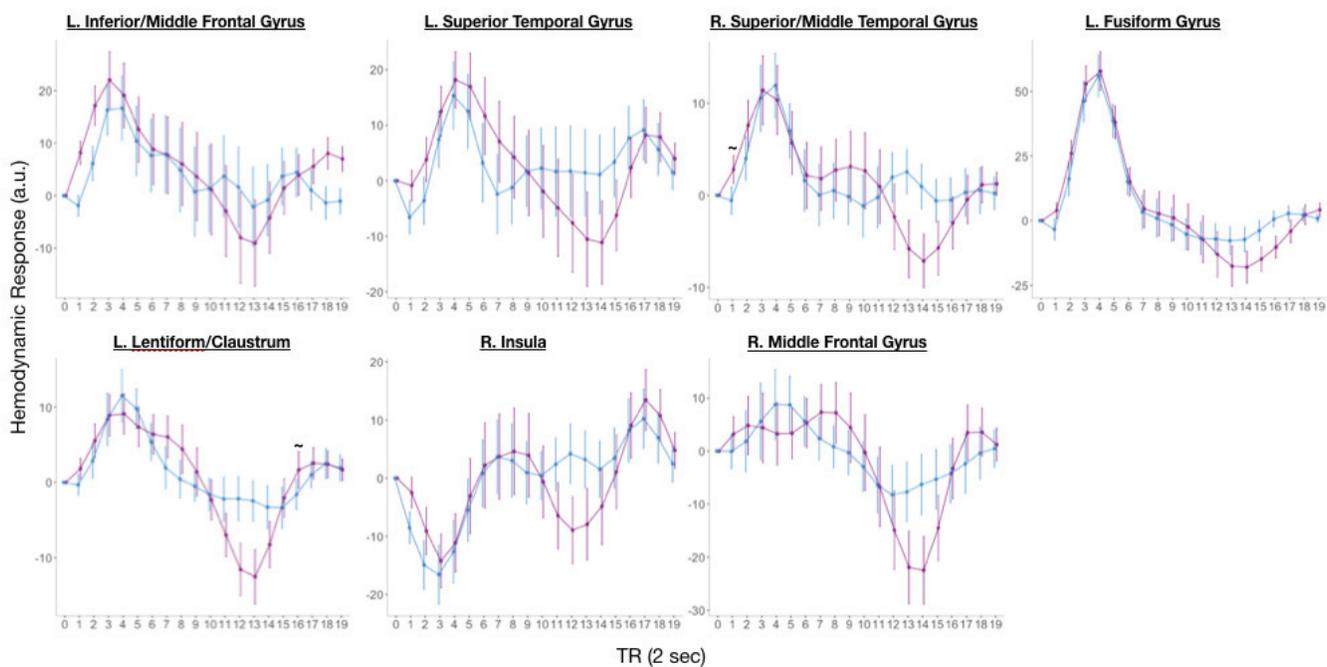
Contrast	TR				
	9	10	12	13	14
Adaptive > Baseline: Mean (SE)	-1.0 (4.1)	-2.1 (3.7)	4.6 (2.8)	4.2 (2.1)	-0.3 (2.4)
Maladaptive > Baseline: Mean (SE)	5.5 (5.2)	2.9 (4.1)	-5.9 (3.2)	-5.7 (3.3)	-5.2 (3.1)
Adaptive vs. Maladaptive t-test (p-value)	-2.5 (0.02)	-2.6 (0.02)	4.1 (0.001)	3.5 (0.002)	2.5 (0.02)
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)

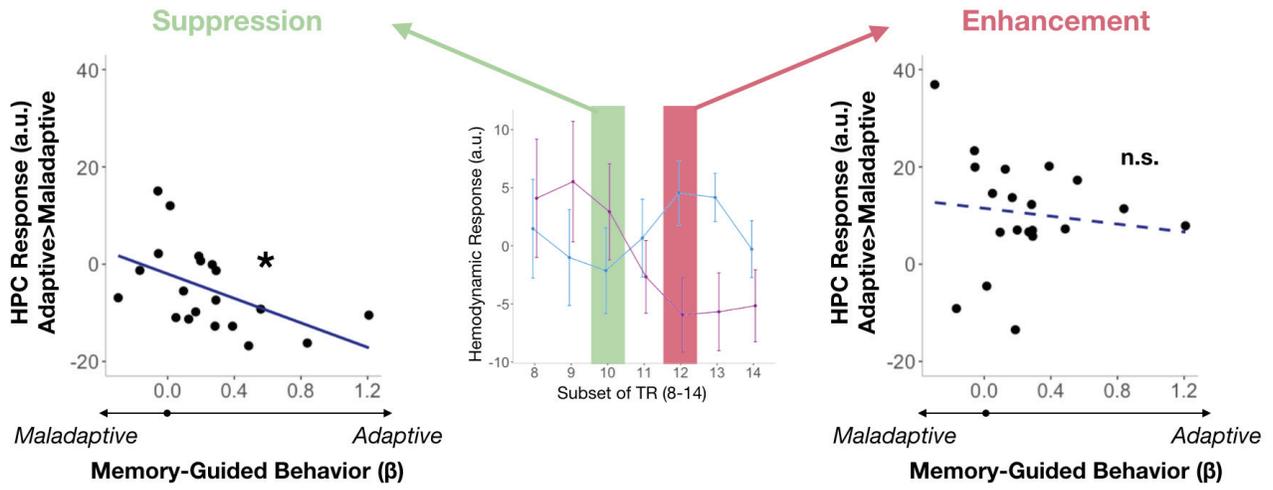
720

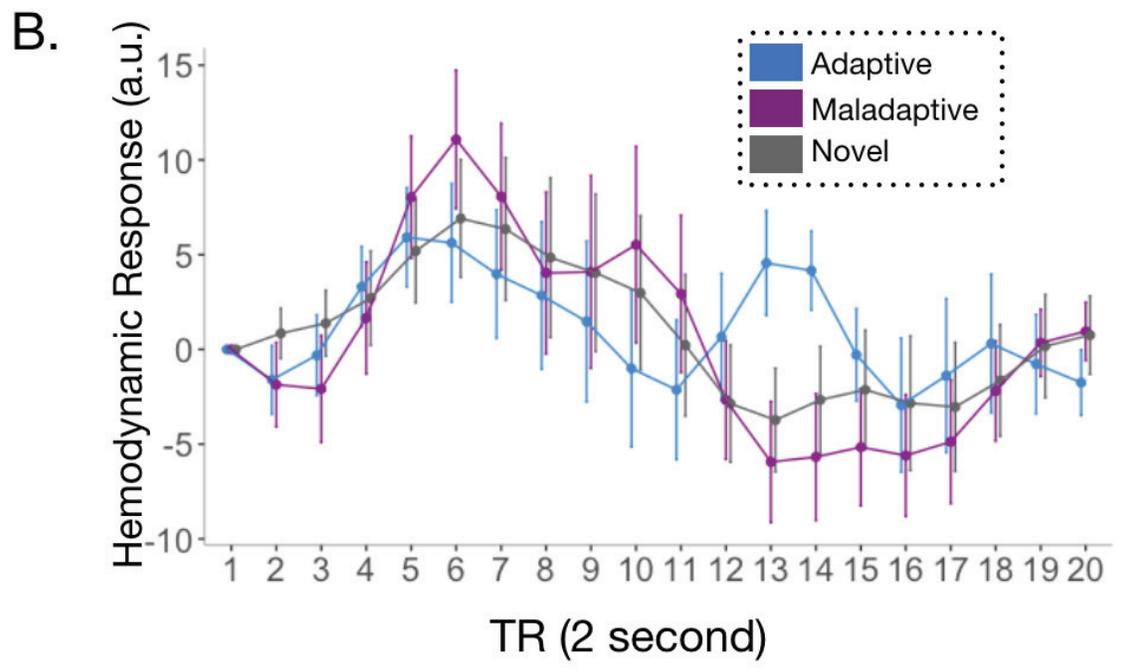
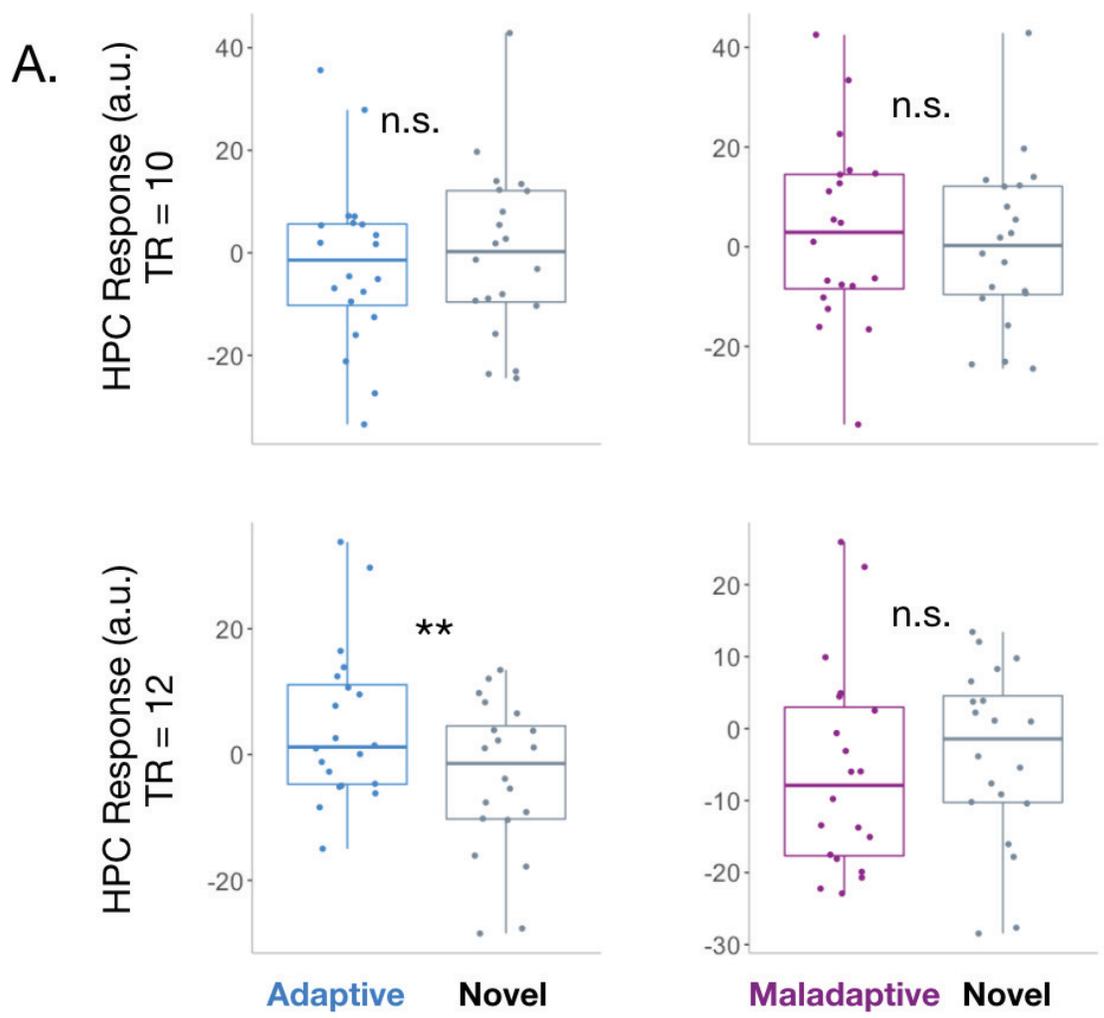




Decision Phase: Adaptive vs. Maladaptive

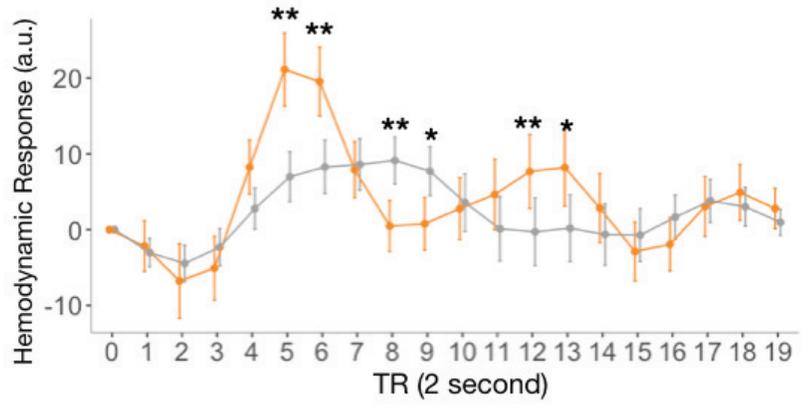
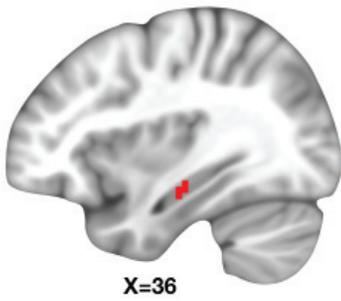






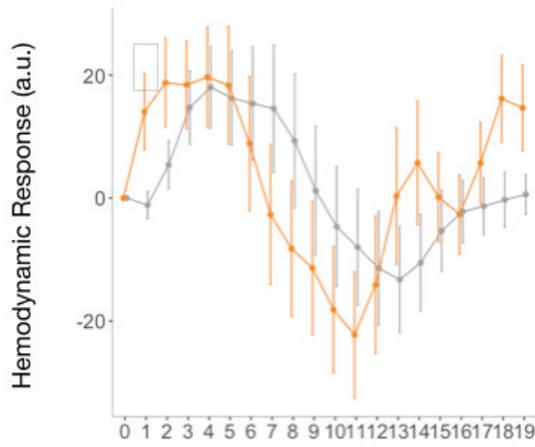
A

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

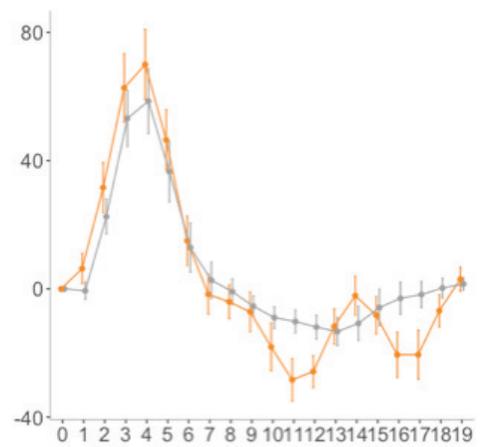


B

L. Middle Frontal Gyrus



R. Middle Occipital Gyrus



TR (2 second)