

**Title (50-word maximum):** Seeing social: A neural signature for conscious perception of social interactions

**Abbreviated title (50-character maximum):** A neural signature for conscious social perception

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# 1 **Seeing social: A neural signature for conscious perception of social** 2 **interactions**

3  
4 Rekha S. Varrier and Emily S. Finn

5 *Abstract (249/250 words)*

6 Percepts of ambiguous information are subjective and depend on observers' traits and mental  
7 states. Social information is some of the most ambiguous content we encounter in our daily lives,  
8 yet in experimental contexts, percepts of social interactions—i.e., whether an interaction is present  
9 and if so, the nature of that interaction—are often dichotomized as correct or incorrect based on  
10 experimenter-assigned labels. Here, we investigated the behavioral and neural correlates of  
11 conscious social perception using a large dataset in which neurotypical individuals viewed  
12 animations of geometric shapes during fMRI and indicated whether they perceived a social  
13 interaction or random motion. Critically, rather than experimenter-assigned labels, we used  
14 observers' own reports of “Social” or “Non-social” to classify percepts and characterize brain  
15 activity, including leveraging a particularly ambiguous animation perceived as “Social” by some  
16 observers but “Non-social” by others to control for visual input. Observers were biased toward  
17 perceiving information as social (versus non-social), and activity across much of the brain was  
18 higher during animations ultimately perceived as social. Using “Unsure” reports, we identified  
19 several regions that responded parametrically to perceived socialness. Neural responses to social  
20 versus nonsocial content diverged early both in time and in the cortical hierarchy. Lastly,  
21 individuals with higher internalizing trait scores showed both a higher response bias towards social  
22 and an inverse relationship with activity in default-mode and limbic regions while scanning for  
23 social information. Findings underscore the subjective nature of social perception and the  
24 importance of using observer reports to study percepts of social interactions.

25 [Significance Statement \(113/120 words\)](#)

26 Simple animations involving two or more geometric shapes have been used as a gold standard to  
27 understand social cognition and impairments thereof. Yet experimenter-assigned labels of what is  
28 social versus non-social are frequently used as a ground truth, despite the fact that percepts of such  
29 ambiguous social stimuli are highly subjective. Here, we used behavioral and fMRI data from a  
30 large sample of neurotypical individuals to show that participants' responses reveal subtle  
31 behavioral biases, help us study neural responses to social content more precisely, and covary with  
32 internalizing trait scores. Our findings underscore the subjective nature of social perception and  
33 the importance of considering observer reports in studying its behavioral and neural dynamics.

34

35 [Introduction: 650/650 words](#)

36 A remarkable feature of human perception is how quickly and automatically we identify social  
37 information in the environment. This is exemplified by pareidolia, the phenomenon of seeing  
38 illusory faces in everyday objects (Liu et al., 2014; Palmer & Clifford, 2020); our sensitivity to  
39 body language and gaze directed at us (e.g., Mona Lisa effect; Todorović, 2006) and our tendency  
40 to overhear salient social cues in otherwise unattended information streams (e.g., cocktail party  
41 effect; Wood & Cowan, 1995).

42 In the brain, regions along the superior temporal sulcus (STS) have been classically associated  
43 with social cognition: the more posterior regions (pSTS) are involved in animacy perception (Lee  
44 et al., 2014; Sugiura et al., 2014) while the more anterior regions are involved in higher-level  
45 processes like mentalizing, language and gaze detection (Carlin et al., 2011; Deen et al., 2015).  
46 The recently proposed third visual stream (Pitcher & Ungerleider, 2021) posits a specialized  
47 pathway for processing social information that emphasizes the role of biological motion. This

48 pathway proceeds from the primary visual cortex (V1) directly to the motion-processing region  
49 (V5/MT) followed by the pSTS and other STS subregions.

50 The association between motion and social perception is best exemplified by our tendency to  
51 spontaneously attribute social intentions to moving stimuli even when they consist of only simple  
52 geometric shapes (Bassili, 1976; Heider & Simmel, 1944; Scholl & Tremoulet, 2000). Whether  
53 such animations are seen as social depends largely on the movement patterns of the agents (Castelli  
54 et al., 2000; Gao et al., 2009). This phenomenon appears to transcend age (Gordon & Roemmele,  
55 2014; Rochat et al., 1997) and culture (Barrett et al., 2005), although interestingly, is not found in  
56 monkeys (Schafroth et al., 2021). Individuals with certain neurological or psychiatric conditions—  
57 most notably autism—are less likely to perceive social interactions in these animations (Abell et  
58 al., 2000; Fong et al., 2017; Klin, 2000; Langdon et al., 2020) and show commensurately lower  
59 activity in typical social processing regions of the brain (Castelli, 2002; Herrington et al., 2007;  
60 Kana et al., 2009, 2015).

61 However, socio-perceptual variability is not limited to clinical populations. Neurotypical  
62 individuals also vary in if and how they perceive social interactions – even when animations are  
63 handcrafted by experimenters to be clearly social or non-social (Li et al., 2020; Nguyen et al.,  
64 2019; Rasmussen & Jiang, 2019). In neurotypicals, social perception covaries with traits like  
65 loneliness, anxiety, psychopathy, and autism-like phenotypes (Desai et al., 2019; Epley et al.,  
66 2008; Gardner et al., 2005; Kanai et al., 2012; Lessard & Juvonen, 2018; Powers et al., 2014;  
67 Sacco et al., 2016). Thus, using participants’ own percepts and individual trait scores will likely  
68 help us understand social perception better than experimenter-assigned labels. Here, we relied on  
69 participants’ responses rather than a “ground truth”. Further, because visual features are often not  
70 well controlled between handcrafted stimuli intended to be seen as social non-social, when

71 possible, we also leveraged stimuli with similar or identical visual properties that nevertheless give  
72 rise to variable percepts across individuals.

73 In this study, we used a large dataset ( $n = 1049$  healthy young adults) from the Human  
74 Connectome Project (Barch et al., 2013; Van Essen et al., 2013) to investigate the behavioral and  
75 neural correlates of conscious social perception. We found that compared to negative reports  
76 (“Non-social”), positive identifications (“Social”) were more frequent, faster and associated with  
77 less uncertainty, indicating a bias toward perceiving information as social. Occipital, temporal and  
78 prefrontal brain regions showed higher activity to “Social” information even when controlling for  
79 visual properties of animations. Some regions showed intermediate activity levels to “Unsure”  
80 reports, suggesting a parametric response to perceived socialness. Differences in activity between  
81 “Social” and “Non-social” percepts emerged early in time and in the cortical hierarchy. Both  
82 percepts and brain activity while viewing animations also correlated with internalizing traits.  
83 Overall, results paint a nuanced and individualized picture of social perception, suggesting that  
84 socialness is “in the eye of the beholder”.

85

## 86 [Materials and Methods](#)

87 We primarily used data from the Social Cognition task of the Human Connectome Project  
88 (henceforth referred to as the “HCP study” or “HCP dataset”). The dataset is openly accessible,  
89 and consists of a large sample of neurotypical individuals, enabling us to study both the dominant  
90 and non-dominant percepts for specific animations. The social task was one of seven cognitive  
91 tasks that were run as part of the HCP task battery (Barch et al., 2013). In this task, participants  
92 watched ten 20s animations, of which five each were considered generally social and generally  
93 non-social (experimenter-assigned labels of Mental and Random, respectively). At the end of each

94 animation, participants indicated whether they perceived a social interaction by pressing buttons  
95 (“Social”, “Non-social”, “Unsure”). To distinguish experimenter-assigned labels from observer  
96 responses, in this paper we use the terms Mental and Random for the former, and “Social”,  
97 “Unsure” and “Non-social” for the latter. In the HCP dataset, participants also completed trait-  
98 level questionnaires, which enable the study of inter-individual differences. Here, we focused on  
99 internalizing symptoms, which include anxiety, loneliness, and social withdrawal (details below  
100 in section *Correlation between traits, behavior, and neural activity*).

101 As participants had to wait until the end of each 20s-long animation to make a response,  
102 the behavioral data in the HCP does not reveal *when* the perceptual decisions were made, and any  
103 differences in decision time are likely to influence the trajectory of brain activity. Hence, we  
104 additionally performed an online study on 100 neurotypical individuals (henceforth referred to as  
105 the “online RT experiment”) to gain insight into when in the course of the animation-watching  
106 decisions might have been made, and how this varied across particular animations and individuals.

## 107 **Participants**

108 This study used the Social Cognition Task dataset publicly available in the online HCP repository  
109 (<https://db.humanconnectome.org/>; for each participant, fMRI data sub-folders:  
110 *tfMRI\_SOCIAL\_RL* and *tfMRI\_SOCIAL\_LR*; behavioral: *\*TAB.txt*). Demographic information  
111 and trait scores used to study inter-individual differences were from the restricted category. We  
112 obtained complete fMRI data from 1049 individuals for the HCP Social Cognition task (ages 22-  
113 37; 562 female and 486 male).

114 For the online RT experiment that we conducted in July 2021, we recruited 100 neurotypical  
115 individuals (ages 18-48, mean = 23.2, SE = 0.64). from the United States and United Kingdom via  
116 the online platform Prolific ([www.prolific.co](http://www.prolific.co) , Palan & Schitter, 2018). Prior to the experiment,

117 all participants read and acknowledged the virtual consent forms in accordance with the  
118 Institutional Review Board of Dartmouth College, Hanover, New Hampshire, USA.

## 119 **Stimuli**

120 Stimuli in the HCP study were ten 20-second-long animations chosen from previous studies  
121 (Castelli et al., 2000; Wheatley et al., 2007). Longer animations had been snipped to 20s by the  
122 HCP researchers (Barch et al., 2013). The animations were presented in two runs with five  
123 animations each (run duration 3min 27s) interleaved with fixation blocks of 15s without jitter. The  
124 order of presentation was maintained across all participants (see Table 1). The number of Mental  
125 (M) and Random (R) animations were balanced within and between runs (run 1: 2M,3R; sequence  
126 M-R-R-M-R; run 2: 3M, 2R; sequence M-M-R-M-R. For a list of the animations as provided by  
127 the HCP and their properties, see Table 1. Note that in this paper, we drop the suffixes in the  
128 filenames (“-A” and “-B”) for convenience.

129 Each animation consisted of two or more shapes in motion (“agents”) with or without  
130 stationary elements (“props”). Seven of them (3M, 4R) had a large red and a smaller blue triangle  
131 as agents, and the remaining three (FISHING, RANDOM MECH, and SCARING) were more  
132 diverse in the number, color, and form of agents and props.

133 For the online RT experiment, we presented the same animations used in the HCP study  
134 and in the same presentation sequence, with a self-timed break after the fifth stimulus in lieu of  
135 the break between the two runs in the HCP study. In the practice phase, we randomly showed  
136 either a generally social or non-social animation (that was not one of the 10 animations used in the  
137 main task) to each participant. For a social practice example, we used MOCKING-B from the HCP  
138 repository, and for a non-social practice example, we created a two-agent animation comparable  
139 in appearance to MOCKING-B using a custom app Psyanim (the latter available here:

140 [https://github.com/rvarrier/HCP\\_socialtask\\_analysis/tree/main/stimuli](https://github.com/rvarrier/HCP_socialtask_analysis/tree/main/stimuli) – link will be made public  
141 on publication. In the meantime, please get in touch with us for the file).

142         The differences in physical properties that we noted above amongst the HCP animations  
143 could have influenced both behavior and brain activity. Hence, we factored these into our data  
144 analyses steps either by comparing the brain activity for “Social” and “Non-social” responses  
145 *within* the same animation (i.e., same visual input) or by regressing out physical properties like the  
146 optic flow and mean brightness before comparing individual pairs of animations in the analysis  
147 comparing timecourses (explained in the sub-section *fMRI Timecourse Analysis* under *fMRI data*  
148 *analysis*).

149         The presence of these visual differences also motivated our decision to perform the online  
150 RT experiment to estimate decision times and consequently the selection of a pair of animations  
151 with similar decision times (details in the *fMRI data analysis* section). Lastly, to address the  
152 physical differences between specific animations, we also included animation as a grouping  
153 variable (“random effect”) in certain behavioral and fMRI data analyses when pooling data from  
154 multiple animations.

155



**Table 1: Animations used in the HCP Social Cognition Task**

Run number	Presentation sequence	Animation file names (.AVI extension)	Experimenter-assigned category	Description of agents
1, <i>tfMRI_SOCIAL_RL</i>	1	COAXING-B	Mental	Bigger red triangle, smaller blue triangle.
	2	BILLIARDS-A	Random	
	3	DRIFTING-A	Random	
	4	FISHING	Mental	1 circle with a “fishing pole”, 1 oblong-shaped “fish”
	5	RANDOM MECHANICAL	Random	4 circles, 1 triangle, 1 long rectangle of multiple colors
2, <i>tfMRI_SOCIAL_LR</i>	1	SCARING	Mental	4 circles: 3 small pink, 1 large blue
	2	SEDUCING-B	Mental	Bigger red triangle, smaller blue triangle.
	3	STAR-A	Random	
	4	SURPRISING-B	Mental	
	5	TENNIS-A	Random	

156

157

## 158 **Experimental design**

159 In the HCP study, participants were given the following instructions about the task: “You will now  
 160 watch short clips and decide if the shapes are having a mental interaction or not. For a mental  
 161 interaction, press the button under your index finger. If you are not sure, press the button under  
 162 your middle finger. For a random interaction, press the button under your ring finger. After each  
 163 clip, there will be a response slide. Please respond while that slide is on the screen.” They had  
 164 three seconds to respond. In our online RT experiment, participants were given similar  
 165 instructions, but were asked to respond *twice* to each animation: once *during* the animation as soon  
 166 as they made a decision (left/right arrows for “Social”/ “Non-social”) and a second time *at the end*  
 167 of each animation within 3 seconds (left/right/down arrows for “Social”/”Non-social”/”Unsure”  
 168 similar to the HCP study).

## 169 **Data acquisition and pre-processing**

170 The fMRI data was acquired using a 3T Skyra scanner with 2mm isotropic voxels and a TR of  
171 0.72s (see Barch et al, 2013 for more acquisition details). Each run comprised 274 scan volumes,  
172 and there were two runs per participant. We used minimally preprocessed voxel-wise fMRI data  
173 (Glasser et al., 2013), parcellated this into 268 parcels spanning the whole brain as per Shen atlas  
174 (Shen et al., 2013) and discarded the first five scan volumes (TRs) within each run to reduce initial  
175 artifacts. Next, to make BOLD response magnitudes comparable across participants, we z-scored  
176 parcel-wise timecourses in each run. Further, since our analyses were to be performed at the trial-  
177 level, we split the run time series into trial-wise timecourses of 40s each – i.e., 20s animations (28  
178 TRs) flanked by 10s fixation periods (14 TRs) on either side (except for the first animation within  
179 each run which included only 6 pre-stimulus TRs). Data preprocessed in this manner was used for  
180 all fMRI analyses except one (the timecourse analysis, explained later) which required comparing  
181 two *individual* animations: COAXING and BILLIARD. Here, the z-normalization was done at the  
182 individual trial-level, to remove differences in mean activity that were due to the order of  
183 presentation (since order was not randomized between participants). In both cases, we lastly  
184 baseline-corrected each trial timecourse by subtracting the signal magnitude at the trial onset (i.e.,  
185 from the TR immediately before stimulus onset).

186 In the online RT experiment, we excluded trials in which either of the two responses (“during”  
187 phase and “after” phase) were missing or where the two responses differed; the latter was done to  
188 ensure that the response time we see in the “during” phase correspond to the percepts reported in  
189 the end (to match the HCP task). Lastly, as a quality check, participants with fewer than 8 out of  
190 10 good-quality (i.e., congruent) responses were also excluded, giving us 90 participants.

## 191 Behavioral data analysis

192 We performed four analyses to measure whether there is a general bias toward social percepts, or  
193 in other words, a shift towards “Social” responses. For these analyses, we included only  
194 participants who responded to all 10 animations and in whom the response times (RT) were not  
195 unrealistically small (i.e., RTs < 100ms were excluded), giving an n=823 for these analyses. Our  
196 dependent variables were:

197 (1) Percentages of “Social” and “Non-social” responses within participants; compared using a  
198 paired t-test

199 (2) Decision criterion, the signal detection theory metric quantified as  
200 
$$\frac{-Z(\text{Hit rate})+Z(\text{False alarm rate})}{2}$$
 (Stanislaw & Todorov, 1999), where Hit rate and False  
201 alarm rate were computed for each participant as fractions of “Social” responses for  
202 animations labelled by the experimenters as Mental and Random, respectively.

203 (3) Response time (RT) differences between “Social” vs. “Non-social” trials. We compared  
204 the RTs both using a non-parametric paired (Wilcoxon signed-rank) test and a more  
205 controlled linear mixed effects (LME) analyses to further account for the differences  
206 between individual animations. The LME model (LMEM) was of the form:  $\log(RT) =$   
207  $f(\text{response}; \text{random intercepts: participant, animation})$ . The factor *response* was  
208 categorical with two levels: “Non-social” (coded as the base level) and “Social”, and  
209 analysis was performed using the Python package `pymr4` (Jolly, 2018). We used the  
210 logarithm of the RT in seconds to bring the residuals of the LMEM closer to a normal  
211 distribution (which is an assumption for LMEMs).

212 (4) Percentage of “Unsure” responses for the two animation labels (Mental, Random). These  
213 were compared using a logistic regression model:  $\text{uncertainty} =$

214  $f(\text{stimLabel}; \text{random intercepts: participant, animation})$  where the factor  
215  $\text{stimLabel}$  was categorical [Mental, Random], and the dependent variable  $\text{uncertainty}$  had  
216 a value of “1” for “Unsure” response trials and “0” otherwise. Keeping Random (0) as the  
217 baseline in the analysis, positive/ negative regression coefficients for  $\text{stimLabel}$  would  
218 indicate a lower/ higher uncertainty in categorizing Random trials.

## 219 **fMRI data analysis**

220 **GLM-based regression:** Our primary approach to fMRI data analysis was a general linear model  
221 (GLM) based on animation onset and offset. We computed the regression coefficients for each  
222 animation separately for the majority of analyses. For each animation, we fitted each parcel’s  
223 activity timecourse to a “slope” regressor (line steadily increasing from 0 to 1 from baseline to the  
224 duration of an animation, i.e., 20s, and padded by zeros before and after) that was convolved by  
225 the Glover HRF (Glover, 1999). (Preliminary analyses had indicated that a steadily increasing  
226 slope regressor captured more variance in the BOLD data than a traditional boxcar regressor.) This  
227 renders one slope regression coefficient ( $\beta$ ) per parcel, participant, and trial (animation). We also  
228 performed a separate GLM analysis across all animations (details in the section below). For this  
229 analysis, we used a *run*-level regressor and estimated coefficients for each parcel, participant, and  
230 *run*. Similar to the slope regressors used at the trial level, regressor values increased (decreased)  
231 steadily during an animation labelled “Social” (“Non-social”) and were 0 at all other timepoints  
232 (including “Unsure” responses) – thus, the run-level regression coefficient here summarizes a  
233 *contrast* between “Social” and “Non-social”. For each participant, we then averaged these  
234 coefficients across the two runs.

235

236 **“Social” vs. “Non-social”**: To identify brain regions showing a consistent and generalizable  
237 difference between “Social” and “Non-social” responses, we compared the regression coefficients  
238 between “Social” and “Non-social” percepts in three analyses: (1) controlled for visual input, (2)  
239 controlled for decision times and (3) across all animations (Table 2). For analyses with individual  
240 animations, we included all participants who gave a valid response to the animation(s) in that  
241 analysis, resulting in slightly different numbers of participants in each analysis. Each analysis is  
242 described in detail below:

243 (1) **Controlled for visual input**: We selected the most ambiguous animation, namely RANDOM  
244 MECH, since it has the relatively most balanced “Social” and “Non-social” response groups.  
245 We excluded participants who gave an “Unsure” response to this stimulus (leaving  $n=777$ )  
246 and then split regression coefficients based on observer responses (“Social”:  $n=107$ , “Non-  
247 social”:  $n=670$ , see Figure 1a), and compared them with two-sample t-tests assuming unequal  
248 variances.

249 (2) **Control for decision time (COAXING vs. BILLIARD)**: We chose two animations which  
250 were most comparable in terms of the time taken to arrive at a decision about whether an  
251 animation was “Social” or “Non-social”. This was based on the data we obtained from the  
252 online RT experiment, where the decision time to report “Social” to COAXING ( $median =$   
253  $3.45s$ ,  $SEM = 0.27s$ ) and “Non-social” to BILLIARD ( $median = 3.7s$ ,  $SEM = 0.25s$ ) were the  
254 closest and did not significantly differ (see Figure 2c and the results sub-section on decision  
255 time for more). Hence, we compared regression coefficients for each of these two animations  
256 within participants using a paired t-test. Note that we excluded participants who gave an  
257 uncertain or non-dominant response for one or both animations (i.e., who responded to

258 COAXING as “Non-social” or “Unsure” or BILLIARDS as “Social” or “Unsure”), giving us  
259  $n = 870$  for this analysis.

260 (3) **Across all animations (ALL):** We also performed a more general comparison between  
261 individuals’ responsiveness to “Social” vs. “Non-social” by identifying brain regions that  
262 show a mean run-level regression coefficient that is different from 0 (for details on how the  
263 run-wise regressor was estimated, see sub-section *GLM-based regression* above). To  
264 minimize biases due to missed responses, we only selected participants who had given all 10  
265 responses and had complete fMRI data from both runs ( $n=814$ ) using a one-sample t-test  
266 compared to 0.

267  
268 Lastly, we identified brain regions that were significant in all three of the above comparisons  
269 and showed changes in the same direction (either “Social” > “Non-social” in all three comparisons  
270 or vice versa) at the FDR-corrected threshold ( $q < .05$ ). We henceforth refer to this procedure as  
271 the “intersection analysis” and the resultant parcels as “social processing regions”.

**Table 2: GLM analyses based on observer responses**

Analysis Nr.	“Social” responder group	“Non-social” responder group	Rationale for the analysis	Statistical comparisons for fMRI	ID for the analysis used in figures and text
1	RANDOM MECHANICAL (within-animation, between-participant)		<ul style="list-style-type: none"> <li>Controls for low-level input</li> <li>Most ambiguous animation</li> </ul>	Two-sample t-test	RANDOM MECH
2	COAXING	BILLIARD	<ul style="list-style-type: none"> <li>Likely similar decision times <i>during</i> animation (as estimated from online RT experiment)</li> </ul>	Paired t-test	COAXING-BILLIARD
	(between-animation, within-participant)				
3	All “Social”	All “Non-social”	<ul style="list-style-type: none"> <li>Maximizes power by comparing all “Social” responses with all “Non-social” responses within participants</li> </ul>	One-sample t-test after averaging run-wise estimates	ALL ANIMATIONS
	Coded 1 (“Social”) and -1 (“Non-social”), in run-wise GLMs.				

272

273

274 **“Social” vs. “Unsure” vs. “Non-social”**: We also leveraged the “Unsure” responses to identify  
 275 brain regions that responded parametrically to level of perceived socialness. We predicted that the  
 276 neural response in such regions during animations ultimately marked “Unsure” would be  
 277 intermediate to that of “Social” and “Non-social” responses. But note that intermediate does not  
 278 necessarily mean halfway, and hence we performed conjunction analyses – i.e., we identified brain  
 279 regions showing “Social” > “Unsure” and “Unsure” > “Non-social” (or vice-versa) and took the  
 280 intersection of these. We performed this analysis across all the animations using an LMEM of the  
 281 form:  $\beta = f(\text{response}, \text{RI}; \text{participant})$  which was performed separately for “Social” vs.  
 282 “Unsure” (LMEM 1) and “Unsure” vs. “Non-social” (LMEM 2). In each LMEM, *response* was a  
 283 categorical variable that has the values “Social” and “Unsure” in LMEM 1 (baseline “Unsure”),  
 284 and “Unsure” and “Non-social” in LMEM 2 (baseline “Non-social”). Thus, a positive LMEM  
 285 estimate for *response* would indicate a higher neural response corresponding to a higher perceived

286 socialness. From this, we identified parcels which showed the same directionality for LMEM 1  
287 and 2 at the multiple comparison-corrected threshold, and which were also in the set of social  
288 processing regions in the GLM analysis above.

289 ***fMRI Timecourse analysis:*** To identify the brain regions where the earliest differences in brain  
290 activity between “Social” and “Non-social” percepts emerged, we performed paired t-tests (within  
291 participant) for each timepoint (TR) between BOLD responses corresponding to a pair of “Social”  
292 and “Non-social” animations (COAXING and BILLIARD, respectively) in which decisions of  
293 whether the animation was social or non-social were likely made at comparable times *while*  
294 watching them as explained previously in the analysis sub-section “*Social*” vs. “*Non-social*”. To  
295 ensure that the differences between BOLD activity between COAXING and BILLIARD are not  
296 due to differences in basic visual input between the two animations, we performed these  
297 comparisons on the residual timecourses obtained after regressing out two low-level visual  
298 features, total optic flow and mean brightness. We first estimated these two features for each  
299 animation frame using the “pliers” package (McNamara et al., 2017), then down-sampled the  
300 resulting timecourses to match the temporal resolution of the fMRI data (i.e., the TR), z-  
301 transformed them and convolved them with an HRF. We then performed a linear regression on  
302 each participant’s trial timecourse (including 14TRs flanking the stimulus duration on either end  
303 like with the slope regressors described earlier) to regress out the changes in BOLD activity related  
304 to these features. We then used the resultant *residual* timecourses for COAXING and BILLIARD  
305 for the timecourse analysis. We compared these at each timepoint (TR) and for each parcel using  
306 paired t-tests (within participant). For each parcel, we thus identified the earliest timepoint at which  
307 BOLD activity begins to diverge. As additional consistency checks, we (1) only performed this  
308 analysis in the social processing regions that consistently differentiated between “Social” and



309 “Non-social” in the GLM analyses, and (2) selected a TR  $t$  as the divergence point only if the  
310 difference between “Social” vs. “Non-social” at  $t+I$  was also significantly different in the same  
311 direction.

312 Note that this analysis does not factor in the hemodynamic lag. This is because although  
313 the HRF *peaks* a few seconds after an event (in our case, the animation onset), the neural responses  
314 to stimulus presentation should have begun instantly (Friston et al., 1994), so here we investigated  
315 where these earliest changes could be observed. Further, in using the median decision times from  
316 the online RT experiment for COAXING and BILLIARD as the expected decision time for the  
317 HCP dataset, we did not factor in the motor response delay (i.e., time taken after a decision has  
318 been made to press a button) in the online RT experiment. Hence it is possible that some of the  
319 pre-decisional processes closer to the decision time may have in fact been post-decisional. While  
320 we cannot exclude this possibility, this was unlikely since motor responses on arriving at a decision  
321 are typically quicker than the TR used in the HCP task (0.72s).

322 We also did not multiple comparison-correct across timepoints in this analysis since the  
323 primary goal was to identify the *earliest* differences in activity, and to infer this correctly, false  
324 negatives are less preferred to false positives. Further, in identifying the earliest timepoints, we  
325 only selected a region if the subsequent timepoint was also significant ( $p < .05$  uncorrected),  
326 limiting the odds of a false positive further by 95%.

327 We also did not perform this analysis within the same animation (RANDOM MECH) and  
328 across all animations like in the GLM analysis (sub-section “*Social*” vs. “*Non-social*”) because  
329 of the heterogeneity in decision times both between reported percepts for the same animation and  
330 across animations (see Figure 2c). This means that the neural processes at each time point could  
331 have also been vastly different between “Social” and “Non-social” animations, thus making the

332 comparison of timecourses less precise both within the same animation (RANDOM MECH) and  
333 across all animations.

### 334 **Correlations between traits, behavior, and neural activity**

335 Past work has shown that individuals high on internalizing traits such as loneliness and anxiety  
336 tend to form illusory social connections by anthropomorphizing inanimate objects (Epley et al.,  
337 2008; Powers et al., 2014) and show smaller grey matter volumes in a brain region typically  
338 associated with social processing, the pSTS (Kanai et al., 2012). Here, we probed whether  
339 internalizing traits affect behavior and/or brain activity associated with social perception using the  
340 internalizing T-score provided by the HCP (Barch et al., 2013). This score is based on participants’  
341 responses to the internalizing dimension questions which is part of the Achenbach Adult Self-  
342 Report questionnaire (ASR; Achenbach et al., 2017). Internalizing symptoms refer to symptoms  
343 like anxiety, depression, and withdrawal, and are typically contrasted with externalizing behaviors  
344 such as rule-breaking and aggression. The ASR was designed to assess behavioral, emotional, and  
345 social functioning across a wide spectrum of the population, so it is sensitive to individual  
346 differences (i.e., produces a range of scores) even in healthy/subclinical populations. We used the  
347 averaged T-scored participant-level internalizing score (labelled “ASR\_Intn\_T” in the HCP  
348 dataset;  $M = 48.72$ ,  $STD = 10.75$ ,  $range = 30-97$ ) for this analysis; see Figure 6a-c for the full  
349 distribution).

350 To assess whether internalizing score relates to a behavioral bias toward “Social” percepts,  
351 we correlated participants’ internalizing scores with the following behavioral variables using  
352 Spearman (rank) correlation: (1) the difference between % of “Social” and % of “Non-social”  
353 responses (calculated as percentages to control for missing data) and (2) the number of “Unsure”  
354 responses for Mental and Random trials, respectively. We also compared the internalizing scores

355 between “Non-social” and “Social” or “Unsure” responders to the most ambiguous animation,  
356 RANDOM MECH. We tested the specificity of these correlations by additionally performing  
357 correlations with externalizing scores and comparing the two using the CorrelationStats package  
358 (<https://github.com/psinger/CorrelationStats>). To quantify if and where internalizing traits relate  
359 to brain activity while scanning animations for social information, for each parcel, we performed  
360 an LME analysis where the dependent variable was the slope regression coefficient, the fixed  
361 factor was internalizing score and the random factor was animation. This yields brain regions that  
362 respond proportionately to internalizing score in that individual across animations and parcels.

### 363 **Code availability**

364 All the code for analyzing data from both the HCP and online RT experiment, as well as the  
365 anonymized data from the online RT experiment, will be made available upon publication here:  
366 [https://github.com/rvarrier/HCP\\_socialtask\\_analysis](https://github.com/rvarrier/HCP_socialtask_analysis). In the meantime, please get in touch with  
367 the authors for these.

368

### 369 **Results**

370 In this study, we used behavior, fMRI data, and individual trait scores from the Human  
371 Connectome Project (HCP) social cognition task to characterize the behavioral and neural  
372 processes underlying conscious perception of social interactions. We started by evaluating the  
373 behavioral data for any response bias: are people more inclined to declare something “Social” (as  
374 opposed to “Non-social”)? We next identified brain regions that robustly differentiated between  
375 “Social” and “Non-social” percepts even when controlled for decision times and sensory  
376 information, including a subset of regions that showed a parametric response pattern to degrees of  
377 perceived socialness. Next, we used a timepoint-by-timepoint analysis to identify where and when

378 brain activity begins to diverge between “Social” and “Non-social” percepts. Lastly, we studied  
379 the relationship between internalizing behavior scores, tendency toward social percepts, and brain  
380 activity while scanning for social information.

### 381 **Some animations are more ambiguous than others**

382 First, we examined the degree to which participants’ percepts of “Social” versus “Non-social”  
383 information agreed with one another as well as the intended stimulus category. In the HCP social  
384 cognition task, participants passively watched ten 20-s animations of geometric shapes (Heider-  
385 Simmel-like; Castelli et al., 2000), see *Materials and Methods* sub-section *Stimuli* for a detailed  
386 description of the animations) and then made a behavioral response — “Social”, “Non-social” or  
387 “Unsure”—to indicate whether they perceived a social interaction in the animation. Five  
388 animations were intended to evoke social interactions (experimenter-assigned Mental) and five  
389 were not (experimenter-assigned Random). Although on average participants’ percepts aligned  
390 with experimenter labels, the degree to which animations were perceived as “Social” and “Non-  
391 social” varied considerably. This was true in both the HCP behavioral data and the secondary  
392 online dataset (online RT experiment) we collected to study the time taken for individuals to arrive  
393 at decisions while watching each animation (Figure 1a and 2a). While animations like DRIFTING  
394 and BILLIARD were seen almost unanimously as “Non-social”, animations like RANDOM  
395 MECH and FISHING had a higher percentage of the non-dominant percept as well as “Unsure”  
396 responses. This underscores the need to use participants’ own percepts to categorize what is or is  
397 not “Social” rather than experimenter-assigned labels. Further, in our analyses, we leverage this  
398 ambiguity by comparing neural activity corresponding to “Social” and “Non-social” responses  
399 within the most variably perceived animation (RANDOM MECH), thereby isolating activity  
400 associated with a conscious social percept while controlling for visual input.

## 401 **Responses are biased toward “Social”**

402 Next, we used behaviorally reported percepts to determine whether there was a response bias  
403 towards “Social”. We hypothesized that evolutionarily, there may be a bias towards perceiving  
404 information as social, since the cost of a false positive (e.g., mistakenly thinking someone is trying  
405 to engage you in a social interaction) is lesser than that of a false negative (e.g., missing out on  
406 social cues that are important for group dynamics, reproduction, and survival). We predicted that  
407 this bias would manifest as a higher “Social” response rate, shorter response times for “Social”  
408 percepts, and more “Unsure” responses to animations labeled Random by experimenters (because  
409 of a reluctance to declare something entirely non-social). Our findings are described below:

410 **(1) 'Social' responses are more frequent:** On comparing the frequency of percepts for each  
411 participant (limited to trials where participants were sure of their response—i.e., excluding  
412 “Unsure” trials), we observed that the percentage of “Social” responses was subtly but  
413 significantly higher ( $M = 52.89\%$ ,  $SE = 0.29\%$ ) than “Non-social” responses ( $M = 47.11\%$ ,  $SE =$   
414  $0.29\%$ ; paired t-test,  $p < 10^{-21}$ ; Figure 1b).

415 **(2) The response criterion further shows a bias towards "Social":** Next, we computed  
416 criterion ( $c$ ), a metric from signal detection theory that quantifies response biases. If the mean  
417 criterion  $\bar{c}$  is significantly different from zero, this suggests a bias in responses towards “Social”  
418 ( $\bar{c} < 0$ ) or “Non-social” ( $\bar{c} > 0$ ). We found that criterion was significantly negative ( $M =$   
419  $-0.047$ ,  $SE = 0.006$ ; Wilcoxon test  $p < 10^{-17}$ ; Figure 1c), further confirming the response bias  
420 towards “Social”. In this computation, we used the experimenter-assigned labels to show that  
421 although the experimenters aimed to create a balanced set of five Mental and five Random  
422 animations, actual observer reports indicate that individuals ended up perceiving more animations

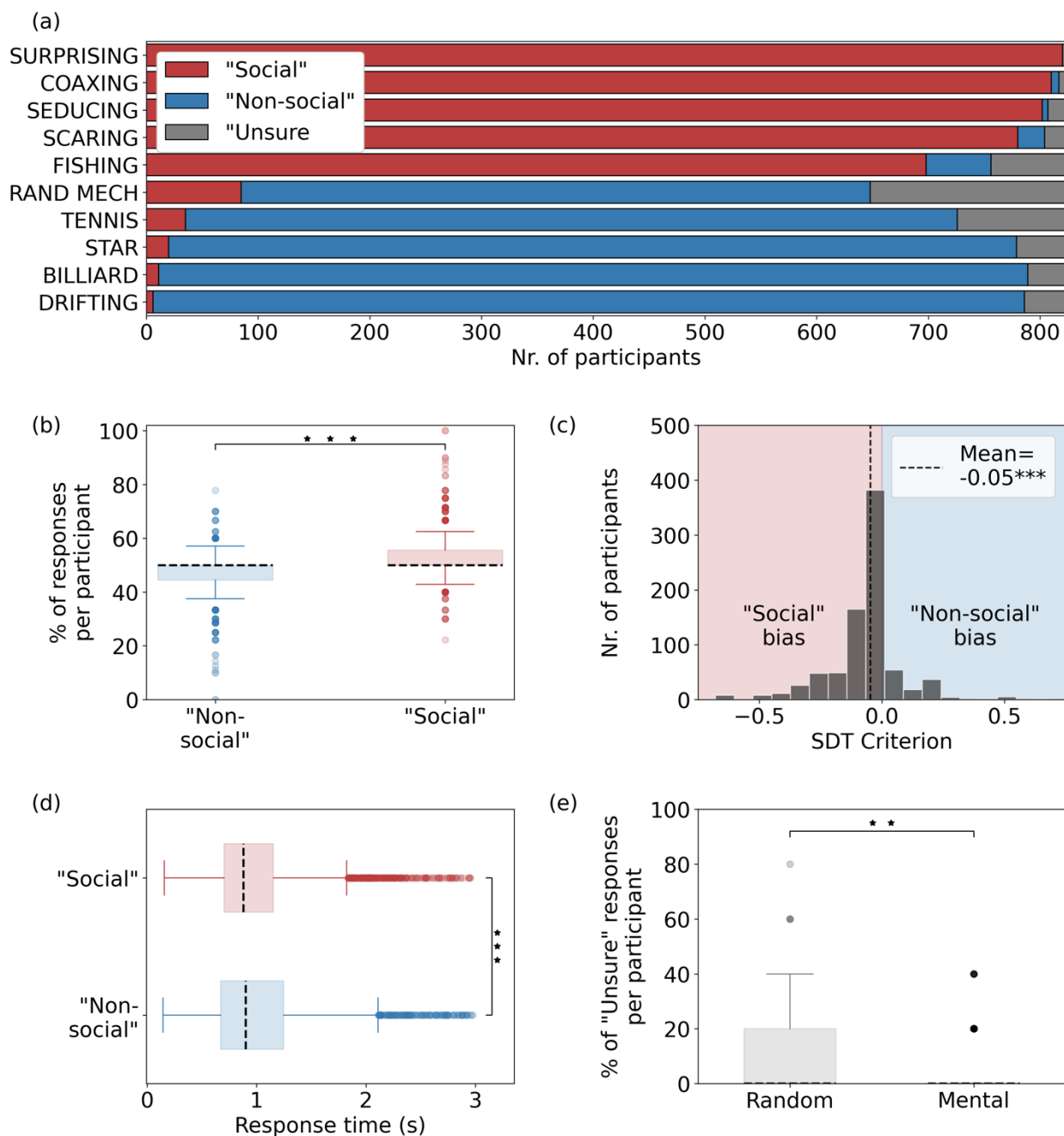
423 as “Social”. Thus, experimenter labels appear to be insufficient to explain all individuals’ “ground  
424 truth” percepts.

425 **(3) Responders may have been quicker to declare something as “Social” than “Non-**  
426 **social”:** Next, to get at a more subconscious measure of perceptual decision-making for social  
427 information, we compared response times between “Social” ( $med = 0.87s$ ,  $SE = 0.009s$ ) and  
428 “Non-social” ( $med = 0.9s$ ,  $SE = 0.012s$ ) responses (Figure. 1d) and found that “Social” responses  
429 were overall faster ( $p < 10^{-3}$ , Wilcoxon signed rank). Since response times could differ by  
430 animation due to their heterogeneity, we additionally performed an LME analysis with response  
431 (“Social” or “Non-social” [baseline]) as the fixed effect, and both animation and participant as  
432 random effects. We observed a trend towards shorter RTs for “Social” responses, but this did not  
433 reach significance ( $Est. = -0.037$ ,  $p = .1$ ).

434 **(4) “Unsure” responses were more common for animations intended as Random**  
435 **compared to those intended as Mental:** We studied the distribution of “Unsure” responses  
436 between animations that were intended to be “Social” (Mental) or “Non-social” (Random) and  
437 noted that there was a higher percentage of “Unsure” responses in the animations intended as  
438 Random ( $M = 9.41\%$ ,  $SE = 0.5\%$ ; Figure 1e) compared to those intended as Mental ( $M =$   
439  $2.70\%$ ,  $SE = 0.26\%$ ). This indicated that people were more reluctant to label something “Non-  
440 social” (as opposed to “Social”) when their confidence is low. In other words, they err on the  
441 side of false alarms rather than misses; this fits with the idea that misses are likely costlier than  
442 false alarms. We formally compared the frequency of “Unsure” responses using logistic  
443 regression with Mental (coded 1) and Random (coded 0) label as the fixed effect and participant  
444 ID and animation as random intercepts. Results showed higher uncertainty on Random trials  
445 even after accounting for the differences in animations ( $Est. = -1.61$ ,  $p = .005$ ).

446

447 To summarize, the behavioral data overall showed a bias towards “Social” responses based on  
 448 percentage of each response type, response times and degree of uncertainty.



449

450 **Figure 1. Behavioral data from the HCP participants (n=823) show a bias toward “Social”**

451 **responses.** (a) Number of responses per type (“Social”, “Non-social”, “Unsure”) and animation

452 sorted from most to least “Social”. (b) Percentages of “Social” and “Non-social” responses.  
453 There was a higher number of “Social” responses ( $p < 10^{-21}$ , paired *t*-test). (c) Signal detection  
454 theory metric “criterion” across participants based on experimenter-assigned labels. Mean  
455 criterion was negative ( $-0.05$ ,  $p < 10^{-17}$ , Wilcoxon signed rank test), indicating a bias toward  
456 false alarms (i.e., declaring an animation labeled Random by experimenters as “Social”). (d)  
457 Response time for “Social” and “Non-social” responses. “Social” responses tended to be  
458 quicker (Wilcoxon signed-rank,  $p < 10^{-3}$ ). (e) “Unsure” responses for animations labelled  
459 Mental and Random by experimenters. There was a higher percent of “Unsure” responses for  
460 Random responses (LMEM: Est. =  $-2.15$ ,  $p < .005$ ). \*\*:  $p < .001$ , \*\*\*:  $p < .0001$

#### 461 **Decision time as to whether an animation is “Social” varies widely between animations**

462 In the HCP study, participants had to wait till the end of each animation (lasting 20s) to make a  
463 behavioral response. However, the decision as to whether an animation was “Social” or “Non-  
464 social” was presumably made sometime during passive viewing, although the decision time  
465 could have varied widely across animations and participants. This variability, in turn, might  
466 influence the timecourse of brain activity (e.g., visual attention for the same animation may be  
467 different when a participant makes a decision 2 seconds after the animation begins vs. 15  
468 seconds after). Hence, getting information as to when decisions could likely have been made  
469 during each animation was critical to modeling and interpreting neuroimaging data. To this end,  
470 we performed an independent online behavioral study using the same animations where  
471 participants (final  $n = 90$ ) were instructed to indicate their percepts as soon as they had arrived at  
472 a decision (“during” phase). To compare the results with the HCP study, participants were also  
473 instructed to respond at the end of each trial (“after” phase).



474           The consensus across participants of which animations were generally “Social” versus  
475 “Non-social” in the online sample was comparable to that of the HCP sample (see Figure 2a). As  
476 a corollary to this, the animations with high variability in decision times in the online RT  
477 experiment also tended to have less consensus across participants in the HCP study – the latter  
478 operationalized as (1) the absolute value of the difference between % “Social” and % “Non-  
479 social” animations (Figure 2b, left) and (2) higher number of “Unsure” responses (Figure 2b,  
480 right). The reaction time data from the “during” phase (Figure 2c) showed that while most  
481 responses were made in the earlier half of the 20 second animations, there was a high variability  
482 in decision time both within and across animations. This means that the brain activity  
483 corresponding to an especially ambiguous animation (e.g., SCARING, RANDOM MECH) could  
484 have been vastly different even amongst participants who reported the same percept for these,  
485 depending on when each participant made their decision and how this affected their attention  
486 before and after the decision. Hence, we identified two animations with the most comparable  
487 decision times, namely, COAXING ( $med = 3.45s$ ,  $SEM = 0.27s$ ), a predominantly “Social”  
488 animation, and BILLIARD ( $med = 3.7s$ ,  $SE = 0.25s$ ), a predominantly “Non-social” animation,  
489 whose decision times were not significantly different (Wilcoxon signed-rank test [paired],  $T =$   
490 1619,  $p = .57$ ). We used this pair of animations in later analyses that required a control for  
491 decision time while watching an animation.

492

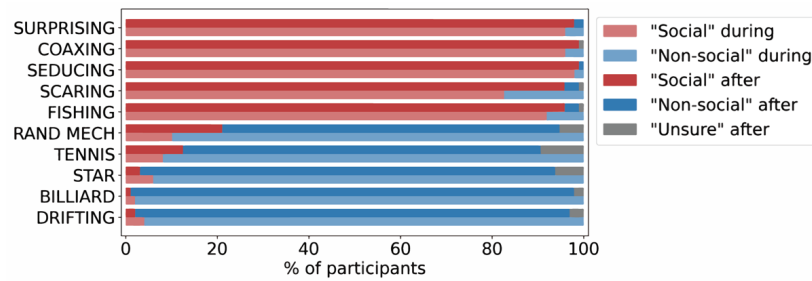
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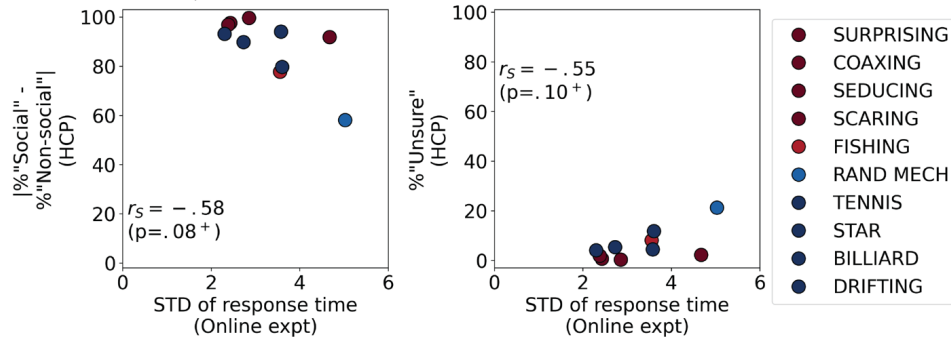
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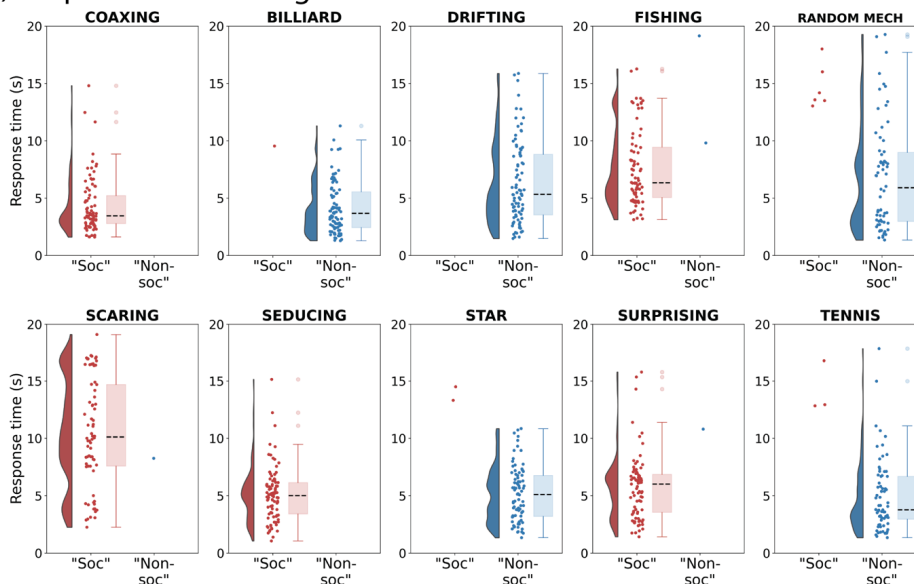
(a) Response time during and after each animation



(b) Uncertainty in decision time during an animation



(c) Response time during each animation



497

498 **Figure 2: Results of the online RT experiment to characterize decision time for each**

499 **animation.** (a) Number of "Social", "Non-social" and "Unsure" responses per animation made

500 during (lighter shades) and after (darker shades) each animation. Order of animations on the Y-

501 axis is the same as for the HCP data in Figure 1a. The degree to which animations were

502 reported "Social" is comparable to the HCP behavioral data in Figure 1a. (b) Standard

503 *deviation of response time while watching each animation (in seconds; X-axis) vs. two indicators*  
504 *of uncertainty from the HCP behavioral data on the Y-axes (left: absolute difference between*  
505 *number of "Social" and "Non-social" responses, an indicator of how definitive responses for this*  
506 *animation were across participants; right: % of "Unsure" responses). Spearman (rank)*  
507 *correlation shows a trend ( $p \leq .1$ , marked with '+') for the animations with higher variation in*  
508 *response times in the online RT experiment (X-axes) to also a less definitive response (left) and a*  
509 *higher % of "Unsure" responses (right) in the HCP behavioral data. (c) Distribution of*  
510 *response times for "Social" and "Non-social" responses while watching each animation (in*  
511 *seconds). As seen in (b), decision times varied more for some animations than others. Note the*  
512 *similarity in the decision times between COAXING "Social" and BILLIARD "Non-social".*

### 513 **Much of the brain responds more strongly to what is perceived as social information**

514 In the next set of analyses spanning this and the next two sections, we used the fMRI data to  
515 understand where and when the brain distinguishes social from non-social information. For all  
516 fMRI analyses, whole-brain data were parcellated into 268 regions covering the cortex, subcortex,  
517 and cerebellum using the Shen atlas (Shen et al., 2013) to ease the computational burden of voxel-  
518 wise analyses.

519 In the first fMRI analysis, we focused on the question of "where" by comparing overall  
520 neural responsiveness while viewing animations ultimately deemed "Social" versus "Non-social".

521 In addition to regions along the STS which are known to be involved in animacy and interaction  
522 perception, we hypothesized that differences might emerge as early as visual regions. We  
523 compared "Social" and "Non-social" responses using a general linear model (GLM) approach—  
524 again, using the participant's reported percept rather than the experimenter-assigned label as input  
525 to the model—in three separate contrasts to ensure results were robust to different confounding

526 factors: 1) within the single most ambiguous animation (RANDOM MECH), which controls for  
527 visual input (since all participants saw the same animation, but reported different percepts; across-  
528 participants); 2) between two animations with similar decision times (COAXING vs BILLIARD),  
529 to control for effect of when the decision was likely made on the timecourse of brain activity during  
530 passive viewing (within-participants); and 3) across all ten animations, to maximize power and  
531 ensure generalizability (within-participants). We then identified social processing regions by  
532 taking the intersection of the regions showing a significant difference in all three analyses.

533 In total, 70 parcels showed "Social" > "Non-social" activity (FDR  $q < .05$ , black contours  
534 in Figure 3) consistently across all three comparisons, and no parcel showed "Non-social" >  
535 "Social" across analyses. Of these, 66 parcels showed positive activations for both the "Social"  
536 ( $\beta^{\text{Social}} > 0$ ) and "Non-social" ( $\beta^{\text{Non-Social}} > 0$ ) responses for both RANDOM MECH and  
537 COAXING-BILLIARD, suggesting that on the whole, much of the brain showed higher *activation*  
538 and not lower *deactivation* to "Social" compared to "Non-social". These parcels spanned the  
539 occipitotemporal and prefrontal cortex, the cerebellum, and some sub-cortical regions (details in  
540 Table 3).

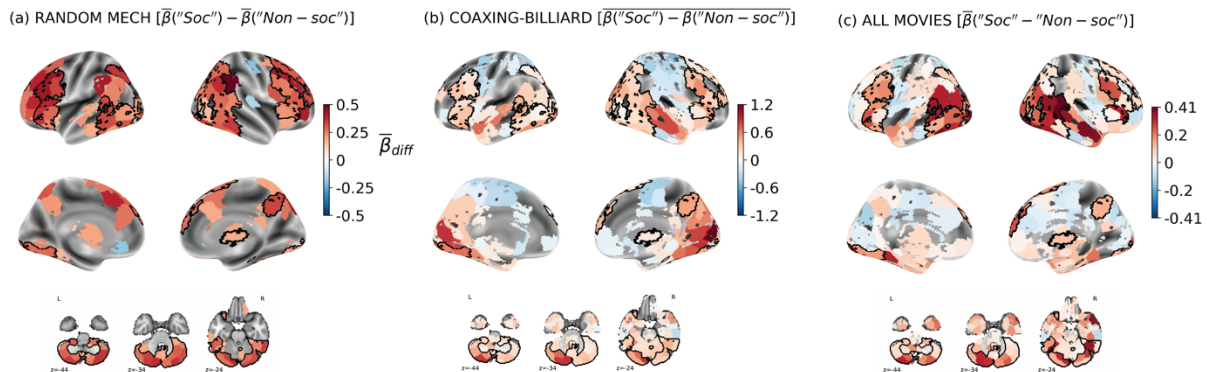
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**Table 3: Brain regions showing robust “Social” v. “Non-social” differences**

Lobe	Regions
Occipital	<ul style="list-style-type: none"> <li>• Bilateral lateral occipital cortex</li> <li>• Bilateral Occipital pole</li> <li>• Bilateral occipital fusiform gyrus</li> </ul>
Temporo-occipital	<ul style="list-style-type: none"> <li>• Bilateral middle and inferior temporal gyrus (temporo-occipital part)</li> <li>• Bilateral temporo-occipital fusiform cortex</li> </ul>
Temporal	<ul style="list-style-type: none"> <li>• Left posterior superior temporal gyrus</li> <li>• Left posterior temporal fusiform cortex</li> <li>• Left temporal pole</li> </ul>
Parietal	<ul style="list-style-type: none"> <li>• Right angular gyrus</li> </ul>
Frontal	<ul style="list-style-type: none"> <li>• Bilateral middle and inferior frontal gyrus</li> <li>• Bilateral lateral precentral gyrus</li> <li>• Bilateral frontal operculum</li> <li>• Bilateral frontal pole</li> <li>• Right superior frontal gyrus</li> <li>• Parts of insula</li> <li>• Left frontal orbital cortex</li> </ul>
Sub-cortical	<ul style="list-style-type: none"> <li>• Bilateral cerebellum (large parts of it)</li> <li>• Bilateral brainstem</li> <li>• Right thalamus</li> </ul>

542

543



544

545 **Figure 3: Identifying regions showing differential activity between “Social” and “Non-social”**

546 **percepts. Mean differences between GLM regression coefficients ( $\beta$ ) for (a) RANDOM MECH**

547 **(mean (RANDOM MECH "Social") – mean (RANDOM MECH "Non-social")), (b) COAXING-**

548 *BILLIARD (mean(COAXING "Social"-BILLIARD "Non-social")) and (c) ALL (estimated from*  
549 *run-level regressors, see Methods). Colored regions are significant at an uncorrected threshold*  
550 *( $p < 0.05$ ) in each of the three analyses, while black contours in a-c show the social processing*  
551 *regions significant after correction for multiple comparisons (FDR  $q < .05$ ) in all three analyses.*  
552 *Note: Colorbar ranges are different between the three subplots, since each was estimated*  
553 *separately using different analyses, and hence the values shouldn't be directly compared.*

### 554 **Some brain regions show parametric responses to degree of perceived socialness**

555 The previous analysis identified social information-processing regions that robustly showed a  
556 higher response to information ultimately reported as “Social”. By leveraging “Unsure” responses  
557 as an intermediate level of perceived socialness between “Social” and “Non-social”, we further  
558 probed the neural correlates of conscious social perception—i.e., an “Unsure” response would  
559 indicate that some evidence for a social interaction was detected, but not enough to be fully  
560 confident in a “Social” response.

561 For this analysis, we probed which brain regions responded proportionately (quantified by  
562 the slope  $\beta$ s) to levels of perceived socialness — “Social”, “Unsure” and “Non-social”.  
563 Specifically, we sought to identify regions showing parametric responses, i.e.,  $\beta^{\text{Social}} > \beta^{\text{Unsure}} >$   
564  $\beta^{\text{Non-social}}$  (condition  $S > U > NS$ ) or  $\beta^{\text{Social}} < \beta^{\text{Unsure}} < \beta^{\text{Non-social}}$  (condition  $S < U < NS$ ) using  
565 conjunction analyses across all animations ( $n=814$ ) using separate LMEMs for “Social” vs.  
566 “Unsure” and “Unsure” vs. “Non-social” (see Methods for details). We further limited this analysis  
567 to the parcels that showed robust differences between “Social” and “Non-social” even when  
568 controlled for visual inputs and decision time ( $n = 70$ ; cf. black contours in Figure 3).

569 38 parcels showed a consistent  $S > U > NS$  response pattern and of these, 35 survived  
570 multiple-comparison correction ( $q < .05$ ) across all parcels (Figure 4a-b). This included posterior

571 and inferior parts of the temporal cortex including parts of the motion-processing region V5/MT  
572 (with more parcels in the right hemisphere), middle and inferior frontal gyrus, precuneus, right  
573 thalamus and postero-lateral parts of the cerebellum.

574 To see if similar trends emerge when controlling for visual input, we plotted the  
575 timecourses for each response type for a subset of the parcels showing parametric responses pattern  
576 to the most ambiguous animation (RANDOM MECH; Figure 4c). We plotted a sub-set of the  
577 parcels in which “Unsure” was the closest to the halfway point between “Social” and “Non-social”  
578 both in terms of the mean regression coefficient and the magnitude of activity at the end of the  
579 stimulus presentation period (20s) for each parcel and response (the rationale being that the signal  
580 during the final timepoints of the animation should be the best reflection of a participant’s  
581 ultimately reported percept). As expected, this results in brain regions which show parametric  
582 neural responses to degrees of reported socialness, albeit with large errorbars for the smaller groups  
583 (“Social” and “Unsure”).

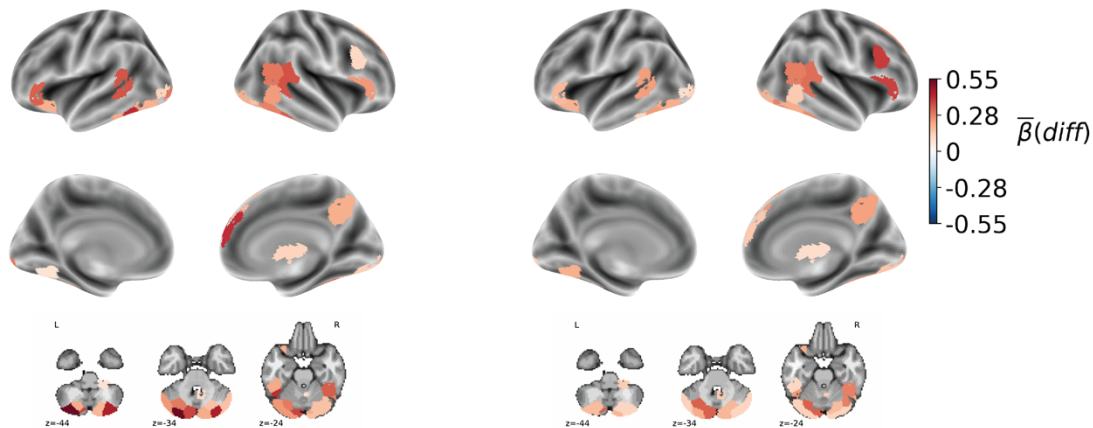
584 Thus, it appears that there are at least some cortical and sub-cortical regions that show a  
585 graded response to degrees of social information. There was a higher number of such parcels in  
586 temporal, occipital and sub-cortical regions, although they were present across the cortex. This  
587 trend can be seen even on plotting the timecourses for the various responses to a single animation.

588

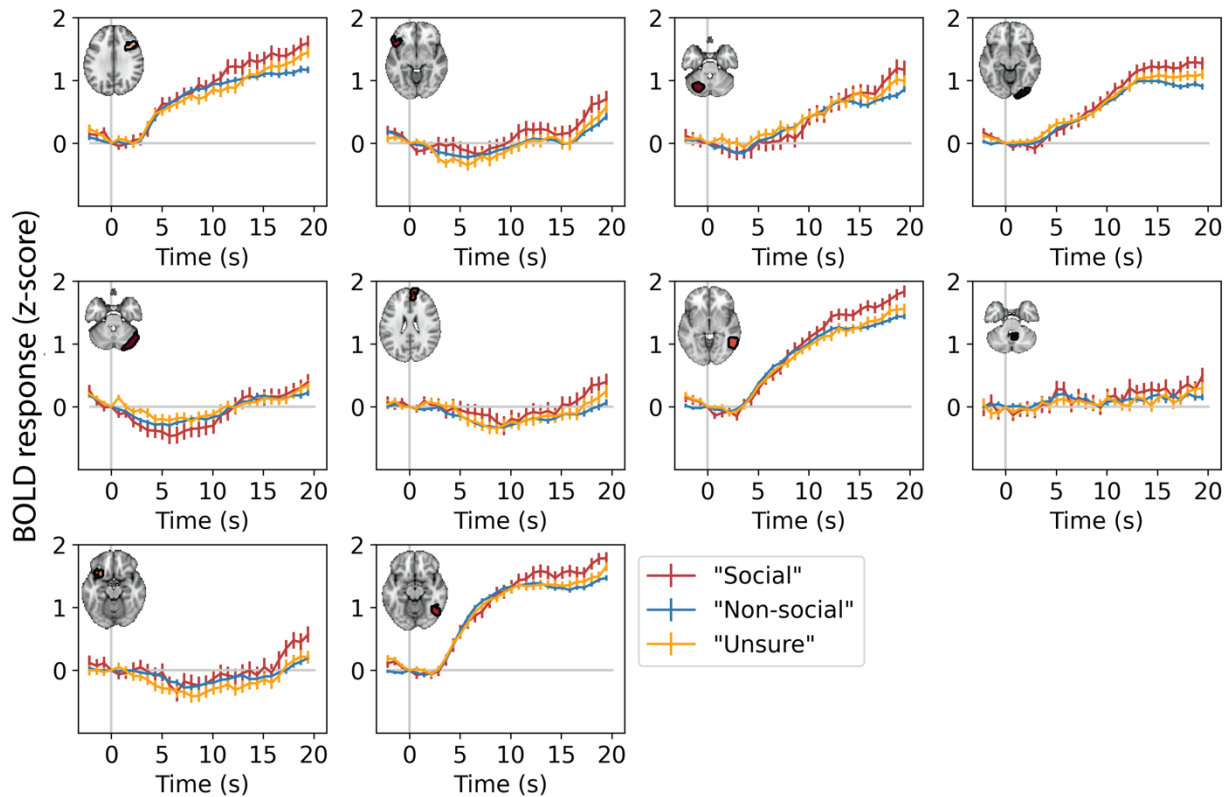


(a) ALL ("Social" - "Unsure")

(b) ALL ("Unsure" - "Non-social")



(c) Timecourses for RANDOM MECH



589

590 **Figure 4. Brain regions showing parametric responses to social content.** (a-b) Colored parcels

591 show mean differences ( $FDR q < .05$ ) in slope regression coefficients ("Social"- "Unsure" and

592 "Unsure"- "Non-social") for the 35 parcels which showed a graded response to perceived



593 *socialness ("Social" > "Unsure" > "Non-social" or vice-versa) across all animations and within*  
594 *the social processing regions obtained from the GLM analysis (cf. black contours in Figure 3).*  
595 *(c) Timecourses for the most ambiguous animation (RANDOM MECH) in 10 of the brain parcels*  
596 *sorted by how close "Unsure" is to the mid-point between "Social" and "Non-social" (details in*  
597 *text). These parcels included bilateral frontal regions, right middle and inferior occipito-*  
598 *temporal regions (including the anterior part of right V5/MT and parts of the cerebellum).*

599 **Processing of social versus non-social information diverges early in time and across the**  
600 **cortex**

601 The whole-trial-based analyses above showed that several regions spanning the whole brain are  
602 more responsive to information that is ultimately reported as social (versus non-social) even  
603 when controlling for decision time and visual input. However, this difference, especially in early  
604 visual regions, could reflect (1) the accumulation of evidence that *led* to the perception of an  
605 animation as "Social", (2) the *consequence* of having perceived an animation as "Social" (i.e.,  
606 top-down attention effects on sensory regions), or (3) a combination of both. To gain a better  
607 understanding of the dynamics of evidence accumulation leading to a "Social" percept, we  
608 compared BOLD activity at each timepoint (TR) after stimulus onset to determine the timepoint  
609 of earliest divergence between "Social" and "Non-social" percepts.

610 To ensure that the differences observed at each timepoint are comparable in terms of the  
611 underlying cognitive processes (i.e., evidence accumulation versus decision-making versus post-  
612 decisional processes), we performed this analysis on the animation pair which likely had  
613 comparable decision times, namely COAXING-BILLIARD. Decision times for these animations  
614 were both early and close in time (as explained in *Materials and Methods* and the *Results* section  
615 for the online RT experiment, also see Figure 2c). These animations were similar visually with

616 the same two triangular agents on the screen (see Table 1) – nevertheless, they did vary in the  
617 temporal dynamics and some low-level visual features. To minimize the effect on these on the  
618 BOLD activity, we regressed out the total optic flow and mean brightness from the BOLD  
619 responses of each animation and participant, and compared the residual COAXING and  
620 BILLIARD timecourses at each TR. To guard against spurious fluctuations early in the  
621 animations, we limited our analysis to the social processing regions (70 parcels) that showed a  
622 consistent difference in activity between “Social” and “Non-social” responses (Figure 3, black  
623 contours).

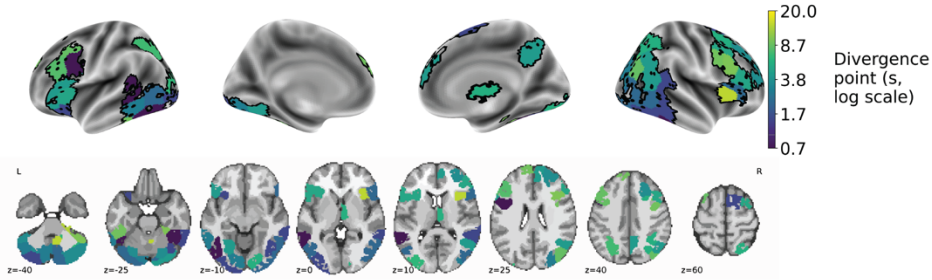
624 Differences in brain activity between “Social” and “Non-social” percepts emerged early,  
625 i.e., in TRs 1-3 after stimulus onset in many regions tested (Figure 5a). There were early  
626 differences between “Social” and “Non-social” in both hemispheres, both in posterior regions  
627 such as the fusiform gyrus, lateral occipital cortex, pSTS and posterior parts of the cerebellum as  
628 well as in frontal areas such as the lateral precentral gyrus, posterior parts of the middle and  
629 inferior frontal gyrus (MFG, IFG), the orbitofrontal cortex (OFC) in the left hemisphere, and the  
630 IFG and supplementary motor area (SMA) in the right hemisphere. Later TRs, which are more  
631 likely to reflect post-decisional activity, showed divergences in the bilateral inferior and superior  
632 frontal regions, the right precuneus, bilateral intraparietal sulcus (IPS) and bilateral posterior  
633 cerebellum. Within the regions that showed a significant overall differential activation for  
634 “Social”, the latest changes were seen in the left IPS and frontal pole and the right IFG and right  
635 anterior and medial cerebellum.

636 To visualize the earliest differences in the posterior regions and to understand how  
637 generalizable these dynamics are, we plotted (Figure 5b) the residual timecourses for  
638 COAXING-BILLIARD (left column, our main analysis) alongside the averaged “Social” and

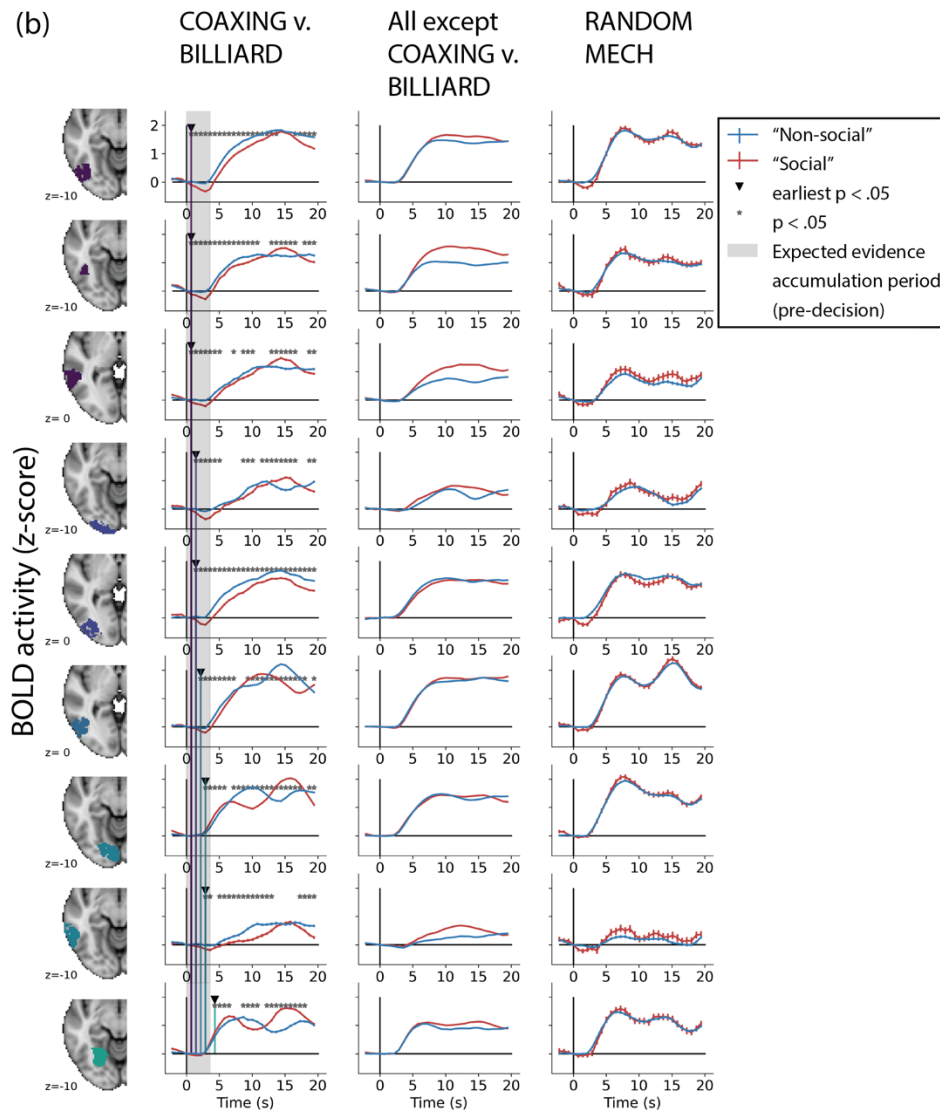
639 “Non-social” timecourses across all the other animations (All except COAXING-BILLIARD;  
640 middle column) and within the most ambiguous animation (RANDOM MECH; right column).  
641 The two latter analyses are not as well suited to pinpointing *when* differences emerged because  
642 decision times were likely more variable across individuals and responses for these animations  
643 (per our online RT experiment), thus making timecourses noisier and less comparable. Despite  
644 this, we see similar relative trends in these posterior regions (each row) as to when and how they  
645 distinguish between “Social” and “Non-social” reports. Responses emerged much later for the  
646 “All except COAXING-BILLIARD” condition in line with the later and more variable decision  
647 times for most animations; see Figure 2c). When comparing within the same animation  
648 (RANDOM MECH), we see trends emerging early on, although the magnitudes are smaller and  
649 the error for the “Social” responder group are large, possible because of the smaller group size ( $n$   
650 = 107) compared to the majority percept of “Non-social” ( $n = 670$ ). Note that the latter two  
651 timecourses are plotted only for visual examination and that we did not perform statistical  
652 analyses here.

653 To summarize, while watching an animation that was eventually reported as “Social”,  
654 differences in brain activity emerged early across much of the brain, involving both ventral  
655 visual processing regions and occipito-temporal regions involved in action and animacy  
656 detection as well as social cognition. The early jump in activity in these regions is in line with  
657 the recently suggested “third visual pathway” that projects directly from early visual cortex to the  
658 superior temporal sulcus and is specialized for social perception (Pitcher & Ungerleider, 2021).

(a) Timepoint of earliest divergence between COAXING and BILLIARD



(b)



659

660 *Figure 5. Timecourse analysis showing when and where differences between “Social” and*

661 *“Non-social” percepts emerge. (a) Brain map of the earliest timepoint at which brain activity*

662 *diverges between "Social" and "Non-social" responses for the COAXING and BILLIARD*  
663 *animations, respectively (within-participant analysis). Analysis was limited to the robust social*  
664 *processing brain regions (cf. Fig. 3, black contours), and BOLD signal timecourses were*  
665 *residualized with respect to the visual features of brightness and optic flow to minimize the*  
666 *effects of any differences in low-level sensory information between the two animations. Colors*  
667 *show how early (purple-blue) or late (yellow-green) activity diverged. (b) BOLD signal*  
668 *timecourses in the left posterior regions illustrating how "Social" and "Non-social" activity*  
669 *diverge in the pre-decisional period for COAXING and BILLIARD. Rows: regions are sorted by*  
670 *the earliest divergence TR and then from posterior to anterior. Columns: left, timecourses for the*  
671 *two animations matched for approximate decision time, COAXING ("Social") and BILLIARD*  
672 *("Non-social"), the main focus of this analysis. Others: timecourses from the same regions*  
673 *shown for two supporting analyses: across all animations except COAXING-BILLIARD*  
674 *("Social" vs. "Non-social" response trials), middle; and for the most ambiguous animation,*  
675 *RANDOM MECH ("Social" vs. "Non-social" responders), right.*

676 **Individual differences in behavior and brain activity while viewing animations covary with**  
677 **internalizing symptoms**

678       Lastly, we explored whether individual differences in behavioral and neural responses to  
679 social animations covaried with trait-level measures. Specifically, we focused on internalizing  
680 symptoms from the Achenbach Adult Self-Report Scale, because past work has shown that certain  
681 internalizing traits (e.g., loneliness, anxiety) are associated with a stronger tendency to perceive  
682 visual cues as socially salient. We hypothesized that individuals with higher internalizing scores  
683 would show stronger behavioral and neural reactivity to potentially social information.

684 Using the behavioral data, we tested whether the response bias towards “Social” (cf.  
685 Figure 1a) was even stronger for individuals higher on internalizing symptoms. Indeed, there was  
686 a positive relationship between the bias toward “Social” responses and internalizing score  
687 (Spearman rank correlation  $r = .104$ ,  $p = .003$ , Figure 6a). We tested the specificity of this  
688 relationship by contrasting it to the correlation with externalizing trait scores, which index more  
689 “acting out” behaviors like rule-breaking and aggression and have not been linked to social  
690 perception tendencies. The correlation with externalizing symptoms was weaker and showed only  
691 trend-wise significance ( $r = .058$ ,  $p = .096$ ), and comparing the correlations showed a trend towards  
692 a significant difference between the two ( $t = 1.317$ ,  $p = .094$ ). Furthermore, individuals with higher  
693 internalizing scores were more likely to give a “Social” or “Unsure” (as opposed to “Non-social”)  
694 response to the most ambiguous animation, RANDOM MECH (“Social” or “Unsure”,  $M = 49.34$ ,  
695  $SE = 0.69$ ; “Non-social”,  $M = 47.65$ ,  $SE = 0.45$ ; unpaired t-test,  $t = 2.054$ ,  $p = .04$ , Figure 6b).  
696 Mean externalizing symptoms were also higher for the “Social” or “Unsure” group ( $M = 49.31$ ,  
697  $SE = 0.57$ ) compared to the “Non-social” group ( $M = 47.98$ ,  $SE = 0.38$ ), although the difference  
698 was smaller (unpaired t-test,  $t = 1.95$ ,  $p = .05$ ).

699 Lastly, individuals with higher internalizing scores were also more likely to give an “Unsure”  
700 response to animations intended as Random ( $r = .098$ ,  $p = .005$ ), but not to animations intended as  
701 Mental ( $r = -.024$ ,  $p = .49$ ), indicating a preference for false alarms over misses when it comes to  
702 detecting social information (difference between correlations:  $t = 2.47$ ,  $p = .007$ ). Demonstrating  
703 specificity to internalizing symptoms, percent “Unsure” responses did not correlate with  
704 externalizing symptoms for either Random (Spearman  $r = .048$ ,  $p = .17$ ) or Mental ( $r = .01$ ,  $p =$   
705  $.75$ ) animations.

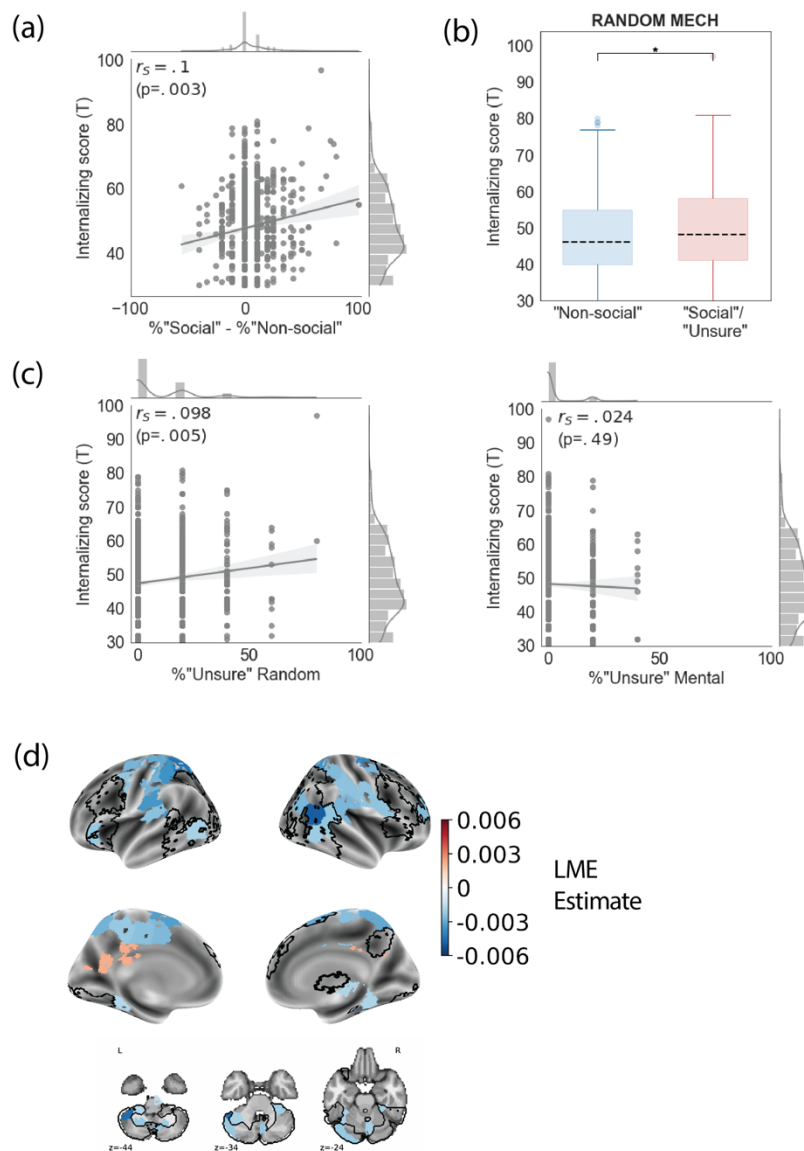
706 Together, these analyses support a link between internalizing symptoms and a greater tendency  
707 to perceive social information, perhaps driven by a homeostatic drive to seek social connections.

708 To understand whether neural activity while scanning for social information also covaried with  
709 internalizing symptoms, we related trial-wise regression coefficients to internalizing symptom  
710 scores in an LMEM (fixed effect: internalizing score; random effect: animation). In a whole-brain  
711 analysis, 50 parcels showed a significant relationship ( $q < .05$ , Figure 6d) between internalizing  
712 score and neural responsiveness. In 48 of these, the LME estimates were negative – i.e., as  
713 internalizing scores increased, the mean regression coefficients for an animation decreased –  
714 although all 48 parcels showed above-baseline activity as evidenced by the positive regression  
715 coefficients ( $\bar{\beta} > 0$  for all parcels). Thus, while individuals with higher internalizing scores showed  
716 positive activity in these regions when scanning animations for social information, the magnitude  
717 of this activity was lower than in individuals with lower internalizing scores. These relationships  
718 were seen in the right angular gyrus, the bilateral superior parietal lobule, supramarginal gyrus,  
719 regions along the dorsal midline, and left cerebellum (colored blue in Figure 6d). The two  
720 remaining parcels, left precuneus and posterior cingulate cortex (colored red in Figure 6d), showed  
721 a mean estimate that was positive but showed a net *deactivation* in the group-level analysis (i.e.,  
722  $\bar{\beta} < 0$ ), indicating that individuals with higher internalizing scores showed less deactivation in  
723 these regions. Thus, in most of the parcels that showed trait-dependent responses, the absolute  
724 magnitude of activity decreased with increasing internalizing symptom scores (which manifests as  
725 positive LME estimates when  $\bar{\beta} < 0$  and negative LME estimates when  $\bar{\beta} > 0$ ).

726 Interestingly, the lateral occipital parcels from the social processing regions (shown as black  
727 contours in Figure 6d) were not as prominent here, showing only a partial overlap (13 parcels)  
728 with the parcels showing trait effects. In the overlapping parcels, which comprised bilateral



729 occipito-temporal regions, the cerebellum and parts of the right superior frontal and left inferior  
730 frontal gyrus, individuals high on internalizing traits showed overall less reactivity in many brain  
731 regions while scanning the environment for social interactions. To reconcile this decrease in neural  
732 reactivity (Figure 6d) with the observed increase in behavioral sensitivity (Figure 6a-c), one  
733 interpretation is that these individuals have a lower threshold for the amount of neural activity  
734 required to declare something “Social”.



735



736 **Figure 6: Relationship between internalizing trait scores, behavior and brain activity.** (a)  
737 *Response bias (% difference between "Social" and "Non-social" responses per participant)*  
738 *correlates positively with internalizing symptom score (Spearman correlation coefficient  $r_s = .1$ ,*  
739  *$p = .003$ ). (b) Internalizing scores across individuals who perceived the most ambiguous*  
740 *animation, RANDOM MECH, as "Non-social" were lower than those for individuals who*  
741 *reported some degree of socialness to RANDOM MECH ("Social" or "Unsure" responses).*  
742 *\* indicates  $p < .05$ . (c) Internalizing score correlates positively with the percent of "Unsure"*  
743 *responses per participant for the generally non-social animations (Random; left; Spearman  $r_s =$*   
744  *$.098$ ,  $p = .005$ ) but not for the generally social animations (Mental; right; Spearman  $r_s = .024$ ,  $p$*   
745  *$= .49$ ). These correlation magnitudes were significantly different ( $t = 2.47$ ,  $p = .007$ ). (d) LME*  
746 *estimates obtained by fitting the slope  $\beta_s$  for each participant and animation to internalizing*  
747 *symptom scores per participant plotted over the brain. Colored parcels showed a significant*  
748 *relationship ( $FDR q < 0.05$ ) and the social processing regions from the GLM analysis (cf.*  
749 *Figure 3) are shown in black. Most regions show a negative relationship with internalizing*  
750 *symptoms and there is only a partial overlap with the parcels that best differentiate "Social" and*  
751 *"Non-social" information.*

752

### 753 Discussion (1197/1200 words)

754 In this study, we investigated behavioral and neural signatures of social signal detection using a  
755 large dataset of neurotypical young adults. Behavioral responses showed a small but consistent  
756 bias toward perceiving information as social (as opposed to non-social), which manifested as a  
757 higher number of "Social" responses and a reluctance to report information as "Non-social". We  
758 used the observers' own labels of what was social and non-social to then identify brain regions

759 that differentiate conscious social percepts, controlling for both visual input (RANDOM MECH)  
760 and decision time (COAXING-BILLIARD), and found that widespread patterns of brain activity  
761 differentiate conscious social percepts. A few brain regions also showed parametric responses to  
762 degrees of perceived socialness (“Social” > “Unsure” > “Non-social” responses). We further  
763 noted that brain activity for information ultimately deemed “Social” diverged from “Non-social”  
764 both early in time and in the cortical hierarchy. Lastly, we found that a trait-level measure of  
765 internalizing symptoms (e.g., loneliness, anxiety) could explain some of the variability in  
766 percepts and brain activity, such that individuals with higher internalizing traits had a higher  
767 tendency to perceive information as social yet lower reactivity in neural systems while scanning  
768 for this information.

769         Humans have been described as an “obligate social” species, evolutionarily tuned to  
770 social interactions (Rutherford & Kuhlmeier, 2013). In our results, both the bias towards  
771 “Social” responses in the behavioral data and the covariation between internalizing symptoms  
772 and sensitivity to social signals, which could reflect a homeostatic drive to seek social  
773 connection (Tomova et al., 2020), are in line with this. Moreover, previous studies have shown  
774 that people who report greater loneliness tend to form illusory social connections (Epley et al.,  
775 2008), overattribute animacy even in the absence of clear humanlike features (Powers et al.,  
776 2014) and have greater attention and memory for social cues (Gardner et al., 2005).

777         Past fMRI studies of animacy and social interaction perception using stripped-down  
778 geometric shape animations have primarily used two types of stimuli: short animations with  
779 simple, controlled motion profiles (e.g., Blakemore et al., 2003; Lee et al., 2014; Schultz et al.,  
780 2005; Tavares et al., 2008) or complex, scripted animations (Castelli et al., 2000; Nguyen et al.,  
781 2019; Osaka et al., 2012). Both sets of studies have primarily identified bilateral pSTS as

782 relevant to intentional motion processing together with the lateral occipital cortex (LOC),  
783 angular gyrus, superior parietal lobule and medial prefrontal cortex. In this study, we observed  
784 differences between social and non-social percepts in these regions but additionally in the  
785 occipital pole, the left temporal pole and dorsolateral and ventrolateral prefrontal cortex. Several  
786 of these regions also showed parametric responses to degrees of perceived socialness. We did not  
787 observe a strong right-hemisphere dominance in this study as in some past work (Lee et al.,  
788 2014; Pitcher & Ungerleider, 2021). These disparities could be the result of the higher sensitivity  
789 we get as a result of the large sample size in the HCP compared to most other studies (n well  
790 below 100) and/or the use of observers' own responses as stimulus labels instead of  
791 experimenter-assigned categories. The latter could be the bigger reason, since several of these  
792 additional regions were not seen even in past studies of the same HCP dataset (Barch et al.,  
793 2013; Li et al., 2020; Westfall et al., 2017). Future users of the HCP social task dataset are hence  
794 cautioned to not rely on experimenter-assigned labels alone.

795 In the timecourse analysis, we observed that the brain starts responding differently to social  
796 information early in time across postero-lateral visual processing regions, even before  
797 participants had likely arrived at a decision about whether an animation was social. Activity in  
798 these regions may therefore reflect pre-decision evidence accumulation processes, in which  
799 participants are using visual cues to determine whether agents are moving in a manner consistent  
800 with an intentional social interaction. Of note, these differences were unlikely to be due to  
801 differences in visual inputs since we regressed out the optic flow and brightness from each  
802 timecourse prior to the analysis. Early differences also emerged in the pSTS—an area critical to  
803 the third visual stream hypothesis (Pitcher & Ungerleider, 2021)—and lateral precentral gyrus,  
804 OFC and SMA. The presence of early differences in frontal regions involving the OFC is in line

805 with previous accounts of a coarse-to-fine visual processing, where an early coarse information  
806 processing wave works in parallel with the slower more detailed processing via the ventral  
807 stream in spontaneous perception (Bar et al., 2006; Baror & He, 2021).

808 Brain activity while scanning animations for social information was lower for individuals  
809 with high internalizing scores in several regions including parts of the default mode network  
810 (angular gyrus, precuneus and posterior cingulate cortex) – some of which have been linked to  
811 depression, early-onset psychosis and anxiety (Collin et al., 2021; Nair et al., 2020; Sheline et al.,  
812 2009; Zhao et al., 2007) – and some of the social information processing regions (occipito-  
813 temporal, frontal, cerebellar) that robustly emerged from the group-level GLM analysis.  
814 Together with the positive correlation between the “Social” bias in behavior and the internalizing  
815 scores, this suggests that individuals with higher internalizing scores may have a lower threshold  
816 for declaring something “Social”.

817 One limitation of this dataset is the heterogeneity of the animations, which were taken from  
818 two studies (Castelli et al., 2000; Wheatley et al., 2007) with vastly different visual features.  
819 Paradoxically these animations are also not optimal to study ambiguous perception since they *did*  
820 have a dominant percept. Nevertheless, the large sample size enabled us to study percept-level as  
821 well as inter-individual differences. Further, the order of animations was not counterbalanced.  
822 Even though the timecourse analysis controlled for key visual differences, we acknowledge that  
823 we used two specific stimuli presented in a certain sequence in the HCP task, and hence cannot  
824 confidently extend these results to *all* social and non-social stimuli. We therefore propose this as  
825 an early step to future studies that investigate social processing pathways using more controlled  
826 stimuli.

827 Another limitation is that in this task, individuals had only three response options. However,  
828 participants' confidence levels in these responses may have been vastly different, especially  
829 since the data showed that some animations were more ambiguous than others. Further, even  
830 given a response of "Social", the nature of the particular interaction perceived could have varied  
831 across individuals, even for the same animation. This could have reduced the effect sizes and can  
832 be overcome in future experiments by using richer behavioral characterizations of percepts (e.g.,  
833 continuous response scales) and/or indirect physiological measures like pupillary responses or  
834 electromyography.

835 In summary, we describe behavioral and neural processes that underlie how people arrive at  
836 conscious percepts of social information. We find evidence that neurotypical individuals are  
837 primed to detect social signals, and that this detection process is reflected in widespread brain  
838 activity that happens early in time and in the cortical hierarchy. We also find considerable  
839 heterogeneity among individuals' percepts of particularly ambiguous information – i.e.,  
840 information that may or may not be social in nature – and describe one trait-level factor that may  
841 influence behavioral and neural tendencies toward social versus non-social percepts. Together,  
842 results indicate the need for a more nuanced view of social perception in which socialness is in  
843 the "eye of the beholder".

844

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