This Accepted Manuscript has not been copyedited and formatted. The final version may differ from this version.



Research Articles: Behavioral/Cognitive

Independent Neural Computation of Value from Other People's Confidence

Daniel Campbell-Meiklejohn^a, Arndis Simonsen^b, Chris D. Frith^{b,c} and Nathaniel D. Daw^d

^aSchool of Psychology, University of Sussex, Falmer, BN1 9QH, United Kingdom

^bDepartment of Clinical Medicine, Aarhus University, Palle Juul-Jensens Boulevard 82, 8200, Aarhus N, Denmark.

^cWellcome Trust Centre for Neuroimaging, University College London, 12 Queen Square, London, WC1N 3BG, United Kingdom

^dPrinceton Neuroscience Institute and Department of Psychology, Princeton University, Princeton, NJ, 08540, USA.

DOI: 10.1523/JNEUROSCI.4490-15.2016

Received: 15 December 2015

Revised: 4 November 2016

Accepted: 1 December 2016

Published: 9 December 2016

Author contributions: D.C.-M., C.D.F., and N.D.D. designed research; D.C.-M. and A.S. performed research; D.C.-M. and N.D.D. analyzed data; D.C.-M., C.D.F., and N.D.D. wrote the paper.

Conflict of Interest: The authors have no conflict of interest.

This research was funded by a *Sapere Aude* Grant to DCM from the Danish Council for Independent Research: Medical Sciences and a Lundbeck Foundation award to DCM and CF.

Corresponding Author: Dr. Daniel Campbell-Meiklejohn, School of Psychology, University of Sussex, Falmer, BN1 9QH, United Kingdom, daniel.cm@sussex.ac.uk

Cite as: J. Neurosci 2016; 10.1523/JNEUROSCI.4490-15.2016

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

Accepted manuscripts are peer-reviewed but have not been through the copyediting, formatting, or proofreading process.

1	
2	
3	
4	Title: Independent Neural Computation of Value from Other People's Confidence
5	Abbreviated Title: Pathways to Value in the Brain
6	Authors: Daniel Campbell-Meiklejohn ^a , Arndis Simonsen ^b , Chris D. Frith ^{b, c} &
7	Nathaniel D. Daw ^d
8	Affiliations:
9	^a School of Psychology, University of Sussex, Falmer, BN1 9QH, United Kingdom
10 11	^b Department of Clinical Medicine, Aarhus University, Palle Juul-Jensens Boulevard 82, 8200, Aarhus N, Denmark.
12 13	^c Wellcome Trust Centre for Neuroimaging, University College London, 12 Queen Square, London, WC1N 3BG, United Kingdom
14 15	^d Princeton Neuroscience Institute and Department of Psychology, Princeton University, Princeton, NJ, 08540, USA.
16 17	Corresponding Author: Dr. Daniel Campbell-Meiklejohn, School of Psychology, University of Sussex, Falmer, BN1 9QH, United Kingdom, daniel.cm@sussex.ac.uk
18	Pages: 36
19	Figures: 7 Tables: 1
20	Number of Words: Abstract (240), Introduction (637): Discussion (1500):
21	Conflict of Interest: The authors have no conflict of interest.
22	Acknowledgements: This research was funded by a Sapere Aude Grant to DCM
23	from the Danish Council for Independent Research: Medical Sciences and a Lundbeck
24	Foundation award to DCM and CF.

26

28

29

30

31

32

33

34

35

36

37

38

39

40

41

42

43

44

45

46

47

27 Abstract

Expectation of reward can be shaped by the observation of actions and expressions of other people in one's environment. A person's apparent confidence in the likely reward of an action, for instance, makes qualities of their evidence, not observed directly, socially accessible. This strategy is computationally distinguished from associative learning methods that rely on direct observation, by its use of inference from indirect evidence. In twenty-three healthy human subjects, we isolated effects of first-hand experience, other people's choices, and the mediating effect of their confidence, on decision-making and neural correlates of value within ventromedial prefrontal cortex (vmPFC). Value derived from first-hand experience and other people's choices (irrespective of confidence) were indiscriminately represented across vmPFC. However, value computed from agent choices weighted by their associated confidence was represented with specificity for ventromedial area 10. This pattern corresponds to shifts of connectivity and overlapping cognitive processes along a posterior-anterior vmPFC axis. Task behavior and self-reported self-reliance for decision-making in other social contexts correlated. The tendency to conform in other social contexts corresponded to increased activation in cortical regions previously shown to respond to social conflict in proportion to subsequent conformity (Campbell-Meiklejohn et al., 2010). The tendency to self-monitor predicted a selectively enhanced response to accordance with others in the right temporoparietal junction (rTPJ). The findings anatomically decompose vmPFC value representations

48 according to computational requirements and provide biological insight into the social 49 transmission of preference and reassurance gained from the confidence of others.

Significance Statement

Decades of research have provided evidence that ventromedial prefrontal cortex (vmPFC) signals the satisfaction we expect from imminent actions. Yet, we have a surprisingly modest understanding of the organization of value across this substantial and varied region. This study finds that using cues of the reliability of other peoples' knowledge to enhance expectation of personal success generates value correlates that are anatomically distinct from those concurrently computed from direct, personal experience. This suggests that representation of decision values in vmPFC is suborganized according to the underlying computation, consistent with what we know about the anatomical heterogeneity of the region. These results also provide insight into the observational learning process by which someone else's confidence can sway and reassure our choices.

63 Introduction

The human brain can use a variety of learning strategies to better its situation. Unifying economic theories suggest that different decision processes converge to a single expectation of satisfaction (or 'value') that will be gained or lost from available actions – correlates of which are found in activity throughout ventromedial prefrontal cortex (Levy and Glimcher, 2012; Bartra et al., 2013), and guide decisions toward options of greater value. Whether this activity represents a single computation of value, a collection of distinct computations, or both, is not clear. But there are both computational and anatomical reasons to suspect sub-regional specialization.

73

74

75

76

77

78

79

80

81

82

83

84

85

86

87

88

89

90

91

92

93

94

95

96

Reward predictions from different types of information are computed differently. For instance, one can learn about an action's value by maintaining a running average of rewards received from performing it. However, some knowledge is only socially and/or inferentially accessible; if one observes someone else perform an action, one can recruit inferential strategies for a judgement of that action's value. For instance, people provide signals of high confidence when they have good knowledge of the likely outcomes to their actions (Patel et al., 2012). So, confident actions of others should have greater influence on our own appraisals (Thomas and Mcfadyen, 1995). So, if the other person appears to know what she is doing (and assuming her intentions are similar to mine), one can employ a rule of imitate-if-appears-confident, or more flexibly, one can infer what she knows from her actions and confidence, then combine this with knowledge inferred from other cues and personal experience. These and similar strategies, unlike directly sampling outcomes, may require steps of indirection and integration of multiple cues (e.g. of others' preference and confidence) but also enable us to compute value in the absence of first-hand experience with prior choice outcomes. We developed a task that provides different types of information for evaluating the value of the same choice: first-hand knowledge, choices of others, and their confidence. We then compared contributions of each information source to decision-making and neural representations of value across vmPFC.

We considered that different computations of value could make use of shifting connectivity, cytoarchitecture, and overlapping cognition toward the anterior of vmPFC (Kringelbach and Rolls, 2004). Cytoarchitecturally, laminar density and granular layer IV volume increase along a posterior to anterior axis (Ongur et al., 2003; Mackey and Petrides, 2010), indicative of increasing inter-area connectivity (Barbas, 2007). Local connectivity required for integrating value signals *in situ* dominates posterior vmPFC.

In contrast, anterior regions maintain a balance of local and distant connectivity that can *additionally* recruit higher-order input (Sepulcre et al., 2010). Correspondingly, moving anterior and dorsal from classical representations of value in area 25 (through areas labelled as area 14m (Mackie, 2010) or 10m and 10r (Ongur et al., 2003)) to medial area 10, known overlapping processes become more abstract, integrative, and inferential (Ramnani and Owen, 2004; Amodio and Frith, 2006; Burgess et al., 2007; Sescousse et al., 2013). Representations of value that require more inferential or integrative processes may map to distinct regions across this cortical landscape.

An anatomical distinction between value from first-hand knowledge and value from agents' confidence-weighted influence would exemplify the mapping of value to cortex as determined by its computational requirements. It would also provide the foundation for investigation of the neural mechanism by which the supporting confidence of others guides our actions. Based on changes of connectivity and overlapping function, value from confidence-weighted influence was predicted to preferentially recruit anterior regions of vmPFC while direct, personal sampling and the main effect of agents' choices (regardless of confidence) was not.

We linked individual differences of influence on task performance to sensitivity of neural responses to corresponding task stimuli. Finally, to establish the relevance of our task and findings to social environments we tested the relationship between observed effects (neural and behavioral) and influence of others on participant behavior (conformity and self-monitoring) outside the lab.

Materials and Methods

119 Participants

Participants were right-handed and had no history of brain injury or psychological disorder. Each gave informed consent. Inclusion criteria for fMRI analysis included at least some use of each information source during the behavioral task to enable contrasts between value-based activation derived from different sources (exclusions were indicated by near-perfect prediction of choice outcomes by only one or two influences, a simple rule-based strategy which precluded quantitative examination of behavior by leading to extremely large and unstable estimates of regression coefficients) (5 participants excluded). Head movements were required to be consistently smaller than a single voxel (2mm) (1 participant excluded). 23 participants (13 male, age: M 26 SD 3.6) met all requirements. Each received 110 Danish Krioner (kr) (20 USD) for time spent participating and 60 kr (10 USD) for winnings on tasks (all subjects were paid this same amount). The study was approved by Central Denmark Region ethics (No. 29718).

Task

The Urn Task (Figure 1) examines how participants make decisions when provided with different sources of information. It asks participants to infer the color of the next marble to be drawn (red or green) for each of a series of 160 mixed urns, with opportunities to do so by inferring other people's information about the likely outcome. Participants had the following information about each urn: a random sample of 8 marbles, four predictions described as being made by past participants (four "agents") based on their own samples from the same urns, and the confidence expressed by those agents. All samples were said to be replaced before the final marble was drawn.

Agents' faces were presented with neutral expressions. To ensure any effects were due to the use of agents' confidence, rather than its inference, we communicated confidence with an explicit cue described to subjects during training: the smug (confident cue) or perplexed (unconfident) animated smiley that appeared within the indicated choice (red or green marble) (See Figure 1). Agents' choices were also said to be presented in the time taken by the agent to make them. Confident response times were between 325 and 1000ms. Unconfident response times were between 1800ms to 2600ms. Once all agents' responses were made, participants had 1300ms to observe them before their own sample appeared. All information was available for 1250ms before a choice could be made, cued by presentation of choice options.

The participant never saw agent samples, and agents were said never to see the participant's sample. Agent choices were seen before personal samples because they were assumed to take longer to process. There was no time limit for participant decisions once the cue for a choice was presented. After a choice, confirmation of the choice was briefly shown and followed by a 1s inter-trial interval. The task took 23 minutes to completion, on average.

After instructions for the task, using visual displays, participants were quizzed by the experimenter on the meaning of each display item and asked what might be in the urn given various combinations of information. Instructions were repeated if necessary. It was critical before progression that participants understood that samples reflected 'randomly mixed' urn contents (the urn shook on arrival for emphasis) and were replaced. No trial outcome was provided to subjects, so participants could not learn to associate outcomes with colors or agents. They were required to make the best use of the information available, and told that a random urn would be selected

and sampled to see if the subject was correct, with a potential reward of 30 Danish Kroner (DKK).

The experimenters actually programmed agents' choices, agents' confidences, and agents' deliberation times in a way that fully counterbalanced the factors of participants' samples, agents' choices, and the confidences of agents favoring either color. Agents were drawn with replacement from a set of 30 images from the Radboud face dataset, in sepia tone (Langner et al., 2010). The use of fictional agents' responses was necessary to achieve sufficient statistical power and ensure that each subject experienced each possible combination of agents' choice, agents' confidence and personal sample. This was explained to participants during debriefing.

The task was designed to study how participants decide across a range of combinations of sample, agents' choice and agents' confidence. Accordingly, trials were generated by creating every possible combination, across trials, of: the number of agents favoring red (vs. green), confidence for agents favoring red, confidence of agents favoring green, and participants' samples – all varying independently of one another. Thus there was no real-world optimal strategy (in the sense that the observations were not actually produced by simulating draws from an urn whose contents could then be predicted), and each participant was paid the maximum reward at the end of the study.

Confidence expressed by any agent was the same as confidence expressed by any other agent that predicted the same color. At the risk of this aspect appearing odd to participants, it enabled us to test our predictions with a clear choice x confidence factorial design that identified independent contributions of each information source to decisions and neural activity. It also kept the task length manageable for an fMRI study.

During debriefing, no participant expressed doubt in the authenticity of the agents' responses.

There were 160 trials in the scanned task. For each number of agents choosing red (0 to 4), there were 32 trials. Sets of 32 were made up of 7 sample distributions (1-7 reds in the participant sample; samples with 4 reds were presented twice as often as the other combinations) evenly distributed over each available combination of agents' confidence. When 1 to 3 agents chose red, there were 4 confident/unconfident combinations. When 0 or 4 agents chose red there were two options (high and low confidence in the agents' chosen color).

Procedure

Prior to scanning, outside the scanner, the participants guessed the next marble from a series of 28 urns *and* indicated confidence in these predictions, based only on a sample of 8 marbles from each (no agents' choices). Participants were told that their own predictions during this task would be used for the Urn Task of future participants. This provided participants with the agents' perspective. Participants were also given a 30 DKK 'prize' for this task. Next, after receiving instructions, the participant practiced for 20 trials before beginning the task in the scanner. Finally, after scanning, the participant filled in questionnaires measuring self-monitoring and the tendency to conform outside the lab before being debriefed.

Behavior Analysis

We performed a factorial, mixed effects logistic regression, which we refer to as the *Component Value Behavioral Model*, to analyze participant choices (dependent variable: per trial choice of red, vs green) as a function of a number of candidate explanatory factors and their interactions. Choices were analyzed in R (v. 3.2.3, R

development Core Team RRID:SCR_001905) using the Ime4 package (v. 1.1.12). The model allows for the measurement of influence of multiple sources of information on the probability of choosing red. This includes added value of a confident agent's choice over an unconfident one. The following predictors of participant choice of red (described below) were added to the regression:

S: proportion of marbles in participant's sample that were red.

O: proportion of agents choosing red.

C_R: confidence of agents choosing red (-0.5 low, 0.5 high)

C_G: confidence of agents choosing green (-0.5 low, 0.5 high)

223 O_RC_R: proportion of agents choosing red x their confidence

224 O_GC_G: proportion of agents choosing green x their confidence

Each predictor was scaled to a range for 0 to 1 and centered around its mean, for each subject. Common scaling allows for the estimated coefficients to be comparable, across predictors, with each expressed in units of change in log odds of choice corresponding to a change from the minimal to the maximal value. Centering is recommended (Cohen, 2003) because it allows main effects to be interpreted as effects when all other effect variables are at their mean, without affecting interaction terms. Interaction terms were calculated from the product of the scaled and centered predictors. $\mathbf{C_R}$ and $\mathbf{C_G}$ had no meaning when no agents chose that color and so these variables were set to their mean (i.e. 0) in these instances, giving them no statistical effect.

237

238

239

240

241

242

243

244

245

246

247

248

249

250

251

252

253

254

255

256

257

258

259

260

The rationale and interpretation of these variables is as follows. S and O are two independent sources of information about the urn in the design; our major question is whether the confidence CR & CG modulates the effect of O. S codes the relative proportion of red (vs green) marbles in the agent's own sample, and a positive regression coefficient for it captures an increasing tendency to choose red when more red marbles are observed. Since the fraction of green marbles is equal to 1 - S, a model with predictors for both effects (and an intercept) would be rank-deficient; however, following mean centering, S codes the difference in red vs green marbles sampled (with a positive value indicating a preponderance of red and negative values the opposite), capturing both effects symmetrically. The same point holds for O. The effect of O captures an increasing tendency to choose red when the relative proportion of agents choosing red (minus those choosing green) is larger. Following mean centering, $O = -O_G$ (proportion choosing green). So interactions O_RC_R and O_GC_G capture the difference of this effect for red and green choices (respectively) between confident vs. unconfident agents. The main effects of confidence, C_R and C_G , capture the baseline effect of confident votes when the votes are evenly split, and control for any overall change in choice tendency when red, or green, votes are confident, independent of the number of votes.

Each effect contained both a fixed and a random effect term, i.e. a mean slope at the group level, an error term allowing that slope to vary from subject to subject, and a full covariance matrix among the random slopes. We verified that all these effects should be included in several ways. First, the significant tests for all regression coefficients (save the intercept) in Table 1 reject the null hypotheses corresponding to the nested models with any one effect being zero. We also present AIC comparisons for the full model against a set of submodels, each omitting one effect. Conversely, we

also tested for progressive improvement in model fit to behavior (by AIC and a likelihood ratio test (χ^2 P < 0.05)) (Vazquez et al., 2010) as effects were added incrementally (in the order: intercept, **S**, **O**, **C**_R and **C**_G, **O**_R**C**_R and **O**_G**C**_G. Each significantly improved the model fit to behavior (detailed results not reported). An additional interaction term between **S** and **O** did not improve the fit.

266 Component Value Behavioral Model:

$$logit(P)_{ij} = \beta_0 + \beta_1 S_{ij} + \beta_2 O_{ij} + \beta_3 C_{Rij} + \beta_4 C_{Gij} + \beta_5 O_R C_{Rij} + \beta_6 O_G C_{Gij} + \epsilon$$

where P is the probability choosing red for the ith trial for subject j, β represents regression coefficients including random effects for all coefficients and ϵ is error.

Individual Difference Measures

Task Behavior: To measure individual differences of information influence, we measured the effect of each information source on the likelihood of each participant's decisions. Using the fixed and random effects of the Component Value Behavioral Model, we calculated the fit (via negative log likelihood) of this model to choices of individual participants. We then calculated the fit of four other models (using the same fitted parameters as the full model): one without S, one without O, one without both CR or CG and one without both ORCR and OGCG. The effect of each model reduction on behavior likelihood (smaller model – full model) represented the impact of the subtracted variable(s) for that participant: S effect, O effect, C effect and OC effect, respectively (Hampton et al., 2008). (The intent of this procedure was to measure the effect of each variable in each subject, but using units of differential log likelihood, analogous to variance explained, rather than estimated regression coefficients. This is because the scaling of the latter can be erratic from subject to subject). These effects

were entered as covariates in a separate group level fMRI analyzes and tested for relation to behavior outside the lab.

Choices in Other Contexts: This study was agnostic to whether findings are unique to social environments, but it was imperative to test the relevance of the results to social behavior outside the lab, given their social context. To test the relevance of task behavior, we used a self-report 'conformity scale' (Mehrabian and Stefl, 1995). The Conformity Scale assesses weight placed on other people's choices relative to one's own information in a variety social contexts. It requires participants to rate agreement or disagreement (on a scale from -4 to 4) with 11 statements referring to reliance on others for decisions. Higher scores mean greater reliance on others. The scale does not assess the use of the others' confidence, so to test its relationship to task behavior we created a simplified model that contained only S and O (removing confidence from the model). Then, similar to above, we calculated the effects of S and O on model fit. We then tested the correlation between these effects (and difference between them) and conformity scale scores. Self-monitoring (Snyder, 1974) was also assessed measuring the tendency to adapt behavior in response to cues from an audience, but no effect was hypothesized given that there was no audience in this task.

Neuroimaging

fMRI Procedure

Participants were instructed and given time to practice until the task was understood and responses could be made in less than 4 seconds. The task was presented with Presentation v.12 software (Neurobehavioral Systems Inc. RRID:SCR_002521). Scanning took place at the Danish Neuroscience Centre, Aarhus, Denmark on a 3 Tesla Siemens Trio Scanner (Siemens Medical Solutions, Erlangen,

Germany) fitted with a 32-channel head coil. The Urn Task displays were backprojected and observed via a mirror and responses were collected from the right-hand using a fibre-optic button box.

Image Acquisition

Functional (Echo Planer Images, EPI) data was collected as T2-weighted echo planar images (EPI) in an interleaved slice acquisition order. Each EPI volume contained 52 slices with the following parameters: voxel size 2x2x2 mm, TE 27 ms, TR 2800ms, Flip Angle: 90°. The small 2mm voxel size efficiently reduced orbitofrontal cortex dropout and distortion. 176-slice 1mm voxel whole-brain anatomical scans were also acquired for co-registration with the EPI data using an MPRAGE sequence on a 256x256x176 grid with the following parameters: TE: 3.7ms, Inversion Time: 900ms, TR: 2420ms, Flip angle: 9°.

First Level fMRI Analysis

All image analysis was carried out with tools of FMRIB's Software Library (FSL RRID:SCR_002823) version 5.0.6 (Smith et al., 2004). Preparation of the EPI data used FSL defaults (FEAT 6.0). Volumes acquired during significant (>1mm) head movements were replaced with neighboring volumes and events with modelled responses occurring during these acquisitions were removed from all models. Independent Component Analysis was used to visually identify and remove remaining artefacts in the data using MELODIC (Beckmann and Smith, 2004). General linear models were fit in pre-whitened data space for each individual participant. Regressors and temporal derivatives were convolved with the default FSL haemodynamic response function (gamma function, delay: 6s, standard deviation: 3s), and filtered by the same high pass filter as the data. Single-participant results were transformed

using nonlinear deformation algorithms into standard space (Montreal NeurologicalInstitute, MNI152).

Component Value fMRI Model

333

334

335

336

337

338

339

340

341

342

343

344

345

346

347

348

349

350

351

352

353

354

In the Component Value Behavioral Model of choices, the dependent variable was choice of red (vs green), and variables were constructed as they related to the evidence in favor of choosing either color. In the fMRI analysis, the dependent measures were neural activity during these choices. However, rather than covarying with the tendency to choose options on the basis of a dimension like color, BOLD activity is widely reported to vary along the dimension of the chosen vs. unchosen option, with larger responses in medial PFC when the chosen (or about to be chosen) option is more likely to be correct, carries more reward, or is otherwise more strongly preferred (Tanaka et al., 2004; Daw et al., 2006; Kim et al., 2006; O'Doherty et al., 2007; Behrens et al., 2008; Wunderlich et al., 2010). Therefore, to test for analogous neural effects as on the behavior, we model the BOLD data using precisely the same set of explanatory variables as the behavioral analysis, but expressed with respect to evidence supporting the chosen vs. unchosen options on each trial, rather than the red vs. green options. So when red is chosen, S_A and O_A (for evidence in "accordance" with the choice) are defined in terms of red samples and choices. When green is chosen, they are defined in terms of green samples and choices. In keeping with the literature on neural correlates of decision variables, we refer to activity correlated with these variables as reflecting their influence as components of "chosen value," meaning the overall supporting evidence that the subject's choice was correct. However, we stress that given the symmetry of our task (where choices are mutually exclusive, and evidence supporting red opposes green), such activity can be understood as reflecting

relative (chosen minus unchosen) value, as indeed has been reported for medial PFC (Boorman et al, 2009).

So the set of variables in the fMRI analysis track those from the behavioral analysis, but coded in terms of accordance of an information source with the subject's choice. Each variable had a parametric weight of accordance that varied trial-by-trial. As in the behavioral model, variables were scaled to a range of 1 and mean centered (orthogonal to a constant term). Like the behavioral model, interaction regressors were calculated by multiplying respective main effect regressors after scaling and mean centering.

The Component Value fMRI Model contained the following variables:

- **S**_A: proportion of marbles in sample in accord with participant's choice
- 366 O_A: proportion of agents' choices in accord with participant's choice
- **C**_A: confidence of accordant agents (-0.5 or 0.5)
- **C**_D: confidence of discordant agents (-0.5 or 0.5)
- **O_AC_A**: accordant agents' choices x their confidence
- **O**_D**C**_D: discordant agents' choices x their confidence
- 371 plus intercept.

'A' and 'D' subscripts represent accordance or discordance of the information source with the choice. Just as in the behavioral analysis, following mean centering S_A codes the relative proportion of accordant (minus discordant) marbles; O_A codes the relative proportion of accordant (minus discordant) other agents' choices; hence S_D (=- S_A) and O_D (=- O_A) are redundant. Also as for behavior, C_A and C_D are mutually independent, and their interactions with O_A (and O_D =- O_A) capture the difference of effect on BOLD from other agents' accordant (vs discordant) choices, when those

agents are confident compared to when they are unconfident. Also, as with behavior \mathbf{C}_A and \mathbf{C}_D had no meaning (and were not presented) when no agents chose the color and so these variable were set to the mean (i.e. 0) in these instances, having no statistical effect.

Integrated Value fMRI Model

Preceding the full model fit described above, which aimed to decompose the influence of different sources of information on value-related BOLD correlates, we wished to verify the presence of activity related to overall value. To define this, we extracted the likelihood assigned by the *Component Value Behavioral Model* to each chosen option of each subject, and took this choice probability as our estimate of the integrated chosen value. Such probabilities reflect the transform of the weighted sum of evidences, through the logistic softmax so as to range from 0 to 1, which provides a well normalized summary of the overall evidence in favor of a red vs green choice, or chosen minus unchosen value, which has been shown to track medial PFC activity (e.g., (Daw and Doya, 2006)).

Accordingly, the fitted model to each subject was:

$$Y_{i} = \beta_{0} + \beta_{1}S_{i} + \beta_{2}O_{i} + \beta_{3}C_{Ri} + \beta_{4}C_{Gi} + \beta_{5}O_{R}C_{Ri} + \beta_{6}O_{G}C_{Gi} + \epsilon$$

- for each ith trial, where β represents fitted mixed and random effect parameters and ϵ is error. If participant chooses red, choice likelihood is $\frac{e^{Y_{ij}}}{1+e^{Y_{ij}}}$. If participant chooses
- 397 green, choice likelihood is $1 \frac{e^{Y_{ij}}}{1 + e^{Y_{ij}}}$. This vector of likelihoods was entered, along
- with a constant, to predict the neural correlates of integrated value (Figure 3A).
- 399 Timing

The modelled fMRI event, for all regressors, was a 1250 ms period when agents' choices and personal samples were concurrently available, before a choice could be made. During this period, both vmPFC sample-driven activation and agent-driven activation were at peak levels (Figure 4). A temporal derivative of each event was added to the model to control for slight errors of fit to the haemodynamic response. The interval between modelled events varied as determined by participant reaction time (M 1.2s, SD 1.6s) and variable time taken for choices of agents to appear (range 0.32 to 2.7s). 80% of participant reaction times were under 1.7s and 90% under 3s. This resulted in a positively skewed distribution of periods between modelled events (M 8.6s, SD 1.7s).

The Spatial Linear Parametric Analysis

To characterize anatomical patterns of activation associated with estimated value from S_A (first-hand experience of sample), O_A (agents' choices alone), and O_AC_A (interaction effect of agents' confidence and agents' choices) we generated five anatomically defined spheres of 10mm diameter linearly traversing an anatomical axis (Nicolle et al., 2012; Sul et al., 2015). This axis spanned the superior medial gyrus, dorsal to the gyrus rectus. It began in area 10m/14m (Ongur et al., 2003; Mackey and Petrides, 2010),at MNI coordinates [0mm, 32mm, -16mm], within a region defined by metanalysis as associated with choice value (Levy and Glimcher, 2012; Bartra et al., 2013). It ended to the frontal pole at the approximate center of ventromedial area 10 (MNI coordinates 0mm, 64mm, 8mm), a region associated with abstract reasoning about mental states (Amodio and Frith, 2006) (Figure 4). Mean percent signal change as extracted from each sphere, for each variable. Percent signal change in response to S, O and OC variables, as well as the contrasts of OC – S and OC – O (to test how the difference of responses to different information change along this axis) was

examined by mixed effect linear regressions (Ime4 with Kenward-Roger approximation of dof).

Fixed impulse response (FIR) sets were then fitted to each regressor in the Component Value fMRI Model. These sets spanned a period of 19.6s divided into 7 time bins, each the length of a TR (2.8s). This period began at the point that agents' responses began to appear on the screen. Mean parameter estimates for each of S_A , O_A and O_AC_A were extracted in each sphere and plotted in Figure 4. To investigate the nature of the interaction between of agents' choice and confidence, we did the same for a second GLM that included separate regressors for confident and unconfident agents supporting the participant's choice. Remaining regressors of the Component Value fMRI Model were included as covariates (S_A , C_D and O_DC_D). We plotted the time courses of the effects of confident agents and unconfident agents in Figure 5.

Group Level fMRI Analysis

Both group models were fitted to parameter estimates from each lower level analysis, using mixed effects in FSL. All group-level Z (Gaussianised T/F) statistical images represent whole-brain searches using cluster corrected statistics (FMRIB's Local Analysis of Mixed Effects (FLAME) 1+2) (Woolrich et al., 2004) (Z > 3.0 voxel threshold, P < 0.05 cluster significance threshold) shown to be robust against false positives (Eklund et al., 2016), using automatic outlier deweighting (Woolrich, 2008).

Individual Differences (Group Level)

Individuals vary on their reliance on others for decision-making, and this is a reasonably stable trait (McGuire, 1967). We harnessed these differences to test

relationships between behavioral influence of specific types of information, their effects neural correlates of value, and social influence on choice in other contexts.

Neural Effects x Behavior: The four measured influences on individual participant behavior (S effect, O effect, C effect and OC effect) were added, mean-centered, as between-participant covariates in a new group-level *Component Value fMRI Model* analysis. We asked if the behavioral O effect, S effect, their difference, and the OC effect predicted the sensitivity of the brain to these influences, highlighted by fMRI effects of O_A, S_A, and O_AC_A. This analysis employed small volume correction within our *a-priori* anatomical region of interest, the vmPFC. This mask was created as the conjunction of all Harvard-Oxford Atlas regions falling within vmPFC with a range along the x axis of -18mm to +18mm and maximum height level of 18mm to cover, with some room for error. regions anatomically specified as vmPFC in prior studies (Mackey and Petrides, 2010).

Conformity and Self-Monitoring: To test the relationship of neural activity during the task to real-world behavior, we tested whether sensitivity to different sources of information during task execution (S_A and O_A) related to self-reported self-reliance for decision-making (Conformity scale) and self-monitoring behavior by adding these as covariates in a separate group level analysis of the *Component Value fMRI Model*. Age and gender were also added as covariates.

vmPFC effects were insensitive to individual differences, so we explored outside this region. For the conformity comparison, we used small volume correction within regions identified to respond more to social conflict in proportion to individual differences of subsequent conformity in an independent study (Campbell-Meiklejohn et al., 2010). Social conflict being a driver of conformity in the brain {Wu}, it was predicted

that those rating high on self-reported conformity would experience greater neural responses to conflict with agents.

While self-monitoring would not affect behavior in our task (with no live audience), individuals high in self-monitoring behavior might react differently social cues. With no *a priori* region of interest for this contrast, we used a whole-brain cluster-corrected analysis.

478 Results

While scanned with fMRI, participants repeatedly predicted the color of marbles to be drawn from an urn by balancing several sources of evidence: their own sample of marbles from the urn, predictions described as made by four other agents based on their private samples from the same urn, and those agents' confidences. We sought to measure subjects' reliance on the subject's sample vs. agents' choices, and particularly to examine the extent to which the influence of the agents' choices was modulated by their confidence. The latter is a key measure in this setting, for distinguishing behavior from simpler heuristics like imitation. This is because an agent's confidence implies the quality of the agent's knowledge informing the choice, and therefore the extent to which their opinion should be trusted. Indeed, a differential effect of confident agents can be captured in a Bayesian ideal-observer model (simulations not shown), which infers the proportion of marbles in the urn from the different sources of evidence, by inferring and marginalizing over the agents' private samples, with confidence as a signal of more decisive evidence.

Behavior

We used a multi-level mixed logistic regression to estimate parameters reflecting how the tendency to predict red was influenced by each information source that should monotonically affect it.

Each variable was established as a distinct contribution to choice behavior (Table 1, Figure 2). At the group level, participants were more likely to predict red following samples with more red (vs. green) marbles (\mathbf{S}), more agents choosing red (vs. green) (\mathbf{O}), higher confidence of agents associated with red (\mathbf{C}_R) (regardless of how many agents chose that color), and lower confidence for green (\mathbf{C}_G). The magnitude of the coefficients for \mathbf{S} and \mathbf{O} indicates that four agents (at average confidence) were relied on roughly the same amount as the sample of eight marbles, meaning each of the agents' choices had impact approximately twice that of observing a single marble in terms of information on this task. Table 1 additionally presents the different variables effects in terms of AIC and variance explained according to McFadden's (1974) pseudo- \mathbf{R}^2 .

Our key question concerned the interaction, which measures whether agents' choices have a differential effect when they are confident. Here, as hypothesized, we found that effect of each agent's choice on participant decisions was greater when that agent was confident (O_RC_R, O_GC_G) .

Conformity and Self-Monitoring Scales

We next considered whether individual differences in this relatively stylized laboratory task tracked an index of real-world social behavior. Greater reliance on personal samples during the Urn Task corresponded greater self-reliance for decision-making in other social contexts (r = -.461, P = .013, Mean Conformity Scale Score -3.7 SD 11.4)

(Figure 7A). Controlling for gender and age, the effect remained significant (r = -.37, P = .049). There was no relationship between the conformity scale and the effect of agents on behavior (P > .4) most likely due to the complication of agent confidence. In contrast, self-monitoring relates specifically to behavioral adjustments to social cues to enhance reputation, would not be expected to show an effect in the absence of a live audience and this was confirmed by the data.

Neuroimaging

We pursued a parallel strategy in the brain to distinguish influence of each information type on neural correlates of estimated value in vmPFC. As vmPFC activity is well known to track the degree to which the chosen option is correct or likely to be rewarded ("chosen value", often relative to the unchosen option) (Tanaka et al., 2004; Daw et al., 2006; Kim et al., 2006; O'Doherty et al., 2007; Behrens et al., 2008; Wunderlich et al., 2010), we redefined all of our explanatory variables in terms of information indicating the chosen (vs unchosen) option will be correct, rather than red vs. green. Therefore, neural results are described with respect to 'accordance' (evidence indicating that the subject's chosen option will be correct) vs 'discordance' (evidence indicating that the subject's choice will be incorrect). (Note that these are symmetric: evidence that the subjects' choice is correct is, equivalently evidence that the other is incorrect.)

Neuroimaging findings are reported as group-level cluster-corrected statistics with a cluster-forming voxel threshold of Z > 3 and cluster significance level of P < 0.05. Results are described in format: [peak location in MNI coordinates (mm)], Z score of peak voxel, P value of cluster, size of cluster in voxels (and minimum cluster size at P < 0.05). Scaling of variables should be considered when interpreting the results (i.e.

a change from 0 to 4 agents' choices is scaled the same as a change from 0 to 8 marbles in a sample). All observed effects relate to when all other variables are at their mean. Mean effect contrasts all endured whole-brain cluster correction. Only activations within the medial prefrontal cortex (mPFC) reported, as this is the focus of our study. Between-subject analysis employed small volume correction using independent masks of regions of interest (detailed in methods).

Integrated Value fMRI Model

Neural correlates of overall chosen value from all information sources were found in central vmPFC ([-8 50 -8], Z_{max} = 4.08, P < .001, 410 voxels (min 76)). Negative correlations (higher activity when evidence favors the unchosen option more) correlated with dmPFC activity ([0 26 48], Z_{max} = 4.82, P < .001, 1345 voxels (min 76). See Figure 3A).

Component Value fMRI Model

We then tested whether these correlates of integrated value could decomposed according to the contribution of the different information sources (Figure 3B). For this we examined the effects of the same explanatory variables as the behavioral model, but expressed in terms of accordance vs. discordance with the subject's choice. Sample accordance (\mathbf{S}_{A}) predicted central vmPFC activity ([2 38 -8], $Z_{max} = 4.12$, P < 001, 446 voxels (min 76). Sample discordance (a negative effect of S_{A}) increased dmPFC activity ([4 30 44], $Z_{max} = 4.1$, P < .001, 276 voxels (min 76)). Accordance of agents' choices (\mathbf{O}_{A}) similarly increased central vmPFC activity (peaks: [-2 22 -12] and [-10 44 -12], $Z_{max} = 4.19$, P < .001, 679 voxels (min 77)), while discordance of agents' choices (the negative effect of O_{A}) increased dmPFC activation ([-2 20 46], $Z_{max} = 6.03$, P<0.01, 797 voxels (min 77)). The conditional main effect of

agent confidence (of accordant or discordant choices) did not produce activation in MFPC at this threshold.

As with behavior, the key question concerned activity corresponding to the differential impact of agents' choices when they are confident vs. unconfident, captured by the interaction (O_AC_A). Such an interaction was observed for BOLD activity only in anterior mPFC (amPFC), primarily occupying ventromedial area 10, with a small extension through anterior 14m (Mackey and Petrides) (peaks [8 58 6] and [4 62 2]], Z_{max} = 3.78, 85 voxels (min 79). This was the only activation for this contrast in the brain. Within this region, unconfident agent choices did little to influence the representation of value, while confident choices had a clear effect (see Figure 5).

The Spatial Linear Parametric Effect

Next, in order to formally examine the impression of spatial separation between the effects of the different information sources, we statistically compared spatial profiles of key effects of Component Value fMRI Model analysis (S_A , O_A , O_AC_A) along an anatomically defined axis from vmPFC to amPFC (Figure 4A). Only O_AC_A increased its effect (in percent signal change) along this axis (β = .03, SE = .01, P= 0.04). (S_A and O_A Ps > .27), and the difference of response between these variables also varied along the axis: $O_AC_A - S_A$ (β = .03, SE = .01, P= 0.045) and $O_AC_A - O_A$ (β = .03, SE = .02, P= 0.026). This rejected the null hypothesis that value-based activity relying on different information sources has a common spatial profile.

Peristimulus plots along this axis reveal that, moving anteriorly, regions of vmPFC respond with increasing selectivity for value derived from confident agents. Neither effects of agents' accordant choices (independent of confidence) nor of accordant samples shared this anatomical specificity. See Figures 4 and 5.

589 Individual Differences

Neural Effects x Behavior: We next tested whether component neural correlates predict component influence on decision-making behavior, using a between-subject analysis. At the group level, the effects of different information sources on choices, as estimated from behavior for each individual, were added as covariates to the *Component Value fMRI Model*. Contrasts were made between them. Within a mask of vmPFC and at a conservative cluster forming threshold (Z > 3), we found that weight placed on personal samples (S effect) predicted a greater neural response to personal sample accordance with choice (S_A) ([-6 54 -4], $Z_{max} = 3.83$, P = 0.03, 32 voxels (min 28). Dorsal and anterior to this, relatively more weight placed on the choices of agents (O effect – S effect) predicted a greater neural response to agents (O_A) ([-4 60 10], $O_{max} = 0.05$, 28 voxels (min 28). See Figure 6.

Conformity and Self-Monitoring Scales: Finally, we sought to test to test whether neural effects during the experiment reflect real-world behavior. Conformity scale scores predicted greater dmPFC activation when going with one's own sample $[0\ 26\ 38]$, $Z_{max}=5.02$, P=0.006, $50\ voxels$ (min 25), and activation just anterior to rTPJ (supramarginal gyrus) in response to conflict with others choices $[66\ -28\ 26]$, $Z_{max}=4.38$, P=0.01, $40\ voxels$ (min 25) (Figure 7B). Self-Monitoring, which reflects the tendency to alter behavior in in response to social cues from an audience, predicted a greater response to increasing accordance with agents in activity extending into rTPJ (peak $[62\ -28\ 36]\ Z_{max}=4.45$ with subpeak $(Z=4.08)\ [56\ -36\ 28]$, P=0.003, $120\ voxels$ (min 74). This indicated differential treatment of social agreement with greater self-monitoring, even without a live audience (Figure 7C).

612 Discussion

This study identified distinct behavioral and neural effects of distinct types of evidence used for making predictions. Behaviorally, each information type influenced decisions in a sensible direction. Confident agents had a greater influence on choices of participants – the hypothesized signature of complex, integrative use of information to evaluate options.

Collectively, increased reward expectancy from all evidence was tracked indiscriminately across a posterior to anterior axis in vmPFC, confirming earlier findings (e.g. Daw et al., 2006; Kim et al., 2006; Behrens et al., 2008; Wunderlich et al., 2010). However, this signal could also be decomposed according to the contribution of distinct components. Increased reward expectancy due to accordant samples and accordant agents' choices (irrespective of confidence) increased activity across vmPFC. In contrast, value that varied with accordant agents' choices but conditional on their confidence was preferentially represented in ventromedial regions of area 10. This is a distinct neurobiological marker of assurance from another person's confidence.

Segregation of value representations over regions of systematically varying cytoarchitecture is consistent with heterogeneity of their computation. The anatomical locations of confidence-based value processes are likely the resolution of computational requirements and connectivity of supporting anatomy. The cytoarchitecture and connectivity of amPFC suggests that value estimates from confident agents specifically involve a form of higher-order cognition (Ongur et al., 2003; Mackey and Petrides, 2010; Sepulcre et al., 2010). While influences of agents in the task can be modelled (as in our regression) simply as the counting of agents'

choices weighted by their confidence – the weighting itself is a signature of the variable's metacognitive treatment.

The nature of this treatment, and how it relates to anterior vmPFC is not yet known. One possibility is the use of inference. The Urn Task can be solved by using statistical inference to infer the contents of the urn given the observed evidence. This requires marginalizing agents' private samples, whose quality is inferred from an interaction of agents' choice and confidence. In principle, Bayes' rule can be invoked to infer (and then marginalize out) the probable state of the agents' samples. This could involve inferences of agents' knowledge from their behavior which would account for BA 10 involvement (Frith and Frith, 2012). Such computations are likely part of a broader class of inferential influences on choice (Tolman, 1948; Hampton et al., 2006, 2008; Daw et al., 2011; Solway and Botvinick, 2012). Additionally, BA 10 involvement could relate the confluence of cognitive processes (Ramnani and Owen, 2004; Zaki, 2013), such as the integration of observed and non-observable information (Burgess et al., 2007).

Both inferential and integrative processes are useful because they flexibly allow a naïve observer to make decisions in new environments. In social contexts, they allow for adaptable valuation using shifting combinations of inferred knowledge, intentions, impulsivity, and optimism of others before deciding how to use their choices to inform one's own. From this perspective, our findings support a theory that the evolution of area 10 could relate to cognitive specialization that optimizes decision-making in human cultures with the complexity of human expression (Povinelli and Preuss, 1995; Dunbar and Shultz, 2007).

It less likely that differences between neural correlates of value relate to a difference of mathematic heuristics: these regions do not come up in fMRI contrasts of

counting methods, addition or multiplication (Piazza et al., 2002; Kawashima et al., 2004). Similarly, while previous studies have examined associative learning in social contexts (Behrens et al., 2008; Hampton et al., 2008; Burke et al., 2010), associative learning was precluded in the present study by the omission of trial outcomes and infrequent repetition of agents.

Previously, however, neuroscience has highlighted the relationship between mPFC and associative learning about the reliability of others. For example, Behrens et al (2008) showed that mPFC is recruited to update beliefs about the accuracy of advice. Meshi et al (2012) and Boorman et al (2013) found that mPFC is related to using and evaluating the another's expertise. It will be interesting to explore how inferential and associative learning about the reliability of others relate.

Nicolle et al (2012) found that ventral-dorsal vmPFC axis delineates action-relevant from action-irrelevant preferences. Subsequent work has shown that individual differences of value representation along a (ventral-dorsal) vmPFC axis also distinguishes self- and other-regarding individuals (Sul et al., 2015). In the present study, we found that ventral area 10 does represent action-relevant preferences, but depending on the computations required. It may be the abstract nature of the calculation (counterfactual choice in the previous study, abstractly inferred or integrated information in the present) that determines amPFC involvement. Indeed, specificity across the posterior to anterior vmPFC axis, may relate to similar anatomical distinctions between primary and secondary rewards (McNamee et al., 2013; Sescousse et al., 2013; Clithero and Rangel, 2014; Li et al., 2015).

dmPFC activity was negatively correlated with estimated value from various sources of information. As in most decision tasks, the value of the action and uncertainty/conflict associated with that value are inversely correlated, though not

perfectly coupled. This is because, for instance, it is more difficult to choose the correct option for choices with conflicting information. Given the literature on correlates of different decision variables in midline prefrontal cortex, the activity we observed in anterior cingulate may reflect a form of conflict (Botvinick et al., 2004) or a cost-benefit process that accounts for both conflict and reduced likelihood of reward (Rushworth et al., 2011).

If a participant was more likely to be influenced by the personal sample, BOLD activity in central vmPFC varied more with the accordance of the sample with their imminent choice. Similarly, if a participant was more likely to be influenced by the choices of agents (relative to the personal sample) BOLD activity in amPFC varied more with accordance of agents' choices with their imminent choice. This suggests that the tendency to be influenced by an information source can be tracked, to an extent, by the sensitivity of that individual to supporting information from that source, within specific mPFC anatomy.

Social behavior outside the lab (i.e. conformity) was inversely correlated with the influence of private evidence during the task. In vmPFC, conformity and self-monitoring in other contexts did predict activations. However, exploration outside of this region revealed a link between neural responses to task influences, and the tendency to be socially influenced in other contexts. The tendency to adopt the decisions of others outside the lab predicted increased supramarginal gyrus responses to conflict with agents, just anterior to rTPJ (Figure 7B). It also predicted increased dmPFC activity when going with one's own sample. These results replicate findings that the tendency to conform socially can be predicted by the neural response to social conflict in these regions (Campbell-Meiklejohn et al., 2010; for meta-analysis see Wu et al., 2016). Activity within rTPJ that correlates with reward expectancy from

observing agent choices (Figure 7C), in high-self-monitors may relate to findings that reward expectancies from observing choices of others can recruit theory-of-mind-like processes (Bruguier et al., 2010; De Martino et al., 2013). This occurs in the absence of a live audience, suggesting that self-monitoring relates to cognitive processes that are somewhat independent of an action's immediate social consequences. Stimulation of the rTPJ region enhances the tendency to take another's perspective (Santiesteban et al., 2012) and its activity has been previously shown to increase when determining the relevance of someone else's behavior for one's decision-making (Carter et al., 2012). Although social interactions in the task were simulated and stylized, their relevance to real-world social settings is supported by these findings.

While results are relevant to real social contexts, we do not suggest that the highlighted processes are exclusive to the social domain. Indeed, the task's logic is based on comparing inferences from different sorts of information rather than social and non-social frames. This reflects the case for the coevolution of general cognitive faculties and social ability (Humphrey, 1976; Emery et al., 2007). Correspondingly, research has shown that the physiology of value representations in 'social' and 'non-social' contexts are similar, when similar processes are employed and similar models applied (Izuma et al., 2008; Zink et al., 2008; Takahashi et al., 2009; Campbell-Meiklejohn et al., 2010; Tricomi et al., 2010; Biele et al., 2011; Lin et al., 2011; Bartra et al., 2013; Boorman et al., 2013). The present results suggest that any differences between social and non-social valuation processes in vmPFC may be proportional to differential use of higher-order computation, and in future this may prove to be the most flexible definition of a 'social' reward.

734 Conclusions

735 The finding that decision-related signals in vmPFC are segmented by the 736 unique cognitive requisites of their computation is an important step in our 737 understanding of the representation of value in the brain. Concurrently, our findings 738 provide new neurobiological insight into the transmission of value information between 739 individuals and the mechanism by which confidence expressed by others assure or 740 discourage us in our decisions. Looking to the future, the findings present new 741 questions as to how distinct valuation processes with separate neural mechanisms 742 can be independently altered by experience, damage, and treatment.

743 References

- 744 Amodio DM, Frith CD (2006) Meeting of minds: the medial frontal cortex and social
- 745 cognition. Nat Rev Neurosci 7:268-277.
- 746 Barbas H (2007) Specialized elements of orbitofrontal cortex in primates. Ann N Y
- 747 Acad Sci 1121:10-32.
- 748 Bartra O, McGuire JT, Kable JW (2013) The valuation system: a coordinate-based
- 749 meta-analysis of BOLD fMRI experiments examining neural correlates of subjective
- 750 value. Neurolmage 76:412-427.
- 751 Beckmann C, Smith S (2004) Probabilistic independent component analysis for
- 752 functional magnetic resonance imaging, IEEE Trans Med Imaging 23:137-152.
- 753 Behrens T, Hunt L, Woolrich M, Rushworth M (2008) Associative learning of social
- 754 value. Nature 456:245-249.
- 755 Biele G, Rieskamp J, Krugel LK, Heekeren HR (2011) The neural basis of following
- 756 advice. PLoS Biol 9:e1001089.
- 757 Boorman ED, O'Doherty JP, Adolphs R, Rangel A (2013) The behavioral and neural
- mechanisms underlying the tracking of expertise. Neuron 80:1558-1571.
- 759 Botvinick MM, Cohen JD, Carter CS (2004) Conflict monitoring and anterior cingulate
- 760 cortex: an update. Trends Cogn Sci 8:539-546.
- 761 Bruguier AJ, Quartz SR, Bossaerts P (2010) Exploring the Nature of "Trader Intuition".
- 762 J Financ 65:1703-1723.
- 763 Burgess PW, Gilbert SJ, Dumontheil I (2007) Function and localization within rostral
- 764 prefrontal cortex (area 10). Phil Trans R Soc B 362:887-899.
- 765 Burke C, Tobler P, Baddeley M, Schultz W (2010) Neural mechanisms of
- 766 observational learning. Proceedings of the National Academy of Sciences of the
- 767 United States of America 107:14431-14436.

- 768 Campbell-Meiklejohn DK, Bach DR, Roepstorff A, Dolan RJ, Frith CD (2010) How the
- opinion of others affects our valuation of objects. Current biology: CB 20:1165-1170.
- 770 Carter RM, Bowling DL, Reeck C, Huettel SA (2012) A distinct role of the temporal-
- 771 parietal junction in predicting socially guided decisions. Science 337:109-111.
- 772 Clithero JA, Rangel A (2014) Informatic parcellation of the network involved in the
- computation of subjective value. Soc Cogn Affect Neurosci 9:1289-1302.
- 774 Cohen J (2003) Applied multiple regression/correlation analysis for the behavioral
- 775 sciences, 3rd ed. / Jacob Cohen ... [et al.] Edition. Mahwah, N.J.; London: L. Erlbaum
- 776 Associates.
- 777 Daw N, Doya K (2006) The computational neurobiology of learning and reward. Curr
- 778 Opin Neurobiol 16:199-204.
- 779 Daw N, O'Doherty J, Dayan P, Seymour B, Dolan R (2006) Cortical substrates for
- 780 exploratory decisions in humans. Nature 441:876-879.
- 781 Daw ND, Gershman SJ, Seymour B, Dayan P, Dolan RJ (2011) Model-based
- 782 influences on humans' choices and striatal prediction errors. Neuron 69:1204-1215.
- 783 De Martino B, O'Doherty JP, Ray D, Bossaerts P, Camerer C (2013) In the Mind of the
- 784 Market: Theory of Mind Biases Value Computation during Financial Bubbles. Neuron
- 785 80:1102-1102.
- 786 Dunbar RIM, Shultz S (2007) Understanding primate brain evolution. Phil Trans R Soc
- 787 B 362:649-658.
- 788 Eklund A, Nichols TE, Knutsson H (2016) Cluster failure: Why fMRI inferences for
- 789 spatial extent have inflated false-positive rates (vol 113, pg 7900, 2016). Proceedings
- 790 of the National Academy of Sciences of the United States of America 113:E4929-
- 791 E4929.
- 792 Emery NJ, Clayton NS, Frith CD (2007) Introduction. Social intelligence: from brain to
- 793 culture. Phil Trans R Soc B 362:485-488.
- 794 Frith CD, Frith U (2012) Mechanisms of social cognition. Annu Rev Psychol 63:287-
- 795 313.
- Hampton A, Bossaerts P, O'Doherty J (2006) The role of the ventromedial prefrontal
- 797 cortex in abstract state-based inference during decision making in humans. J Neurosci
- 798 26:8360-8367.
- 799 Hampton A, Bossaerts P, O'Doherty J (2008) Neural correlates of mentalizing-related
- 800 computations during strategic interactions in humans. Proc Natl Acad Sci USA
- 801 105:6741-6746.
- 802 Humphrey NK (1976) The Social Function of Intellect. In: Growing points in ethology
- 803 (P.P.G. B, R.A. H, eds), pp 303-317. Cambridge, UK: Cambridge University Press.
- 804 Izuma K, Saito D, Sadato N (2008) Processing of social and monetary rewards in the
- 805 human striatum. Neuron 58:284-294.
- 806 Kawashima R, Taira M, Okita K, Inoue K, Tajima N, Yoshida H, Sasaki T, Sugiura M,
- 807 Watanabe J, Fukuda H (2004) A functional MRI study of simple arithmetic--a
- 808 comparison between children and adults. Brain Res Cogn Brain Res 18:227-233.
- 809 Kim H, Shimojo S, O'Doherty JP (2006) Is avoiding an aversive outcome rewarding?
- Neural substrates of avoidance learning in the human brain. PLoS Biol 4:e233.

- Kringelbach M, Rolls E (2004) The functional neuroanatomy of the human orbitofrontal
- 812 cortex: evidence from neuroimaging and neuropsychology. Prog Neurobiol 72:341-372.
- 813 Langner O, Dotsch R, Bijlstra G, Wigboldus DHJ, Hawk ST, van Knippenberg A (2010)
- Presentation and validation of the Radboud Faces Database. Cogn Emot 24:1377-
- 815 1388.
- 816 Levy DJ, Glimcher PW (2012) The root of all value: a neural common currency for
- 817 choice. Curr Opin Neurobiol 22:1027-1038.
- 818 Li Y, Sescousse C, Amiez C, Dreher J-C (2015) Local Morphology Predicts Functional
- 819 Organization of Experienced Value Signals in the Human Orbitofrontal Cortex. The
- 820 Journal of Neuroscience 35:1648-1658.
- 821 Lin A, Adolphs R, Rangel A (2011) Social and monetary reward learning engage
- 822 overlapping neural substrates. Soc Cogn Affect Neurosci.
- 823 Mackey S, Petrides M (2010) Quantitative demonstration of comparable architectonic
- 824 areas within the ventromedial and lateral orbital frontal cortex in the human and the
- 825 macague monkey brains. Eur J Neurosci 32:1940-1950.
- 826 McGuire M (1967) Personality and Susceptability to Social Influence. In: Handbook of
- 827 Personality Theory and Research (Borgatta EF, Lambert WW, eds). Chicago: Rand
- 828 McNally.
- 829 McNamee D, Rangel A, O'Doherty JP (2013) Category-dependent and category-
- 830 independent goal-value codes in human ventromedial prefrontal cortex. Nat Neurosci
- 831 16:479-485.
- 832 Mehrabian A, Stefl CA (1995) Basic Temperament Components of Loneliness,
- 833 Shyness, and Conformity. Soc Behav Personal 23:253-263.
- 834 Meshi D, Biele G, Korn CW, Heekeren HR (2012) How expert advice influences
- 835 decision making. PloS one 7:e49748.
- 836 Nicolle A, Klein-Flugge MC, Hunt LT, Vlaev I, Dolan RJ, Behrens TE (2012) An agent
- 837 independent axis for executed and modeled choice in medial prefrontal cortex. Neuron
- 838 75:1114-1121.
- 839 O'Doherty J, Hampton A, Kim H (2007) Model-based fMRI and its application to
- reward learning and decision making. ANYAS 1104:35-53.
- Ongur D, Ferry AT, Price JL (2003) Architectonic subdivision of the human orbital and
- medial prefrontal cortex. J Comp Neurol 460:425-449.
- Patel D, Fleming SM, Kilner JM (2012) Inferring subjective states through the
- observation of actions. Proc R Soc Lond, Ser B: Biol Sci 279:4853-4860.
- 845 Piazza M, Mechelli A, Butterworth B, Price CJ (2002) Are subitizing and counting
- implemented as separate or functionally overlapping processes? NeuroImage 15:435-
- 847 446.
- Povinelli DJ, Preuss TM (1995) Theory of mind: evolutionary history of a cognitive
- 849 specialization. Trends Neurosci 18:418-424.
- 850 Ramnani N, Owen AM (2004) Anterior prefrontal cortex: insights into function from
- anatomy and neuroimaging. Nat Rev Neurosci 5:184-194.
- 852 Rushworth MFS, Noonan MP, Boorman ED, Walton ME, Behrens TE (2011) Frontal
- 853 cortex and reward-guided learning and decision-making. Neuron 70:1054-1069.

- Santiesteban I, Banissy MJ, Catmur C, Bird G (2012) Enhancing social ability by
- stimulating right temporoparietal junction. Curr Biol 22:2274-2277.
- 856 Sepulcre J, Liu H, Talukdar T, Martincorena I, Yeo BT, Buckner RL (2010) The
- 857 organization of local and distant functional connectivity in the human brain. PLoS
- 858 Comput Biol 6:e1000808.
- 859 Sescousse G, Caldu X, Segura B, Dreher JC (2013) Processing of primary and
- 860 secondary rewards: a quantitative meta-analysis and review of human functional
- 861 neuroimaging studies. Neurosci Biobehav Rev 37:681-696.
- 862 Smith S, Jenkinson M, Woolrich M, Beckmann C, Behrens T, Johansen-Berg H,
- 863 Bannister P, De Luca M, Drobnjak I, Flitney D, Niazy R, Saunders J, Vickers J, Zhang
- Y, De Stefano N, Brady J, Matthews P (2004) Advances in functional and structural
- MR image analysis and implementation as FSL. NeuroImage 23 Suppl 1:S208-219.
- 866 Snyder M (1974) Self-Monitoring of Expressive Behavior. JPSP 30:526-537.
- 867 Solway A, Botvinick MM (2012) Goal-directed decision making as probabilistic
- 868 inference: a computational framework and potential neural correlates. Psychol Rev
- 869 119:120-154.
- 870 Sul S, Tobler PN, Hein G, Leiberg S, Jung D, Fehr E, Kim H (2015) Spatial gradient in
- 871 value representation along the medial prefrontal cortex reflects individual differences in
- 872 prosociality. Proceedings of the National Academy of Sciences of the United States of
- 873 America 112:7851-7856.
- 874 Takahashi H, Kato M, Matsuura M, Mobbs D, Suhara T, Okubo Y (2009) When your
- gain is my pain and your pain is my gain: neural correlates of envy and schadenfreude.
- 876 Science (New York, NY) 323:937-939.
- 877 Tanaka SC, Doya K, Okada G, Ueda K, Okamoto Y, Yamawaki S (2004) Prediction of
- 878 immediate and future rewards differentially recruits cortico-basal ganglia loops. Nat
- 879 Neurosci 7:887-893.
- 880 Thomas JP, Mcfadyen RG (1995) The Confidence Heuristic: A Game-Theoretic
- Analysis. J Econ Psychol 16:97-113.
- Tolman EC (1948) Cognitive maps in rats and men. Psychol Rev 55:189-208.
- 883 Tricomi E, Rangel A, Camerer C, O'Doherty J (2010) Neural evidence for inequality-
- averse social preferences. Nature 463:1089-U1109.
- 885 Vazquez AI, Bates DM, Rosa GJM, Gianola D, Weigel KA (2010) Technical note: an R
- 886 package for fitting generalized linear mixed models in animal breeding. J Anim Sci
- 887 88:497-504.
- 888 Woolrich M (2008) Robust group analysis using outlier inference. NeuroImage 41:286-
- 889 301.
- Woolrich MW, Behrens TE, Beckmann CF, Jenkinson M, Smith SM (2004) Multilevel
- 891 linear modelling for FMRI group analysis using Bayesian inference. NeuroImage
- 892 21:1732-1747.
- 893 Wu H, Luo Y, Feng C (2016) Neural signatures of social conformity: A coordinate-
- 894 based activation likelihood estimation meta-analysis of functional brain imaging studies.
- 895 Neurosci Biobehav Rev 71:101-111.

896 897	Wunderlich K, Rangel A, O'Doherty JP (2010) Economic choices can be made using only stimulus values. Proc Natl Acad Sci USA 107:15005-15010.
898 899	Zaki J (2013) Cue Integration: A Common Framework for Social Cognition and Physical Perception. Perspect Psychol Sci 8:296-312.
900 901	Zink C, Tong Y, Chen Q, Bassett D, Stein J, Meyer-Lindenberg A (2008) Know your place: neural processing of social hierarchy in humans. Neuron 58:273-283.
902	

Figure Legends

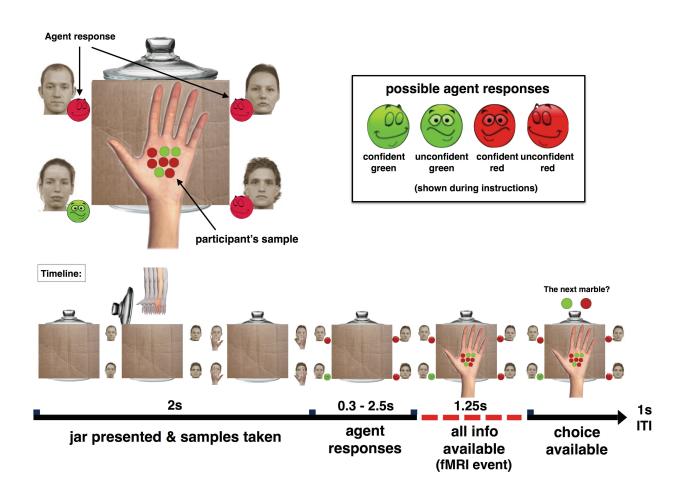
Figure 1. Urn Task. On each trial: (i) A new urn of randomly mixed marbles is presented. Contents are hidden. (ii) Animation of five hands individually reaching for five different samples from the urn occurs (parts i and ii last 1.5 to 2s). (iii) Predictions of the *next* marble drawn from the urn, and their associated confidence in those predictions of four agents shown. Agents were represented as sepia toned faces with neutral expression. Agents' predictions were expressed by the colour of the circle positioned next to their face. Confidence indicated as the expression within that circle and the speed at which the answer was shown (rapid + smug = high confidence). Agents' answers took between 300 and 2500ms to appear. Once agents' choices were in, they remained on the screen for 1250s. (iv) Next, the participant's own sample of marbles appeared from the bottom of the screen was displayed with all other information for a further 1250ms. The sample contained 8 marbles, with one to seven of them being red. This was the event modelled in the fMRI analysis. (v) Finally, the participant is asked to make a prediction (red or green). No choice feedback was provided.

Figure 2. Behavioural Effects. Probability (mean proportion) of choices for red as a function of: reds in sample, frequency and confidence of red choices by agents, and frequency and confidence of green choices by agents. Error bars are standard error.

Figure 3. Neural Representation of Value in vmPFC. Activations colour-coded with respect to amount of evidence supporting the likelihood of the participant's choice being correct (Clusters Defined by Z > 3.0, Cluster Sig P< 0.05) A: neural representation of value from the *Integrated Value fMRI Model* combining all available information. B: Distribution and overlap of activity correlating with increasing value computed from information sources of the *Component Value fMRI Model*. C:

928 Distribution and overlap of activity correlating with increasing value computed from 929 information sources of the Component Value fMRI Model. 930 Figure 4. Effect Time-Courses Across vmPFC. A. Anatomically defined spherical 931 regions of interest spanning the superior medial gyrus from area 14m (Mackey and 932 Petrides, 2010) to ventromedial area 10. B. Plots of mean effects of interest within the 933 Component Value fMRI Model across 5 Time bins are 2.8s (1 TR) beginning at the 934 onset of agents' responses. Figure shows relative non-specificity of SA and OA across 935 the region, the increasing specificity of O_AC_A toward dorsoanterior regions, and the 936 sustained response to agents' choices O_A into the response window of S_A. Error bars 937 are standard error. 938 Figure 5. Effects of Confident and Unconfident Agents across vmPFC. Mean 939 effect of an adapted Component Value fMRI Model that separates effects of confident 940 agents' choices from unconfident agents' choices across the 5 spheres and time bins 941 of Figure 4. Figure shows the increasing specificity of socially-learned value that is 942 contingent on agents' confidence toward dorsoanterior regions of vmPFC. Error bars 943 are standard error. 944 Figure 6. Individual Differences of Task Behavior: Effects of information sources 945 on choices, for each individual, were added as covariates to the Component Value 946 fMRI Model analysis. vmPFC responses to SA are predicted by the influence of samples on choice behavior. amPFC responses to OA are predicted by the relative 947 948 influence of agents (O effect – S effect) on choice behavior. 949 Figure 7. Social Influence in Other Situations. A. Scatterplot showing relationship 950 between the use of one's own sample during the Urn Task (arbitrary units) and self-951 reported reliance on agents outside the lab. B Between-subjects those more likely to

conform in other social situations respond more to conflict with agents and less conflict
with personal samples within regions previously shown predict conformity from social
conflict responses (Campbell-Meiklejohn et al., 2010). C. Between subjects, rTPJ
responds more to accordance of agents' choices in proportion to tendency to adapt
behaviour to social cues in real-world situations (self-monitoring).



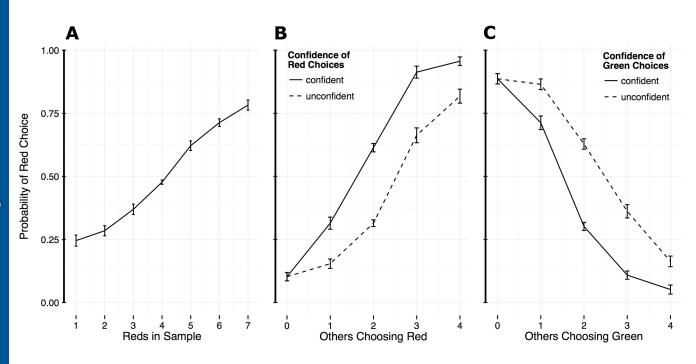


Table 1. Fixed Effects from Mixed Effects Logistic Regression of Each Variable's Effect on Choice of Red

Variable	β	SE	P	Partial R2	Δ ΑΙC
(Intercept)	-0.03	0.07	0.62		
Proportion of Sample That is Red (S)	10.26	0.87	<0.001	0.38	1160
Proportion of Agents Choosing Red (O)	9.96	0.75	<0.001	0.55	2297
Confidence of Agents Choosing Red (C _R)	2.57	0.30	<0.001	0.15	321
Confidence of Agents Choosing Green (C _G)	-2.61	0.30	<0.001	0.15	332
Proportion of Agents Choosing Red x Confidence (O _R C _R)		0.53	<0.001	0.01	8.2
Proportion of Agents Choosing Green x Confidence (O _G C _G)		0.53	0.01	0.01	0.4

R² of full model is .68 (McFadden's Pseudo R²)

Partial R² calculated as 1 - (log likelihood of full model / log likelihood of model without designated predictor). Corresponding change in AIC value also provided.

