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5 **Contributions of the medial prefrontal cortex to social influence in economic**
6 **decision-making**

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25 **Author Contributions**

26 M.A.J.A and N.R. designed the study. M.A.J.A collected and analysed the data. M.A.J.A and
27 N.R. wrote the manuscript.

28                                              **Abstract**

29     Economic decisions are guided by highly subjective reward valuations (SVs). Often these SVs

30     are overridden when individuals conform to social norms. Yet, the neural mechanisms that

31     underpin the distinct processing of such normative reward valuations (NV) are poorly

32     understood. The dorsomedial and ventromedial portions of the prefrontal cortex

33     (dmPFC/vmPFC) are putatively key regions for processing social and economic information

34     respectively. However, the contribution of these regions to economic decisions guided by

35     social norms is unclear. Using fMRI and computational modelling we examine the neural

36     mechanisms underlying the processing of SVs and NVs. Subjects (n = 15) indicated either

37     their own economic preferences or made similar choices based on a social norm - learnt

38     during a training session. We found that that the vmPFC and dmPFC make dissociable

39     contributions to the processing of SV and NV. Regions of the dmPFC processed *only t*he

40     value of rewards when making normative choices. In contrast, we identify a novel

41     mechanism in the vmPFC for the coding of value. This region signalled both subjective and

42     normative valuations, but activity was scaled positively for SV and negatively for NV. These

43     results highlight some of the key mechanisms that underpin conformity and social influence

44     in economic decision-making.

**Introduction**

45

46    Behaviour is frequently driven by evaluations of the value of different courses of action

47    (Kahneman and Tversky 1984; Rushworth and Behrens 2008). In humans, these evaluations

48    form part of our everyday lives when we make economic decisions and place value on

49    behaviours that result in rewarding outcomes. Such decisions can be highly subjective

50    (Green et al. 1994; Mazur 2001). For example, whilst some people are impulsive and favour

51    small immediate rewards to larger delayed benefits, others are patient and prefer to wait

52    much longer in order to obtain only slightly larger rewards.

53    The neural basis of such subjective impulsivity in economic decision-making is becoming

54    increasingly understood (McClure et al. 2004; Kable and Glimcher 2007, 2010; Kim et al.

55    2008; Peters and Buchel 2009; Figner et al. 2010; Louie and Glimcher 2010). However, such

56    economic decisions are often made in the context of groups of individuals interacting

57    together. Within these groups behaviour is often dictated by social norms which determine

58    what behaviours are permissible or preferred (Asch 1956; Kahneman and Miller 1986; Boyd

59    et al. 2003; Fehr and Fischbacher 2004). Such normative preferences often override

60    subjective evaluations, with people flexibly switching between making economic decisions

61    based on subjective or normative valuations. However, there is currently a very limited

62    understanding of how reward valuations based on normative preferences are recalled and

63    influence activity in the brain (Izuma 2013; Ruff and Fehr 2014). How does the brain process

64    rewards that are valued subjectively, or through recalled social norms?

65    The medial prefrontal cortex (mPFC) is understood to contribute to the processing of social

66    norm information, but also to impulsive economic decision-making (Izuma 2013). The

67    prevailing view of functional organisation in the mPFC suggests that these functions are

68    localised to distinct zones of the mPFC (Rudebeck et al. 2008). It is often claimed that dorsal

69    sub-regions (DmPFC) are specialised for processing social information, whereas ventral

70    portions (VmPFC) are specialised for processing information about the value of rewards

71    (Amodio and Frith 2006; Rushworth and Behrens 2008).

72    Anatomical evidence supports the notion of a functional dissociation between the DmPFC

73    (comprising areas BA 6,8 and 9) and VmPFC (area 11 and 32). These regions contain distinct

74    cytoarchitectonic zones and each have a distinct connectional fingerprint (Barbas et al. 1999;

75    Cavada et al. 2000; Petrides and Pandya 2006, 2007; Sallet et al. 2013; Neubert et al. 2015).

76    Notably, portions of the VmPFC are strongly connected to regions implicated economic

77    decision-making but have weaker connections to areas engaged when processing social

78 information (Barbas et al. 1999; Cavada et al. 2000; Petrides and Pandya 2006, 2007; Kable

79 and Glimcher 2007; Sallet et al. 2013; O'Doherty 2014; Neubert et al. 2015). In contrast, sub-

80 regions of the DmPFC (Ongur et al. 2003; Petrides and Pandya 2006) - are strongly

81 connected to areas of the brain that are more typically engaged during social information

82 processing (Apps and Sallet, 2017; Barbas et al. 1999; Cavada et al. 2000; Petrides and

83 Pandya 2006, 2007; Behrens et al. 2009; Kilner 2011; Apps and Tsakiris 2013; Sallet et al.

84 2013; Neubert et al. 2015). Functional evidence also supports claims of a dissociation (Frith

85 and Frith 2006; Izuma 2013; Ruff and Fehr 2014). Portions of areas 6, 8 and 9 are engaged

86 when processing others intentions or mental states (Ramnani and Miall 2004; Behrens et al.

87 2008; Hampton et al. 2008; Gabay et al. 2014), when learning what attitudes are normative

88 (Spitzer et al. 2007; Klucharev et al. 2009), and when social norms are violated (Berthoz et al.

89 2002; Spitzer et al. 2007; Buckholtz et al. 2008; Prehn et al. 2008; Buckholtz and Marois

90 2012). In contrast, the ventral portions of the mPFC (VmPFC), including BA 32 and 11 (Ongur

91 et al. 2003; Petrides and Pandya 2006), have been shown to signal the value of both primary

92 and secondary reinforcers and particularly in processing the subjective value of economic

93 rewards (Kable and Glimcher 2007; Luhmann et al. 2008; Pine et al. 2009; Smith et al. 2010;

94 O'Doherty 2011; Peters 2011; Hunt et al. 2012; Strait et al. 2014). Moreover, damage to this

95 region in humans has been linked to impulsive economic decisions (Koenigs et al. 2010; Mar

96 et al. 2011).

97 More recent evidence has cast doubt on whether there is such a strong dissociation. Studies

98 examining the neural mechanisms that underlie the learning of another's subjective

99 valuation of a reward (Garvert et al. 2015), or choosing on behalf of another based on their

100 preferences (Nicolle et al. 2012) have shown the involvement of both the VmPFC and

101 DmPFC. They found that both the DmPFC and VmPFC can be engaged by the value of a

102 reward according to either ourselves or another person. However, these results suggest that

103 DmPFC is engaged when this valuation is not guiding the execution of one's current actions

104 (it is engaged in 'offline' valuations) and the VmPFC is engaged by the value guiding one's

105 current choices ('online' valuation'). This would therefore point to neither the VmPFC nor

106 DmPFC being engaged by social or non-social information specifically. However, these

107 decisions were made either to reward the subjects themselves, or one other person. The

108 mechanisms that underlie how the brain processes the value of a reward when required to

109 conform to a norm are unclear. Moreover, it is unclear how different regions of the mPFC

110 contribute to the processing of both subjective and normative valuations.

111    In this study we dissect out the contribution of different regions of the mPFC to making

112    decisions based on subjective (SV) and normative valuations (NV). We designed a paradigm

113    based on previous delay-discounting economic decision-making tasks that have been used

114    to examine subjective impulsive behaviours (Mazur 2001; Kable and Glimcher 2007).

115    Subjects made inter-temporal economic decisions choosing between a small immediate

116    reward, and a larger, delayed reward. On half of the trials these choices were made based

117    on their subjective preferences, and on half of the trials they were made based on a

118    normative valuation that was learnt during a training session. Using this design in

119    conjunction with functional magnetic resonance imaging (fMRI) and computational

120    modelling, we were able to examine the contribution of different regions of the mPFC to the

121    processing of subjective or normative reward valuations.

**Methods**

123 *Subjects*

124 Sixteen healthy right-handed participants were screened for neurological, psychiatric and

125 psychological disorders (ages 18-32; 13 female). This study was approved by the Royal

126 Holloway, University of London Psychology Department Ethics Committee and conformed to

127 the regulations set out in the CUBIC MRI Rules of Operation. We excluded participants who

128 made translations or rotations of >3mm (or >3°) volume to volume, or subjects who's total

129 movement was greater than 3mm. One (male) subject was excluded for failing to respond

130 on 30% of the trials and excessive head motion. Subjects were paid for their participation

131 (see 'payment' in supp. Methods). Subjects were informed that a previous behavioural

132 experiment had taken place with 100 participants. They were told that these participants

133 received payment in the same manner that they had. However, in fact no previous study

134 was conducted.

135 *Task*

136 The aim of this experiment was to examine the processing of rewards, the value of which

137 was either discounted by temporal delays subjectively, or in a manner that conformed to a

138 social norm. Subjects were engaged in the experiment over two consecutive days. On the

139 first day, subjects performed two tasks. First they indicated their own preferences on a

140 temporal discounting task and second they learnt by trial and error what they believed was

141 normative preferences on a similar delay-discounting task. Subjects were told that this

142 preference reflected what 'at least 69% of people chose to do in the prior pilot experiment'.

143 On the second day, subjects performed similar trials of a temporal discounting task but on

144 half of the trials they were required to indicate their own preferences (Subjective trials) and

145 on the other half they were required to conform to the "normative" preferences that they

146 had learnt during the training session and not their own preferences. Although it should be

147 noted that subjects were free to choose on both types of trial.

148 For the temporal discounting task, subjects were required to choose between an immediate

149 reward (£3) and a delayed reward that was shown on the screen (sup. Fig.1 and Fig.1). The

150 magnitude of the delayed options were £3.10, £3.75, £5, £8, £12 and £20 and were available

151 at delays of 1 day, 15 days, 30 days, 60 days, 100 days and 180 days. Thus there were 36

152 different combinations of delay and magnitude that were used as the delayed options. The

153 same options were used in both the training tasks and the task inside the scanner in both

154 conditions, although trials were presented in different pseudo-randomised orders.

155

156 *Payment*

157 Subjects were told that their payment would be based on their choice on one trial each from
158 the normative or subjective trials during the training or scanning session. This payment
159 would be determined by them selecting numbers at random "out of a hat". The number
160 would correspond to one of the trials during the training and scanning session and their
161 payment would be based on whichever choice they indicated on that trial. This approach has
162 previously been used to ensure that subjects are incentivised to accurately indicate their
163 preferences on all trials. Subjects were informed that they would be paid by cheque for their
164 participation. If on the selected trial they chose the delayed option, they would be paid that
165 higher reward value, but the cheque would be dated such that it could not be cashed until
166 the delay had passed. If they chose the immediate option then the cheque would be dated
167 the same day. All of this information was provided to the subjects before the experiment,
168 thus subjects were aware that their decisions during the experiment were real economic
169 decisions. Importantly, subjects were not rewarded during the training or scanning session
170 for making responses that were congruent or incongruent with the norm. This was
171 important, as we did not want subjects to associate making decisions on the normative trials
172 with any additional rewards – other than that being offered in association with a delay. Such
173 additional associations could have distorted behaviour and the processing of delayed
174 rewards in the main experiment, as they would only be present in the normative condition
175 and not in the subjective condition. Subjects were told that one trial from the normative
176 condition would be selected at random and would affect their payment, in exactly the same
177 manner as on the subjective trials. The subjects were not, therefore, incentivized to conform
178 but were simply instructed to do so.  This ensured that subjects believed that the economic
179 choices made during the main tasks were the only choices that influenced their payment for
180 the experiment.

181

182 *Apparatus*

183 Subjects lay supine in an MRI scanner (3T Siemens Trio, CUBIC, Royal Holloway, University of
184 London) with the fingers of the right hand positioned on an MRI-compatible response box.
185 Stimuli were projected onto a screen behind the subject and viewed in a mirror positioned
186 above the subjects face. Presentation software (Neurobehavioral Systems, Inc., USA) was

187    used for experimental control (stimulus presentation and response collection). A custom-

188    built parallel port interface connected to the Presentation PC received transistor-transistor

189    logic (TTL) pulse inputs from the response keypad. It also received TTL pulses from the MRI

190    scanner at the onset of each volume acquisition, allowing events in the experiment to

191    become precisely synchronized with the onset of each scan. The timings of all events in the

192    experiment were sampled accurately, continuously and simultaneously (independently of

193    Presentation) at a frequency of 1 kHz using an A/D 1401 unit (Cambridge Electronic Design,

194    UK). Spike2 software was used to create a temporal record of these events. Event timings

195    were prepared for subsequent general linear model (GLM) analysis of fMRI data (see event

196    definition and modelling in the main text).

197

198    *Trial Structure*

199    During the scanning session, each trial began with a trial-type cue (either the word "YOU" or

200    "GROUP"), that indicated whether subjects were required to make subjective preferences

201    ("YOU") or indicate normative preferences ("GROUP") on the trial. Following the trial-type

202    cue, after a variable delay, an offer cue was presented that indicated the magnitude and

203    delay of the delayed option. After a further variable delay, a trigger cue was presented

204    where subjects were required to indicate their choice (for full timings see Fig.1). A "now"

205    stimulus was used to signify the £3 immediate option and a "wait" stimulus was used for the

206    delayed option. Subjects were required to indicate their choice at the time of the trigger

207    cue, by pressing one of two buttons on a keypad. The trigger cue was presented for 1000ms,

208    any responses before or after this time period resulted in the trials being classified as

209    "missed" (All subjects included missed less than 3% of trials). Subjects were instructed to

210    press the button that corresponded to "now" if the preference was the £3 immediate option

211    or "wait" for the larger delayed option. In order to prevent subjects from preparing a

212    specific motor response at the time of the offer cue, the position of the "now" and "wait"

213    stimuli were pseudorandomly organised, such that subjects could not predict which button

214    would be "now" and which would be "wait" at the time of the offer cue. All stimuli were also

215    colour-coded to ensure that is was clear whether a subjective or normative preference was

216    required on each trial. Yellow cues indicated that a normative choice should be made and

217    white cues indicated that a subjective choice should be made. By introducing variable jitters

218    between offer cues and responses we decreased the possibility of finding reaction time

219    related behavioural or neuroimaging findings, due to extended and variable fore-periods

220 before subjects indicated choices. As expected, therefore, we found no behavioural effects
221 on reaction times.

222

223 *Procedure*

224 *Training*

225 Subjects were trained in two phases one day prior to scanning. In the first phase the subject

226 was presented with a series of visual stimuli on a monitor and performed a series of delay-
227 discounting trials where they were required to indicate their own preferences between the
228 delayed and an immediate options. Each trial consisted of an offer cue (an amount of money
229 and a delay period) and a trigger cue (two lines corresponding to two buttons on the
230 keypad, with the words "wait" above one line and "now" above the other line). During this
231 phase of training subjects performed 108 trials. This stage of the training enabled subjects to
232 familiarise themselves with performing delay-discounting trials. This task allowed us to
233 examine the stability of subjective preferences pre and post the learning of normative
234 preferences.

235

236 In the second phase of training, subjects performed a task where they learned the normative
237 preferences for each delayed option. The subjects were informed that a previous
238 behavioural experiment had taken place with 100 participants and that there was always at
239 least 69% agreement on whether people should wait for the delayed reward or take the
240 immediate one. Their task was to learn what this majority/group of people would choose to
241 do through trial and error. Each trial consisted of a delayed offer cue and a trigger cue but
242 also an additional feedback cue. The feedback cue indicated the social norm preference for
243 the delayed option on each trial. The cue was either the word "NOW" or "WAIT", which
244 indicated whether the normative preference was for the immediate or delayed option
245 respectively. Subjects were instructed to indicate the normative preferences by learning
246 from the feedback. The normative preferences learnt during this session were based around
247 the behaviour of subjects during a pilot experiment (see "computational modelling" below
248 for more details). During this session, subjects performed 108 trials, with the same options
249 presented as during the first phase of the training, in a pseudo-random order. During
250 training every subject correctly indicated the norm response at greater than 95% accuracy

251    after the first 10 trials during this session. Moreover, in the subsequent scanning session,

252    subjects performed a further 20 trials of this task with feedback, ensuring that subjects

253    learnt and recalled the norm during the main experiment (See below).

254

255    *Scanning Session*

256    On the day following the training session, subjects performed a similar delay-discounting

257    task inside the MRI scanner. There were 216 pseudorandomly organised trials, 108 where

258    they indicated their own preference (subjective trials) and 108 where they indicated the

259    preferences according to the majority behaviour they had learnt during the training

260    (normative trials). The large number of trials, and the parametric analysis, were approaches

261    employed that can increase power to detect within-subject effects (although no formal

262    power analysis was conducted, due to difficulties in interpretation; Mumford 2012). In this

263    session, there was no feedback cue on the normative trials. Subjects were therefore

264    required to recall the normative preferences they had learned during training. In this

265    session, all stimuli were colour-coded, with a different coloured font used for each

266    condition, ensuring that subjects were able to distinguish between the subjective and

267    normative conditions. This design enabled us to examine activity in the brain when subjects

268    made identical decisions, but when these decisions were based on subjective or normative

269    valuations.

270

271

272    *Computational Modelling*

273    Previous research has shown that behaviour in delay-discounting tasks can be modelled

274    using a number of different functions (Green et al. 1994; Mazur 2001) that contain discount

275    factors (free parameters that explain how rewards are idiosyncratically discounted by time).

276    Two models were compared separately in terms of their fit to the subjective preferences of

277    the subjects and also the subject's behaviour on the normative trials. The first was a

278    hyperbolic model (Mazur 2001) in which the subjective value of a reward (V) is a function of

279    its magnitude (M) and the delay (d) on a given trial:

280

281

282      (1) $$V_{(t)} = \frac{M_{(t)}}{(1+kd_{(t)})}$$

283      In this model k is the discount factor, an idiosyncratic free parameter that discounts the

284      magnitude (M) of the reward, such that the subjective value (V) is less than its objective

285      magnitude. The value of k therefore reflects the extent to which a subject discounts a

286      delayed reward, such that a high k decreases the value of the reward quickly as the delay

287      becomes greater.

288      We compared the hyperbolic model with an alternative model, to examine whether he

289      hyperbolic model best reflected choice behaviour in both the normative and subjective

290      trials. In this second model, the subjective value of the rewards (V) was a function of the

291      exponential effect on the delay where:

292

293      (2) $$V = e^{-k.d(t)} \text{ x } M_t$$

294

295      In (2) the discounting effect of the delay is expressed as an exponential transform ($e$) of the

296      discount factor (k) multiplied by the delay period (d). As such, the magnitude of a reward

297      (M) is idiosyncratically, but exponentially discounted by the length of delay before its

298      receipt. The hyperbolic and exponential models were fitted separately to the preferences on

299      the subjective trials and the choices on the normative trials. Thus, separate discount factors

300      (k) could be estimated for the subjective and normative trials and also each model could be

301      compared in terms of it's fit to the data.

302      As in previous studies the models were fit to the data using the softmax algorithm and

303      Maximum Likelihood Estimation (Apps et al. 2015). To fit the two models to the behaviour of

304      the subjects on both the subjective and normative trials, the softmax algorithm (Sutton and

305      Barto 1998) was used. The softmax approach was employed separately for estimation of the

306      normative and subjective discount factors. This method assigns a probability to the choices

307      made by the subjects:

308

309      (3)

310 $$P_a(n) = \frac{e(\beta.V_{o1(t)})}{e(\beta.V_{o1(t)}) + e(\beta.V_{o2(t)})}$$

311

312   This equation converts the subjective values of the choices made by the subjects ($V_{o1}$) into

313   a probability ($P_a$), as a function of the value of both options. On trials where the delayed

314   option is chosen $V_{o2}$ is the value of the immediate option and equal to 3 (£3 was always the

315   immediate option). On trials where the immediate option is chosen $V_{o2}$ is the value of the

316   delayed option. The coefficient β represents the stochasticity (or temperature) of the

317   behaviour (i.e. the sensitivity to the value of each option). This algorithm therefore

318   compared the value of the chosen option to the other options, the output is the probability

319   of that option being chosen, given the value of the free parameters (k and β). The values

320   were taken from the two models (see equation (1) and (2)) outlined above and fitted

321   separately to both the subject's own preferences and also the behaviour on the normative

322   trials. This allowed for comparisons to be made between the fit of the exponential and

323   hyperbolic models for both the subjective and normative behaviours.

324   Importantly the normative preferences that subjects learnt during the training session were

325   based on a hyperbolic model which was set with a fixed discount factor (k = 0.023). Thus, it

326   would be expected that a hyperbolic, rather than an exponential model would better explain

327   subjects behaviour on the normative trials, as we found.

328   This approach allowed us to examine the BOLD response that covaried with value n each

329   trial. Thus, we could examine activity that covaried with the subjective value (SV) of a

330   reward on subjective trials and with the value of a reward according to the social norm on

331   the normative trials (NV).

332

333   It is important to note that we did not compare these models, in which there were separate

334   parameters for subjective and normative choices, with those in which the same parameters

335   could account for choices on both types of trial. Whilst such models may have provided a

336   parsimonious account of the choice data, such an approach may not be theoretically valid or

337   allow us to examine shifts in preferences. The changes in subjective preferences from the

338   training session to the scanning session reveal that (i) the source of the valuation guiding the

339   decisions is distinct and (ii) subjects value rewards *very* differently prior to learning the norm

340   compared to how they do after learning it. As such, assuming a single discount function or

341   single temperature parameter may be parsimonious for explaining the data, but, would not

342   allow us to examine these changes in behaviour.

343    *Functional imaging and analysis*

344    *Data acquisition*

345

346    878 EPI scans were acquired from each participant. 38 slices (10% distance factor) were

347    acquired in an ascending manner, at an oblique angle (≈30˚) to the AC-PC line to decrease

348    the impact of susceptibility artefact in the subgenual mPFC (Deichmann et al. 2003).  A voxel

349    size of 3×3×3 mm (20% slice gap, 0.6 mm) was used; TR=3s, TE=32ms, flip angle=85°. The

350    functional sequence lasted 51 minutes. T1-weighted structural images were also acquired at

351    a resolution of 1×1×1 mm using an MPRAGE sequence. Immediately following the functional

352    sequence, phase and magnitude maps were collected using a GRE field map sequence ($TE_1 =$

353    5.19ms, $TE_2 = 7.65$ms).

354

355    *Image preprocessing*

356

357    Scans were pre-processed using SPM8 (www.fil.ion.ucl.ac.uk/spm). The EPI images from

358    each subject were corrected for distortions caused by susceptibility-induced field

359    inhomogeneities using the FieldMap toolbox (Andersson et al. 2001). This approach corrects

360    for both static distortions and changes in these distortions attributable to head motion

361    (Hutton et al. 2002). The static distortions were calculated using the phase and magnitude

362    maps acquired after the EPI sequence. The EPI images were then realigned, and coregistered

363    to the subject's own anatomical image. The structural image was processed using a unified

364    segmentation procedure combining segmentation, bias correction, and spatial normalization

365    to the MNI template (Ashburner and Friston, 2005); the same normalization parameters

366    were then used to normalize the EPI images. Lastly, a Gaussian kernel of 8 mm FWHM was

367    applied to spatially smooth the images in order to conform to the assumptions of the GLM

368    implemented in SPM8.

369

370    *Event definition and modelling*

371

372    In this study, two GLM analyses were performed to investigate activity that varied

373    parametrically with the subjective (SV) and normative values (NV) of temporally discounted

374     rewards. The first GLM was employed to examine activity that varied with the normatively

375     and subjectively discounted values. In the second GLM an analysis was performed to

376     examine whether activity on subjective and normative trials might be better explained by

377     "offline" vs "online" valuations as in Nicolle et al., (2012) – see supplementary materials.

378

379     Each GLM design matrix contained regressors modelling:

380     • Trial-type cue (informing the subject whether they should indicate their own
381         preference or the normative preference on the trial)
382     • Subject offer cue (the delayed reward option on the trials where the subjects
383         indicated their own preferences)
384     • Norm offer cue (cuing the subject to indicate the normative preference)
385     • Subject trigger cue (the trigger cue when the subject indicated their own
386         preference)
387     • Norm trigger cue (cuing the subject to indicate the normative preference)
388     • Missed trials (a regressor modelling the onsets of the trial-type cue, option and
389         trigger cues of missed trials)

390

391     Regressors were constructed for each of these events by convolving the event timings with

392     the canonical Haemodynamic Response Function (HRF). The residual effects of head motion

393     were modelled in the analysis by including the six parameters of head motion acquired

394     during preprocessing as covariates of no interest. We ran two GLMs at the single-subject

395     level that each contained different additional parameters. In addition to the regressors

396     defined for the event types outlined above, each GLM also contained regressors which were

397     first order parametric modulations of the offer cue and trigger cue events. These modulators

398     scaled the amplitude of the HRF in line with either the SV and NV on the subjective or

399     normative trials respectively. The values from SV and NV were taken from the hyperbolic

400     model as outlined above. Thus, we were able to examine whether the BOLD signal covaried

401     with SV and NV at the time the options were presented and at the time when subjects

402     indicated their choices.

403

404    The second GLM had the same structure except that different parametric modulators were

405    used. Specifically, we used the offline SV as a parametric modulator on the normative option

406    and trigger cues, and the offline NV was used as a parametric modulator of the subjective

407    option and trigger cues. This allowed us to examine whether different regions of the mPFC

408    showed the same 'online/offline' profile as suggested by Nicolle et al., (2012).

409    *Group analysis, Contrasts and Thresholding*
410

411    Random effects analyses were applied to determine voxels significantly different at the

412    group level. SPM{t} images from all subjects at the first-level were input into second-level

413    Flexible Factorial design matrices. T and F-contrasts were conducted on the regressors to

414    examine differences between SV and NV and the effects of SV and NV independently. These

415    contrasts identified voxels in which activity varied parametrically in the manner predicted by

416    the subjective or normative value parameters. The main analysis is reported from activity

417    time-locked to the offer cues. An additional analysis from the trigger cues was also

418    conducted (**supplementary table.1**). To examine the effects of shifts in subjects' preferences

419    in subjective value from before and after learning the social norm, covariates were entered

420    on t-tests for SV and NV in second-level design matrices.

421    To correct for multiple comparisons we first identified a large cluster by using a cluster-

422    threshold as recommended by Woo et al. 2014 to identify an initial, large mPFC cluster. To

423    then be more anatomically specific we used masks of putatively areas 8, 9, 11, 32 and pre-

424    SMA from Neubert et al. (2015) as small volume corrections. In addition, we used these

425    same masks in a region of interest (ROI) analysis. The masks of Neubert et al., (2015) were

426    created based on resting-state and diffusion-weighted imaging in both humans and

427    macaques, and highlight the largely preserved connectional properties of these regions

428    across species. These masks therefore provide a detailed anatomically derived parcellation

429    of the mPFC that we can use to delineate the contributions of different regions of the mPFC

430    to value processing in this study. Note that by using this approach we could examine the

431    effects of SV and NV in different regions of the mPFC in a manner that would not be possible

432    using the traditional approach of contrasting SV with NV and examining the peak response

433    or averaging over the effects across the whole cluster.

434

435    In addition to the small volume correction approach, we also performed a ROI analysis using

436    MARSBAR. In this approach, we averaged over the effects of all of the voxels in each mask.

437    This analysis is reported in full in Supp. Fig.2.

438

439  **Results**

440  We designed a novel version of an inter-temporal decision-making task to investigate

441  activity covarying with subjective or normative valuations of rewards (**fig.1**). During fMRI,

442  subjects made choices between a low (£3), immediately received reward, and a larger in

443  magnitude (£3.10 - £20) but delayed (1 – 180 days) reward. On half of the trials subjects

444  were instructed to indicate their own preference, but crucially, on the other half of the trials,

445  subjects were required to indicate the preference. The normative preferences had been

446  learnt through trial and error during a training session (**See Methods & Supp. material**).

447  Thus on half the trials subjects choices were made based on a subjective valuation of a

448  delayed reward, but on the other half of the trials the same kind of valuation was dictated

449  by a social norm.

450

451

452  *Behavioural Results*

453  *Rewards are hyperbolically discounted by delays*

454  Are rewards devalued by temporal delays? Consistent with a large body of previous work,

455  rewards were subjectively devalued by the temporal delay before receipt (**fig.2a,b; Supp.**

456  **Results**). Crucially, however, there was no difference between subjects' choices on the

457  subjective and normative trials at the group level during scanning (*p > 0.1*). This result

458  importantly ensures that activity identified in neural analyses is not driven by systematic

459  differences in valuation of delayed rewards by subjects in the normative and subjective

460  conditions (see **Supp. results**).

461  To characterise the nature of the discounting effect, we fitted hyperbolic and exponential

462  'discount' models separately to the choices on the normative and subjective trials, using the

463  softmax algorithm and maximum likelihood estimation (see **Methods**, (**fig.2c**) and **Supp.**

464  **Table** 2.). Thus, for each model we estimated a "discount factor ('*k*')" which dictates the

465  extent to which a reward is devalued by a delay and a stochasticity parameter (β), which

466  represents how noisy valuations are.   To determine which function best fitted the

467  behavioural data, (**fig.2c**) we conducted a 2x2 repeated measures ANOVA on the log-

468  likelihood for each condition (subjective, normative) and function (exponential, hyperbolic).

469  We found a marginal effect of condition and a main effect of function, and a marginal

470    interaction (Condition ($F$(1,14) =  4.391, $p$ = 0.055); Function ($F$(1,14) = 17.554, $P$<0.001);

471    Condition x Function ($F$(1,14) = 3.874, $p$ = 0.07). Examination of the log-likelihood estimates

472    shows that the effect was driven by a better fit of the hyperbolic model to both the

473    subjective and normative choice data, in line with previous studies examining inter-temporal

474    choice data (Mazur 2001). Further analyses were therefore completed using only the

475    hyperbolic model.

476

477    *Social norms are accurately reproduced*

478    For the aims of this study it was important that subjects were able to reproduce the

479    normative preferences that they had learnt during the training session accurately on the

480    normative trials inside the scanner. To examine this we compared the estimated discount

481    factor from the hyperbolic model on the normative trials during scanning with the discount

482    factor which was used to create the normative behaviour that subjects learnt through trial

483    and error during training ($k$ = 0.023). We found no significant difference between these

484    discount factors ($t$(14) = 0.36, $p$ > 0.7), highlighting that subjects' choices on the normative

485    trials were not significantly different from the behaviour that they had learnt as normative

486    during training. (**fig.2d**)

487    Were subjects making the same choices on both the normative and subjective trials? There

488    was no significant difference between the discount factors in the normative and subjective

489    conditions (U(14) = 0.47, $p$ > 0.6). However, this absence of a difference can most likely be

490    attributed to the high levels of variability across subjects in the subjective valuation trials.

491    Importantly, there was also no correlation between the subjective discount parameters and

492    the normative discount parameters across subjects ($r_{s}$ = 0.23, $p$  = 0.4). This indicates that

493    whilst at the group level there was no difference in behaviour in the two conditions, subjects

494    were not simply performing the normative trials using the same discount function as they

495    were on the subjective trials. Thus, they were behaving differently in the two conditions, and

496    performing the normative trials in accordance with the normative discount function they

497    had learned.

498

499

500

501     *Shifts in subjective preferences after learning norms*

502     Seventy-three percent of subjects shifted their preferences in the direction of the norm

503     between the subjective preferences task at the beginning of the training session and the

504     subjective trials inside the scanner after they had learnt the norm (**fig.2**). A Mann-Whitney U

505     test on the difference of subjective discount factors from the norm discount factors prior to

506     learning the norm, compared to the difference between the parameters after learning the

507     norm discount factor, showed a significant effect (U(14) = -1.7, *p* < 0.042, one-tailed). Overall

508     subjects were significantly closer to the norm in the scanning session, after they had learnt

509     the norm, than they were during the training session before being exposed to the norm.

510     However, there was a correlation between a subjects discounting parameter prior to

511     learning the norm and post learning the norm, suggesting that whilst there was a shift in

512     behaviour overall, subjects remained relatively impatient or patient with respect to the

513     other subjects after learning the normative preferences ($R_s$ = 0.8, *p* < 0.001). Thus, in line

514     with research showing that minimal group exposure can have powerful effects on behaviour

515     (Hewstone et al. 2002), our results suggest that subjects shifted their subjective preferences

516     towards the norm following the learning of normative preferences, rather than shifting their

517     performance on the normative trials towards their original subjective preferences. However,

518     we note that given the sample size that inferences made upon all analyses related to this

519     shift in preferences should be made with caution.

520

521

522     **fMRI results**

523     In this study we were interested in examining activity time-locked to the offer cue when

524     subjects evaluated either the subjective value (SV) or normative value (NV) of an offered,

525     delayed, reward (analysis of the response cues are included in the supplementary material).

526     To examine the processing of SV and NV we used the values taken from the hyperbolic

527     model fitted to the subjects behaviour, and used them as parametric modulators of activity

528     at the time of the offer cue on the corresponding trials (**see supp. Table 1** for results from

529     the response cue). That is, we examined activity that parametrically varied with NV on

530     normative trials and activity that parametrically varied with SV on subjective trials.

531

532    *Main Analyses*

533    *The mPFC differentially codes subjective and normative value*

534    The first hypothesis was that sub-regions across the DmPFC and VmPFC might signal value

535    differently on subjective and normative trials. To examine this question we first performed a

536    whole-brain corrected comparison between SV and NV. An F-contrast between the SV and

537    NV parametric modulators revealed a large cluster extending over both the dorsal and

538    ventral portions of the mPFC (3095 voxels) that was significant at a cluster-wise threshold (Z

539    = 4.09, *P* < 0.001 uncorrected voxel-wise threshold, *P* < 0.05 FWE cluster threshold (as

540    recommended by Woo et al. 2014)). Although other regions also showed a significant

541    difference between SV and NV (See **Supp. Results**), for the aims of this paper we focus on

542    the mPFC cluster. However, we note that we also found a similar pattern of results in the

543    posterior superior temporal sulcus to those we report in the mPFC, and at a reduced

544    threshold we found a cluster in the ventral striatum that coded SV only (**Supp. Figs. 3 and 5**)

545    In line with our hypotheses, the mPFC cluster contained multiple peaks which corresponded

546    putatively with divisions of the mPFC based on cytoarchitectonic and connectional anatomy

547    Neubert et al .,(2015). In line with our predictions peaks were identified in areas BA 8, 9, 11

548    and 32. (see **Supp.fig.2** for masks of these regions). In the following sections we

549    demonstrate that each of these 5 zones did in fact signal SV and NV differently, however,

550    they clustered into three sub-regions that each had a distinct signature for signalling SV and

551    NV. For each region we highlight a small volume corrected result to demonstrate the

552    difference in signalling of SV and NV in each region before then highlighting the specific

553    nature of value signalling in each region.

554

555    *Coding of normative, but not subjective, value in the anterior DmPFC*

556    To examine effects in the anterior DmPFC we used masks corresponding to BA 8 and 9, both

557    regions which have been identified in studies examining the neural basis of social norm

558    processing (Izuma 2013). Details of the extent of these masks are shown in supplementary

559    material (**see Supp.Fig.2**). We identified a peak within the spatial extent of each mask for the

560    contrast between SV and NV (Area 8 mask: x = -4, y = 32, z = 52; Z = 3.88, *p < 0.05* small

561    volume correction (SVC); Area 9: x = 6, y = 52, z = 38; Z = 3.80 SVC) demonstrating that both

562    sub-regions differentially signaled NV and SV. Examination of the response in the peak voxel

563    in each region (**fig.3**) suggested that activity in both areas covaried only with NV on

564 normative trials and not with SV on the subjective trials. Statistically, this was demonstrated

565 by clusters in the same regions, with the same peak voxels, showing an effect of NV (Area 8:

566 x = -4, y = 32, z = 52; Z = 3.8, *p < 0.05* SVC); Area 9: x = 6, y = 52, z = 38; Z = 3.69 svc) but no

567 voxels in these regions showing any effect of SV even at a considerably reduced threshold (*p*

568 < 0.05 uncorrected). Thus, anterior DmPFC sub-regions were specifically sensitive to NV on

569 normative trials, but not SV on subjective trials. That is the region was sensitive to value but

570 only in the normative condition.

571

572 *Opposing coding of subjective and normative value in the VmPFC*

573 We applied the same approach to examine activity in the VmPFC, using masks of areas 11

574 and 32 (See **Supp.Fig.2** for spatial extent). Both of these regions have been identified as

575 signalling subjective value (Kable and Glimcher 2007; Neubert et al. 2015) in human

576 neuroimaging tasks.

577

578 Similar to the DmPFC, clusters in both regions showed a significant difference between SV

579 and NV (Area 32 mask: x = 6, y = 46, z = 10; Z = 3.56, *p < 0.05* svc; Area 11: x = -8, y = 42, z =-

580 10; Z = 3.58, *p* < 0.05 svc). Activity in these regions showed an effect of both SV and NV, but

581 in the opposite direction (**fig.3**). This was demonstrated statistically by clusters within the

582 spatial extent of both masks - each containing the peak voxel from the contrast between SV

583 and NV - showing a positive effect of SV and a negative effect of NV alone, albeit at a slightly

584 reduced threshold (p < 0.002 uncorrected). Activity in these regions showed an effect of

585 both SV and NV, but in the opposite direction (fig.3). This was demonstrated statistically by

586 clusters within the spatial extent of both masks - each containing the peak voxel from the

587 contrast between SV and NV - showing a positive effect of SV and a negative effect of NV

588 alone, albeit at a slightly reduced threshold (p < 0.002 uncorrected). This suggests that both

589 sub-regions of the VmPFC showed a significant effect of value, but activity covaried in the

590 opposite direction for SV and NV in both regions. Our claim is supported by the ROI analyses

591 in which both clusters had significant effects of SV and NV when correcting for multiple

592 comparisons (See Methods, Supp. Results and Supp. Fig.2). Although the effects for SV in the

593 VmPFC were slightly weaker than our other reported results, there is considerable evidence

594 that the VmPFC does signal such information, particularly in temporal discounting tasks

595 (Kable & Glimcher, 2007) and in this study the reduced significance may have been driven by

596 the variability in this region for signalling SV (see below).

597

598

599 *Subjective and Normative value in the posterior DmPFC*

600 To examine whether any regions processed the value of rewards regardless of whether the

601 valuation was normative or subjective we performed a conjunction between SV and NV. This

602 contrast revealed voxels in in a more posterior region of the DmPFC ($p < 0.001$ uncorrected

603 voxel-wise threshold, $P < 0.05$ FWE cluster corrected). This region lying anterior to the

604 border between the precentral gyrus and the superior frontal gyrus on the medial surface

605 fell within the region often referred to as the pre-supplementary motor area (Pre-SMA; (x = -

606 8, y = 20, z = 44; Z = 4.96, *p < 0.05* SVC). A cluster and also the peak voxel from the

607 conjunction was also identified independently as showing a significant effect of both SV and

608 NV in the same direction ($p < 0.001$ uncorrected). Activity in the posterior regions of the

609 DmPFC therefore covaried both with SV on subjective trials and NV on the normative trials in

610 the same manner.

611 *Shifts in subjective valuations and conformity to social norms*

612 Behaviourally we found a shift of subjects' valuations towards the normative valuations on

613 the subjective trials after learning the normative preferences. Previous studies have shown

614 that regions of the DmPFC and VmPFC are engaged when updating behaviour in order to

615 conform to social norms (Klucharev et al. 2009; Garvert et al. 2015). To examine whether

616 this effect was related to the processing of SV and NV in the mPFC, we used the difference in

617 discount factors between subjective discount factor during the first part of training to that

618 during scanning as a covariate. We then examined whether the extent to which activity that

619 varied with SV on subjective trials or NV on normative trials covaried with the extent to

620 which subjects shifted their choices. We found 3 separate clusters in the mPFC that survived

621 correction for multiple comparisons using the masks of area 32 (14,48, 4, Z = 3.69, *p <*

622 0.05svc), 8 (-12, 32, 50, Z = 4.11, *p < 0.05*svc) and 9  (-10, 48, 42 Z = 3.64, *p < 0.05*svc) in

623 which activity was correlated with SV on subjective trials (**see supp.fig.4**). Clusters in the

624 same regions also showed a significant correlation between the degree of SV coding and the

625 extent to which subjects got closer to the norm from the first to the second session, at a

626 reduced threshold ($p<0.005$ uncorrected. We found no clusters in which activity covarying

627  with NV correlated with shifts in subjective valuations. ). These findings are consistent with

628  the notion that activity in these regions is related to shifts in behaviour based on learning a

629  norm. However, we note that given the sample size that inferences made upon all analyses

630  related to this shift in preferences should be made with caution.

631

632

633  ***Supplementary and Control Analyses***

634  *Memory demands*

635  To examine whether our effects could be driven simply by memory demands on the

636  normative trials compared to the subjective trials, we performed a contrast between activity

637  at the time of the offer cues on the normative trials to those on the subjective trials. We

638  found no voxels in the medial prefrontal cortex showing a significant effect (p<0.05FWE-svc

639  corrected for each ROI). This would therefore argue against the notion that activity may be

640  related to simply recalling what decision to make against choosing one based on one's own

641  valuation.

642

643  *Value not Conflict*

644  Could activity on either trial-type be related to 'conflict' between the choice options? To

645  examine this we performed two additional analyses. We created a parametric regressor of

646  the difference between the subjective and normative valuation on each trial. In these

647  regressors covarying activity would be dependent on the degree of conflict between the two

648  valuations. We then examined in the ROIs used in the main analyses whether activity

649  covaried with these regressors on the subjective or normative trials. We found that none of

650  the ROIs showed a significant effect of these "conflict regressors" even at a reduced

651  threshold (P<0.01 uncorrected) on either type of trial. Secondly, we then examined whether

652  activity in these regions signalled "decision conflict/difficulty", regardless of trial type. This

653  decision difficulty regressor was the absolute value on each trial type subtracted from the

654  value of the immediate offer (£3). This examined activity that would be highest when the

655  value of the immediate and delayed option was closest to each other and thus choosing

656  between them would be most difficult. None of the ROIs in the mPFC showed activity that

657  significantly covaried with this this decision difficulty/conflict regressor, even at a reduced

658    threshold (p<0.01 uncorrected). There is therefore little evidence of any conflict related

659    signals in the regions we examined.

**Discussion**

660

661  In many social situations our subjective valuations of economic rewards are overridden by

662  our desire to conform to social norms. In this study, we examined how the brain processes

663  the value of rewards according to a social norm and whether such valuations are coded

664  similarly to subjective value in the mPFC. Subjects performed inter-temporal choices that

665  were either based on their own subjective preferences or on a learnt social norm. We found

666  that a large portion of the mPFC was sensitive to reward valuations and showed a difference

667  between the processing of subjective and normative valuations. Across this region, three

668  distinct sub-regions were identified that processed the value of rewards differently if the

669  valuation was driven by subjective or normative information. In support of previous research

670  examining the processing of social norms, our results implicated the anterior portions of the

671  DmPFC (areas 8 and 9). However, we show that this region covaried exclusively with value

672  on the normative trials, and not on the subjective trials. However, activity in posterior

673  regions of the DmPFC covaried with value on both subjective and normative trials and

674  activity in the VmPFC varied with subjective value positively but normative values negatively.

675  In addition, we found that the extent to which parts of the anterior DmPFC, and area32 of

676  the VmPFC, signal SV is correlated with shifts in subjective preferences. Specifically how

677  much individuals have shifted their subjective valuations after being exposed to a norm

678  correlates with the degree to which these regions signal SV. These results highlight that

679  normative valuations are coded distinctly from subjective valuations in the mPFC.

680  Research examining the neural basis of social norm processing, social influence and

681  conformity has consistently implicated the DmPFC (Izuma 2013). Neuroimaging studies have

682  shown that activity across the Pre-SMA, BA 8 and BA 9 tracks how different one's opinions

683  are from those of another group or individual, and these regions are engaged when

684  updating one's own, or when learning another group or persons opinions (Berns et al. 2005;

685  Klucharev et al. 2009; Campbell-Meiklejohn et al. 2010; Zaki et al. 2011; Nicolle et al. 2012;

686  Izuma and Adolphs 2013; Garvert et al. 2015; Nook and Zaki 2015). Moreover, Transcranial

687  Magnetic Stimulation (TMS) studies have shown that information processing in the DmPFC is

688  causally linked to social norm guided behaviours and conformity (Klucharev et al. 2011;

689  Izuma et al. 2015). As a result, it is often argued that the DmPFC processes information that

690  guides behaviours when operating in social groups and when under social influence.

691  Alternatively, some have argued that the mPFC plays an important role in signalling decision-

692  difficulty or conflict monitoring (Botvinick et al. 2004). However, we found little evidence of

693 such signals in this experiment. This may be down to the fact that the region which has often

694 been debated as signalling conflict, lies in the ACC in areas 24 or 32, and not in areas 8 and 9.

695 Our results are therefore much more consistent with the DmPFC signalling social

696 information that guides behaviour when interacting in social groups. We show that such

697 social specificity is only present in the anterior portions of the DmPFC (areas 8 and 9). In

698 addition, we show that specificity for processing NV in the DmPFC may depend on the extent

699 to which people's subjective preferences are influenced by normative information. That is,

700 the extent to which activity in sub-regions of the DmPFC (area 9) varied with SV was

701 dependent on how much an individual's subjective preferences were influenced by the

702 learning of normative information. This suggests that the extent to which people are

703 influenced by social information might influence how the DmPFC codes our own valuations.

704 This is in line with evidence that the DmPFC may be a key region for learning about the social

705 norms (Izuma 2013; Izuma et al. 2015) and also by how influenced people are by the

706 behaviour of another individual (Garvert et al. 2015)

707 However, our results suggest that these properties are not shared across all of the DmPFC.

708 Specifically, we found that a more posterior portion of the DmPFC (putatively in the pre-

709 SMA), signalled value on both subjective and normative trials. This would support accounts

710 that suggest this region is important for the processing the value of choices, but does not

711 play any specific role in social or non-social behaviours (Nachev et al., 2008). Specifically,

712 there is evidence that neurons that direct actions towards rewards are present in this region

713 and also that this region is important for initiating behaviours (Wang et al. 2001; Nachev et

714 al. 2008). Supporting this claim, anatomical evidence shows that the pre-SMA is strongly

715 connected to parts of the motor system, with connections of the premotor cortex and parts

716 of the basal-ganglia that are putatively important for valuing and selecting actions (Nachev

717 et al. 2008). Our results support the notion that the pre-SMA is sensitive to value. However,

718 we show the importance of accurate localisation for understanding DmPFC function. Using

719 the approach implemented here and localising activity to specific regions that are known to

720 have distinct functions, connections and anatomical properties, we were able to show that

721 the Pre-SMA may signal value regardless of the source of the valuation with greater

722 precision.

723 A wealth of research has suggested that the VmPFC processes information that is consistent

724 with a role in value-guided choice (Kable and Glimcher 2007; Rushworth and Behrens 2008;

725 O'Doherty 2014; Strait et al. 2014; Manohar and Husain 2016). Such a notion is supported by

726   its anatomical connections to other regions of the brain that process the subjective value of

727   rewards including portions of the intraparietal sulcus, amygdala nuclei, both medial and

728   lateral portions of the orbitofrontal cortex, and the ventral striatum (Haber et al. 2006;

729   Kable and Glimcher 2007, 2010; Petrides and Pandya 2007; Kim et al. 2008; Hunt et al. 2012;

730   Neubert et al. 2015). In addition a plethora of neuroimaging studies highlight that activity in

731   this region scales with the subjective value of a chosen reward (O'Doherty 2014). These

732   findings have led many to suggest that this region plays a crucial role in integrating

733   information about the value of rewards in order to select behaviours that have the highest

734   value. Our results do not support this account. Instead, activity in both areas 11 and 32 in

735   the VmPFC scaled positively with SV but crucially scaled *negatively* with the NV of rewards.

736   This suggests that this region is sensitive to the value of rewards, but its processing of value

737   is context-dependent and the nature of the value-computations performed in this region

738   may differ depending on whether a reward valuation is a function of social information or is

739   subjective.

740   There is in fact a plethora of evidence supporting the notion that the VmPFC processes

741   information that influences social behaviour is supported by anatomical and functional

742   evidence. Medial portions of areas 11 and 32 in the VmPFC have connections to portions of

743   the amygdala, dysgranular portions of the anterior insula, posterior portions of the superior

744   temporal sulcus, the anterior cingulate gyrus, and regions in the DmPFC that we found to

745   process only normative value (Morecraft et al. 1992; Petrides and Pandya 2007). These

746   regions are well known for their roles in processing social information (Amodio and Frith

747   2006; Behrens et al. 2009; Hurlemann et al. 2010; Apps and Tsakiris 2013; Blair 2013; Gu et

748   al. 2015; Lockwood et al. 2015; Apps et al. 2016). Neuroimaging studies have also shown

749   that the VmPFC processes information about the value of rewards that others will receive

750   and is engaged by the value of monetary rewards donated to charity and when enforcing

751   social norms (Krajbich et al. 2009; Cooper et al. 2010; Hare et al. 2010; Tricomi et al. 2010;

752   Baumgartner et al. 2011; Buckholtz and Marois 2012; Janowski et al. 2013; Zaki et al. 2014;

753   Apps et al. 2015). In addition, there is considerable evidence that lesions to the VmPFC, and

754   structural changes to this region in healthy individuals, are linked to antisocial behaviour and

755   influence the extent to which people conform to social norms (Blair 2013; Gu et al. 2015;

756   O'Callaghan et al. 2016). Our results therefore go against the viewpoint that the VmPFC does

757   not process social information (Rudebeck et al. 2008) and support emerging evidence that

758   this region may play an important role in processing value-related information during social

759   interactions.

760     Recently studies have examined the processing of value in a context where the beneficiary

761     of the value-guided choice was either the subject themselves, or another individual. Sul et

762     al., (2015) suggested that when choosing to benefit either ourselves or another, when the

763     choices are based on our own preferences, more ventral portions of the mPFC encode value

764     for ourselves but more dorsal portions signal value for other people – although this differs

765     between prosocial and selfish individuals. In contrast, Nicolle et al.,(2012) and Garvert et al.,

766     (2015) found that value was coded in an 'offline', modelled frame of reference in more

767     dorsal portions of the mPFC and in a more 'online' executed frame of reference in the

768     VmPFC. That is, the VmPFC coded the value of rewards according to whoever might receive

769     the outcome of a decision, whereas the DmPFC signalled value according to the preferences

770     of the person who would not receive the reward on that trial. Our results, however, do not

771     fully support either viewpoint. Our results support the suggestion that DmPFC is specialised

772     for processing social information, as argued by Sul et al., (2015), but would not support their

773     claim that the VmPFC processes rewards only when they are subjectively valued. Likewise,

774     we did not find evidence to strongly support the claim that the findings of Garvert et al.,

775     (2015) and Nicolle et al., (2012) that the DmPFC and VmPFC encode value in an offline and

776     online reference frame respectively.

777     How can we reconcile these previous studies findings with our results? One possible

778     explanation is that there is a substantial difference in the nature of decisions that conform

779     to norms compared to decisions made that benefit another. Specifically, when making

780     normative decisions an individual is both the beneficiary of the choice and decisions-maker,

781     whereas when choosing for others the individual is not the beneficiary of the outcome. This

782     key distinction in the frame of reference for the beneficiary of the choice may explain why

783     we do not find similar results. In addition, it is also plausible that our results are referring to

784     different regions of the mPFC from those of Sul and colleagues and Nicolle and colleagues.

785     Specifically, our results extended across a large portion of the mPFC (areas 8,9,32 and 11),

786     whereas the distinctions identified in previous studies refer to a smaller circumscribed

787     region potentially restricted to distinctions within areas 32 and area 9. Thus, our results

788     extend these previous findings by examining regions that extend over a larger spatial extent

789     of the mPFC. Moreover our findings highlight the contributions of several mPFC regions to

790     making decisions based on a social norm guided valuation are somewhat distinct from the

791     contributions made when making decisions to benefit another.

792

793   Lastly, could these results be accounted for by differences in the memory demands between

794   subjective and normative decisions? Notably, we did not find any main effect differences in

795   the mPFC when comparing activity time-locked to the offer cues on subjective or normative

796   trials. This suggests that the differences in activity in the mPFC related to the discounted

797   value of delayed rewards and not purely to the requirement to recall a response from

798   memory. Moreover, subjects showed conformity to the norm even on subjective trials,

799   suggesting that recall of the norm was guiding behaviour on both subjective and normative

800   trials. Behaviourally therefore, our results suggest that the normative and subjective trials

801   were comparable in terms of their memory demands. Finally, whether the dmPFC processes

802   information in a domain-general way (i.e. is engaged by memory processes including those

803   that are socially relevant) or processes exclusively social information is a question that has

804   been examined extensively in social neuroscience. There is considerable debate over

805   whether parts of the mPFC operate in a domain-general or socially specific manner (Amodio

806   and Frith 2006; Izuma 2013), and whether operating in larger social groups was an

807   evolutionary pressure for greater memory capacity and the expansion of the prefrontal

808   cortex (Dunbar and Shultz 2007). Theoretical accounts also directly link the evolution of the

809   mPFC to the requirement to process increasingly abstract rules about how to interact with

810   others (Murray et al. 2016) and prefrontal cortex development is linked to the degree to

811   which social influence changes behaviour through ageing (Steinberg and Monahan 2007;

812   Steinberg 2008; Tamnes et al. 2017). To base one's behaviour on recalled information rather

813   than one's own preferences may therefore be a fundamental aspect of social norm guided

814   behaviour and a key mechanism underlying the functional properties of the mPFC. The issue

815   of whether information processing in the dmPFC is exclusively 'social' in nature, or is a more

816   domain-general process, cannot be resolved by this study alone. However, crucially either of

817   these possibilities does not contradict our key argument, that the neural mechanisms

818   underlying subjective valuations may be different than those that underlie the social norm

819   recalled valuations.

820   In summary, we have identified three zones in the mPFC that process value-related signals

821   but each has a different profile for processing subjectively or normatively valued rewards.

822   Our results highlight some of the key neural and computational mechanisms that may

823   underpin reward valuation and social influence. Moreover, this may pave the way for

824   understanding why people can make much more impulsive or patient economic decisions

825   when interacting with others than they would when making the same decisions alone.

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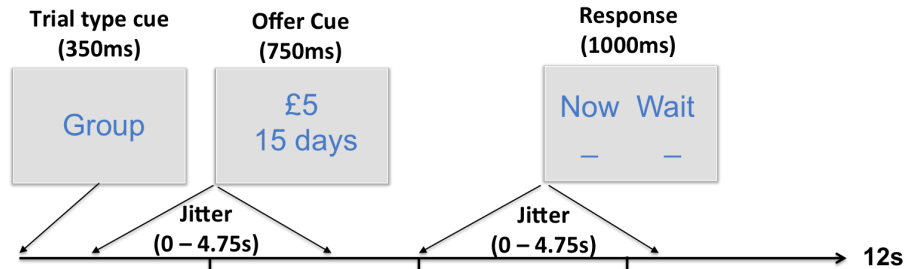
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1032    Figure Legends

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1037    **Fig.1. Trial Structure.** *Each trial began with a cue that indicated whether a choice should be*

1038    *made based on a subjective preference ("YOU") or normative ("GROUP") valuation. The font*

1039    *used throughout the trial was colour coded to also indicate the trial-type to the participant.*

1040    *Following a temporal jitter, an offer cue indicated the magnitude (£3.10 - £20) and delay*

1041    *(1day – 180days) that was on offer on the trial. On each trial subjects were required to*

1042    *evaluate whether they would prefer this offer or a fixed baseline of (£3) following no delay.*

1043    *Following another temporal jitter subjects were required to indicate their response by*

1044    *making a button press on a keypad. To avoid activity at the time of the offer cue being*

1045    *confounded by preparatory motor activity, which button corresponded to taking the delayed*

1046    *offer ("wait") or the immediate offer ("now") varied randomly on each trial.*



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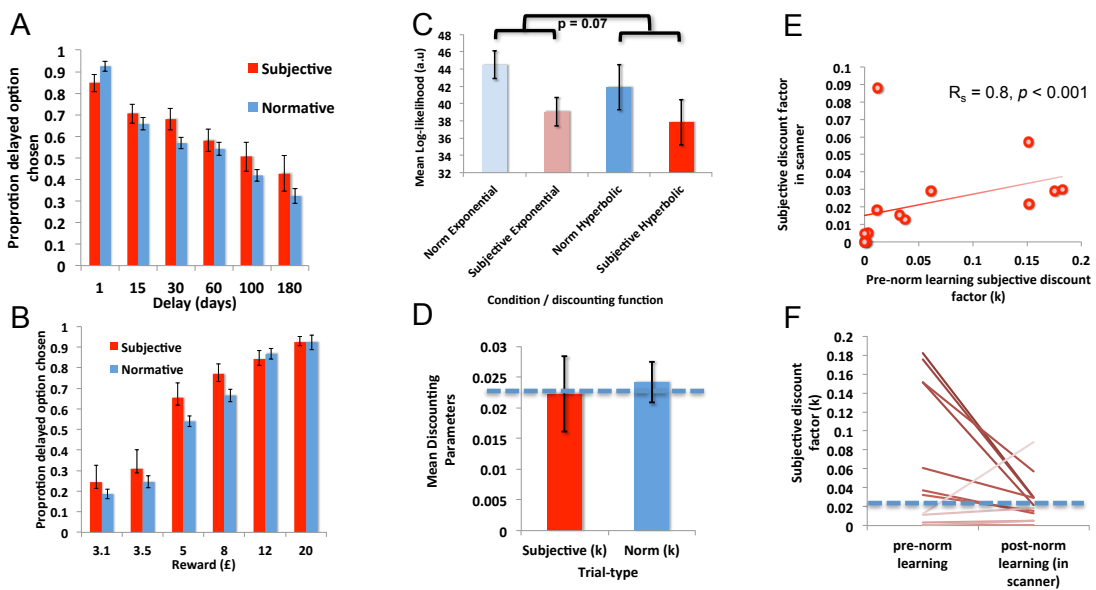
*Figure 2. Behavioural Results. Subjects devalued rewards as a function of temporal delays. As delays increased subjects were more likely to choose the immediate option (A) and as rewards increased they were more likely to take the delayed option (B). Overall choices on the inter-temporal choice trials were better explained by a hyperbolic, rather than exponential model (C). (D) Subjective or normative discount parameters estimated based on the subjects choice behaviour did not differ from the normative discount factor that was learnt during training (dotted blue line). Subjective discount factors in the scanning session correlated with subjective discount factors during the training before subjects had learnt the normative behaviour (E). However, there were substantial shifts in subjective discount factors from before to after learning the norm (F). 73% of subjects discount factors were closer to the norm after learning normative preferences during training, suggesting they were influenced by the social norm based preferences. Error bars depict standard error of the mean (SEM).*
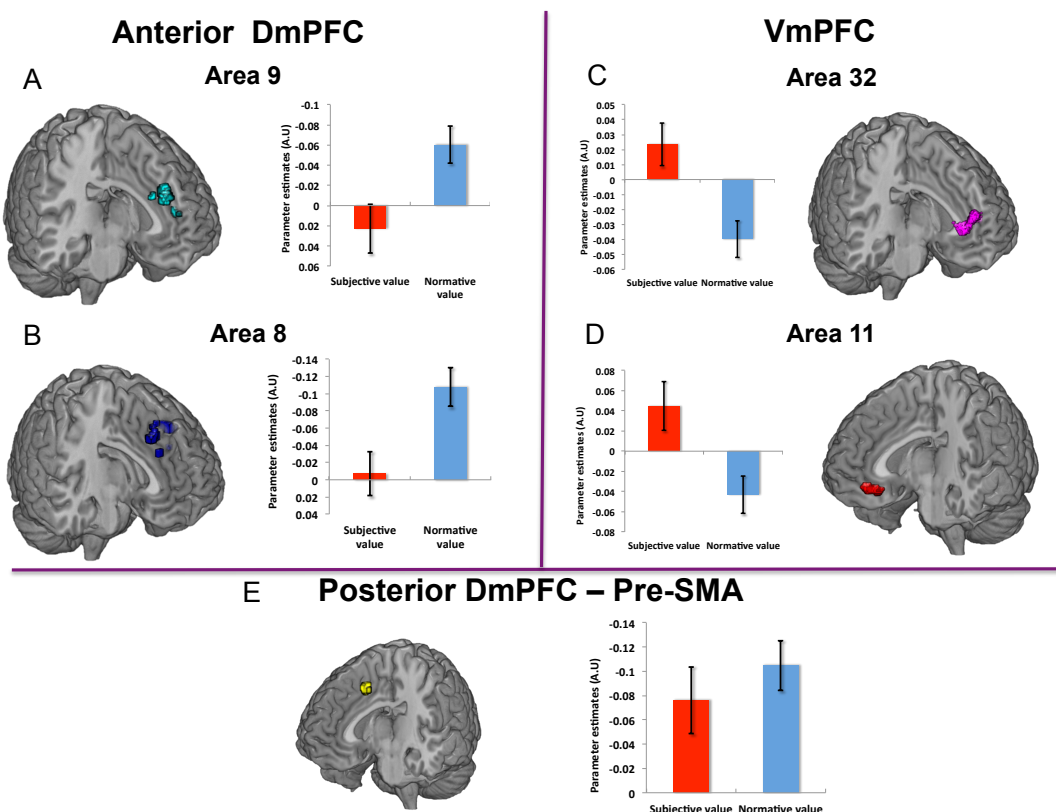


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*Figure 3. Subjective and Normative value in mPFC. Different profiles of response to SV and NV in different mPFC sub-regions at the time the options were evaluated. Clusters in anterior regions of the DmPFC - areas 9 (A) and 8 (B) - showed a significant negative effect of Normative value (NV) on the normative trials but no effect of Subjective value (SV) on the subjective trials. Plots show response from the peak voxel (responses of the whole clusters*

1067 *are reported in **supp. fig.2**). Clusters in the VmPFC - areas 32 (C) and 11 (D) - showed a*

1068 *significant negative effect of NV on the normative trials and a significant positive effect of SV*

1069 *on the subjective trials. A region in the posterior DmPFC showed a significant conjunction (E),*

1070 *signalling both SV and NV and no difference between the two. Thus, the mPFC is sensitive to*

1071 *reward valuations in inter-temporal choice. Error bars depict SEM. Results are shown at p <*

1072 *0.001 uncorrected for display purposes.*

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