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The neural basis of aversive Pavlovian guidance during planning

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5 **The neural basis of aversive Pavlovian guidance during planning**

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Abstract

Important real-world decisions are often arduous as they frequently involve sequences of choices, with initial selections affecting future options. Evaluating every possible combination of choices is computationally intractable, particularly for longer multi-step decisions. Therefore, humans frequently employ heuristics to reduce the complexity of decisions. We recently used a goal-directed planning task to demonstrate the profound behavioral influence and ubiquity of one such shortcut, namely aversive pruning, a reflexive Pavlovian process that involves neglecting parts of the decision space residing beyond salient negative outcomes. However, how the brain implements this important decision heuristic, and what underlies individual differences have hitherto remained unanswered. Therefore, we administered an adapted version of the same planning task to healthy male and female volunteers undergoing functional magnetic resonance imaging (fMRI) to determine the neural basis of aversive pruning. Through both computational and standard categorical fMRI analyses, we show that when planning was influenced by aversive pruning, the subgenual cingulate cortex was robustly recruited. This neural signature was distinct from those associated with general planning and valuation, two fundamental cognitive components elicited by our task but which are complementary to aversive pruning. Furthermore, we found that individual variation in levels of aversive pruning were associated with the responses of insula and dorsolateral prefrontal cortex to the receipt of large monetary losses, and also with sub-clinical levels of anxiety. In summary, our data reveal the neural signatures of an important reflexive Pavlovian processes that shapes goal-directed evaluations, and thereby determines the outcome of high-level sequential cognitive processes.

Significance Statement

Multi-step decisions are complex because initial choices constrain future options. Evaluating every path for long decision sequences is often impractical; thus, cognitive shortcuts are often essential. One pervasive and powerful heuristic is aversive pruning, in which potential decision-making avenues are curtailed at immediate negative outcomes. We used neuroimaging to examine how humans implement such pruning. We found it to be associated with activity in the subgenual cingulate cortex, with neural signatures that were distinguishable from those covarying with planning and valuation. Individual variations in aversive pruning levels related to sub-clinical anxiety levels and insular cortex activity. These findings reveal the neural mechanisms by which basic negative Pavlovian influences guide decision-making during planning, with implications for disrupted decision-making in psychiatric disorders.

Introduction

Most important decisions are difficult as they involve sequences of consequential choices. For example, to go to university, where, and what to study? Such planning is complex as the outcomes of earlier decisions (e.g. degree) can affect the availability of later options (e.g. income), and the resulting tree of future possibilities to be evaluated grows quickly with decision sequence length. To manage this intricacy, we often have to abandon rational calculation in favour of hard-wired approximations. We recently identified one such powerful Pavlovian heuristic that humans ubiquitously use during complex planning, which we term "aversive pruning" (Huys *et al.*, 2012). Aversive pruning entails excising from consideration decision tree branches that contain important negative events (here, large monetary losses; **Figures 1A-B**). Individual variation in aversive pruning levels predicted the severity of subclinical depressive symptoms (Huys *et al.*, 2012), suggesting a possible role in depression (Dayan and Huys, 2008, Eshel and Roiser, 2010). These behavioural and computational studies raise the question as to how aversive pruning is implemented in the brain. Therefore, we sought to identify the neural basis of aversive pruning using fMRI.

Aversive pruning is reflexive, akin to Pavlovian responses, as it persists above and beyond loss aversion, even when it is highly suboptimal (Huys *et al.*, 2012). Our central expectation therefore was that aversive pruning would be mediated via regions known to be involved in orchestrating emotional reactions to aversive events. Thus, our predictions focused first on the subgenual anterior cingulate cortex (SGC; part of the ventromedial prefrontal cortex). The SGC is anatomically well placed to subserve the impact of affective aversive values on planning. It is connected to areas involved in mediating Pavlovian behavioural inhibition such as the periaqueductal grey (PAG) and amygdala, as well as regions involved in the evaluation required for planning (Schultz, 2015), such as orbitofrontal cortex (OFC) and dorsolateral prefrontal cortex (DLPFC; (Johansen-Berg *et al.*, 2008, Ongur *et al.*, 2003). The SGC is known to both represent aversive stimuli and mediate their impact: neurons in the homologous region of the macaque brain (ventral bank of the pregenual anterior cingulate) specifically represent negatively-valenced motivational value (Amemori and Graybiel, 2012). These neurons increased in activity during decisions to avoid a punishment (facial air puff), which also entailed forsaking a reward (food). Importantly, stimulation of these neurons triggered maladaptive decision-making, increasing levels of avoidance even when potential concomitant rewards were high.

There is also evidence that the SGC participates in aversive processing in humans (Talmi *et al.*, 2009). Additionally, and consistent with some theoretical accounts of the role that Pavlovian inhibition plays in the development of affective disorders (Dayan and Huys, 2008, Eshel and Roiser, 2010, Huys *et al.*, 2015a), the SGC has consistently been shown to be overactive in patients with mood disorders (Drevets et al., 1997, Drevets et al., 2008), with its degree of activation to negative stimuli predicting treatment response in depression (Roiser et al., 2012). Since aversive pruning is a form of reflexive behavioural inhibition, we additionally expected the involvement of regions directly implicated in this process, notably the PAG and amygdala. The PAG participates in fear (Mobbs *et al.*, 2007) and increases

107 in activation with anxiety in humans (Mobbs *et al.*, 2010). The amygdala has been
108 reported to be recruited during human conditioned inhibition (Geurts *et al.*, 2013).
109 Both structures have also been implicated in affective disorders (Krishnan and
110 Nestler, 2008).

111 Finally, as planning depends on multiple cognitive systems, we anticipated
112 that the neural architecture subserving aversive pruning would operate in addition
113 to, yet distinct from, established networks governing other cognitive processes.
114 Specifically, we expected to distinguish the neural correlates of aversive pruning
115 from those associated with executive functioning (Newman et al., 2003) and
116 mnemonic processes (Tolman, 1948) (DLPFC, parietal cortex, dorsal striatum),
117 sequence planning (Fermin *et al.*, 2016, Matsuzaka *et al.*, 2012) (pre-supplementary
118 motor area (SMA), SMA, motor cortex, cerebellum), as well as goal-directed
119 evaluation (Schultz, 2015) (ventral striatum, OFC, insula).

Materials and methods

Participants

Forty-one healthy volunteers (21 female; M = 23.30 years, SD = 3.70) were recruited via the University College London Psychology participant pool. Participants were screened for past and present psychiatric disorders, including substance/alcohol dependence/abuse, using the Mini International Neuropsychiatric Inventory (Sheehan *et al.*, 1998). Past or present psychopathology was an exclusion criterion and one participant was excluded on this basis (previous substance dependence), leaving 40 participants in the analysis. Participants completed the State-Trait Anxiety Inventory (STAI; (Spielberger *et al.*, 1970); state: M = 9.50, SD = 7.20, trait: M = 14.00, SD = 7.53), Beck Depression Inventory (BDI; (Beck *et al.*, 1961); M = 3.13, SD = 4.21), the revised Neuroticism-Extraversion-Openness Personality Inventory (NEO PI-R; (Costa and McCrae, 1992); openness: M = 33.28, SD = 5.84, conscientiousness: M = 29.90, SD = 7.88, extraversion: M = 31.45, SD = 6.54, agreeableness: M = 34.18, SD = 4.84, neuroticism: M = 17.98, SD = 8.13) and the Wechsler Test of Adult Reading (WTAR; (Wechsler, 2001)), which was used to evaluate intelligence quotient (IQ; M = 111, SD = 4.2). The study was approved by the UCL Graduate School Ethics Committee and all participants provided written, informed consent. Participants were compensated based on task performance, up to a maximum of £40, with a minimum payment of £15.

Figure 1 about here

Task

The reinforced sequential planning task was adapted for fMRI from one described in detail previously (Huys *et al.*, 2012) and programmed in Cogent 2000 (www.vislab.ucl.ac.uk/Cogent), a stimulus presentation toolbox for Matlab (version 7.1). Participants moved throughout a hexagonal maze via button presses (U/I during training, left/right in the scanner; **Figure 1C**) in an attempt to maximize earnings. Possible outcomes (**Figure 1D**) comprised one large reward (+140 pence, top blue arrow), three large losses (-70 pence, red arrows), and several small gains and losses (20 pence each, green (+) and black (-) transitions, respectively). During free plan trials (of which there were 90; **Figure 1E**), participants had nine seconds to devise a sequence of moves so as to maximize their earnings (planning phase); a countdown timer from 9 to 1 indicated the amount of time left in seconds. Following this planning phase, participants had 2.5 seconds to input their responses, via a series of button presses on an MRI-compatible button box. We biased the free plan trials by starting position and difficulty, such that for 60 trials it was optimal to transition through the large loss, while for the remaining 30, the optimal sequence avoided the large loss.

During restricted plan trials (40; **Figure 1F** and **1G**), participants were presented with two possible multi-step routes (equal length; 3-5 moves) through the maze, one coloured blue and the other green (**Figure 1F**), and had to choose between just these. As in the free plan trials, participants had nine seconds to evaluate the best route (one path always yielded more money than the other). Subsequently, two coloured boxes appeared, one blue, the other green, and the participant then selected their chosen route with a single button press (either left or

5

165 right option, **Figure 1G**; again, as per free plan trials, participants had 2.5 seconds to
166 input their response). Twenty of the restricted plan trials involved deciding between
167 two routes that both transitioned through a large loss (restricted plan large loss). In
168 the other 20 restricted plan trials, both paths avoided the large loss (restricted plan
169 no large loss).

170 For both free plan and restricted plan trials, participants were then shown
171 the selected sequence of moves and their corresponding monetary outcome (0.8 s
172 for each move; **Figure 1H**). Every trial finished with a fixation cross, which varied in
173 duration depending on the number of moves (0.5-2.1 s), such that the trial duration
174 was always 16 seconds. Twenty fixation trials, also 16 seconds in duration, were
175 included to constitute an implicit baseline in the fMRI analysis. Trials were
176 randomized into three runs of 50 trials, each lasting 13.5 minutes and with the
177 constraint that no trial (i.e. number of moves, starting position and trial type) was
178 repeated consecutively. Participants were paid according to their earnings, but the
179 running net income was not displayed until the end of each run. Not entering
180 enough moves on free plan trials, or failing to respond on restricted plan trials,
181 incurred a £2 loss on each occasion.

182 Participants received extensive training on the task before entering the
183 scanner: 30 trials without reinforcement, followed by a test, to learn the transitions
184 (**Figure 1C**); and 34 trials to learn the transition values (**Figure 1D**), including 18 free
185 plan and two restricted plan trials with no time restriction, and 14 with the same
186 time restriction as in the scanner, two of which were restricted plan trials.

187

188 **Behavioural analyses**

189 **Basic behavioural outcome measures**

190 Free plan trials were classified according to the following categories: correct
191 decisions (participants executed the best possible sequence), suboptimal decisions
192 (participants did not execute the best possible sequence), and misses (participants
193 failed to enter enough moves). Correct decisions were further sub-categorised as
194 "optimal large loss" (OLL) correct trials, on which the participant transitioned
195 through at least one large loss to gain the maximum amount of money, and "optimal
196 no large loss" (ONLL) correct trials, where the maximum was attained by avoiding
197 large losses. Suboptimal decisions were further classified into "aversive pruning"
198 trials and "error" trials. Aversive pruning trials were defined when it was optimal to
199 transition through the large loss, but participants selected the best available option
200 that avoided the large loss (e.g. **Figure 1A-B**). Errors were defined as all other
201 instances of suboptimal choices and were subdivided into trials where the optimal
202 decision would avoid (ONLL error, though these occurred very rarely) or entail (OLL
203 error, excluding aversive pruning trials) transitioning through a large loss. Restricted
204 plan trials were classified as either correct or errors. Please see **Table 1** for a list of
205 trial outcome classifications.

206 The main behavioural outcome measures were proportion correct (OLL and
207 ONLL) scores (after removing the small number of missed trials: mean = 4.65%, SD =
208 2.55%) and reaction times (calculated at the time of the first move entered). We

209   determined a proxy (trial-based) measure of each individual's sensitivity to large
210   losses by calculating the difference between ONLL and OLL correct scores (averaged
211   across depth). We excluded three participants who scored below 50% correct across
212   all ONLL trials, indicating an inability to perform the task.

213   **Table 1**. Basic behavioural outcome measures

Type	Abbreviation	Explanation
Optimal no large loss correct	ONLL correct	Optimal sequence chosen where this does not include a large loss
Optimal large loss correct	OLL correct	Optimal sequence chosen where this includes a large loss
Aversive pruning	-	The best sequence that avoids large losses chosen when the optimal sequence includes at least one
Optimal no large loss error	ONLL error	Suboptimal sequence chosen for this trial type, not including aversive pruning
Optimal large loss error	OLL error	All suboptimal sequences chosen for this trial type

214

215   **Basic behavioural data analyses**

216   Behavioural data from the scan (i.e. excluding training trials) were analysed using
217   SPSS (Software Package for Statistics and Simulation; Version 21. NY, USA: IBM
218   Corp). Only free and restricted plan trials on which participants entered the correct
219   number of moves were included in this analysis. Accuracy, reaction time (RT) and
220   earnings data across conditions were analysed using paired-sample *t*-tests and
221   analysis of variance (ANOVA). Due to low trial numbers, RT and earnings data were
222   not analysed for ONLL error trials. Where appropriate, RT data were log transformed
223   to meet parametric assumptions (assessed using the one-sample Kolmogorov-
224   Smirnov test). Where transformations were not sufficient to correct normality
225   violations, non-parametric tests were applied, including the Friedman test and
226   Wilcoxon Signed-rank test. To test the relationship between psychometric variables
227   and task performance, we used multiple linear regression, with the following
228   variables included in the model: age, sex, IQ, STAI trait, STAI state and BDI. For all
229   analyses, $P < 0.05$ was considered significant and $0.05 < P < 0.1$ a trend towards
230   significance. Where appropriate, Greenhouse-Geisser correction of degrees of
231   freedom was used to accommodate violations of sphericity.

232

233   **Model-based behavioural data analyses**

234   *Overview of model-based behavioural data analyses*

235   Here, we focussed our analyses specifically on aversive pruning and fMRI; detailed
236   analyses of alternate planning strategies are described elsewhere (Huys *et al.*,
237   2015b). Computational modelling was based on our previous approach (Huys *et al.*,
238   2012). Only free plan trials on which participants entered sufficient moves were
239   included; restricted plan trials were not modelled. Following model fitting, models
240   were compared using the integrated Bayesian information criteria (iBIC; (Huys *et al.*,

241 2012), in which models of greater complexity are penalized more strongly, and thus
242 are required to have higher log likelihoods for the choices than simpler models.

243 We initially provide a brief overview of our modelling approach, and explain
244 this in more detail in the section below. Our analyses focussed on the creation of
245 four distinct computational models and their evaluation in relation to our
246 behavioural data based on our previous results with this task reported in Huys et al.,
247 (2012). First, we constructed an optimally performing model, called "Lookahead",
248 which fully evaluated each sequence within the maze and chose the path with the
249 highest net total value. As optimal sequence planning is unrealistic, especially at
250 higher decision depths, we next calculated a "Discount" model, in which sequence
251 planning is probabilistically terminated at each depth, with the likelihood of
252 termination determined by the "general discount" parameter. Most relevant to the
253 hypothesis examined here, we then created a "Pruning" model, in which participants
254 stopped planning sequences specifically if they contained a large monetary loss, in
255 addition to general discounting. This tendency is governed by the "pruning" (specific
256 discount) parameter. Finally, we constructed a "Loss sensitive" model to control for
257 any overweighting of negative relative to positive outcomes, a phenomenon
258 commonly known as loss aversion.

259 For the fMRI analyses, we exploited the best-fitting, Pruning model, to
260 quantify the "inclination to prune" on a trial-by-trial basis. This involved computing
261 the distribution of probabilities over all possible paths for a particular problem
262 (starting state and depth), given that individual's pruning parameter. This
263 distribution was calculated from the "Pruning" model. We also computed this
264 distribution assuming that the pruning parameter was identical to the general
265 discount parameter – in other words, assuming no specific discounting when
266 encountering large monetary losses, equivalent to the "Discount" model. The
267 difference between these two distributions, calculated for every trial, was our metric
268 of the inclination to prune in our model-based fMRI analyses, and is called the
269 Kullbach-Leibler (KL) divergence.

270 *Details of model-based behavioural data analyses*

271 Compared with our previous approach (Huys *et al.*, 2012), the models were adapted
272 to take into account the fact that participants had to emit an entire action sequence
273 at once; the models therefore had to specify distributions over entire action
274 sequences. That is, rather than choosing from one of the two actions *d* times (as
275 previously (Huys *et al.*, 2012), *D* corresponds to decision depth), participants chose
276 one sequence from the entire set of 2^D available sequences. We write the probability
277 of emitting sequence $\mathbf{a}^i$ as:

278 $$p(\mathbf{a}^i) = \frac{\exp(\beta \mathcal{Q}(\mathbf{a}^i))}{\sum_j \exp(\beta \mathcal{Q}(\mathbf{a}^j))}$$ [1]

279 where β is the inverse temperature which determines the steepness of the softmax
280 function.

281 The Q value was defined as follows. For model "Lookahead", a standard tree-
282 search algorithm was used. This completely evaluates each possible sequence
283 according to the sum of all *D* outcomes $r_d(\mathbf{a}^i)$ that would be encountered:

$$Q^{\text{look}}(\mathbf{a}^i) = \sum_{d=1}^{D} r_d(\mathbf{a}^i)$$

[2]

However, it is computationally unrealistic for human participants to perform such a search, given the large number of possible sequences (8, 16 or 32 sequences, for 3-, 4- and 5-move trials respectively). Thus, we fitted a "Discount" model, which captures the tendency not to plan fully, forcing the tree search to terminate at each depth with probability 1-γ (hence γ here represents the continuing probability; note that in Huys et al. 2012 it was formulated as the complementary stopping probability). The 'Discount' model captured such uniform search curtailment with a single γ parameter:

$$Q^{\text{disc}}(\mathbf{a}^i) = \sum_{d=1}^{D} \gamma^{d-1} r_d(\mathbf{a}^i)$$

[3]

The next model, "Pruning" is central to the hypothesis we aimed to test here: it splits the γ parameter into γ_G ("general pruning") representing the general tendency not to plan (as in model discount), and γ_S (termed "specific pruning" in our previous report (Huys *et al.*, 2012); here "aversive pruning") the probability of tree-search continuation specifically on encountering a large loss. The "Pruning" model incorporated these two separate γ parameters:

$$Q^{\text{prune}}(\mathbf{a}^i) = \sum_{d=1}^{D} \gamma_\text{G}^{d-l(d)-1} \gamma_\text{S}^{l(d)-1} r_d(\mathbf{a}^i)$$

[4]

with $l(d)$ indexing the number of times a large loss outcome had been encountered up to the point d in the sequence. That is, a probabilistic reduction in planning beyond a large loss is captured by a lower continuing probability (γ_S) after a large loss.

Next, a "Loss sensitive" model with values $Q^{\text{prune+LA}}(\mathbf{a})$ additionally allowed the sensitivities to each of the outcomes r in equation 4 to be fitted separately for every participant. For this model, β in equation 1 was fixed at unity. This ensured that any aversive pruning was not simply due to a relatively stronger weighting of losses compared to rewards (i.e. loss aversion (Tversky and Kahneman, 1991), the well-known tendency for humans to overweight losses relative to gains of equivalent magnitude).

Finally, we considered an additional Pavlovian attraction parameter that had proved important in the behavioural study (Huys *et al.,* 2012). This captured the attraction of states based on their average future consequences, irrespective of whether sufficient choices remained on a trial to exploit those consequences. Most critically, this captured participants' tendency to move from state 6 to state 1 (-20p) rather than to state 3 (+20p) when there was only one choice left in this state. We found this effect in our current data too, with participants choosing the transition from state 6 to state 1 on 53% of trials when only one choice remained, despite the relative 40p cost entailed. However, there were fewer such trials in the current version of the task, thus weakening its evidentiary basis.

322   The reader is referred to Huys *et al.* (2012) for a detailed discussion of these
323   models. The fitting procedures and the rationale for the group-level iBIC are also
324   discussed there.

325   Additional behavioural modelling was performed to generate parameter
326   estimates to approximate the aversive pruning on each particular trial, to include in
327   model-based fMRI analyses (O'Doherty *et al.*, 2007). As a marker for the engagement
328   of the neural circuits that are involved, we examined the inclination the subject had
329   to aversively prune on each trial, whether or not this behaviour actually occurred.
330   This inclination should depend on the trial type (being greater when there are more
331   opportunities for aversive pruning - e.g., on deeper trials) and should be higher the
332   stronger the individual's overall tendency to engage in aversive pruning. Short of a
333   validated process model for aversive pruning, we considered a surrogate measure of
334   trial- and subject-specific propensity that at least exhibits these two critical
335   properties. Specifically, we computed (using a set of parameters tailored to each
336   subject) two probability distributions over all possible sequences for every trial: first,
337   the distribution assuming that aversive pruning had no influence (i.e. fixing γ_S at
338   zero); and second, the distribution calculated using their fitted γ_S. The difference
339   between these two distributions, the Kullback-Leibler (KL) divergence, is our index of
340   the likely predilection to engage in aversive pruning on any given trial. Note that we
341   do not assume that subjects actually compute the distributions with and without γ_S
342   – they are simply used here as a tractable proxy of the trial-by-trial variation in
343   inclination to engage in aversive pruning. The KL divergence was calculated between
344   the action distribution probability for models with and without aversive pruning. If
345    $p(\mathbf{a}|s_0, d, \gamma)$ is the probability of all possible action sequences of length *d* starting
346   from state s_0 given by equation 3 (the Discount model, with only one γ), and
347    $p(\mathbf{a}|s_0, d, \gamma_G, \gamma_S)$ is the same for equation 4 (the Pruning model, where γ is split),
348   the KL divergence D_{KL} is then:

$$D_{KL} = \sum_{\mathbf{a}} p(\mathbf{a}|s_0, d, \gamma) \log \frac{p(\mathbf{a}|s_0, d, \gamma)}{p(\mathbf{a}|s_0, d, \gamma_S, \gamma_G)}$$

349   [5]

350   This KL divergence value was calculated for each successfully completed free
351   plan trial, including the training trials, and then Z-transformed such that the mean
352   was equal to zero and the standard deviation equal to 1 for each individual.
353   Importantly, the summed KL divergence value across trials for each participant was
354   highly correlated with the difference between their γ_G and γ_S values ($r_{(37)}$ = 0.74, *P* <
355   0.001). Note that the KL divergence measure should be high on trials where the
356   possibility of aversive pruning is likely to have influenced subjects' behaviour to a
357   greater degree (e.g. with increased complexity), given their estimated overall
358   tendency to engage in aversive pruning.

359

MRI data acquisition

361   Brain images were acquired using a Siemens 1.5 Tesla Avanto MRI scanner with a 32-
362   channel sense head coil at the Birkbeck-UCL Neuroimaging Centre.

363   The task was presented via a head coil mirror and a front-of-bore projection
364   system. Two hundred and twenty-five T2* weighted echo-planar imaging (EPI)

365 volumes (42 slices per volume, slice repetition time (TR) = 87 ms, volume TR = 3.654
366 s, echo time (TE) = 50 ms, slice tilt = -30°, flip angle = 90°, field of view = 192 mm)
367 were collected per run. The EPI sequence used was optimized to reduce signal
368 dropout in both orbitofrontal cortex and amygdala regions (Weiskopf *et al.*, 2006).
369 Phase oversampling (12%) was applied. Slices were positioned to maximally
370 encompass ventral prefrontal and subcortical regions as these included our *a priori*
371 hypothesized regions of interest (ROIs). Following task completion, field maps (short
372 TE = 10 ms, long TE = 14.76 ms) were acquired in order to assess the inhomogeneity
373 of the magnetic field. Finally, a 3D T1-weighted anatomical scan (magnetization
374 prepared rapid gradient echo; 176 slices; slice thickness = 1 mm; gap between slices
375 = 0.5 mm; TR = 2,730 ms; TE = 3.57 ms; field of view = 256 × 256 mm^2; matrix size =
376 256 × 256; voxel size = 1 × 1 × 1 mm resolution) was acquired at the end of each
377 scanning session.

378

379 **fMRI preprocessing**

380 EPIs were pre-processed prior to analysis using Statistical Parametric Mapping (SPM)
381 8 (release 4010; www.fil.ion.ucl.ac.uk/spm) in MATLAB (7.1; Natick, MA). The first
382 three volumes from each run were discarded to allow for T1 equilibrium effects,
383 leaving 222 volumes per run. Images were spatially realigned to the fourth volume of
384 the session and unwarped (using field maps), in order to correct for motion and
385 geometric distortions caused by inhomogeneities in the magnetic field, respectively.
386 Volumes corrupted due to movement (0.01% of all volumes) were excluded and
387 replaced by linear interpolation of the surrounding images. Images were then
388 normalized to Montreal Neurological Institute (MNI) co-ordinate space and
389 smoothed with a Gaussian kernel of 4 mm full-width at half-maximum (FWHM).

390

391 **fMRI statistical analyses**

392 All fMRI analyses were conducted using SPM.

393 **First-level modelling**

394 *Model-based fMRI – aversive pruning*

395 We first constructed an fMRI model to explore the impact of aversive pruning on
396 planning on a trial-by-trial basis using the computationally derived KL divergence
397 estimates, Z-transformed within each subject (i.e. model-based fMRI). In this model,
398 all valid free plan trials were included in a single regressor, which was modulated
399 first by difficulty (i.e. the number of sequences to evaluate; 2^d = 8, 16 or 32 for 3-, 4-
400 and 5-move problems, respectively, where d = depth), to account for the linear
401 effects of the expanding tree upon the KL divergence value. The difficulty-modulated
402 regressor was then parametrically modulated by the KL divergence value. This, and
403 all other models (except the model examining value itself), contained a separate
404 parametric regressor representing the net monetary outcome of the chosen
405 sequence across all trials (also time-locked to the planning period with the same
406 duration). Specifically, the linear effect of anticipated reward on planning-related
407 responses was modelled via a parametric regressor, with magnitude proportional to
408 the net outcome provided by the chosen sequence. The inclusion of such a regressor

409   removes value-related response variance from the analysis; this is important
410   because aversive pruning is, by definition, monetarily disadvantageous. We also
411   examined the effect of depth on KL divergence-related responses by computing the
412   interaction of the KL divergence value and difficulty (again, 2^d) and entering it as a
413   third parametric modulator.

414   *Distinguishing aversive pruning from planning and value-related networks*

415   In order to confirm established findings and the distinctiveness of our aversive
416   pruning fMRI results from other networks and processes elicited by the task, we also
417   constructed further models testing for the neural effects of planning and valuation.
418   To examine responses related to difficulty during complex planning, we examined
419   the first parametric modulator (difficulty: 2^d), which modulated the regressor
420   containing all successfully completed free plan trials (time-locked to the planning
421   period with the same duration (9 s)). The aim here was to locate the regions of the
422   brain that scaled with the increasing cognitive demands of planning in our task. We
423   constructed an additional model to explore outcome value-related networks. This
424   value model contained a further parametric modulator time-locked to the outcome
425   phase (2.4-4 s following the end of response input), which allowed us to examine
426   value-related responses during both the planning and outcome phases (each in a
427   separate regressor); we parametrically modulated the relevant portions of the trial
428   by the net monetary outcome of each trial.

429   *Trial-based fMRI – aversive pruning*

430   For the trial-based fMRI analyses, the subject-level design matrix included separate
431   regressors for the different trial types (defined according to participants' in-scanner
432   choices - see "Basic behavioural analyses" above and Table 1) corresponding to the
433   planning phase of the task. The following regressors of interest were included: OLL
434   correct; ONLL correct; aversive pruning; OLL error; correct restricted plan large loss;
435   and correct restricted plan no large loss. ONLL error trials were not included due to
436   low trial numbers for this category and were included in a separate regressor of no
437   interest. To model increasing cognitive demands with increasing depth, we entered
438   trial difficulty as a parametric modulator. This parametric regressor on OLL correct,
439   ONLL correct, aversive pruning, and OLL error entailed a modulation by the number
440   of sequences that needed to be evaluated (i.e. difficulty, 2^d). Contrasting conditions
441   parametrically modulated by depth should yield a more sensitive analysis of neural
442   responses as the likelihood of aversive pruning grows with the branching or
443   complexity of the decision tree.

444   *Model- and trial-based fMRI*

445   For both model-based and trial-based fMRI analyses, we also included regressors to
446   model the response input phase (duration 2.5 s, in a single regressor for all trials)
447   and outcome phase (duration 2.4-4 s). The outcome phase was categorised into the
448   same six regressors as the planning phase for the trial-based fMRI analysis (free plan:
449   OLL correct, ONLL correct, aversive pruning and OLL error; restricted plan: correct
450   restricted plan large loss and correct restricted plan no large loss), again separately
451   modelling the linear effect of net outcome across trial types. Additionally, to assess
452   the impact of receiving a large loss, we contrasted OLL and ONLL correct trials during
453   the outcome phase of the task. For both the model- and trial-based fMRI analyses,

454 regressors of no interest included missed/no-response trials, ONLL error trials and
455 incorrect restricted plan trials combined into a single regressor (whole-trial duration:
456 16 s), as well as regressors modelling null scans for the two scans immediately
457 before and after the second run, and interpolated images following removal of
458 corrupted scans (if any). Fixation trials were not modelled explicitly and constituted
459 an implicit baseline. The six realignment parameters were also included in the
460 model. All regressors were modelled as boxcars time-locked to the trial phase
461 (planning, input, and outcome) with the corresponding duration (9 s, 2.5, and 2.4-4
462 s, respectively), and convolved with SPM's canonical hemodynamic response
463 function.

464   Estimation incorporated a high-pass filter at 1/128 Hz and serial correlations
465 intrinsic to the fMRI time series were accounted for using an AR(1) model. The three
466 runs were modelled as a single concatenated run to avoid non-estimation of entire
467 runs for participants with low numbers of event types.

468

469 **Second-level modelling**

470 Following estimation, subject-level contrast images were smoothed with a 7 mm
471 FWHM kernel, and entered into group-level one-sample *t*-tests. Activations were
472 localized with reference to the group-averaged anatomical scan and the atlas of Mai
473 and colleagues (2003). Given our *a priori* hypotheses regarding the neural basis of
474 aversive pruning (Dayan and Huys, 2008), we applied an initial threshold of *P* = 0.005
475 and applied family-wise error (FWE) correction for multiple comparisons at the
476 voxel-level, adjusted for small volume (SVC) across our ROIs. For the planning phase
477 analysis, the SGC ROI was defined as an 8 mm box centred on of the peak coordinate
478 from a study reporting altered glucose metabolism in patients with depression (MNI
479 coordinates, [x = -2, y = 32, z = -2]; (Drevets *et al.*, 1997)). The PAG ROI was defined
480 as an 8 mm box centred on the peak coordinate previously identified as activating to
481 increasing threat using fMRI in healthy human participants (MNI coordinates, [x = -
482 3,y = -25, z = -11] (Mobbs *et al.*, 2007). A bilateral amygdala ROI was created from
483 the Wake Forest University (WFU) Pickatlas toolbox for SPM
484 (http://www.fmri.wfubmc.edu/download.htm) with the Automated Anatomical
485 Labelling atlas. We anticipated very robust responses for the more general planning
486 and value-related networks; thus, for the purposes of inference, outside our ROIs,
487 we increased our threshold such that only voxels surviving whole-brain voxel-level
488 FWE correction < 0.05 survived. All second-level analyses incorporated an explicit
489 binary grey matter mask.

490   For the trial-based analyses, the main contrasts we report are derived from
491 linear combinations of the ONLL correct, OLL correct and aversive pruning
492 regressors, which are comparable in terms of visual input during the planning and
493 outcome phases, and the correct restricted plan trials. Since trials were categorised
494 according to participants' decisions, some participants had fewer than four trials in a
495 given condition; these participants were excluded from the relevant contrasts,
496 resulting in slightly different numbers of subjects across analyses. For the outcome
497 phase analysis, we anticipated that activation in the insula would be elicited during
498 the receipt of large losses (Garrison *et al.*, 2013). Therefore, for this analysis we

499   created a bilateral insula ROI from the WFU Pickatlas and applied SVC as described
500   above.

501   For the trial-based planning analyses our primary contrast of interest was the
502   comparison of aversive pruning trials (on which participants avoided the optimal
503   sequence that contained a large loss and instead chose the best available large-loss-
504   free sequence), relative to OLL correct trials (on which participants chose an optimal
505   sequence transitioning through a large loss). To control for the effects of
506   transitioning through a large loss *per se* on OLL correct trials we included the
507   restricted plan trials to create the following contrast: aversive pruning + restricted
508   plan large loss > OLL correct + restricted plan no large loss. We ensured that
509   difficulty was matched across this contrast by selecting trials that provided an equal
510   ratio of 3:4:5 move problems for each participant across the aversive pruning and
511   OLL correct conditions. For restricted plan trials, the inclusion threshold was set at
512   chance level (50%); two participants failed to meet this criterion due to a failure to
513   understand trial instructions and were excluded from analyses including this trial
514   type. To control for possible difficulty differences between restricted plan trials,
515   (because there were more divergent arrows in the restricted plan large loss
516   condition), trials were chosen to match the number of divergent arrows between the
517   two restricted plan trial types.

518   Finally, we constructed additional contrasts to test how the above planning
519   contrasts were modulated by difficulty (2^d). These contrasts are derived from linear
520   combinations of the OLL correct, ONLL correct and aversive pruning parametric
521   modulator regressors, but exclude the restricted plan trials; the latter are
522   unnecessary here as the parametric modulator already entails a contrast (between
523   more difficult and easier trials) within each condition, controlling for the transition
524   through the large loss *per se* on OLL correct trials. As above, three main contrasts
525   were examined: 1) aversive pruning parametric modulator > OLL correct parametric
526   modulator; 2) OLL correct parametric modulator > ONLL correct parametric
527   modulator; and 3) ONLL correct parametric modulator > aversive pruning parametric
528   modulator.

Results

We describe two broad collections of behavioural analysis, and through this, associated fMRI responses. Following a brief description of the broad patterns of behaviour observed on the task, which paralleled our previous findings (Huys et al., 2012) we initially consider a computational model-based treatment that aimed to characterize the whole structure of behaviour using a parsimonious model whose parameters are intended to capture the general tendencies of each subject. Imaging analyses associated with this model duly indicated the general architecture of control. We then explore the specificity of our imaging analyses in the context of other known neural architecture underlying the cognitive components implicated in our task. Finally, for completeness, we provide complementary behavioural and fMRI analyses based on categorisations of trials (see Table 1).

Behavioural and modelling evidence for pruning

Participants chose the correct sequence on average 78% (SD = 18%) of the time on free plan trials on which the optimal sequence did not include a large loss (ONLL); on these trials aversive pruning would not be disadvantageous. By contrast, on free plan trials on which the optimal sequence did include a large loss (OLL), for which aversive pruning would be disadvantageous, performance was impaired for every participant (mean OLL correct = 37% (SD = 18%)). The difference between performance on these trial types was substantial and highly significant (mean difference = 41% (SD = 20%), $t_{(36)}$ = 12.51, $P < 0.001$, d = 2.06; **Figure 2A**), confirming our previous findings (Huys et al., 2012). As expected, performance also became worse with increasing difficulty ($F_{(2,72)}$ = 132.75, $P < 0.001$, η_p^2 = 0.787; **Figure 2B**), but remained high even for depth 5 choices, where there are 32 different paths. Critically, there was a significant interaction between trial type and difficulty ($F_{(2,72)}$ = 5.58, $P = 0.009$, η_p^2 = 0.134). Planned contrasts revealed that the requirement to transit through a large loss to attain the optimal amount had an increasingly detrimental effect on decision-making at higher difficulty (depth 3: mean difference = 34% (SD = 25%), $t_{(36)}$ = 8.26, $P < 0.001$, d = 1.36; depth 4: mean difference = 40% (SD = 22%), $t_{(36)}$ = 11.29, $P < 0.001$, d = 1.86; depth 5: mean difference = 49% (SD = 29%), $t_{(36)}$ = 10.33, $P < 0.001$, d = 1.70). Note, though, that this analysis does not examine where the loss appeared in the tree.

Figure 2 about here

Model-based aversive pruning behaviour and associations with psychometric variables

Consistent with our previous report (Huys *et al.*, 2012), there was substantial evidence for aversive pruning based on our computational model (see **Figure 2C-D**; Pruning and Pruning+Loss models). That is, the most parsimonious model (smallest negative model evidence iBIC; red star in **Figure 2E**; see **Table 2** for model performance overview) incorporated aversive pruning, with steeper discounting after large losses than after other outcomes (γ_G is significantly larger than γ_S, $t_{(36)}$ = 5.12, $P < 0.001$, d = 0.84; **Figure 2F**; improvement in $\log_{10}$ model evidence between model Discount and model Pruning (ΔiBIC) = 77.5, indicative of decisive evidence in favour of the Pruning model). Loss aversion was also evident (**Figure 2G**), such that the best model incorporated fitted reward and loss sensitivities (ΔiBIC between

573 model Pruning and Pruning+Loss) = 5.8). It is important to distinguish between these
574 two loss-related processes that are included in our model. Aversive pruning, as
575 instantiated in the model, is not simply a discounting of the value associated with
576 transitions (or subsequent paths). Instead, the aversive pruning parameter controls
577 whether paths following large losses are actually explored at all, regardless of the
578 possible gains that lie behind them. We consider such a reflexive avoidance of even
579 considering options to be Pavlovian in nature, as it is elicited automatically and not
580 related to the overall value of the path. Excessive discounting of the value of
581 negative transitions (equivalent to loss aversion) does occur in our data, but this is
582 controlled by a different set of parameters and is conceptually separate from
583 pruning.

584 Importantly, our computationally-derived general planning parameter (γ_G)
585 was positively correlated with its trial-based equivalent (ONLL percent correct: $r_{(37)}$ =
586 0.73, $P < 0.001$; **Figure 2H**). The difference between OLL and ONLL percent correct
587 was strongly correlated with the equivalent metric derived from the computational
588 analyses (γ_G-γ_S: $r_{(37)}$ = 0.63, $P < 0.001$; **Figure 2I**), providing convergent validity for the
589 two approaches. However, due to the uncertainty attached to both choice frequency
590 and model parameter estimates this correlation is not perfect and some subjects
591 with small or even negative difference between γ_S and γ_G still show a positive
592 difference between ONLL and OLL frequencies. It would be interesting to examine
593 subjects who do and do not show aversive pruning separately, or indeed look for
594 changes over time in the strength of pruning. Unfortunately, the present sample size
595 does not allow for this; therefore, we concentrate here on correlational analyses.
596 Finally, further validation of the model comes from sampling surrogate data (Figure
597 2J-L).

598 Overall, these results are consistent with our previous report in an
599 independent sample (Huys *et al.*, 2012), and provide complementary evidence for
600 the presence of aversive pruning. The slow degradation of performance with depth
601 on the ONLL trials is compatible with the fact that the number of trials without a
602 large loss increases slowly with depth, and that aversive pruning allows the
603 concentration of resources on these paths.

604

605 **Table 2.** Model performance values

Model	Number of parameters	Choice log likelihood	% variance explained	iBIC
Pruning + Loss	6	1151	55.3	2466
Pruning	3	1173	54.4	2472
Discount	2	1221	52.5	2549
Lookahead	1	1502	41.7	3052

606 ⬜
607 iBIC: integrated Bayesian information criteria

608 A multiple regression analysis revealed that state anxiety, but no other
609 included variable (IQ, gender, age, depression and trait anxiety), correlated with the
610 difference between ONLL and OLL percent correct ($t_{(37)}$ = 2.12, P = 0.042); variance
611 inflation factor (VIF) values were less than 3.0 for all independent variables,

612 suggesting an adequate lack of collinearity. Contrary to our expectations, however,
613 no psychometric variables correlated with the computationally derived aversive
614 pruning estimate (γ_G–γ_S). In particular, we did not replicate our previous finding that
615 this statistic was correlated with subclinical depression scores, though we note that
616 the range of scores in the present study was relatively low.

617 **Aversive pruning recruits the subgenual cingulate cortex**

618 We used the computational model to construct, separately for each participant's
619 maximum *a posteriori* parameters, a measure of the inclination to engage in aversive
620 pruning on each trial. This is the Kullback-Liebler (KL) divergence between the
621 distributions of trajectories assuming discounting based on depth alone (discount
622 model) vs discounting based on losses encountered (pruning model). **Figure 3A**
623 confirms that the KL divergence increases with depth ($F_{(2, 72)}$ = 223.82, *P* < .001, η_p^2 =
624 0.86), with all three groups significantly different from each other, *P* < 0.001), as
625 expected from the likely extra opportunities for aversive pruning with longer
626 sequences. **Figure 3B** shows that the measure was indeed higher on aversive pruning
627 trials (based on participant choices – see Table 1); however, there were no
628 significant differences between trial types ($F_{(3,108)}$ = 0.74, *P* = 0.48, η_p^2 = 0.02).
629 Negative KL divergence values shown here arise due to the mean correction applied
630 to the metric used for fMRI analyses.

631   We entered the KL divergence value on each trial as a parametric regressor
632 across all successfully completed free plan trials, controlling for difficulty (which was
633 entered as the first parametric regressor) and trial net value. Consistent with our
634 primary hypothesis, this analysis revealed that SGC activation increased with our
635 metric of inclination to engage in aversive pruning, the KL divergence ([x = -6, y = 29,
636 z = -2]; $t_{(36)}$ = 3.87, P_{SVC} = 0.004; **Figure 3C**). The interaction between KL divergence
637 and difficulty also revealed a greater modulation of SGC activation by inclination to
638 engage in aversive pruning at higher depth ([x = -6, y = 35, z = -5]; $t_{(36)}$ = 3.47, P_{SVC} =
639 0.009; **Figure 3D**.

640   In summary, our computational fMRI analyses revealed that SGC activation
641 was higher on trials on which our model indicated that there was a greater
642 inclination to indulge in aversive pruning, and this was particularly the case on more
643 difficult trials. In the following analyses we show that this activation in the SGC is
644 separate to responses related to planning and valuation.

645   **Figure 3 about here**

646 **Planning and valuation responses**

647 We next explored the specificity of our aversive pruning results relative to other
648 neural networks known to be associated with cognitive processes required during
649 successful undertaking of our task, namely planning and valuation. We first explored
650 the effect of planning by examining the first parametric modulator, which indexed
651 difficulty (2^d). As expected, increasing difficulty robustly activated a network of
652 regions identified in previous studies of planning. This included the bilateral dorsal
653 cerebellum, primary visual, supplementary motor, and DLPFC, thalamus, dorsal
654 caudate and putamen, all of which survived whole-brain (WB) voxel-level correction
655 for multiple comparisons (all $t_{(36)}$ > 5.45, P_{WB} < 0.05; **Figure 4A**).

656   To examine responses related to receipt of outcomes, we constructed a
657 separate model in which the net monetary value of the chosen sequence was
658 entered as a parametric regressor, time-locked to the outcome period. Increasing
659 monetary outcome robustly activated the VS (left [x = -12, y = 8, z = -8]; $t_{(36)}$ = 7.74,
660 P_{WB} < 0.001; right [x = 12, y = 8, z = -8]; $t_{(36)}$ = 5.52, P_{WB} = 0.027; **Figure 4B**, left panel),
661 the medial orbitofrontal cortex (mOFC; [x = 0, y = 44, z = -14]; $t_{(36)}$ = 5.88, P_{WB} =
662 0.013; **Figure 4B**, middle panel), and the head of the caudate ([x = -6, y = 20, z = 7];
663 $t_{(36)}$ = 7.17, P_{WB} < 0.001; **Figure 4B**). Given the wealth of research establishing the
664 existence of value signals in the VS and OFC (Schultz, 2015), we correlated the large
665 reward (+140p) sensitivity parameter from our winning computational model with
666 the net outcome-related activation at the peak voxel within these regions. This was
667 significant in the mOFC ($r_{(37)}$ = 0.46, *P* = 0.004; **Figure 4B,** right panel), but not the VS
668 ($r_{(37)}$ = 0.13, *P* = 0.45).

669   **Figure 4 about here**

670 **Neural response to large losses is associated with aversive pruning tendency**

671 During the outcome phase, participants would no longer have any reason to plan,
672 but instead had just to observe their executed plan being replayed with feedback on
673 the monetary consequence of each box-to-box move. We next asked whether the
674 tendency to engage in aversive pruning might impact on activation during this phase.
675 To do this, we examined trials on which volunteers could have aversively pruned but
676 (correctly) chose not to. Thus, again controlling for net objective outcome, we
677 compared trials on which subjects correctly avoided aversively pruning, therefore
678 receiving at least one large loss during the entire sequence (OLL correct), with
679 correct trials that avoided all large losses (i.e. aversive pruning was helpful, ONLL
680 correct) (note that all of the trials in this contrast involved optimal decisions).

681   This contrast revealed activation in our insula ROI ([x = 33, y = 23, z = -5]; $t_{(36)}$
682 = 4.70, P_{SVC} = 0.011; **Figure 4C**, left panel), as well as robust responses that survived
683 whole-brain correction in the inferior parietal lobule (IPL; [x = 39, y = -52, z = 46]; $t_{(36)}$
684 = 4.78, P_{WB} = 0.01) and DLPFC [x = 45, y = 44, z = 4]; $t_{(36)}$ = 4.32, P_{WB} < 0.001). We next
685 asked whether the tendency to engage in aversive pruning might be related to
686 activation to the receipt of large losses (**Figure 4C**, middle panel). Activation in the
687 insula ($r_{(37)}$ = 0.47, *P* = 0.003; **Figure 4C**, right panel) and DLPFC ($r_{(37)}$ = 0.35, *P* =
688 0.034), but not in IPL ($r_{(37)}$ = 0.22, *P* = 0.20), correlated significantly with our
689 computationally derived measure of aversive pruning, γ_G-γ_S (although the
690 correlations between activation in the insula (Z = 1.58, *P* = 0.113) and DLPFC (Z =
691 0.85 *P* = 0.39) and aversive pruning behaviour were not significantly greater than
692 that in the IPL).

693

694 **Confirmatory trial-based behavioural and fMRI analyses**

695 **Trial-based behaviour provides further evidence of pruning**

696 Further evidence consistent with aversive pruning comes from a finer classification
697 of suboptimal choices. Of course, it is not possible to be definitive as to the
698 processes that underlie any particular suboptimal (or indeed optimal) choice.
699 However, trials for which it would have been optimal to transition through a large

loss, but participants selected the best available option that avoided large losses (e.g. **Figure 1B**) are at least suggestive of aversive pruning-influenced planning. We call these aversive pruning trials. All other instances of suboptimal selection we term as errors (separated into trials for which the optimal decision entailed (OLL error; excluding aversive pruning trials, i.e. this category did not include trials where the next best available option that did not entail transitioning through a large loss was chosen) or avoided (ONLL error) transitioning through a large loss: see Table 1). Due to low trial numbers ONLL errors were not considered further.

A clear example of aversive pruning occurs in the scenario depicted in **Figure 5A**. Placed in state 2 with 3 moves to plan, the optimal solution is to go from state 2 to state 5 (-70p), from state 5 to state 1 (-70p) and from state 1 back to state 2 (reaping the only large reward in the maze: +140p). This sequence results in breaking even, and participants chose it 41% (SD = 33%) of the time (**Figure 5A**, blue outcome). However, in spite of the relative ease of the problem (only 8 sequences needed evaluating), participants had a strong tendency to engage in aversive pruning, presumably because the optimal sequence contains two large losses. The best available option that avoided the large loss involved moving from state 2 to state 3 (-20p), from state 3 to state 4 (-20p), and from state 4 back to state 2 (+20p) (resulting in a net loss of 20 pence). Such aversive pruning arose on 37% (SD = 31%; aversive pruning percentage) of trials (**Figure 5A**, red outcome), i.e., nearly as often as the optimal choice. By way of comparison, subjects selected the optimal and the next best available sequence 80% (SD = 23%) and 14% (SD = 20%) of the time, respectively, on the ONLL trial requiring 3 moves to plan from state 5.

Participants displayed a strong tendency towards aversive pruning, choosing the best sequence that avoided a large loss on around 52% (SD =23%) of OLL trials in which they chose suboptimally (chance = ~11% across depths). All subjects engaged in aversive pruning, however the extent of the predilection was highly variable across the sample (4-93%); nevertheless, the aversive pruning percentage was very consistent within subjects between the 1st and 2nd half of the trials ($r_{(37)}$ = 0.69, $P <$ 0.001). Interestingly this fraction, which we call the aversive pruning percentage, did not depend on depth ($F_{(2,72)}$ = 1.15, P = 0.32, η_p^2 = 0.03; **Figure 5B**), thus supporting the hypothesis that aversive pruning acts as an adaptive heuristic to reduce the number of options to be considered, allowing participants to maintain reasonable, if not perfect, planning performance across depths (Huys *et al.*, 2012). We also examined the average earnings, which revealed a significant main effect of trial type (**Figure 5C**; $F_{(3,108)}$ = 320.538, $P <$ .001, η_p^2 = 0.90). Perhaps surprisingly, aversive pruning choices earned participants significantly more money than OLL correct choices ($t_{(36)}$ = 6.74, $P <$ 0.001, d = 1.11). Although by definition optimal choices would have earned more on aversive pruning trials (**Figure 5C**, light red bar; mean difference = 33p, SD = 9p), this pattern arises because aversive pruning occurred more frequently with increasing depth (while OLL correct trials were rarer to be performed at higher depth), and the average net value largely increases with depth (OLL correct: depth 3 = 33p, depth 4 = 67p, depth 5 = 93p; aversive pruning: depth 3 = -20p, depth 4 = 13p, depth 5 = 50p; OLL error: depth 3 = -84p, depth 4 = -59p, depth 5 = -47p) (although this is not the case for ONLL correct trials (depth 3 = 100p, depth 4 = 80p, depth 5 = 60p)).

746   If aversive pruning is indeed a heuristic that reduces the number of evaluated
747   sequences, then we might see an effect on reaction times (RT: **Figure 5D**; note
748   though, that subjects could not enter choices until the 9s of planning had elapsed,
749   which could reduce the magnitude of this effect). There was a main effect of trial
750   type (Friedman χ^2(3) = 33.876, *P* < 0.001). Post-hoc tests revealed that ONLL correct
751   RTs were significantly shorter than OLL correct RTs (*Z* = 2.105, *P* = 0.035) and
752   aversive pruning RTs (*Z* = 4.413, *P* < 0.001). However, contrary to our expectations,
753   the difference in RT between OLL correct and aversive pruning choices was non-
754   significant (*Z* = -1.335, *P* = 0.182). Nevertheless, aversive pruning choices were made
755   significantly faster than OLL error trials (*Z* = 2.844, *P* = 0.004).

756   Finally, we note that the difficulty in planning transitions through large losses
757   was even evident on the much easier restricted plan trials (on which only two
758   sequences required evaluation). Participants made the optimal choice significantly
759   more often on restricted plan trials that did not feature large losses (mean = 90%, SD
760   = 9%) than on those that did (mean = 84%, SD = 8%; $t_{(34)}$ = 3.74, *P* < 0.001, d = 0.63).
761   However, there was no effect on RT (correct trials only: $t_{(34)}$ = 1.12, *P* = 0.27, d =
762   0.19).

763   **Figure 5 about here**

764   **Trial-based fMRI confirms a role for the SGC in aversive pruning**

765   A contrast between aversive pruning and OLL correct trials during the planning
766   period (incorporating restricted plan control trials, controlling for net outcome;
767   N=31) revealed no significant activation in our ROIs, and no cluster survived whole-
768   brain correction for multiple comparisons. However, an analysis of the parametric
769   modulation of aversive pruning trials by difficulty (contrasted against the parametric
770   modulation of OLL correct trials by difficulty, again controlling for net income: N=33)
771   revealed a cluster in the SGC extending into pregenual ACC ([x = -3, y = 35, z = -2];
772    $t_{(32)}$ = 3.08, P_{SVC} = 0.023; left panel of **Figure 5E**). We also note the presence of a
773   cluster in the right amygdala, though this did not survive correction for multiple
774   comparisons and therefore we do not consider it further ([x = 21, y = 2, z = -20]; $t_{(32)}$ =
775   2.85, P_{SVC} = 0.144). The result in the SGC was driven by a progressive reduction in
776   response with increasing difficulty on OLL correct trials (i.e. a negative modulation by
777   difficulty; one-sample *t*-test against zero: $t_{(32)}$ = 3.72, *P* = 0.001), while difficulty did
778   not affect activation on aversive pruning trials ($t_{(32)}$ = 1.09, *P* = 0.285; right panel of
779   **Figure 5E**). This finding that aversive pruning elicits a (relative) increase in SGC
780   activation as depth increases, complements the one arising in our computationally-
781   motivated analysis based on the KL divergence, where a robust modulation by
782   difficulty was also identified. Taken together, these results suggest that inhibiting
783   aversive pruning may require deactivation of the SGC, particularly when decisions
784   are more complex.

785   None of our other comparisons yielded significant activation in our ROIs, or
786   activation in other regions that survived whole-brain correction for multiple
787   comparisons. Contrasting the parametric effect of difficulty between aversive
788   pruning and ONLL correct trials (N=35) did not reveal any effect surviving correction
789   for multiple comparisons. The equivalent parametric contrast between ONLL and

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790   OLL correct trials (N=35) revealed an effect in the right amygdala that narrowly
791   missed significance ([x = 33, y = -1, z = -20]; $t_{(34)}$ = 3.25, P_{SVC} = 0.062).

Discussion

Multi-step decision-making is fundamental to human behaviours. However, fully solving complex planning problems is often too arduous, thus necessitating heuristics. We used a combination of neuroimaging and computational modelling of behaviour to characterise the neural basis of one such simple approximation, aversive pruning. This is the inflexible, reactive curtailment of search when a large loss is encountered during planning. Aversive pruning represents a computationally well-defined influence of a Pavlovian inhibitory response on high-level cognitive manipulations during planning. We replicated previous findings that aversive pruning was ubiquitous across subjects (Huys *et al.*, 2012). As expected, it served to preserve computational resources, being more prevalent on harder problems, and was associated with faster responses than other suboptimal decisions. Both computational model- and trial-based neuroimaging analyses showed that aversive pruning was associated with haemodynamic responses in the SGC during planning. By contrast, distinct circuits were activated by planning and valuation. Further, the responses to the receipt of large losses in the insula and DLPFC correlated with one of our computationally-derived behavioural measures of overall aversive pruning. Our results reveal the neural and computational architecture underlying a profoundly influential heuristic that enables humans to make complex planned decisions with reasonable speed and accuracy.

The aversive pruning-related activation that we identified in the SGC through both computational and categorical analyses exists over and above planning- and value-related responses. Closer examination of the parametric modulation by difficulty sheds further light on the nature of this finding. In comparison to correct decisions that transitioned through a large loss, aversive pruning was associated with higher SGC activation especially on more difficult problems. Intriguingly, our trial-based analyses suggest that this effect was largely driven by a relative decrease in SGC response on correct decisions that transitioned through a large loss as planning complexity increased (**Figure 5E**). This is consistent with studies examining the trade-off between appetitive and aversive outcomes. In humans, Talmi et al. (2009) also found SGC inhibition when participants chose to endure a punishment in order to obtain a gain. In non-human primates, Amemori and Graybiel (2012) reported that neurons in the homologous area of the ACC in the macaque (BA24b) responded to aversive stimuli in an approach-avoidance decision task; localized microstimulation of these neurons increased the negative impact of aversive consequences on choice. Thus, it appears that planning through a negative outcome in order to achieve an overall positive outcome is facilitated when the SGC is deactivated.

Importantly, the SGC is a key node where cognition and emotion are thought to interact pathologically, for example in mood disorders (Drevets *et al.*, 2008, Roiser *et al.*, 2012). The anatomical correspondence between resting-state findings in depressed patients, punishment-driven anticipatory responses in healthy humans, and aversive signals in non-human primates is striking. The SGC may be an important mediator of the inhibitory effect of aversive expectations not just on behaviour, but also on higher-level cognitive function in mood disorders. In the context of depression, it has been suggested that inhibitory control is impaired and that this underlies some of depressed subjects' inability to disengage from aversive

838 information (Dayan and Huys, 2008, Joormann and Gotlib, 2010). However, the SGC
839 appears to be hyperactive during rumination, and in depression more generally
840 (Cooney *et al.*, 2010), possibly suggesting a reduced efficiency of these mechanisms
841 rather than a lack of engagement.

842 Complex decision-making processes recruit a diverse set of hierarchical
843 cognitive components (Solway and Botvinick, 2012) and neural structures (Newman
844 *et al.*, 2003). We note here at least two neural network processes on top of which
845 aversive pruning occurs. First, planning a complex sequence of actions requires
846 considerable cognitive control. Unsurprisingly, as planning difficulty increased in our
847 task, structures such as the cerebellum, DLPFC, dorsal striatum, motor cortex, and
848 thalamus were increasingly activated (**Figure 4A**). These brain regions are frequently
849 implicated in planning tasks which require cognitive control (Newman *et al.*, 2003)
850 and in goal-directed approaches to problem solving (Solway and Botvinick, 2012). A
851 second important component process of decision-making is the evaluation of
852 outcomes associated with action sequences. Increasing net monetary outcome was
853 associated with activation in a network of structures commonly activated in
854 reinforcement learning tasks and thought to underlie valuation, including the VS and
855 the mOFC (Schultz, 2015). Interestingly, activation in mOFC, but not VS, at the time
856 of outcome was associated with our computationally-derived behavioural measure
857 of sensitivity to large reinforcements. This finding is consistent with the hypothesis
858 that mOFC is critical for processing outcomes *per se*, while VS is more closely aligned
859 with prediction error signalling (Schultz, 2015).

860 When we focused our analysis on the outcome phase (contrasting optimal
861 decisions with and without large losses) we found that a number of regions (insula,
862 IPL and DLPFC) were significantly more activated during the receipt of large losses,
863 even after accounting for trial-by-trial monetary earnings. Even though the actual
864 planning would have terminated before this point, activations in the structures that
865 responded positively to large losses (insula and DLPFC) also correlated positively
866 with our computationally derived estimate of overall aversive pruning (γ_G-γ_S). Of
867 particular relevance is the insula, which is thought to play a role in interoceptive
868 perception and the production of subjective negative feeling states (Medford and
869 Critchley, 2010), and has been reported to influence decision-making (Yu *et al.*,
870 2010). For example, individuals with insula damage have been reported to exhibit a
871 selective impairment in avoiding stimuli associated with monetary losses (Palminteri
872 *et al.*, 2012). We had not predicted activation of DLPFC and IPL in the outcome
873 phase, but this pattern would be consistent with the engagement of inhibitory
874 processes during cognitive control (Guitart-Masip *et al.*, 2012). We speculate that
875 these results may indicate a similar involvement in aversive pruning, though this
876 needs to be tested in future studies. The activation of the DLPFC is particularly
877 noteworthy with respect to depression. Fales and colleagues (2008) showed a failure
878 to activate the DLPFC during suppression of irrelevant aversive information in
879 depression. As aversive pruning might relate to the ability to inhibit the processing of
880 aversive information, and hence correlate negatively with rumination (Gotlib and
881 Joormann, 2010), a clear prediction is that a similar pattern would be observed when
882 depressed patients aversively prune.

883   Taking the above results together, a possible model accounting for our fMRI
884   results is that the DLPFC and insula might co-ordinate to mark parts of the decision
885   tree that contain large losses. Once the tree is demarcated, these signals may then
886   be used during the planning phase where SGC responses drive the decision to prune.
887   Meanwhile, deactivation of the SGC appears critical to choosing to engage with the
888   large loss in order to make an optimal decision. The consistency of the SGC response
889   between our computational and categorical fMRI analyses during planning supports
890   the notion that this region participates in curtailing the decision tree search on
891   encountering a large loss. Although we cannot directly exclude an additional causal
892   influence, whereby it is the overloading of cognitive control that leads to the release
893   of the pruning reflexes, the structure of the findings still argue for a shaping
894   influence of the pruning reflexes on the process of evaluation.

895   A limitation of the current work is that the aversive pruning time-point(s)
896   during planning are not clearly temporally delineated; we therefore cannot make
897   temporal causality claims about the neural effect. Aversive pruning is a meta-
898   reasoning process involving multiple repeated decisions about what to evaluate next
899   (Russell and Wefald, 1991). The ambiguity surrounding the precise point at which
900   aversive pruning occurs could be resolved more directly, possibly using a
901   combination of eye-tracking and neuroimaging methods with higher temporal
902   resolution such as EEG or MEG. A further limitation is that our study was performed
903   in healthy participants and was not designed to detect correlations with symptoms
904   of mood or anxiety disorders. In a previous study (Huys *et al.*, 2012) aversive pruning
905   correlated with subclinical measures of depression, while in the current study, it
906   correlated with state anxiety. We originally hypothesised (Dayan and Huys, 2008)
907   that aversive pruning might relate to both symptoms of depression and anxiety
908   because features of impaired inhibition of aversive processing are prominent in both
909   disorders. The failure to confirm our previous finding of a correlation with depressive
910   symptoms might be due to a restricted range of scores in the present sample.

911   In summary, it is tremendously difficult to plan optimally in complex
912   problems; heuristics are frequently mandatory. We confirmed the pervasive
913   influence of one such shortcut, aversive pruning, over goal-directed behaviour,
914   distinguishing its impact from those of other decision-making biases. Our
915   neuroimaging results revealed that aversive pruning recruits neural structures
916   implicated in decision-making and mood disorders, specifically the SGC. DLPFC and
917   insula responses to large losses and anxiety levels, an established risk factor for
918   mood disorders, were related to the degree of aversive pruning across participants.
919   Taken together, our results suggest a novel circuit in which emotionally salient
920   information is used to facilitate decision-making, albeit only approximating
921   optimality. Activation of this circuit could prevent optimal decision-making during
922   planning and may contribute to psychopathological conditions characterized by
923   aberrant decision-making.

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934

935 **Author Contributions**

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937 Q.J.M.H.; Data collection, N.L., and P.F.; Writing – Original Draft, J.P.R., N.L., N.E., P.D., P.F.,
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940

941 **Competing Interests**

942 The authors declare that no competing interests exist.

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1056 **Figure 1**. Aversive pruning example and fMRI task design. **(A)** Decision tree and
1057 monetary outcomes up to a depth of three, from starting state 2. Purple and
1058 orange coloured lines indicate pressing the left and right buttons, respectively.
1059 The totals earned for the two best paths (thicker lines; breaking even and losing
1060 20 pence) are shown in blue and red. **(B)** An example of disadvantageous
1061 aversive pruning. The red line shows the curtailment of search within the
1062 decision tree upon encountering a large monetary loss (-70p), such that the
1063 more advantageous break-even sequence is not considered. **(C)** Button presses
1064 and transitions within the maze. **(D)** Monetary outcomes within the maze. **(E)**
1065 Free plan trial. Beginning in a selected white box, participants had 9 seconds to
1066 plan a sequence of moves (3-5; indicated centrally) to maximise income. Plusses
1067 and minuses below each box indicate the potential outcomes possible from
1068 moving from there, but are not indicative of directionality. Coloured sidebar
1069 arrows were included to match visual input with restricted plan trials. **(F)**
1070 Restricted plan trial. Participants had 9 seconds to decide between two maze
1071 routes (green and blue), one of which provided higher net income. **(G)** For
1072 restricted plan trials, the selection of either the blue or green route involved
1073 choosing either the left or right button. **(H)** After entering their moves or path
1074 selection, participants were shown their selected path with the corresponding
1075 monetary outcome for each box-to-box transition for both free and restricted
1076 plan trials. Summed path totals were not shown.

1077 **Figure 2**. Initial model-free and model-based computational model comparison and
1078 parameter estimates for behaviour analysis. **(A)** Percentage of trials on which the
1079 correct sequence was chosen, split by whether it did not include a large loss (green:
1080 optimal no large loss; ONLL) or did (blue: optimal large loss; OLL). Black dots
1081 represent individual performance and grey lines connect the two trial types. **(B)**
1082 ONLL and OLL performance split by decision depth. **(C)** Average likelihood of
1083 participants' choices. Chance model performance level is shown by the black dashed
1084 line; "Lookahead" represents optimal planning; "Discount" incorporates random
1085 stopping of the tree search; "Pruning" additionally incorporates a specific chance of
1086 stopping when a large loss (-70p) is encountered; and "Pruning+Loss" additionally
1087 incorporates individual reinforcement value sensitivities to account for loss aversion.
1088 **(D)** Proportion of variance explained by the different models. **(E)** Model evidence
1089 measured by group-level iBIC; red star indicates the best performing (i.e. lower iBIC)
1090 model. **(F)** Pruning parameters (values indicate the probability of continuing to
1091 evaluate the decision tree). Black dots in F show individual data (parameters taken
1092 from the Pruning+Loss model), connected by black dashed lines. **(G)** Reinforcement
1093 sensitivity parameter estimates. **(H)** Relationship between the trial-based measure
1094 of general planning ability, optimal no large loss (ONLL), and its computational
1095 equivalent, γ_G. **(I)** Relationship between the trial-based measure of aversive pruning
1096 (ONLL minus optimal large loss (OLL)) and its computational equivalent, the
1097 difference between γ_G and γ_S. **(J)** Comparison of ONLL and OLL correct between the
1098 observed data and data generated from our winning model. **(K)** Observed and
1099 generated data for each individual subject plotted for ONLL and OLL correct trials.
1100 **(L)** The fraction of times the winning model gave the highest probability to the
1101 action chosen by the subject; red line shows chance level. Red and green error bars
1102 indicate one standard error and 95% confidence intervals of the mean, respectively.

1103   **Figure 3**. Neural responses during aversive pruning: model-based fMRI results.
1104   **(A)** Kullback-Leibler (KL) divergence value increased linearly with depth, and, **(B**)
1105   based on participant behaviour, was highest on trials classified as aversive
1106   pruning trials. **(C)** Activation in pregenual and subgenual cingulate (SGC) cortex
1107   increased linearly with KL divergence value. **(D)** There was an interaction
1108   between KL divergence value and difficulty in the SGC, with greater impact of
1109   the former on more difficult trials. Overlays are presented at a threshold of $P <$
1110   0.005 (uncorrected). Error bars represent one standard error of the mean and
1111   colour bars indicate t-values.

Figure 4. Neural responses to increasing difficulty and value and relationship between aversive pruning and loss receipt at outcome. **(A)** Bilaterally, cerebellum (left panel), motor cortex (left panel), dorsal striatum (middle panel), and dorsolateral prefrontal cortex (right panel) activation increased linearly with task difficulty during the planning phase. Overlays are presented at a threshold of $P_{WB} < 0.05$. **(B)** Ventral striatum (VS; left panel) and medial orbitofrontal cortex (mOFC, middle panel) activation increased linearly with the net monetary value during the outcome phase. Overlays are presented at a threshold of $P < 0.005$ (uncorrected) but VS and mOFC results survive voxel-level $P_{WB} < 0.05$. Peak voxel mOFC activation to increasing reward (B, right panel) correlated with the sensitivity to large rewards (+140p) parameter derived from our computational model. **(C)** Contrasting feedback on the correct trial types (OLL vs ONLL correct) revealed responses in the right insula (C, left panel), and right dorsolateral prefrontal cortex (DLPFC; C, left panel). Response in the insula was driven by increased activation during OLL correct outcomes (C, middle panel). The difference in insula activation between OLL and ONLL correct trials at outcome correlated with γ_G-γ_S, our computationally-derived measure of overall aversive pruning (C, right panel). Overlays are presented at a threshold of $P < 0.005$ (uncorrected). Error bars represent one standard error of the mean and colour bars indicate t-values.
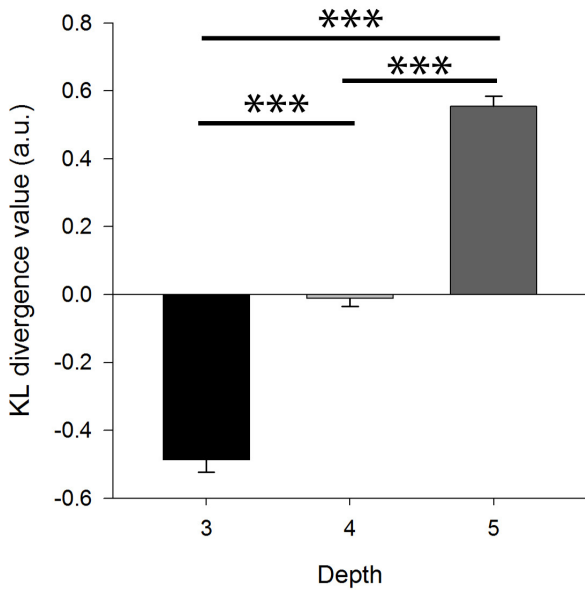
1129   **Figure 5**. Confirmatory trial-based behavioural and fMRI results. **(A)** Decision
1130   tree showing path selection starting from state 2 with 3 moves to go; line width
1131   is proportional to selection frequency. The optimal route (break-even, blue) and
1132   the sub-optimal aversive pruning route (net income -20p, red) were selected
1133   with similar frequency. **(B)** Aversive pruning percentage [aversive
1134   pruning/(aversive pruning+OLL error)*100], split by depth. **(C)** Mean trial
1135   earnings across the four conditions. The light red bar behind aversive pruning
1136   depicts the possible earnings if participants had performed optimally on the
1137   trials classified as aversive pruning. OLL error represents incorrect choices on
1138   OLL trials that could not be classified as aversive pruning. **(D)** Reaction times for
1139   the first button press across trial types. **(E)** Difficulty-related response in the
1140   subgenual cingulate (SGC: left panel) contrasting aversive pruning trials against
1141   optimal large loss (OLL) correct trials. Overlay is presented at a threshold of $P <$
1142   0.005 (uncorrected). The finding in the SGC was driven by a negative
1143   modulation by difficulty for OLL correct trials ($P = 0.001$), with no significant
1144   effect of difficulty on aversive pruning trials ($P = 0.285$, right panel). Error bars
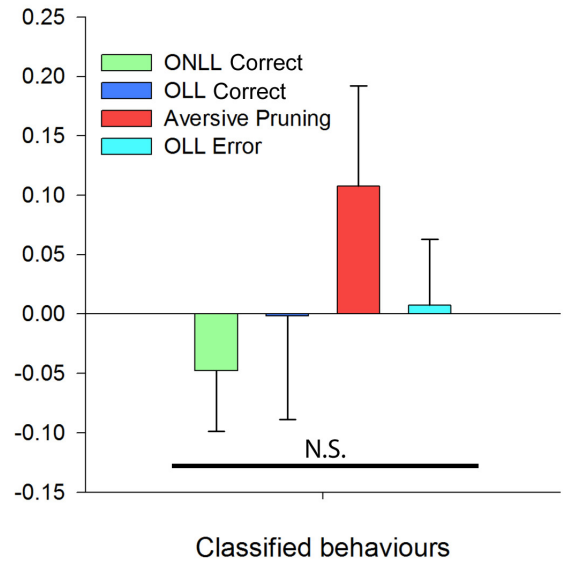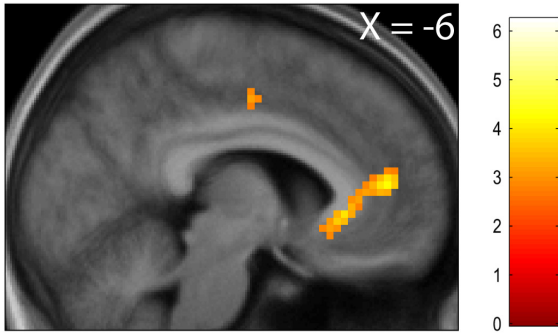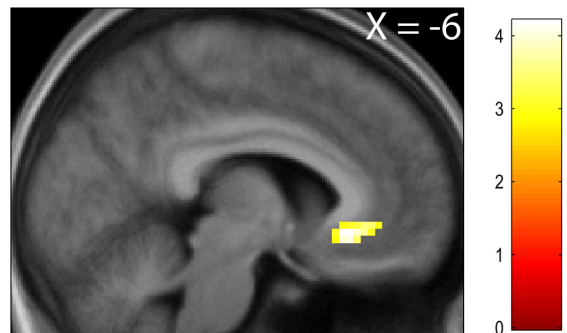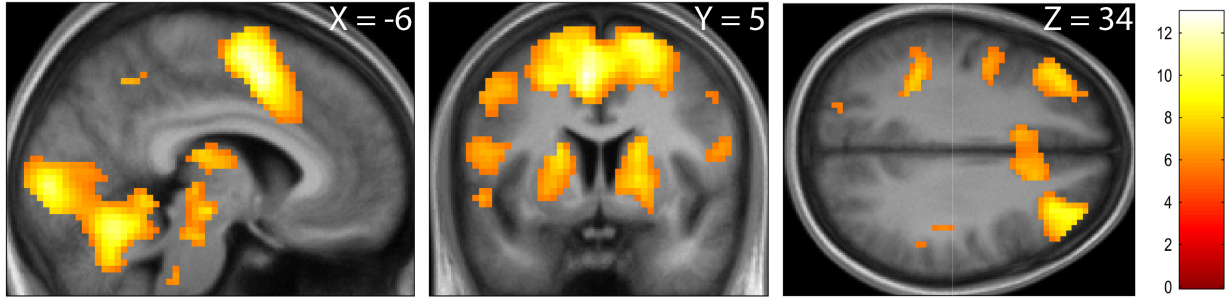1145   represent one standard error of the mean and the colour bar indicates t-values.

A

Current choice

Next choice

Two choices ahead

Totals: -110 -70 -120 **0** -60 **-20** -110 -70

B

Aversive
Pruning

-110 -70 -120 0 -60 **-20** -110 -70

C

D

E

3 moves
9

F

3 moves
9

G

H

A

State

L
R

Totals: -110 -70 -120 0 -60 -20 -110 -70

B

% correct (from remaining)

Aversive Pruning

N.S.

Depth

C

Mean money per trial (pence)

ONLL Correct
OLL Correct
Aversive Pruning
OLL Error

*

Classified behaviours

D

RT from enter choice onset time (ms)

***
*
**

E

X = -3

SGC parameter estimates (beta)

*

Classified behaviours