Supplemental Discussion

*A comparison of parameter selection for the biophysical decision model*

In addition to the comparison with other classes of decision model, we also explored the effects of variations in model parameters on the qualitative predictions made by the model. Specifically, we varied the synaptic constant $J_{A,i}$ which controls the degree to which self excitation dominates in the biophysical decision model; variation in this parameter drove the cross-subject predictions mentioned in the above section. Three different instantiations of the model (low, $J_{A,i}=0.3243$; medium, $J_{A,i}=0.3436$; high, $J_{A,i}=0.3629$) produced broadly similar results in terms of the key qualitative prediction of a transition from overall value to value difference effects, even though the speed and accuracy of the network responses varied across these instantiations (supplementary figures S1-S3). This suggests that the model predictions were robust to variation in the degree of recurrent excitation. Notably, although all three models varied with respect to the precise location of the value difference and overall value peak, they nevertheless concurred that the overall value effect should be seen earlier in time and at a higher frequency than value difference (supplementary table S1). This was also true in the data from pSPL and VMPFC (supplementary table S1). The variation in the lower part of panel c from figures S1-S3 also explains the cross-subject effect of median reaction time on value difference (see ‘speed-accuracy tradeoff in the parietal cortex’, above). Finally, we also found that these
qualitative predictions held when other model parameters were adjusted, such as the scaling constant $k_{dec}$ (data not shown).

**Speed-accuracy tradeoff in the parietal cortex**

In addition to the analysis presented in figure 1, which focuses on the predictions made by a single implementation of the biophysical network model, we also investigated variation in network behaviour caused by manipulating a few key model parameters. By varying the strength of recurrent excitation in the network model, we found that networks with stronger recurrent excitation were faster in making decisions but typically made more mistakes\(^1\), giving rise to a speed-accuracy tradeoff (fig S6). We assumed that such a mechanism might account for cross-subject variability in task performance. Behaviourally, we found that in our subjects there was indeed a cross-subject speed-accuracy tradeoff: subjects who on average would choose the option with the higher subjective expected value more often would also have longer average RTs ($R=0.5756, p<0.001$; fig S7A).

We used this variation to generate model predictions that relate to how network activity might vary across subjects. To do this, we took the parameter estimates from the first-level regression of value difference for each of the different network model instantiations, and regressed these parameter estimates onto the models’ median RTs. This is equivalent to performing a higher-level analysis (as is frequently performed on neuroimaging data), looking for cross-subject variation in the expression of a particular response. Here, instead, using the biophysical model, we are looking for cross-network variation in the expression of a response, elicited by varying the degree of recurrent
excitation within the network. The dependent variable is the circuit’s sensitivity to value difference, and the independent variable is the network’s median RT. The analysis yielded the prediction that networks with a higher median RT had first a weaker correlate of value difference (blue area in fig S6B), and then a stronger one (red area in fig S6B), at these relatively low frequencies. (This is equivalent to saying that the effect of value difference is later to emerge in network models that exhibit slower temporal dynamics.)

We tested the same cross-subject predictions in source-reconstructed MEG data. We found that in the pSPL, subjects with a longer median reaction time had a more negative correlate of value difference initially, followed by a more positive one (fig S7B), matching predictions elicited by varying the degree of self-excitation relative to inhibition within the model’s selective neuronal pools (cf. fig S6B). We did not find a similar effect in VMPFC. However, the same caveats with regards to signal to noise ratio in VMPFC relative to pSPL, expressed in the main paper, also apply to this analysis.

Importantly, such a signal could not be explained by a simpler model in which non-decision time varied across subjects (rather than recurrent excitation), as this would predict a similar effect on the overall value signal, which was not observed (data not shown). Also, it is important to note that such a mechanism depends upon long-lasting variation in the strength of synaptic weights across models, and so might complement (rather than contradict) neural mechanisms recently proposed for more rapid adjustment of speed versus accuracy in perceptual decision tasks².³.
A comparison of different decision models

It is important to note that the main objective of the present study was not to make specific claims about the accuracy (or otherwise) of the biophysical decision model, but was instead to use a whole-brain imaging technique to compare predictions from this model with activity recorded from across the entire cortex, and infer which cortical regions were involved in value comparison. It was not our intention to perform a strong ‘model comparison’ to infer that the biophysical decision model was better at explaining cortical activity than other decision models.

Nevertheless, alternative models are commonly used to explain neural activity in other studies, so it is interesting to see which of the predictions from the biophysical decision model are present in other classes of decision model, particularly as they have been shown to be closely related in terms of behavioural predictions\(^4\). We considered three other classes of decision model, using the simplified descriptions taken from \(^4\). These were:

(i) the drift diffusion model (DDM) (where the difference in subjective value determined the drift rate of the decision particle)\(^5\);

(ii) a race model, in which two (non-competing) units accumulate information for each alternative (where the subjective value of each option determined the rate of accumulation for each unit)\(^6\);

(iii) a feedforward inhibition model, in which value-related inputs both excite the selective unit and inhibit the non-selective unit\(^7\).

Results from this analysis are presented in fig S13. We found that the simple DDM made starkly different predictions to the biophysical decision
model, in that it predicted only an effect of value difference on neural activity and reaction times, and no effect of overall value (fig S13B). This is, in many ways, to be expected, as the two values are subtracted before being used to determine the drift rate in the DDM, so the model has no information about the overall value of the trial. Similar predictions were made by an extended DDM (although we did not consider whether alternative DDMs, such as those containing a time-varying urgency signal, would make different predictions).

By contrast with the DDM, the race model made the opposite prediction: a strong effect of overall value on neural activity, but no effect of value difference (fig S13C). A similar set of predictions were made by the feedforward inhibition model (fig S13D). Thus, the temporal dynamics shown by the biophysical decision model appear to be unique in exhibiting a transition from an overall value signal to value difference. Such predictions may also generalize to other models of mutual inhibition, but we did not test these predictions here.

We make this claim with a few caveats. We did not exhaustively test the entire parameter space of the models presented in fig S13 (instead we selected parameters that provided a reasonable fit to our behavioural data), nor did we considered more sophisticated variants of these models, of which there are many examples in the literature. We also assigned the same noise structure to data prior to the decision and after reaching the decision bound, so that the measured signal was related to decision-related activity rather than noise. An exhaustive test of variations of model parameters and model structures is beyond the scope of this paper. It is possible that further adaptations or variations of the DDM, race and feedforward inhibition models might be able to
make similar predictions to the biophysical decision model, but we leave this topic to future studies. Full MATLAB code for the simulations is available on request.
Supplementary Tables

*Supplementary table S1* Central frequency and time of signals relating to overall value and value difference, using three different instantiations of the biophysical decision model

<table>
<thead>
<tr>
<th>Degree of recurrent excitation</th>
<th>Central time/frequency (overall value)</th>
<th>Central time/frequency (value difference)</th>
</tr>
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<tbody>
<tr>
<td>Low ($J_{A,ii}=0.3243$)</td>
<td>740 ms/4.50 Hz</td>
<td>860 ms/3.25 Hz</td>
</tr>
<tr>
<td>Medium ($J_{A,ii}=0.3436$)</td>
<td>680 ms/5.00 Hz</td>
<td>780 ms/3.75 Hz</td>
</tr>
<tr>
<td>High ($J_{A,ii}=0.3629$)</td>
<td>640 ms/5.75 Hz</td>
<td>740 ms/4.50 Hz</td>
</tr>
<tr>
<td>Data (pSPL)</td>
<td>600 ms/5.50 Hz</td>
<td>690 ms/4.25 Hz</td>
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<tr>
<td>Data (VMPFC)</td>
<td>570 ms/5.75 Hz</td>
<td>610 ms/5.50 Hz</td>
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### Supplementary table S2 Parameter fits for Prospect theory parameters

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<tr>
<th>Subject</th>
<th>$\gamma$</th>
<th>$\alpha$</th>
<th>$\tau$</th>
<th>Log likelihood (subjective)</th>
<th>Log likelihood (objective)</th>
<th>BIC (subjective)</th>
<th>BIC (objective)</th>
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<td>191.2</td>
<td>208.6</td>
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<tr>
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<td>-115.3</td>
<td>224.8</td>
<td>235.9</td>
</tr>
</tbody>
</table>

Parameters $\gamma$, $\alpha$ and $\tau$ refer to probability weighting, utility and temperature parameters respectively in Prospect theory model; log likelihood is compared between this model and an 'objective value' model with only one free parameter (softmax temperature); Bayesian Information Criteria (BIC – lower numbers indicate better fit), which compare models whilst penalizing those with higher numbers of free parameters, showed a strong preference for the subjective model over the objective model (paired T(58)=3.79, p<0.0005).
**Supplementary table S3** Prospect theory parameters and log reaction times, split between first and second halves of experiment.

<table>
<thead>
<tr>
<th>Parameter</th>
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<th>Half 2</th>
<th>Paired T(58)</th>
<th>p value</th>
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<tr>
<td>$\gamma$</td>
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<td>0.74+/-0.08</td>
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<td>0.2280 (n.s.)</td>
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<td>$\alpha$</td>
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<td>0.42+/-0.05</td>
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<tr>
<td>$\tau$</td>
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<td>0.24+/-0.05</td>
<td>1.43</td>
<td>0.1593 (n.s.)</td>
</tr>
<tr>
<td>LogRT(ms)</td>
<td>7.27+/-0.04</td>
<td>7.07+/-0.04</td>
<td>3.53</td>
<td>0.0008 (**)</td>
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</tbody>
</table>

Whilst there is a highly significant decrease in reaction times in the second half of the task, there is no significant change in behavioral parameters describing choice parameters.
Supplementary Movies

**Supplementary movie S1** shows the temporal evolution of stimulus-locked activity, showing the main effect of task performance (2-10Hz activity) relative to a pre-stimulus baseline. Snapshots are presented in main figure 3 A/B.

**Supplementary movie S2** shows the temporal evolution of response-locked activity, showing the main effect of task performance (2-10Hz activity) relative to a post-response baseline. Snapshots are presented in main figure 3 C-F.
Supplementary Figures

Figure S1. Main figure 1, with low degree of recurrent excitability ($J_{Aii}=0.3243$). Layout is as per main figure 1. The observed transition from overall difference to value difference signaling is still present in this model, and the central frequency/time for the two effects differs (see supplemental table S1).
Figure S2. Main figure 1, with medium degree of recurrent excitability ($J_{\text{hi}}=0.3436$). Layout is as per main figure 1. The observed transition from overall difference to value difference signaling is still present in this model, and the central frequency/time for the two effects differs (see supplemental table S1).
Figure S3. Main figure 1, with high degree of recurrent excitability ($J_{el}=0.3629$). Layout is as per main figure 1. The observed transition from overall difference to value difference signaling is still present in this model, and the central frequency/time for the two effects differs (see supplemental table S1).
Figure S4. Prospect theory function fits for individual subjects. (A) Probability weighting function, converting objective probability $p_o$ to subjective weighting $w(p_o)$. (B) Expected utility function, converting objective reward magnitude $r_o$ to subjective expected utility $v(r_o)$. Parameter fits are given in table S2.
**Figure S5.** Results of a linear regression on reaction time, in which subjective values were orthogonalized with respect to objective values, allowing separate interrogation of the effects of the linear and non-linear components of the subjective value function on reaction time. There is an additional effect of the non-linear component of value difference (although no significant effect of the non-linear component of overall value). Additional co-regressors included whether subject chose left or right, the linear effect of trial number, a term accounting for autocorrelation (RT on previous trial), and the effect of ‘no brainer’ trials. Bars show mean +/- s.e. across subjects. ** denotes *p*<0.005; *** denotes *p*<0.0005.
**Figure S6. Cross-subject effect in biophysical model.** (A) Median reaction time and mean accuracy (probability of choosing higher valued option) in 30 different instantiations of the biophysical model, obtained by varying the degree of recurrent excitation in selective neuronal populations (i.e. varying $J_{A,II}$ in the biophysical model). A speed-accuracy tradeoff is obtained. (B) ‘Cross-subject’ regression of median reaction time on value difference, derived from biophysical model; the plot reflects the result of a first level regression of value difference onto network activity, and then submitting the parameter estimates from this regression to a second-level regression with model median RT as the independent variable. Color indicates group Z-statistic. (C) Effect from figure S6B, collapsed across frequencies from 3-10Hz.
**Figure S7.** Cross-subject effect in parietal cortex (MNI 18, -44, 62mm). (A) Behavioural cross-subject speed accuracy tradeoff ($R=0.5756$, $p<0.001$); (B) Cross-subject effect of reaction time on value difference time-frequency spectrum, analysis equivalent to figure S6B. Color indicates group Z-statistic. (C) Effect from figure S7B, collapsed across frequencies from 3-10 Hz; equivalent to figure S6C.
Figure S8. Effect of task performance, stimulus-locked, on activity in 2-10Hz range in VMPFC (relative to -300ms to -100ms pre-stimulus baseline). Trials are subdivided into first, second, third and fourth quarters of the experiment. A steady decrease in the recruitment of VMPFC through the experiment can be seen.
Figure S9. Contrast of value difference and overall value activity between first and second halves of experiment in VMPFC. In the main paper (figure 4E-F), we report similarities between the model and data recorded from VMPFC during the first half of the experiment. Here, we show a direct contrast for overall value (blue) and value difference (green), collapsed across relevant frequencies, for 1st half>2nd half experiment. We found that value difference, but not overall value, was significantly stronger in VMPFC during the 1st half than during the 2nd half of the experiment ($p<0.05$, permutation test).
**Figure S10.** Lateral IPS correlates with value difference more strongly in second half of experiment. (A) Results from a whole brain analysis looking for brain regions coding value difference more strongly in the second half of the experiment than the first half. Cross-section at MNI $z=58$mm, $t=725$ms post-stimulus onset. Thresholded at $T(29)>2.3$ (peak $T(29)=3.79$ (675 ms post stimulus), MNI $(50,-46,48)$ (left); $T(29)=2.69$ (750ms post stimulus), MNI $(-50,-38,56)$ (right)). (B) Time-frequency effect of value difference in left IPS peak in first half of experiment; color indicates group Z-statistic. (C) Time frequency effect of value difference at same location in second half of experiment.
Figure S11. Lateral IPS main effect responses are stable throughout experiment. Responses are from left lateral IPS peak presented in figure S10. (A) Main effect of task performance relative to pre-stimulus baseline. Top panel=first half of trials; bottom panel=second half of trials. (B) Main effect of task performance relative to pre-stimulus baseline. Top panel=harder trials; bottom panel=’no brainer’ trials. Color indicates group Z-statistic.
Figure S12. Value-related and reaction-time dependent signals in other cortical regions. Value correlates can be seen elsewhere, but do not match with predictions from the biophysical model. Time frequency spectra show group Z-statistics for effects of overall value (left), value difference (middle) and reaction time (right) on cortical activity in 2-10 Hz range, estimated using multiple regression. (A) Right premotor cortex, MNI (38, -2, 64 mm) – shows a correlate of overall value, but no difference signal; (B) right inferior frontal sulcus, MNI (50, 10, 30 mm) – shows a correlate of overall value, but no difference signal; (C) left sensorimotor cortex, MNI (-50, -28, 58 mm) shows a correlate of value difference, but this signal is noticeably at the same time as a corresponding negative correlate of reaction time, suggestive of a role in response execution; (D) left primary visual cortex, MNI (-12, -94, -2 mm) – shows a weak correlate of value difference, but a stronger positive correlate of correlate of reaction time, suggestive of increased attentional demands on trials of longer duration.
**Figure S13. Comparison of different decision models.** Left column: Effect of value difference (VD) and overall value (OV) on reaction times for each model, estimated using linear regression. Y-axis is flipped, so positive values equate to a negative effect on reaction time. See main figure 1B. Middle column: Effect of overall value (top panel for each model) and value difference (bottom panel for each model) on time-frequency decomposed model data. See main figure 1C. Right column: Model details. For further details of model parameters, see (Bogacz et al., 2006). In each case, x is the variable submitted to time-frequency decomposition and linear regression; cdW is white noise, normally distributed with mean 0 and variance $c^2dt$. $v_1$ and $v_2$ are values of options 1 and 2. (A) Biophysical model, as used in main paper; (B) Simple drift diffusion model; (C) Race model; (D) Feedforward inhibition model.


