

1 SUPPLEMENTARY MATERIALS

2

3 **Supplementary Note 1: Choice of circuit elements.** Using a reductionist approach, we selected
4 circuit elements *crucial to the regulation of dopamine by dorsomedial striosomes*. Thus, we
5 prioritized the direct connection between striosomes and daSNC and the regulation of daSNC via
6 GPe and GPI→LHb→RMTg.

7 Notably, we exclude from our model the substantia nigra reticula (SNr), another basal ganglia
8 region that receives projections from the striosomes^{24,95} and the subthalamic nucleus⁹⁶ and feeds
9 back to daSNC neurons⁹⁷, forming an additional secondary striosome→daSNC connection. In the
10 context of our model, sSPN→SNr→daSNC helps to determine *how many* decision-dimensions
11 are included in the parallel direct and indirect pathway decision-spaces, in conjunction with the
12 modeled operation assigned to the GPI→LHb→RMTg pathway. The connection through SNr, by
13 introducing a striosome→SNr→daSNC→striosome loop, would add an additional set of dynamics
14 on a longer time scale than the modeled striosome→daSNC→striosome loop. The analysis using
15 **Instance 1** of the model (full connectivity, no dynamics), however, would remain similar, with
16 similar selective effects of striosomes, GPI, LHb, RMTg, and daSNC on the decision-space and
17 choice.

18 Other regions that might be included in a future expanded model are the central nucleus of the
19 amygdala, the paraventricular thalamic nucleus, the rhomboid, and the paratenial thalamic
20 nucleus, each of which provides input to the striosomes more so than matrix^{70,98–101}. In the context
21 of our model, these connections would help to influence *which* decision-dimensions are included
22 in decision-space, in conjunction with cortical neurons, FSIs, sSPNs, and daSNC neurons.

23 More broadly, our model does not include certain brain regions that are relevant to decision-
24 making such as the dorsolateral striatum, ventral striatum, dopaminergic neurons in the ventral
25 tegmental area (VTA), subthalamic nucleus, and other basal ganglia regions. There are also brain
26 regions outside the basal ganglia that are implicated in decision-making¹⁰² that we do not
27 consider.

28 We did not consider neuronal molecular heterogeneity or gene expression.

29

30 **Supplementary Note 2: Choice of cortical inputs to the striatum.** We focus on the processing
31 of information by the striatum rather than the specific information encoded by each region of the
32 cortex. This allows us to retain focus on the processing of information by the striatum. Additionally,
33 our model assumes that cortical inputs are roughly similar between the striosomes and matrix.
34 This assumption allows us to assign the same decision-dimensions to striosome subpopulations
35 as to matrix subpopulations. As shown in **Table 2**, in reality, several striatum-projecting cortical
36 regions have been found to project more strongly to either striosomes or matrix^{2,67,69}, although the
37 experimental data on many of these regions is mixed⁷⁰. However, we suggest that there are
38 somewhat similar representations of decision-dimensions in sSPNs and mSPNs.
39 Computationally, as shown in **Extended Data Fig. 4**, average population activities can
40 successfully encode information mapped to the principal components of cortical activity even
41 when cortex→SPN connectivity is sparse and different cortical neurons project to each SPN. So,
42 provided that the cortical information encoded in striosome- and matrix-projecting regions is

43 somewhat similar, the decision-dimensions formed by the population should, on average, be
44 similar. To speculate on the function role of the different connectivity, it could be that the regions
45 that are more mSPNs-projecting relay more detailed representations of information, while the
46 regions that are more sSPNs-projecting relay information about how many decision-dimensions
47 to use (a similar effect to the b_{sSPN} term in eq. (1)). This hypothesis might align with functional
48 differences in the regions that project mostly to striosomes versus matrix. For instance, the
49 prefrontal cortex, associated with complex cognitive function, projects mostly to striosomes and
50 inhibits striosomes during conflict¹¹, perhaps suggesting a functional role in increasing the
51 dimensionality of the decision-space based on internal representations of task difficulty. Similarly,
52 the orbitofrontal cortex, associated with high-level decision-making schema¹⁰³ and hyperactive
53 during anxiety, projects mostly to striosomes and may communicate contextual information
54 related to the decision.

55

56 **Supplementary Note 3: Modulation of SPNs by dopamine during the decision to form**
57 **decision-space.** We make several hypotheses about dopamine in order to form our model. First,
58 we hypothesize that dopamine plays a role in modulating SPN activity during decision-making.
59 This follows based on the existing work linking dopamine to second-by-second modulation of SPN
60 firing¹⁰⁴ including work that demonstrates an opposite effect in striosome versus matrix²⁰. A recent
61 experiment demonstrated that midbrain dopamine neurons selectively modulate a subpopulation
62 of SPNs⁸⁹, perhaps corresponding to a decision-dimension (see **Table 7**). Second, we
63 hypothesize that this modulatory effect occurs variably over time and is most pronounced when
64 new important cues appear. This aligns with the literature on RPE¹⁰⁵. Third, we hypothesize that
65 dopamine modulation should only occur in complex tasks (that require one or more decision-
66 dimension), compatible with evidence that suggests minimal effect of dopamine release on SPNs
67 in simple tasks⁸⁹. Fourth, we hypothesize that dopamine plays an important role in largescale
68 sSPN modulation of mSPN compared to including collaterals, interneurons (choline
69 acetyltransferase interneurons, somatostatin expressing interneurons, and parvalbumin-positive
70 interneurons cross compartment boundaries but likely have primarily local effects¹⁰⁶), or other
71 possible connections through other brain regions.

72

RESOURCE AVAILABILITY

73

74 **Lead Contact**

75 Further information and requests for resources and reagents should be directed to and will be
76 fulfilled by the lead contact, Alexander Friedman (afriedman@utep.edu)

77 **Materials availability**

78 Code used to construct, analyze, and test the model is deposited to
79 https://github.com/dirkbeck/DM_space_model.

80 Code used to analyze neural data from the Corticostriosomal Circuit Stress Experiment database
81 is deposited to https://github.com/dirkbeck/DM_space_model.

82 Data from the Corticostriosomal Circuit Stress Experiment data, prepared for use in the current
83 paper, is deposited to <https://doi.org/10.7910/DVN/SMKW0I>.

84 **Data and code availability**

- 85
- 86 • This paper analyzes existing, publicly available data. These accession numbers for the
87 datasets are listed in the key resources table.
 - 88 • All original code has been deposited at https://github.com/dirkbeck/DM_space_model and
89 is publicly available as of the date of publication. DOIs are listed in the key resources table.
 - 90 • Any additional information required to reanalyze the data reported in this paper is available
from the lead contact upon request.

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92

93 **METHODS**

94

95 **Outline.**

- 96
- **Decision-dimensions and decision-space.** Explanation of the foundational concept of the model.
 - 97
 - 98 • **Analyzed instances of the model.** We conduct our analysis using three instances of the
 - 99 conceptual model. In the following sections, we formally define the model in each instance,
 - 100 then detail the methods behind our related analyses.
 - 101
 - **Instance 1: full connectivity and feedforward.** Related to **Figs. 1-3,5, Extended**
 - 102 **Data Figs. 1-3,7.** Used to link neural activity, the decision-space, and choice.
 - 103
 - **Modeled Circuit Manipulation using Instance 1.**
 - 104
 - **Instance 2: sparse connectivity and feedforward.** Related to **Extended Data**
 - 105 **Fig. 4.** Used to demonstrate how a large network might encode the decision-
 - 106 space.
 - 107
 - **Modeling SPN encoding of data, using Instance 2.**
 - 108
 - **Instance 3: full connectivity and dynamics.** Related to **Fig. 4, Extended Data**
 - 109 **Fig. 6.** Used to demonstrate how the decision-space might form over time.
 - 110
 - **Modeling time-variant input, using Instance 3.**
 - 111 • **Movement of Circuit Activity Across Multiple Trials.** An extension of the model to view
 - 112 possible changes of the circuit between trials in the context of decision-space. Related to
 - 113 **Fig. 6, Extended Data Fig. 8.**
 - 114 • **Rationale for the computational framework.** Reasoning behind our modeling
 - 115 strategies.
 - 116 • **Inferring decision-space from SPN activity and choice.** A method we designed in
 - 117 which decision-space can be inferred from experimental data. Related to **Extended Data**
 - 118 **Figs. 1q,r.**
 - 119 • **Testing the Model Through Analysis of Neural Data.** Analysis of neural data which
 - 120 supports our model. Related to **Figs. 2e,f, Extended Data Figs. 2a-n, 3a-p.**

121

122 **Decision-dimensions and decision-space.**

123 The physiologies of the circuit elements produce two abstractions which we use, for convenience,

124 throughout our work:

- 125
- A *decision-dimension* is an axis of the coordinate system with which SPNs (dsSPNs,

126 isSPNs, dmSPNs, imSPNs; see **Table 1** for anatomical definitions) encode data projected

127 from the cortex. A decision-dimension is equivalent to a principal component of cortical

128 activity. In our analysis, separate groups of SPNs encode data along the first, second,

129 third, and fourth principal components. (Arbitrarily, we do not consider principal

130 components beyond the first four). Each of the dsSPN/isSPN/dmSPN/imSPN subgroups

131 have neurons corresponding to each of the four principal components.

 - The *decision-space* is the mathematical space formed by mSPNs (both dmSPNs and

132 imSPNs) after dopamine signaling from daSNC. Modeled dopamine signaling determines

133 whether to include or exclude neurons encoding each decision-dimension during a

134 decision. Thus, from the mathematical space formed by all decision-dimensions, a

135

136 mathematical subspace (i.e. the “decision-space”) is formed with which to define action
137 values.

138 We use the prefix “decision” because the circuit uses decision-space, formed from a basis of
139 decision-dimensions, to define action values during decision-making.

140

141 ***Analyzed Instances of the Model.***

142 The general case of the model (although not formally used for analysis) is a dynamic network of
143 cortical neurons, FSIs, dsSPNs, isSPNs, GPi, LHb, daSNCs, dmSPNs, imSPNs, and mSPN-
144 projecting neurons which encode action values.

145 We conduct our analyses using three instances of this general case, which are each equivalent
146 to the general case under the specific conditions we outline. The three instances, tailored to our
147 various analyses, each allow for a different mathematical simplification. This allows us to
148 conceptually and formally define the instances individually in a way that is intuitive and relates
149 directly to our analyses.

- 150 1) Instance 1 has full cortex→FSI→SPN connectivity and constant activity in each circuit
151 element throughout the decision. In this instance, the model can be defined equivalently
152 using a smaller set of network elements and a feedforward network. See ***Instance 1: full***
153 ***connectivity and feedforward.***
- 154 2) Instance 2 has constant activity in each circuit element throughout the decision. In this
155 instance, the model can be defined equivalently using a feedforward network. See
156 ***Instance 2: sparse connectivity and feedforward.***
- 157 3) Instance 3 has full cortex→FSI→SPN connectivity. In this instance, the model can be
158 defined equivalently using a smaller set of network elements. See ***Instance 3: full***
159 ***connectivity and dynamics.***

160

161 ***Instance 1: full connectivity and feedforward.***

162 In this section, we describe the instance of the model where each cortical neuron projects to each
163 FSI, each FSI projects to each SPN (for dsSPN, isSPN, dmSPN, imSPN), and each cortical
164 neuron projects to each SPN. Additionally, cortical input to the system does not change over time,
165 and the activities of other circuit elements do not decay over time.

166 This instance of the model leads to a convenient formation of the model as a circuit of fewer
167 elements (one FSI, one dsSPN, isSPN, dmSPN, and imSPN per the four decision-dimensions),
168 and no time component. In this section, we frame this instance mathematically and then describe
169 our related analysis.

170

171 **Input: cortical activity.**

172 During a decision, a vector of cortical input $\mathbf{x}_P \in \mathbb{R}^{p \times 1}$ enters each pathway P in the network (
 173 $\mathbf{x}_{\text{direct}}$ to direct pathway SPNs and $\mathbf{x}_{\text{indirect}}$ to indirect pathway SPNs). The elements of \mathbf{x}_P are the
 174 activities of p cortical neurons. Each neuron encodes a different sensory input.

175

176 **Outputs.**

177 We use this instance of the model to examine: 1) the activities of the circuit elements depending
 178 on the activities of other circuit elements (**Fig. 1, Extended Data Figs. 1a-i**); 2) the modulation of
 179 mSPNs by dopamine (i.e. decision-space, **Figs. 1a,b**); 3) action values given decision-space
 180 (**Extended Data Figs. 1j-l**), and 4) choice given action values (**Extended Data Figs. 1m-p**).

- 181 1) The activities of circuit elements during a decision are related to each other based on
 182 anatomically realistic connections (eqs. (1),(2),(3),(5),(23)).
- 183 2) A decision-space is formed probabilistically. The probability a given decision-dimension i
 184 being used during a decision is equivalent to the activity of daSNC (see eq. (2)), which
 185 ranges from 0 to 1. Probabilities are realized in the connection from daSNC to mSPN (see
 186 eq. (3)), when each decision-dimension is probabilistically assigned a weight (in most
 187 analyses, either 0 or 1). Decision-space is defined as the space formed from the basis of
 188 decision-dimensions that were not assigned a weight of 0.
- 189 3) Action value is derived based on mSPN activity during a decision.
- 190 4) Choice is derived from action values. Action values are treated as Merton processes¹⁰⁷
 191 using eq. (6). Several possible actions are assigned action values and the corresponding
 192 process that hits the threshold first is enacted.

193

194 **Defining FSI activity.**

195 FSI activity, c_P , is set to the magnitude of \mathbf{x}_P for each pathway, multiplied by a weight of
 196 cortex→FSI connection a_{FSI} plus an additive shift b_{FSI} :

197

$$198 \quad (23) \quad c_P = a_{\text{FSI}} \cdot \|\mathbf{x}_P\| + b_{\text{FSI}}$$

199

200 where:

- 201 • c_P is relative activities of FSIs that project to SPNs of pathway P (activity arb. u.)
- 202 • a_{FSI} is the weight of cortex→FSI connection. Similar for both P . (dimensionless)
- 203 • \mathbf{x}_P is the activities of cortical neurons that project to SPNs of pathway P . (activity arb. u.)
- 204 • b_{FSI} affects the relative activity of all sSPN neurons. Similar for both P . (activity arb. u.)

205 In the current instance of the model, there are 2 FSIs, one that receives input from $\mathbf{x}_{\text{direct}}$ and
 206 projects to dsSPNs and dmSPNs, and the other than receives input from $\mathbf{x}_{\text{indirect}}$ and projects to
 207 isSPNs and imSPNs.

208 For use in our analysis, see
 209 https://github.com/dirkbeck/DM_space_model/blob/main/algorithmic_model.m.

210

211 Defining sSPN activity.

212 To get the activities of sSPNs in each pathway, \mathbf{x}_P is normalized via division by c_P and multiplied
 213 by $\mathbf{W}_P \in \mathbb{R}^{p \times q}$, which linearly transforms and reduces cortical input from the p -dimensional
 214 coordinate space of cortex to the smaller q -dimensional coordinate space of sSPN. In the sSPN
 215 coordinate space, each coordinate is a principal component of a training set of historical cortical
 216 input across n time steps $\mathbf{X}_P \in \mathbb{R}^{n \times p}$ (uncorrelated, for simplicity). For each pathway, \mathbf{W}_P contains
 217 the truncated first q columns (corresponding to the first q principal components) of $\mathbf{W}_{\text{full}, P} \in \mathbb{R}^{p \times p}$
 218 after the decomposition $\mathbf{X}_P \mathbf{X}_P^T = \mathbf{W}_{\text{full}, P} \mathbf{\Lambda} \mathbf{W}_{\text{full}, P}^T$ is made to obtain the full principal component
 219 matrix. Experimental work has revealed dimensionality reduction the order of ~ 100 times from
 220 cortex to SPNs¹⁰⁸, so $q \ll p$. Note that in our analysis using the current instance of our model, \mathbf{X}_P
 221 is not explicitly generated because we specify the inputs to the system in terms of the coordinate
 222 space of decision-dimensions.

223 For each pathway, the components of an sSPN activity vector $\mathbf{s}_{\text{sSPN}, P} \in \mathbb{R}^{q \times 1}$ each correspond to
 224 the activity of an sSPN circuit element. A constant $b_{\text{sSPN}, P}$, used in analyses where modeled sSPN
 225 activity is stimulated or inhibited, adjusts overall sSPN activity:

226

$$227 \quad (1) \quad \mathbf{s}_{\text{sSPN}, P} = \frac{1}{c_P} \mathbf{W}_P^T \mathbf{x}_P + b_{\text{sSPN}, P} \quad (\text{copied from **Results** for convenience})$$

228

229 where:

- 230 • c_P is the relative activity of the FSI projecting to SPNs of pathway P (activity arb. u.)
- 231 • \mathbf{W}_P is a matrix of weights from cortical neurons to SPNs of pathway P . Each column is
 232 equivalent to a principal component of cortical activity. (dimensionless)
- 233 • \mathbf{x}_P is the activities of cortical neurons that project to SPNs of pathway P . (activity arb. u.)
- 234 • $b_{\text{sSPN}, P}$ affects the relative activity of all sSPN neurons (activity arb. u.)

235 In the current instance of the model, activities are defined based on a feedforward network, so
 236 the simplification is made that sSPN activities are not affected by daSNC activities.

237 In the current instance, there is one sSPN per decision-dimension per pathway. So, there are q
 238 dsSPNs and q isSPNs. The dsSPNs receive input from x_{direct} and c_{direct} . The isSPNs receive input
 239 from x_{indirect} and c_{indirect} .

240 For use in our analysis, see
 241 https://github.com/dirkbeck/DM_space_model/blob/main/algorithmic_model.m.

242

243 Defining GPI, LHb, and RMTg activities.

244 The GPI→LHb→RMTg→daSNC pathway performs a series of operations which influence RMTg
 245 activity RMTg, which is an input to daSNC activity in eq. (2). Weights $w_{\text{GPI},P} \in \mathbb{R}^{2q \times 1}$, not
 246 necessarily positive, are combined with the activities of the q dsSPNs and q isSPNs, forming
 247 scalar representations of dsSPN or isSPN activity. z_{GPI} , z_{LHb} , and z_{RMTg} terms reflecting the
 248 activities of those circuit elements are combined with this scalar representation:

249

$$250 \quad (5) \quad \text{RMTg} = z_{\text{RMTg}} + z_{\text{LHb}} + z_{\text{GPI}} \cdot w_{\text{GPI}} \cdot \begin{bmatrix} s_{\text{sSPN,direct}} \\ s_{\text{sSPN,indirect}} \end{bmatrix}$$

251 (copied from **Extended Data Fig. 1** for convenience)

252

253 where:

- 254 • z_{RMTg} is an additive shift that affects relative RMTg activity (activity arb. u.)
- 255 • z_{LHb} is an additive shift that affects relative LHb activity (activity arb. u.)
- 256 • z_{GPI} is a coefficient that affects relative GPI activity (activity arb. u.)
- 257 • w_{GPI} is the weights of connection from sSPNs of pathway P to the GPI neuron
 258 (dimensionless)
- 259 • $s_{\text{sSPN},P}$ is the activity of sSPNs corresponding to decision-dimension i and pathway P
 260 (activity arb. u.)

261 This pathway contains one GPI element, one LHb element, and one RMTg element, as visualized
 262 in **Fig. 1a**. All sSPN elements project to GPI. GPI activity is an input to LHb, which after the z_{LHb}
 263 addition, is an input to RMTg, which itself has a z_{RMTg} addition. For simplicity, these series of
 264 operations are presented together in eq. (5).

265 For use in our analysis, see
 266 https://github.com/dirkbeck/DM_space_model/blob/main/algorithmic_model.m.

267

268 **Defining daSNC activity.**

269 daSNC neurons incorporate the output of the GPI→LHb→RMTg→daSNC pathway with direct
270 inputs from sSPN elements. There are q sSPN elements of each pathway and q daSNC elements
271 corresponding to each pathway. For each pathway, the i th sSPN element connects to the i th
272 daSNC element, but not to other daSNC elements (see **Fig. 1a**). These connections have weights
273 $w_{\text{sSPN} \rightarrow \text{daSNC}, i, P}$ for $i = 1, 2, \dots, q$. RMTg, on the other hand, connects to each daSNC element. The
274 output of the i th daSNC element, constrained to between 0 and 1 via a logistic function, captures
275 the importance of a single decision-dimension:

276

277 (2)
$$\text{daSNC}_{i,P} = \frac{1}{1 + \exp(w_{\text{sSPN} \rightarrow \text{daSNC}, i, P} \cdot s_{\text{sSPN}, i, P} + \text{RMTg} - z_{\text{daSNC}, i, P})}$$

278 (copied from **Results** for convenience)

279

280 where:

- 281 • $w_{\text{sSPN} \rightarrow \text{daSNC}, i, P}$ is the weight of connection from the sSPN corresponding to decision-
282 dimension i and pathway P to the daSNC corresponding to decision-dimension i and
283 pathway P . The weight is fixed in this instance of the model. (dimensionless)
- 284 • $s_{\text{sSPN}, i, P}$ is the activity of sSPNs corresponding to decision-dimension i and pathway P
285 (activity arb. u.)
- 286 • $z_{\text{daSNC}, i, P}$ is an additive shift applied to the daSNC neuron corresponding to decision-
287 dimension i and pathway P (activity arb. u.)
- 288 • RMTg is RMTg activity, as defined in eq. (5). (activity arb. u.)

289 This pathway is modeled using one neuron per decision-dimension per pathway. So, there are q
290 daSNC neurons that each receive projection from a dsSPN, and q daSNC neurons that each
291 receive projection from an isSPN. daSNC elements also receive input from RMTg.

292 For use in our analysis, see
293 https://github.com/dirkbeck/DM_space_model/blob/main/algorithmic_model.m.

294

295 **Defining mSPN activity and decision-space.**

296 In each pathway, decision-space is formed probabilistically. The conversion from daSNC activity
297 to realization of decision-space occurs in the connections from daSNC to mSPN. There are q
298 daSNC elements corresponding to each pathway and q mSPN elements, and, in each pathway,
299 the i th daSNC element connects to the i th mSPN element, but not to other mSPN elements (see
300 **Fig. 1a**).

301 Like sSPNs, mSPNs encodes the cortical input normalized by an FSI and is transformed to a
 302 coordinate space of the first q principal components. The difference is that for each of dmSPNs
 303 and imSPNs, a diagonal matrix $S_P \in \mathbb{R}^{q \times q}$ is multiplied by the cortical input after transformation:

304

305 (3) $s_{\text{mSPN},P} = \frac{1}{c_P} S_P W_P^T x_P$ (copied from **Results** for convenience)

306

307 where:

- 308 • c_P is the relative activity of the FSI projecting to SPNs of pathway P (activity arb. u.)
- 309 • S_P is a diagonal matrix that applies dopamine release (via daSNC activity) to mSPN
 310 activity in pathway P . (dimensionless)
- 311 • W_P is a matrix of weights from cortical neurons to SPNs of pathway P . Each column is
 312 equivalent to a principal component of cortical activity. (dimensionless)
- 313 • x_P is the activities of cortical neurons that project to SPNs of pathway P . (activity arb. u.)

314 In the current instance, there is one mSPN per decision-dimension per pathway. So, there are q
 315 dmSPNs and q imSPNs. The dmSPNs receive input from x_{direct} and c_{direct} . The imSPNs receive
 316 input from x_{indirect} and c_{indirect} .

317 The diagonal elements of S_P are set probabilistically to either 1 (dimension in decision-space) or
 318 0 (dimension not in decision-space) such that $P(S_{P,ii} = 1) = \text{daSNC}_{i,P}$.

319 Thus, in the portions of our analysis where we set the activities of the q daSNC elements to be
 320 equal, the decision-dimensions each have the same probability of being included in decision-
 321 space, i.e. $\text{daSNC}_1 = \text{daSNC}_2 = \dots = \text{daSNC}_q = d$. In this case, we treat the probability of a certain
 322 decision-space dimensionality forming as a binomial distribution:

323

324 (18) $P(m \text{ DM-dimensions used to form DM-space}) = \binom{q}{m} d^m (1-d)^{q-m}$ for $m=0, 1, \dots, q$

325 (copied from **Extended Data Fig. 8** for convenience)

326

327 where:

- 328 • q is the number of possible decision-dimensions
- 329 • d is the (equal) probability that each decision-dimension is used to form decision-space

330

331 **Defining action value.**

332 Action value (or, in the indirect pathway, inaction value) $v_{j,P}$ for each of k potential actions is
333 defined based on the activities of dmSPNs (or imSPNs). During this process, elements of a
334 coefficient matrix $\beta_P \in \mathbb{R}^{k \times q}$ are applied to mSPN activities for each decision-dimension, action,
335 and pathway. Bias $\alpha_{j,P}$ is subtracted. Below, $\beta_{j,P}$ is used to indicate row j of β_P .

336

337 (4)
$$v_{j,P} = \frac{1}{1 + \exp(-\beta_{j,P} s_{\text{mSPN},P} - \alpha_{j,P})}$$
 (copied from **Results** for convenience)

338 where:

- 339 • $\beta_{j,P}$ is a matrix of weights from dmSPNs to downstream action value encoding neurons
340 for the direct pathway, or imSPNs to downstream inaction value encoding neurons for the
341 indirect pathway. (dimensionless)
- 342 • $s_{\text{mSPN},P}$ is the activity of sSPNs corresponding to decision-dimension i and pathway P
343 (activity arb. u.)
- 344 • $\alpha_{j,P}$ is an additive shift corresponding to the neuron encoding action j for the direct
345 pathway or inaction j for the indirect pathway. (activity arb. u.)

346 There is one neuron encoding each $v_{j,P}$. So, there are k neurons encoding action values and k
347 neurons encoding inaction values. Each of these neurons receives projection from all mSPNs of
348 the corresponding pathway.

349

350 **Defining choice.**

351 k Merton process¹⁰⁷ are run to determine whether each action should be taken, and another k to
352 determine whether each action should be refrained from. Progress to choice for each action (or
353 inaction), $Y_{j,P}$, is related to its corresponding action (or inaction) value $v_{j,P}$ and an uncorrelated
354 Brownian component $dW_{j,P}$ scaled by a coefficient σ .

355

356 (6)
$$dY_{j,P} = v_{j,P} dt + \sigma dW_{j,P}, Y_{j,P}(t=0) = 0, \text{ where } W_{j,P} \text{ is a standard Wiener process}$$

357 (copied from **Extended Data Fig. 1** for convenience)

358

359 where:

- 360 • $Y_{j,P}$ is the progress to enaction of action j in the direct pathway, and progress to refraining
361 from action j in the indirect pathway.

- 362 • $v_{j,P}$ is the action (or inaction) value corresponding to action j and pathway P . (activity arb.
- 363 u.)
- 364 • σ is the coefficient of noise.

365 The time it would take to enact action j , $t_{\text{action},j}$, is defined as the first hit time of a threshold h for
 366 process j of the direct pathway:

367

$$(7) \quad t_{\text{action},j} = \min_t \{ t \mid Y_{j,\text{direct}} \geq h \}$$

(copied from **Extended Data Fig. 1** for convenience)

369

370 The time it takes to exclude action j from consideration, $t_{\text{inaction},j}$, is calculated similarly using the
 371 indirect pathway:

372

$$(8) \quad t_{\text{inaction},j} = \min_t \{ t \mid Y_{j,\text{indirect}} \geq h \}$$

(copied from **Extended Data Fig. 1** for convenience)

374

375 The enacted action is the first to reach h , given that the corresponding inaction process has not
 376 first reached h :

377

$$(9) \quad \text{action} = \arg \min_{j \in J} (Y_j(t_{\text{action},j})), \text{ where } J \text{ is the subset of actions s.t. } t_{\text{action},j} < t_{\text{inaction},j}$$

379 (copied from **Extended Data Fig. 1** for convenience)

380

381 where:

- 382 • $Y_{j,P}$ is the progress to enaction of action j in the direct pathway, and progress to refraining
- 383 from action j in the indirect pathway.
- 384 • t is time (s)
- 385 • h is a threshold at which an action is considered taken (progress to decision arb. u.)

386 In our analysis, we run simulations using a constant time step discretization of eq. (6).

387 For code, [see](https://github.com/dirkbeck/DM_space_model/blob/main/weiner_process_model.m)
 388 https://github.com/dirkbeck/DM_space_model/blob/main/weiner_process_model.m.

389

390 **Modeled Circuit Manipulation using Instance 1.**

391 To get a sense of the functional role of the circuit elements, we conducted sensitivity analyses by
392 changing parameters in the model individually and determining their effect on the activities of
393 other circuit elements, decision-space formation, action values, and/or choice.

394

395 **Common parameters.**

396 The values specified here, arbitrarily chosen, are used in the analyses in **Instance 1** unless
397 otherwise indicated:

- 398 • throughout, $k = 4$
399 • in eq. (23): $a_{\text{FSI}} = 1$
400 • in eq. (23): $b_{\text{FSI}} = 0.5$
401 • in eq. (1): $b_{\text{sSPN}} = 0$
402 • in the inputs to eq., $q = 4$
403 • in eq. (5): $z_{\text{GPi}} = 1$
404 • in eq. (5): $z_{\text{LHb}} = 0.5$
405 • in eq. (5): $z_{\text{RMTg}} = 0.5$
406 • in eq. (2): $w_{\text{sSPN} \rightarrow \text{daSNC}, i, P} = 1$ for all i and P
407 • in eq. (2): $z_{\text{daSNC}, i, P}$ for all i and P
408 • in eq. (4): $\beta_{\text{direct}} = \begin{pmatrix} 1 & -1 & 0 & 0 \\ -1 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix}$,

409 whose rows correspond to, for example: turning left, turning right, turning around, wandering;
410 and whose columns correspond to, for example: a reward-predominant decision-dimension 1,
411 a cost-predominant decision-dimension 2, a novelty-predominant decision-dimension 3, and
412 a location-predominant decision-dimension 4. The coefficients model a T-maze where a
413 choice is made to turn right or left based on relative values of cost and reward.

- 414 • in eq. (4): $\alpha_{j, P} = -3$ for all j and P
415 • in eq. (6): $\sigma = 1$
416 • in eq. (7), (8): $h = 2$

417

418 **Effect of reward/costs on LHb/RMTg/daSNC activity.**

419 In **Extended Data Figs. 1e,f**, we modeled the effect of incrementing reward or cost on the
420 activities of LHb, RMTg, and daSNC.

421 The inputs enter the model circuit in two ways: 1) reward and cost are mapped to decision-
422 dimensions; and 2) cost level leads to changes in LHb and RMTg activities, similar to what has
423 been demonstrated in experimental work^{75,82,109–111}. The modeled LHb and RMTg responses to
424 cost are proportional to cost level with an arbitrary coefficient (set to 1 for LHb and 0.9 for RMTg
425 for the purposes of plotting).

426 The modeled results show that the mean activity of a daSNC subpopulation encoding reward-
427 predominant data responds positively to increases in reward and negatively to decreases in
428 reward, similar to experimental evidence¹¹². LHb and RMTg respond negative linearly to reward
429 level and positive linearly to cost level, similar to experimental evidence^{109,113}. Sudden changes
430 in reward or cost level, therefore, lead to shifts in activities that track changes to expectations of
431 future reward or cost value, including reward or cost currently received, i.e. reward or cost
432 prediction error.

433 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_model.m), see
434 [https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_model.m)
435 [model.m](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_model.m).

436

437 **Effect of LHb/RMTg/daSNC activity on decision-space.**

438 In **Extended Data Figs. 1g-i**, we modeled the effect of incrementing GPi, LHb, RMTg, or daSNC
439 activity on the type of decision-space formed during a decision.

440 In the plotted analysis, we altered z_{GPi} in eq. (5), z_{LHb} in eq. (5), z_{RMTg} in eq. (5), and $z_{\text{daSNC},i,P}$
441 (uniform change for all i , a single pathway is considered) in eq. (5) such that they took 10 values
442 incremented from 0 to 1. Parameters not altered took default values (see **Common parameters**).

443 We also examined the role of each component in decision-space formation through the
444 perspective of a series of steps, each carried out by a different circuit element. For this analysis,
445 we substituted eq. (5) into eq. (2) and altered each parameter in turn. The plots illustrate the value
446 of $\text{daSNC}_{i,P}$ if the other parameters were set to 1 (z_{GPi}) or 0 ($z_{\text{RMTg}}, z_{\text{daSNC},i,P}$). b_{LHb} is set to 0.5
447 (control), -5 (lesioned LHb), or 5 (stimulated LHb).

448 See **Tables 6,7** for alignment to the experimental literature.

449

450 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_model.m), see
451 [https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_model.m)
452 [model.m](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/GPi_LHb_RMTg_DA_model.m).

453

454 **Effect of sSPN activity on decision-space.**

455 In the analysis plotted in **Fig. 2a**, we incremented b_{sSPN} in eq. (1) and, for each increment,
456 recorded daSNC_i in eq. (2). Then, using the approach in eq. (6), we converted the probability that
457 one decision-dimension is used in the formation of decision-space to the probability that a
458 decision-spaces of a certain dimensionality is formed.

459 For code, see
460 [https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/friedman2015optogenetic](https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/friedman2015optogenetic_manipulation.m)
461 [manipulation.m](https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/friedman2015optogenetic_manipulation.m).

462

463 **Effect of decision-space on choice.**

464 In the analysis plotted in **Fig. 2b**, we changed which decision-space was formed by mSPNs and
465 measured choice.

466 The excitation group was modeled using a non-dimensional decision-space (dopamine→mSPN
467 weights of 0 reward-predominant decision-dimension, 0 cost-predominant dimension). The
468 control group was modeled using a 1D direct pathway decision-space (dopamine→mSPN weights
469 of 0.5 reward-predominant dimension, 0 cost-predominant dimension). The inhibition group was
470 modeled using a 2D direct pathway decision-space (dopamine→mSPN weights of 1 reward-
471 predominant dimension, 1 cost-predominant dimension). The modeled T-maze task was a choice
472 between reward=2, cost=1 (high reward, high cost) and reward=1, cost = 0.5 (low reward, low
473 cost). 20 simulations were run per modeled subject for 100 subjects. Other parameters for forming
474 decision-space and calculating action value are set to their defaults (see **Common parameters**).
475 For simplicity, the indirect pathway is not modeled in this analysis.

476 For code, see
477 [https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/friedman2015optogenetic](https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/friedman2015optogenetic_manipulation.m)
478 [manipulation.m](https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/friedman2015optogenetic_manipulation.m).

479 In the analysis in **Figs. 3b,c**, we modeled changes to decision-space and choice after stress.

480 Here, modeled control rodents made decisions using a 2D direct pathway decision-space formed
481 from reward-predominant and cost-predominant decision-dimensions. This correspond
482 mathematically to a truncation of β_{direct} (see eq. (4) and **Common parameters**) to two columns.
483 The first subset of modeled stress-group rodents made decisions without forming direct pathway
484 decision-space. This corresponds to an elimination of β_{direct} such that action value is defined
485 purely based on priors ($\alpha_{j,\text{direct}}$ in eq. (4)). The second subset made decisions without forming
486 direct pathway decision-space until they reached a critical threshold, beyond which they formed
487 a 1D direct pathway decision-space with a reward-predominant dimension. Action values are
488 derived for the three groups across multiple reward and cost combinations (**Fig. 3c**) via eqs. (3)
489 and (4). Then choices are modeled using eqs. (6), (7), and (9) across 2000 simulations per group
490 for each reward concentration (each incremented from 0 to 1 arbitrary units, 7 increments). Cost
491 concentration is set to 0.5 arbitrary units (set at this level to resemble the steepness of increase
492 in the experimental psychometric function). Default parameters are used for action value

493 formation and the Merton process model. For simplicity, the indirect pathway is not modeled in
494 this analysis. **Fig. 3b** plots the averages of the simulations.

495 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/Friedman2017_lo), see
496 https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/Friedman2017_lo
497 [wD_space.m](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/Friedman2017_lo).

498 In the analysis plotted in **Figs. 3d,e**, we modeled the effect on choice of shifts in decision-space
499 after a small cost is added to a reward (experimental data is plotted in **Extended Data Fig. 3j**).

500 Rodents in the only-reward task were modeled as forming a lower-dimensional direct pathway
501 decision-space (decision-dimension 1 weight = 0.5, decision-dimension 2 weight = 0.2) while
502 animals in the reward-and-cost task formed a higher-dimensional direct pathway decision-space
503 (decision-dimension 1 weight = 1, decision-dimension 2 weight = 0.5).

504 To do this, we truncated β_{direct} (see eq. (4) and **Common parameters**) to two columns or derived
505 action value purely based on priors ($\alpha_{j,\text{direct}}$ in eq. (4)). A cortical input of reward = 0.7, cost = 0.3
506 is shown in the plots. For simplicity, the indirect pathway is not modeled in this analysis.

507 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/alterd_choice_a), see
508 https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/alterd_choice_a
509 [fter_space_transition.m](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/alterd_choice_a).

510 In the analysis plotted in **Fig. 3h**, we modeled changes to choice after aging in young and old
511 groups.

512 Here, we truncated β_{direct} (see eq. (4) and **Common parameters**) to two decision-dimensions,
513 the first corresponding to a reward-predominant decision-dimension and the second
514 corresponding to a cost-predominant decision-dimension. In the current analysis, the first row of
515 β_{direct} corresponded to licking while the second row corresponds to performing a different action,
516 e.g. movement. The licking action was assigned a larger prior, $\alpha_{1,\text{direct}} = 0$, $\alpha_{2,\text{direct}} = -3$, due to
517 the strong association developed in the rodents between the experimental apparatus and licking.
518 For the modeled “learned, young” group, no decision-space is formed during the reward-cue task
519 and a decision-space using only a cost-predominant decision-dimension is formed during the
520 cost-cue task (i.e. $s_{\text{mSPN},\text{reward},\text{direct}} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, $s_{\text{mSPN},\text{cost},\text{direct}} = \begin{bmatrix} 0 \\ 1 \end{bmatrix}$ in eq. (3)). For the modeled
521 “learned, old” group, no decision-space is formed during the reward-cue task and a decision-
522 space involving a cost-predominant decision-dimension is partially formed during the cost task (
523 $s_{\text{mSPN},\text{reward},\text{direct}} = \begin{bmatrix} 0 \\ 0 \end{bmatrix}$, $s_{\text{mSPN},\text{cost},\text{direct}} = \begin{bmatrix} 0 \\ 0.5 \end{bmatrix}$). For the “not learned” group, a decision-space
524 involving a cost-predominant decision-dimension is partially formed during both tasks (
525 $s_{\text{mSPN},\text{reward},\text{direct}} = \begin{bmatrix} 0 \\ 0.5 \end{bmatrix}$, $s_{\text{mSPN},\text{cost},\text{direct}} = \begin{bmatrix} 0 \\ 0.5 \end{bmatrix}$). For simplicity, the indirect pathway is not
526 modeled in this analysis.

527 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/Friedman2020_lo_wD_space.m), see
528 [https://github.com/dirkbeck/DM_space_model/blob/main/disorder hypotheses/Friedman2020 lo](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/Friedman2020_lo_wD_space.m)
529 [wD_space.m](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/Friedman2020_lo_wD_space.m).

530

531 **Effect of decision-space on sSPN-mSPN correlation**

532 In the analysis plotted in **Fig. 2d**, sSPN-mSPN correlation is compared across decision-spaces
533 with different dimensionality.

534 It is assumed in the plotted examples that a 1D decision-space is only formed from the first
535 decision-dimension, a 2D decision-space is only formed from the first and the second, and a 3D
536 decision-space is only formed from the first, second, and third. The analysis assumes a
537 comparison of SPNs of the same pathway (that is, either dsSPN-dmSPN or isSPN-imSPN). For
538 this analysis, eigenvalues of cortical activity are set to 2, 1, 0.5, 0.2, and 0.1, respectively.
539 Weighted averages of example signals (left panel) and correlation for different decision-spaces
540 (right panel) are formed using the identity that eigenvalues of principal components are equivalent
541 to their variances.

542 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/ctx_sSPN_mSPN_coordinated_activity.m), see
543 [https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/ctx_sSPN_mSPN_coordin](https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/ctx_sSPN_mSPN_coordinated_activity.m)
544 [ated_activity.m](https://github.com/dirkbeck/DM_space_model/blob/main/model_tests/ctx_sSPN_mSPN_coordinated_activity.m).

545

546 **Effect of FSI activity on decision-space.**

547 In the analysis plotted in **Fig. 3f**, we incremented FSI activity a_{FSI} in eq. (23) and determined the
548 response of $daSNC_i$ in eq. (2) (a single pathway is considered). The activity parameters related to
549 other circuit elements were held constant (see **Common parameters**).

550 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/space_dimensionality_vs_FSI.m), see
551 [https://github.com/dirkbeck/DM_space_model/blob/main/disorder hypotheses/space dimension](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/space_dimensionality_vs_FSI.m)
552 [ality vs FSI.m](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/space_dimensionality_vs_FSI.m).

553

554 **Effect of cortical SNR on choice.**

555 In the analysis plotted in **Extended Data Figs. 5a-e**, cortical signal to noise ratio (SNR) is altered
556 and the effect on choice is simulated.

557 Merton process simulations (see **Defining Choice**) are run across ten increments of reward and
558 cost from -1 to 1 arbitrary units for a modeled cost-benefit conflict task. Parameters related to
559 action value are set to their defaults and the T-maze task is used (see **Common parameters**).
560 Here, “turn right” corresponds to receiving the reward and cost combination, while other actions
561 correspond to receiving no reward and no cost. For simplicity, only the direct pathway is used to

562 influence choice. 100 simulations are run for each of 100 reward and cost combinations, and for
563 each combination, choice is averaged.

564 The above process is replicated with changes to two sets of parameters. First, the effect of
565 changes to decision-space were considered. A different S in eq. (3) was used depending on

566 specified decision-space: $S = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & \vdots \\ 0 & \dots & 0 \end{bmatrix}$ for 1D decision-spaces, and $S = \begin{bmatrix} & 0 \\ I_2 & \vdots \\ 0 & \dots & 0 \end{bmatrix}$ for 2D

567 decision-spaces. Second, changes to cortical noise were considered by adding i.i.d. Gaussian
568 noise to x_{direct} (with mean 0 and standard deviation σ) at every time step, then recalculating action
569 values in eq. (4) based on the mSPN activities calculated at that time step. Simulations were run
570 for $\sigma = 1, 2, \dots, 10$. Default parameters were used for calculating action value (see **Common**
571 **parameters**).

572 Examples of single simulations at each level of reward and cost are shown for the $\sigma = 1$ (high
573 cortical SNR) and $\sigma = 5$ (low cortical SNR) cases in **Extended Data Figs. 5a-d**. In **Extended Data**
574 **Fig. 5e**, expected value is averaged across the 100 simulations for each noise level. Expected
575 value here is defined as reward minus $0.75 \cdot \text{cost}$ (to add preference for reward compared to cost,
576 coefficient is arbitrary) achieved across reward and cost levels. In the plot, SNR is set to the
577 inverse of σ .

578 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/cortical_snr.m), see
579 [https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/cortic](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/cortical_snr.m)
580 [al_snr.m](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/cortical_snr.m).

581

582 **Effect of dopamine on action/inaction values.**

583 In the analyses plotted in **Extended Data Figs. 6c-f**, we measured the effect of high versus low
584 dopamine on action and inaction values across a range of cortical inputs to the system.

585 We modeled a cost-benefit conflict task with increasing reward (scale of 0 to 1 arbitrary units, 100
586 increments) and constant cost (set to 0.25 arbitrary units). Experimental work has shown that
587 dopamine increases direct pathway activity while decreasing indirect pathway activity and vice
588 versa⁴². Therefore, we set coefficients relating to overall activity of the pathways oppositely: in the
589 low dopamine case, the direct pathway coefficient was 0.1 arbitrary unit and the indirect pathway
590 coefficient 5 arbitrary units; and in the high dopamine case, the indirect pathway coefficient was
591 5 arbitrary units and the direct pathway coefficient 0.1 arbitrary unit. These coefficients were
592 multiplied by β_{direct} or β_{indirect} in eq. (4), increasing or decreasing the overall sensitivity of action
593 value on data along cortical principal components. In the model, changes to dopamine also
594 involved a change in decision-space: due to their opposite effects on mSPN activity, dopamine
595 biases the direct pathway towards forming higher-dimensional decision-spaces and the indirect
596 pathway towards forming lower-dimensional decision-spaces. For the purpose of this analysis,

597 eq. (3) is reframed to incorporate the effects of dopamine in scaling action value score (A , set to

598 either 5 or 0.1 arbitrary units in our analysis) and changing decision-space (B , set to 1 arbitrary
 599 unit when dopamine is high and 0 when dopamine is low). Here, individual elements are
 600 referenced through subscripts based on their j th row and column corresponding to the reward
 601 or cost dimension.

602

603 (24)
$$v_{j,\text{direct}} = \frac{1}{1 + \exp(-A \cdot (\beta_{j,\text{reward,direct}} + B \cdot \beta_{j,\text{cost,direct}}) - \alpha_{j,\text{direct}})}$$

604

605 (25)
$$v_{j,\text{indirect}} = \frac{1}{1 + \exp(-A \cdot ((1 - B) \cdot \beta_{j,\text{reward,indirect}} + \beta_{j,\text{cost,indirect}}) - \alpha_{j,\text{indirect}})}$$

606

607 where:

- 608 • A is the multiplicative effect of dopamine released to mSPNs (dimensionless)
- 609 • B is the effect of dopamine on decision-space (dimensionless)
- 610 • β_j is the connection weight from mSPN to an action value neuron. Each $\beta_{j,\text{reward}}$ or $\beta_{j,\text{cost}}$
 611 corresponds to an element of the connection weight matrix β_P .
- 612 • prior_j is an additive shift corresponding to the neuron encoding action j (activity arb. u.)

613 The plot in **Extended Data Fig. 6c** compares the high dopamine and low dopamine cases. The
 614 plot in **Extended Data Fig. 6d** shows a similar analysis but for changes in parameters: cost is
 615 fixed at 0.5 arbitrary units, and A is set to either 2 arbitrary units (corresponding to the pathway
 616 not disconnected) or 0 (corresponding to the pathway disconnected). The plots in **Extended Data**
 617 **Figs. 6e,f** show progress to action in the case where reward = 1 arbitrary unit and cost = 0.25
 618 arbitrary unit for low versus high dopamine. Deliberation time distributions are formed by
 619 aggregating the deliberation times across the 100 simulations. For parameters used for subjective
 620 valuation and deliberation time simulation, see **Common parameters**.

621 For [https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct_vs_indirect_pathway_SV.m)
 622 [vs_indirect_pathway_SV.m](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct_vs_indirect_pathway_SV.m), see
 623 [https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct_vs_indirect_pathway_SV.m)

624

625 **Effect of decision-dimensions on choice.**

626 In the analysis plotted in **Extended Data Fig. 6i**, we altered the connections between mSPN and
 627 action/inaction encoding neurons on choice.

628 A modeled approach/avoid experiment is conducted by offering an option with reward = 1 arbitrary
 629 unit, cost = 1 arbitrary unit, and varying (10 values incremented from [0, 2] arbitrary units)
 630 physically proximity to another reward. An additional column is added to β_{direct} and β_{indirect} in eq.
 631 (4) to reflect the fact that additional proximity to the other reward increases approach rate:
 632 $\beta_{\text{direct}} = \beta_{\text{indirect}} = \begin{bmatrix} 1 & -1 & 1 \\ -1 & 1 & -1 \end{bmatrix}$, where the upper row corresponds to approaching, the bottom row
 633 corresponds to not approaching, and the columns correspond to, from left to right, a reward-
 634 predominant decision-dimension, a cost-predominant decision-dimension, and a location-
 635 predominant decision-dimension. Reward is assigned a greater relative importance than cost or
 636 location (score of 3 arbitrary units versus 1 versus 1) in sSPNs, while cost is assigned a greater
 637 relative importance than reward or location (score of 3 arbitrary units versus 1 versus 1). daSNC
 638 activity is incremented by changing $z_{\text{daSNC}, i, P}$ in eq. (2) for all i and both pathways. Action and
 639 inaction values are calculated, and then choice is formed by averaging the results of 1000 Merton
 640 process simulations.

641 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct_vs_indirect_pathway_proximity_theory.m), see
 642 [https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct_vs_indirect_pathway_proximity_theory.m)
 643 [_vs_indirect_pathway_proximity_theory.m](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/direct_vs_indirect_pathway_proximity_theory.m).

644

645 **Effects of sSPN, LHb, and daSNC activity on decision-space.**

646 In **Figs. 5a,b**, b_{sSPN} (eq. (1)), z_{LHb} (eq. (5)), and $z_{\text{daSNC}, i, P}$ (for all i and a single pathway, eq. (2))
 647 are incremented from 0 to 5 arbitrary units with 20 evenly spaced increments along each axis.
 648 Each of the 20x20x20 points are used to derive daSNC_i in eq. (2) and converted to decision-
 649 spaces via eq. (18). To limit the number of points in **Fig. 5a**, each point is shown with 0.5%
 650 probability.

651 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/decision_space_by_circuit_activity.m), see
 652 [https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/decision](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/decision_space_by_circuit_activity.m)
 653 [_space_by_circuit_activity.m](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/decision_space_by_circuit_activity.m).

654

655 **Effect of decision-space on choice profiles.**

656 In **Figs. 5c,f**, **Extended Data Figs. 7d,f**, we form decision-spaces using various decision-
 657 dimensions across incremented cortical reward and cost inputs, then classified the action values
 658 formed across those reward/cost inputs using a scoring system.

659 The scoring system, visualized in **Extended Data Fig. 7c**, is as follows:

660 Scores for “explore,” “riskiness,” “high action,” “exploit,” “safety,” “low action” are calculated by
 661 incrementing reward and cost on [-1 1] (arbitrary units) scales (9 increments are used for each of
 662 reward and cost in **Fig. 5c**, **Extended Data Fig. 7d**, 6 increments in **Figs. 5f**, **Extended Data**

663 **Fig. 7f).** The notation used here treats $v_{r,c,j}$ as the action value of the j th action at a certain
 664 reward and cost increment and $v_{r,c}$ as the set of those action values. In the plotted analysis, $k=4$
 665 actions are assigned action values.

- 666 • Explore. The tendency to pursue multiple actions simultaneously. Scored as the area of
 667 the region of reward and cost combinations with a Gini coefficient less than 0.25.
 668

$$669 \quad (26) \quad \text{explore} = \sum_{r=-1}^1 \sum_{c=-1}^1 [\text{gini}(v_{r,c}) < 0.25]$$

$$670 \quad (27) \quad \text{gini}(v_{r,c}) = \frac{\sum_{i=1}^k \sum_{j=1}^k |v_{r,c,i} - v_{r,c,j}|}{2k \sum_{j=1}^k v_{r,c,j}}$$

- 672 • Exploit. The tendency to pursue only one action. Scored at the area of the region of reward
 673 and cost combinations with a Gini coefficient greater than 0.5.
 674
 675

$$676 \quad (28) \quad \text{exploit} = \sum_{r=-1}^1 \sum_{c=-1}^1 [\text{gini}(v_{r,c}) > 0.5]$$

- 677 • Riskiness. The combined value of actions when reward and cost are high. Scored by
 678 examining the combinations where both reward and cost are greater than 0.
 679
 680

$$681 \quad (29) \quad \text{riskiness} = \sum_{r=0}^1 \sum_{c=0}^1 \sum_{j=1}^k v_{r,c,j}$$

- 682 • Safety. The combined value of actions when reward and cost are low. Scored by
 683 examining the combinations where both reward and cost are less than 0.
 684
 685

$$686 \quad (30) \quad \text{safety} = \sum_{r=-1}^0 \sum_{c=-1}^0 \sum_{j=1}^k v_{r,c,j}$$

- 687 • High action. How often actions will have high action values. Scored as the area of the
 688 region of reward and cost combinations that have combined action value greater than 0.5.
 689
 690

$$691 \quad (31) \quad \text{high action} = \sum_{r=-1}^1 \sum_{c=-1}^1 \left[\sum_{j=1}^k v_{r,c,j} > 0.5 \right]$$

- 692 • Low action. How often actions will have low action values. Scored as the area of the region
 693 of reward and cost combinations that have combined action value less than 0.2.
 694
 695

696 (32) high action = $\sum_{r=-1}^1 \sum_{c=-1}^1 \left[\sum_{j=1}^k v_{r,c,j} < 0.2 \right]$

697

698 In the analyses plotted in **Fig. 5c** and **Extended Data Fig. 7d** and the examples in **Fig. 5d**, action
 699 value scores, as measured by the scoring definitions above, are compared when different
 700 decision-spaces are constructed but cortical input and system parameters are unchanged. The
 701 underlying action values across reward and cost levels resembles those from other analyses (see
 702 **Common parameters**) except for an addition of normal random noise (mean = 0, standard
 703 deviation = 1) to every element of β_{direct} (see eq. (4)).

704 The analysis in **Extended Data Fig. 7d** is similar, except for here, a weighted average is taken of
 705 action value scores, as measured by the scoring definitions above, between scenarios where
 706 different decision-spaces are constructed. A different S in eq. (3) is used depending on the

707 specified dimensionality of direct pathway decision-space: $S = \begin{bmatrix} 1 & 0 & 0 \\ 0 & 0 & \vdots \\ 0 & \dots & 0 \end{bmatrix}$ for 1D,

708 $S = \begin{bmatrix} I_2 & 0 \\ \vdots & \vdots \\ 0 & \dots & 0 \end{bmatrix}$ for 2D, $S = \begin{bmatrix} I_3 & 0 \\ \vdots & \vdots \\ 0 & \dots & 0 \end{bmatrix}$ for 3D, and $S = I_4$ for 4D. A weighted average of the

709 five decision-spaces is calculated for three levels of sSPN activity (-1, 0, and 1).

710 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective_value_scores_by_space.m), see
 711 [https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective_value_scores_by_space.m)
 712 [e_value_scores_by_space.m](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective_value_scores_by_space.m).

713 In the analyses plotted in **Fig. 5f**, **Extended Data Fig. 7f**, for each of 1000 simulations,
 714 uncorrelated Gaussian white noise (mean = 0, standard deviation = 1) is added to every element
 715 of β_{direct} (see eq. (4)) and 6 by 6 grids of action values across reward and cost combinations are
 716 scored by the “explore,” “riskiness,” “high action,” “exploit,” “safety,” and “low action” metrics.
 717 Scores for each metric are compared across simulations and between decision-space groups.
 718 Observations that score in the top 10% by a metric are considered outliers. Outlier proportion is
 719 plotted in **Fig. 5f**. The means across the simulations of each score are plotted in **Extended Data**
 720 **Fig. 7f**.

721 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective_value_score_extremes.m), see
 722 [https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective_value_score_extremes.m)
 723 [e_value_score_extremes.m](https://github.com/dirkbeck/DM_space_model/blob/main/day_to_day_space_sampling/subjective_value_score_extremes.m).

724

725 **Instance 2: sparse connectivity and feedforward.**

726 In this section, we describe the instance of the model where cortex input to the system does not
 727 change over time and the activities of other circuit elements do not decay over time.

728 This instance of the model leads to a convenient formation of the model as a circuit with no time
729 component. In this section, we frame this instance mathematically and then describe our related
730 analysis examining the process of formation of the decision-space over time.

731 To focus on the portions of the circuit we analyze using this instance, we define here the subset
732 of the circuit involving cortex, FSI, sSPN, daSNC, and mSPN.

733 For https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_network_model.m, see
734 https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_network_model.m.
735

736

737 **Cortical input.**

738 A set of 4 cortical neurons, notated as C , is sampled at random from a population of 50 cortical
739 neurons. Each neuron in C projects to one FSI and each of Q SPNs, which each correspond
740 to a decision-dimension. In our analysis, Q is set to 4. This process is repeated 10,000 times
741 per each pathway, forming 10,000 groups of 4 cortical neurons, 1 FSI, 4 dsSPNs (or isSPNs),
742 and 4 dmSPNs (or imSPNs) for each pathway.

743

744 **Defining FSI activity.**

745 FSI activity is defined as a weighted sum of the activities of connected cortical neurons:

746

$$747 \quad (33) \quad \text{FSI}_C = \sum_{q \in C} w_{\text{cortex} \rightarrow \text{FSI}} \text{cortex}_q + b_{\text{FSI}}$$

748

749 where:

- 750 • C is a randomly sampled subset of cortical neurons.
- 751 • FSI_C is the activity of the FSI which receives projection from the cortical neurons in C
752 (activity arb. u.)
- 753 • $w_{\text{cortex} \rightarrow \text{FSI}}$ is the connection weight between cortical neurons and FSIs (dimensionless)
- 754 • cortex_q is the activity of cortical neuron q (activity arb. u.)
- 755 • b_{FSI} affects the relative activity of all sSPN neurons (activity arb. u.)

756 In the current instance of the model, there are 10,000 FSIs that project to each of dSPNs and
757 iSPNs. Each cortical neuron in C projects to FSI_C .

758

759 **Defining sSPN activity.**

760 sSPN activity is defined as a weighted sum of the activities of connected cortical neurons, divided
761 by a weighted sum of the activities of connected FSIs, plus an additive shift b_{sSPN} applied to all
762 sSPNs:

763

764 (10)
$$\text{sSPN}_{s,C} = \frac{1}{|C|} \sum_{q \in C} \frac{w_{q \rightarrow s}^{\text{cortex}_q}}{\text{FSI}_C} + b_{\text{sSPN}}$$

765 (copied from **Extended Data Fig. 4** for convenience)

766

767 where:

- 768 • C is a randomly sampled subset of cortical neurons.
- 769 • $\text{sSPN}_{s,C}$ is the activity of an sSPN s that receives projection from cortical neurons in C .
770 (activity arb. u.)
- 771 • $w_{q \rightarrow s}$ is the connection weight between cortical neuron q and sSPN s . The weight is
772 equivalent to one of the first four principal components of the cortical activity of the four
773 connected cortical neurons. sSPNs are separated into equal populations that correspond
774 to the first, second, third, or fourth principal component. (dimensionless)
- 775 • FSI_C is the activity of the FSI which receives projection from the cortical neurons in C
776 (activity arb. u.)
- 777 • cortex_q is the activity of cortical neuron q (activity arb. u.)
- 778 • b_{sSPN} represents the relative activity of all sSPN neurons (activity arb. u.)

779 In the current instance of the model, there are 40,000 neurons for each of dsSPNs and isSPNs.
780 Activities are defined based on a feedforward network, so the simplification is made that sSPN
781 activities are not affected by daSNC activities. All cortical neurons in C project to $\text{sSPN}_{s,C}$ for all s
782 , and similarly, FSI_C projects to $\text{sSPN}_{s,C}$ for all s .

783

784 **Defining daSNC activity.**

785 The activity of the daSNC element corresponding to decision-dimension i and pathway P is
786 defined as the weight from sSPNs corresponding to decision-dimension i and pathway P :

787

788 (11)
$$\text{daSNC}_{i,P} = \frac{1}{1 + \exp\left(\frac{1}{n_{\text{sSPN}}} \sum_{s \in i,P} w_{s \rightarrow \text{daSNC},i,P} \cdot \text{sSPN}_s + \text{RMTg} - z_{\text{daSNC},i,P}\right)}$$

789 (copied from **Extended Data Fig. 4** for convenience)

790

791 where:

- 792 • $\text{daSNC}_{i,p}$ is the activity the daSNC neuron corresponding to decision-dimension i and
 793 pathway P . (activity arb. u.)
 794 • n_{sSPN} is the count of sSPNs in each of the direct/indirect pathways
 795 • $w_{s \rightarrow \text{daSNC},i,P}$ is the connection weight from sSPN s to the daSNC neuron corresponding to
 796 decision-dimension i and pathway P . The weight is fixed in this instance of the model.
 797 (dimensionless)
 798 • sSPN_s is the activity of SPN s (activity arb. u.)
 799 • RMTg is RMTg activity. (activity arb. u.)
 800 • $z_{\text{daSNC},i,P}$ is the bias in the activity of a daSNC neuron corresponding to decision-
 801 dimension i and pathway P . (activity arb. u.)

802 In the current instance of the model, there are q daSNC neurons that receive projection from the
 803 10,000 dsSPNs corresponding to each decision-dimension, and likewise q daSNC neurons that
 804 receive projection from the 10,000 isSPNs corresponding to each decision-dimension. RMTg also
 805 projects to all daSNC neurons.

806 In our analysis using this instance of the model, we arbitrarily set $w_{\text{sSPN} \rightarrow \text{daSNC},i} = 1$ arbitrary unit
 807 for both pathways and $z_{\text{daSNC},i} = -5$ arbitrary units for all i for the direct pathway, and $z_{\text{daSNC},i} = 5$
 808 arbitrary units for all i for the indirect pathway. For simplicity, RMTg is set to 0.

809

810 **Defining mSPN activity and decision-space.**

811 mSPN activity is defined as a weighted sum of the activities of connected cortical neurons, divided
 812 by a weighted sum of the activities of connected FSIs. Here, unlike in the definition of sSPN
 813 activity in eq. (10), a $d_{i,P}$ term is multiplied to incorporate the weighting of mSPNs by dopamine:

814

815 (12)
$$\text{mSPN}_{m,C} = \frac{d_{i,P}}{|C|} \sum_{q \in C} \frac{w_{q \rightarrow m}^{\text{cortex}_q}}{\text{FSI}_C}$$

816 (copied from **Extended Data Fig. 4** for convenience)

817

818 where:

- 819 • C is a randomly sampled subset of cortical neurons.
- 820 • $mSPN_{m,C}$ is the activity of mSPN m that receives projection from cortical neurons in C .
821 (activity arb. u.)
- 822 • $d_{i,P}$, which takes the value 0 or 1, is dopamine signaling to mSPNs corresponding to
823 decision-dimension i and pathway P . $d_{i,P}$ is the realization of probabilistic weighting of
824 decision-dimensions based on daSNC activity (see **Conceptual Model**). (dimensionless)
- 825 • $w_{q \rightarrow m}$ is the connection weight between cortical neuron q and mSPN m . The weight is
826 equivalent to one of the first four principal components of the cortical activity of the four
827 connected cortical neurons. As described in **Conceptual Model**, sSPNs are separated
828 into equal populations that correspond to the first, second, third, or fourth principal
829 component. (dimensionless)
- 830 • FSI_C is the activity of the FSI which receives projection from the cortical neurons in C
831 (activity arb. u.)
- 832 • $cortex_q$ is the activity of cortical neuron q (activity arb. u.)

833 In the current instance of the model, there are 40,000 neurons for each of dmSPNs and imSPNs
834 All cortical neurons in C project to $mSPN_{m,C}$ for all m , and similarly, FSI_C projects to $mSPN_{m,C}$ for
835 all m .

836

837 **Modeling SPN encoding of data, using Instance 2.**

838 To explore the ability of SPNs to successfully encode data along decision-dimensions, even when
839 cortex and SPNs are sparsely connected, we constructed networks with different degrees of
840 dimensionality reduction (**Extended Data Fig. 4g**). A single pathway is considered. One type of
841 network had 2 times dimensionality reduction (20 cortical neurons, 10 SPN), another had 10 times
842 dimensionality reduction (100 cortical neurons, 10 SPN), and another had 100 times
843 dimensionality reduction (1000 cortical neurons, 10 SPN), similar to what is found in the human
844 brain^{61,108}.

845 For each type, we constructed modeled networks with cortex→SPN connections equal to principal
846 components of cortical activity by simulating, for each analyzed pathway, a random symmetric
847 positive definite matrix that is used as the cortical covariance matrix Σ_p (see **Defining sSPN**
848 **activity**) via MATLAB's sprandsym() with density=1. Eigenvalues are arbitrarily specified as $\lambda_1=2$
849 , $\lambda_2=2$, $\lambda_3=0.5$, $\lambda_4=0.2$, and $\lambda_5=\lambda_6=\dots=\lambda_p=0$, i.e. the first and second principal components are
850 very important, the third somewhat important, the fourth slightly important, and the others
851 unimportant. The weights W_p from cortical neurons to the Q SPN circuit elements per pathway
852 are then derived as the first Q eigenvectors of Σ_p .

853 We incremented the number of cortical neurons that connected to each SPN from 2 to 10. The
854 network was connected sparsely based on the specified number of connections from randomly

855 selected cortical neurons to each SPN. For simplicity in this analysis, we created a cortical signal
 856 that resembled the first principal component of cortical activity as a whole (regardless of
 857 connectivity to SPNs) and let the first cortical principal component to have large eigenvalue
 858 compared to the others (i.e. $\lambda_1=1, \lambda_2=0.1, \lambda_3=\lambda_4=\dots=\lambda_p=0$).

859 For each of the modeled networks (3 network types by 9 increments from 2 to 10), we simulated
 860 the process 1000 times. During each simulation, we calculated the ability of the network to
 861 discriminate between the large signal along the first cortical principal component and the absence
 862 of signal along the second cortical principal component, given its access to only a subset (2 to 10
 863 cortical neurons) of the complete signal.

864 Then the SPNs encoding data along the first versus second decision-dimension were assessed
 865 in their ability to distinguish between signals along the first cortical principal component versus
 866 the second. This was quantified using the Bhattacharyya distance of the activity among SPNs
 867 encoding data along the first decision-dimension versus the second, assuming the subpopulations
 868 have mean activities μ_1 and μ_2 and standard deviations σ_1 and σ_2 , respectively.

869

870 (34)
$$D_B = \frac{1}{4} \frac{(\mu_1 - \mu_2)^2}{\sigma_1^2 + \sigma_2^2} + \frac{1}{2} \ln \left(\frac{\sigma_1^2 + \sigma_2^2}{2\sigma_1\sigma_2} \right)$$

871

872 where:

- 873 • μ_1 is the mean activity of activities in the first subpopulation (activity arb. u.)
- 874 • μ_2 is the mean activity of activities in the second subpopulation (activity arb. u.)
- 875 • σ_1 is the standard deviation of activities in the first subpopulation (activity arb. u.)
- 876 • σ_2 is the standard deviation of activities in the second subpopulation (activity arb. u.)

877 For the current analysis, a_{FSI} is arbitrarily set to 1 arbitrary unit and b_{FSI} is arbitrarily set to 0.

878 For `code`, see
 879 [https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/dime](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/dimension_discrimination_vs_sparsity.m)
 880 [nsion_discrimination_vs_sparsity.m](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/dimension_discrimination_vs_sparsity.m).

881

882 ***Instance 3: full connectivity and dynamics.***

883 In this section, we describe the instance of the model where each cortical neuron projects to each
 884 FSI, each FSI projects to each SPN (for dsSPN, isSPN, dmSPN, imSPN), and each cortical
 885 neuron projects to each SPN.

886 This instance of the model leads to a convenient formation of the model as a circuit of fewer
 887 elements (one FSI, one dsSPN, isSPN, dmSPN, and imSPN per the four decision-dimensions),

888 with a time component. In this section, we frame this instance mathematically and then describe
 889 our related analysis.

890 To focus on the portions of the circuit we analyze using this instance, we define here the subset
 891 of the circuit involving cortex, sSPN, daSNC, and mSPN.

892

893 **Defining SPN and daSNC activity.**

894 Here, the activities of SPN and daSNC elements and the weights from sSPN to daSNC are
 895 represented as a system of differential equations. Because FSI activity is not measured in the
 896 related analyses, cortical activity to pathway P after FSI normalization $x_{i,P}(t)$ is used as input to
 897 the system in the equations below.

898 For a model diagram, see **Fig. 4a**. Note that daSNC activity of 0 (i.e. average activity) leads to 0
 899 change in SPN activity (due to the $1/2$ terms in eqs. (13) and (14).

900

901 (13)
$$\tau \cdot \frac{ds_{\text{sSPN},i,P}(t)}{dt} = -s_{\text{sSPN},i,P}(t) + x_{i,P}(t) - w_{\text{daSNC} \rightarrow \text{sSPN},i,P} \cdot \left(y_{\text{sSPN},i,P}(t) - \frac{1}{2} \right)$$

902 (copied from **Extended Data Fig. 6** for convenience)

903

904 (14)
$$\tau \cdot \frac{ds_{\text{mSPN},i,P}(t)}{dt} = -s_{\text{mSPN},i,P}(t) + x_{i,P}(t) + w_{\text{daSNC} \rightarrow \text{mSPN},i,P} \cdot \left(y_{\text{sSPN},i,P}(t) - \frac{1}{2} \right)$$

905 (copied from **Extended Data Fig. 6** for convenience)

906

907 (15)
$$\frac{d}{dt} w_{\text{sSPN} \rightarrow \text{daSNC},i,P}(t) = \kappa \cdot s_{\text{sSPN},i,P}(t)$$

908 (copied from **Extended Data Fig. 6** for convenience)

909

910 where:

911

912 (16)
$$y_{\text{sSPN},i,P}(t) = \frac{1}{1 + \exp\left(w_{\text{sSPN} \rightarrow \text{daSNC},i,P}(t) \cdot s_{\text{sSPN},i,P}(t) + \text{RMTg} - z_{\text{daSNC},i,P} \right)}$$

913 (copied from **Extended Data Fig. 6** for convenience)

914

- 915 • τ is the time constant related to the decay rate of activity (dimensionless)
- 916 • $s_{i,P}(t)$ is the SPN activity (either dsSPN, isSPN, dmSPN, or imSPN) corresponding to
- 917 decision-dimension i and pathway P , as a function of time. (activity arb. u.)
- 918 • t is time (seconds)
- 919 • $x_{i,P}(t)$ is the cortical activity input, after FSI normalization, to an SPN corresponding to
- 920 decision-dimension i and pathway P (activity arb. u.)
- 921 • $w_{\text{daSNC} \rightarrow \text{sSPN}, i, P}$ is the connection weight from a daSNC neuron corresponding to
- 922 decision-dimension i and pathway P to an sSPN (either dsSPN or isSPN) corresponding
- 923 to decision-dimension i and pathway P . (dimensionless)
- 924 • $y_{i,P}(t)$ is the activity of the daSNC neuron corresponding to decision-dimension i and
- 925 pathway P , as a function of time. (activity arb. u.)
- 926 • $w_{\text{sSPN} \rightarrow \text{daSNC}, i, P}(t)$ is the connection weight from an sSPN (either dsSPN or isSPN) to a
- 927 daSNC neuron corresponding to decision-dimension i and pathway P , as a function of
- 928 time. (dimensionless)
- 929 • K is a coefficient that determines the rate at which the connection from sSPNs to daSNC
- 930 neurons change depending on sSPN (dsSPN or isSPN) activity. (dimensionless)
- 931 • $z_{\text{daSNC}, i, P}$ is the bias in the activity of a daSNC neuron corresponding to decision-
- 932 dimension i and pathway P . (activity arb. u.)
- 933 • RMTg is the output of RMTg, per eq. (5). (activity arb. u.)

934 In the current instance of the model, there are q dsSPNs, q isSPNs, q dmSPNs, q imSPNs, q
935 daSNC neurons that each receive projection from a dsSPN, and q daSNC neurons that each
936 receive projection from an isSPN. daSNC neurons corresponding to decision-dimension i and
937 pathway P project to sSPNs and mSPNs of the same i and P .

938

939 **Defining decision-space.**

940 A decision-dimension is used to form decision-space at times when daSNC activity corresponding
941 to the decision-dimension exceeds a threshold:

942

$$943 \quad (17) \quad S_{i,P}(t) = \begin{cases} 0 & y_{i,P}(t) < \text{threshold} \\ 1 & y_{i,P}(t) \geq \text{threshold} \end{cases}$$

944 (copied from **Extended Data Fig. 6** for convenience)

945

946 where:

- 947 • $y_{i,P}(t)$ is the activity of the daSNC neuron corresponding to decision-dimension i and
948 pathway P , as a function of time. (activity arb. u.)
- 949 • $S_{i,P}(t)$ is the application of dopamine release (via daSNC activity) to mSPN activity
950 corresponding to decision-dimension i and pathway P . The notation here is used to match
951 the notation in **Instance 1**; $S_{i,P}(t)$ is the (i,i) element of the diagonal matrix $S_P(t)$ whose
952 elements correspond to the weights assigned to the decision-dimensions, similar to in eq.
953 (3). (dimensionless)

954

955 **Defining action value.**

956 Action value is defined here like in **Instance 1**, except mSPN activity (for dmSPN and imSPN) is
957 defined as a function of time:

958

$$959 \quad (35) \quad v_{j,P} = \frac{1}{1 + \exp(-\beta_{j,P} s_{\text{mSPN},P}(t) - \alpha_{j,P})}$$

960

961 where:

- 962 • $\beta_{j,P}$ is a matrix of weights from dmSPNs to downstream action value encoding neurons
963 for the direct pathway, or imSPNs to downstream inaction value encoding neurons for the
964 indirect pathway. (dimensionless)
- 965 • $s_{\text{sSPN},P}$ is the activity of sSPNs corresponding to decision-dimension i and pathway P
966 (activity arb. u.)
- 967 • t is time (seconds)
- 968 • $\alpha_{j,P}$ is an additive shift corresponding to the neuron encoding action j for the direct
969 pathway or inaction j for the indirect pathway. (activity arb. u.)

970 As in the other instances of the model, there is one neuron encoding each $v_{j,P}$. So, there are k
971 neurons encoding action values and k neurons encoding inaction values. Each of these neurons
972 receives projection from all mSPNs of the corresponding pathway.

973

974 **Modeling time-variant input, using Instance 3.**

975 In **Figs. 4d-i**, simulated responses of dsSPN, isSPN, dmSPN, and imSPN are derived using the
976 forward Euler method with step size 0.001s.

977 In **Figs. 4d,e**, the cortical input to sSPN elements corresponding to each of four example direct
978 pathway decision-dimensions is represented by a vector of length 5001 (corresponding to 0s to

979 5s with increments 0.001s). Four arbitrary input vectors are used, one corresponding to each
980 plotted decision-dimension:

981

$$982 \quad (36) \quad 2 + \sin(t), 1 + \cos(t), \sin(2t), \cos(2t)$$

983

984 The first vector corresponds to a reward-predominant dimension (shown in green in **Fig. 4i**). A
985 relatively large positive average value (2 arbitrary units) is assigned to it as an example of an
986 important decision-dimension to a decision. A cost-predominant decision-dimension (second
987 vector) is specified to be important, but less so, and novelty-predominant and location-
988 predominant decision-dimensions (third and fourth vectors) are assigned to be relatively
989 unimportant. The number of decision-dimensions used to form decision-space is averaged across
990 time steps in the 5s simulation. In **d**, simulations are run across 100 evenly spaced increments of
991 an addition to each vector at all timesteps. In **e**, simulations are run across 100 evenly spaced
992 increments of $z_{daSNC,i}$ (for each pathway, depending on the simulation) in eq. (16) from -1 to 1
993 arbitrary units.

994 **Figs. 4f,g** show examples of the response of dsSPN, isSPN, dmSPN, and imSPN elements to
995 different cortical inputs. In **Fig. 4f**, a cortical input of 10 arbitrary units for 2.5s is followed by an
996 input of 20 arbitrary units for 2.5s. In **Fig. 4g**, a cortical input of 10 arbitrary units for 2.5s is
997 followed by an input of 0 for 2.5s.

998 In the analysis shown in **Fig. 4h**, cortical inputs of 10 arbitrary units for 2.5s are followed by cortical
999 inputs with prediction errors incremented by 0.1 from -1 to arbitrary units. These prediction errors
1000 are relative to the original cortical input of 10 arbitrary units. For example, for the prediction error
1001 of -1, there is a signal of 0 for 2.5s, and for the prediction error of 1, there is a signal of 20 for 2.5s.
1002 To find the change in the activities of circuit elements, their activities at 2.5s are subtracted from
1003 their activities at 5s.

1004 **Fig. 4i** shows simulations for an example input with $\kappa=0$ in eq. (16) versus $\kappa=0.1$ arbitrary units.
1005 The cortical input is as follows: in decision-dimension 1 (e.g. reward-predominant), a cortical
1006 signal of 10 arbitrary units for the 0-1.23s timeframe and elsewhere a signal of 0; in decision-
1007 dimension 2 (e.g. cost-predominant), a cortical signal of 10 arbitrary units for the 1.25-2.43s
1008 timeframe and elsewhere a signal of 0; in decision-dimension 3, a cortical signal of 10 arbitrary
1009 units for the 2.5-3.73s timeframe and elsewhere a signal of 0; and in decision-dimension 4, a
1010 cortical signal of 10 arbitrary units for the 3.75-5s timeframe and elsewhere a signal of 0.

1011 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/sSPN_DA_mSPN_dynamic_interaction.m), see
1012 [https://github.com/dirkbeck/DM_space_model/blob/main/dynamic model and neural net/sSPN](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/sSPN_DA_mSPN_dynamic_interaction.m)
1013 [_DA mSPN dynamic interaction.m](https://github.com/dirkbeck/DM_space_model/blob/main/dynamic_model_and_neural_net/sSPN_DA_mSPN_dynamic_interaction.m).

1014

1015 Parameters are set to common values, chosen arbitrarily, with physiologically accurate signs:

- 1016 • in eqs. (13), (14): $\tau = 1$
- 1017 • in eq. (13): $w_{\text{daSNC} \rightarrow \text{sSPN}, \text{direct}} = -1$
- 1018 • in eq. (13): $w_{\text{daSNC} \rightarrow \text{sSPN}, \text{indirect}} = 1$
- 1019 • in eq (14): $w_{\text{daSNC} \rightarrow \text{mSPN}, \text{direct}} = 1$
- 1020 • in eq. (14): $w_{\text{daSNC} \rightarrow \text{mSPN}, \text{indirect}} = -1$
- 1021 • in eq. (15): $\kappa = -0.01$
- 1022 • in eq. (16): $\text{RMTg} = 0$
- 1023 • in eq. (16): $z_{\text{daSNC}, i, P} = 0$ for all i and P
- 1024 • in eq. (17): $\text{threshold} = 0.5$

1025 Additionally, the following initial conditions, also chosen arbitrarily, are used across analyses:

- 1026 • $s_{\text{sSPN}, i, \text{direct}}(0) = s_{\text{sSPN}, i, \text{indirect}}(0) = s_{\text{mSPN}, i, \text{direct}}(0) = s_{\text{mSPN}, i, \text{indirect}}(0) = 0$
- 1027 • $w_{\text{sSPN} \rightarrow \text{SNc}, i, \text{direct}}(0) = w_{\text{sSPN} \rightarrow \text{SNc}, i, \text{indirect}}(0) = 1$

1028

1029 ***Movement of Circuit Activity Across Multiple Trials.***

1030 Here, we model changes in circuit activity between trials. We begin by forming advantage and
 1031 cost functions that guide the realignment of the circuit. Using these, we explore how vulnerability
 1032 versus resilience in disorder formation could be interpreted through the lens of the model.

1033

1034 **Defining advantage and cost of circuit activity.**

1035 *Advantage* is defined here as the ability of the circuit to produce beneficial decision-spaces at a
 1036 certain activity. The goal of the sSPN-GPi-LHb-RMTg-daSNC circuit in the model is to produce
 1037 preferred decision-spaces for action valuation (**Figs. 6a-d**). For instance, in a laboratory
 1038 environment when an animal routinely makes a choice to approach depending on reward level, a
 1039 one-dimensional direct pathway decision-space with a reward dimension may be helpful. During
 1040 a decision it may make sense for this animal to reach a circuit activity where forming a one-
 1041 dimensional direct pathway decision-space is probable.

1042 We represent this logic mathematically as a function of an n -element circuit $\{X_1, X_2, \dots, X_n\}$. In
 1043 our analysis, we focus on either FSI and sSPN, holding the rest of the circuit elements fixed at
 1044 default values (see **Common parameters**); or sSPN, LHb, and daSNC, holding the rest of the
 1045 circuit elements fixed at default values. The advantage of a certain circuit activity is defined as a
 1046 weighted sum of probabilities the direct pathway decision-space occurs and the benefit of forming
 1047 each decision-space:

1048

1049 (19) $\text{advantage}(X_1=x_1, X_2=x_2, \dots, X_n=x_n) = \sum_{l=1}^{2^q} \text{score}_l \cdot P(\text{space}_l | (X_1=x_1, X_2=x_2, \dots, X_n=x_n))$

1050 (copied from **Extended Data Fig. 8** for convenience)

1051

1052 where:

- 1053 • $\{X_1, X_2, \dots, X_n\}$ are elements of the circuit with activities x_1, x_2, \dots, x_n . (activity arb. u.)
- 1054 • q is the count of decision-dimensions
- 1055 • $score_l$ is a coefficient corresponding to the preference for a given direct pathway decision-
- 1056 space. (dimensionless)

1057

1058 The probability each decision-space forms is derived from probability its decision-dimensions
1059 individually are used during the decision (daSNC_{*i*} in eq. (2), here notated as d_i):

1060

1061 (37) probability of formation of a decision-space $l = d_1(1 - d_1)d_2(1 - d_2) \cdot \dots \cdot d_m(1 - d_m)$

1062

1063 The rationale for this formation of advantage is theoretical. Elsewhere, we show that direct
1064 pathway decision-spaces of different dimensionality are beneficial (and may be used by rodents)
1065 for tasks of different difficulties (**Fig. 2**). We also show that certain decision-spaces are beneficial
1066 with certain levels of cortical noise (**Extended Data Fig. 5**) and for obtaining different types of
1067 action values (**Figs. 5c-f**). We represent this as an assignment of greater value to certain decision-
1068 spaces, given external and internal contexts and the task at hand.

1069 *Cost*, here, is defined as the difference between the circuit activity and a baseline activity. For
1070 most scenarios, the circuit might be best served searching for the circuit activity with the highest
1071 advantage. However, there is an obvious counterexample: it could be that it is easiest to form
1072 preferred decision-spaces at extremely unusual circuit activity (e.g. very high sSPN, very high
1073 LHb, very high daSNC), and only slightly more difficult to form that decision-space at closer to
1074 average circuit activity (average sSPN, low LHb, average daSNC). It may be more advantageous
1075 for the circuit to shift to the latter activity.

1076 Therefore, we introduce a cost function to form *net advantage*. We then use net advantage to
1077 define the circuit activities that are the most beneficial. The concept of baseline circuit activity is
1078 introduced here in order to define cost. This can be interpreted as the circuit activity outside of
1079 decision-making.

1080

1081 (20) $\text{cost}(X_1=x_1, X_2=x_2, \dots, X_n=x_n) = \left\| \begin{bmatrix} x_1 & x_2 & \dots & x_n \end{bmatrix}^\top - \begin{bmatrix} x_{1,\text{baseline}} & x_{2,\text{baseline}} & \dots & x_{n,\text{baseline}} \end{bmatrix}^\top \right\|_2$

1082 (copied from **Extended Data Fig. 8** for convenience)

1083

1084 where:

- 1085 • $\{X_1, X_2, \dots, X_n\}$ are elements of the circuit with activities x_1, x_2, \dots, x_n . (activity arb. u.)
- 1086 • Outside of decision-making, $\{X_1, X_2, \dots, X_n\}$ have baseline activities
- 1087 $x_{1, \text{baseline}}, x_{2, \text{baseline}}, \dots, x_{n, \text{baseline}}$. (activity arb. u.)

1088

1089 Net advantage is defined as advantage minus cost multiplied by a constant:

1090

1091 (21) $\text{net advantage}(X_1=x_1, \dots, X_n=x_n) = \text{advantage}(X_1=x_1, \dots, X_n=x_n) - \text{constant} \cdot \text{cost}(X_1=x_1, \dots, X_n=x_n)$

1092 (copied from **Extended Data Fig. 8** for convenience)

1093

1094 where:

- 1095 • Functions for reward and cost are taken from eqs. (19) and (20), respectively.
- 1096 • constant alters the weight given to cost compared to reward. (dimensionless)

1097

1098 **Visualizing advantage, cost, and net advantage.**

1099 **Fig. 6b** shows an example of how a circuit forms advantage per eq. (19). The advantage scores
1100 score_i are randomly generated (normal distribution, mean 0, standard deviation 1) for each of the
1101 16 possible decision-spaces formed from four decision-dimensions. sSPN and daSNC activity are
1102 incremented across a 10x10 grid of sSPN and daSNC activities which each range from 0 to 10
1103 arbitrary units. The activities of other circuit elements are set to default values in **Instance 1** of
1104 the model (see **Common parameters**).

1105 Cost in **Fig. 6c** is formed using eq. (20). Distance from the circuit baseline point is measured as
1106 Euclidean distance in the two plotted decision-dimensions.

1107 Net advantage in **Fig. 6d** is calculated per eq. (21). For this example, the cost coefficient
1108 $\text{constant} = 1$ (dimensionless coefficient).

1109 **Fig. 6f** similarly shows net advantage but after incrementing sSPN, LHb, and daSNC activities.
1110 Similar to in the example in **Fig. 6d**, a set of scores are independently randomly generated and
1111 constant in eq. (21) is set arbitrarily to 1 (dimensionless coefficient).

1112 For [https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/advantage_cost_net](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/advantage_cost_net_advantage_example.m)
1113 [_advantage_example.m](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/advantage_cost_net_advantage_example.m).
1114

1115

1116 **Defining direction of circuit movement.**

1117 The direction of movement is defined as a search for the most optimal circuit activity to produce
1118 advantageous direct pathway decision-spaces. To understand how a circuit governed by eq. (21)
1119 might adjust over the course of multiple trials, we relate the adjustment of circuit activity to net
1120 advantage. We specify that the circuit adjusts so that it can more easily reach advantageous
1121 decision-spaces. This constitutes a movement in the baseline activity of eq. (20).

1122 Thus, the circuit adapts in the direction of the gradient of net advantage.

1123

$$1124 \quad (22) \quad \frac{\Delta [x_{1, \text{baseline}} \quad x_{2, \text{baseline}} \quad \dots \quad x_{n, \text{baseline}}]^T}{\text{trial}} = \text{rate} \cdot \nabla \text{net advantage}(X_1=x_1, \dots, X_n=x_n)$$

1125 (copied from **Extended Data Fig. S8** for convenience)

1126

1127 where:

- 1128 • $\{X_1, X_2, \dots, X_n\}$ are elements of the circuit with activities x_1, x_2, \dots, x_n . (activity arb. u.)
- 1129 • Outside of decision-making, $\{X_1, X_2, \dots, X_n\}$ have baseline activities
1130 $x_{1, \text{baseline}}, x_{2, \text{baseline}}, \dots, x_{n, \text{baseline}}$. (activity arb. u.)
- 1131 • rate is a coefficient that affects the speed of movement of the circuit per trial. (trial⁻¹)

1132

1133 **Effect of initial circuit activity on future trials.**

1134 In **Figs. 6e,g, Extended Data Fig. 8a**, several examples illustrate trajectories of circuit movement,
1135 as defined in eq. (21).

1136 In these analyses, we assume that decision-dimensions are assigned equal importance by sSPN,
1137 i.e. (1) in eq. $b_{\text{sSPN}}=0$. The probability that an individual decision-dimension is used to form
1138 decision-space is calculated using eq. (2). Advantage scores score_i are randomly generated
1139 (normal distribution, mean = 0, standard deviation = 1 arbitrary unit) for each of the 16 possible
1140 decision-spaces created from four dimensions. The value of constant in eq. (21) is set to 1
1141 arbitrary unit. For each increment of a 15x15 grid of sSPN and FSI (**Fig. 6e**) or 15x15x15 grid of
1142 sSPN, LHb, and daSNC (**Fig. 6g, Extended Data Fig. 8a**), net advantage is calculated for the
1143 scenario where that activity is the circuit baseline, i.e. $X_1=x_{1, \text{baseline}}, X_2=x_{2, \text{baseline}}, \dots, X_n=x_{n, \text{baseline}}$.

1144 The gradient of this grid is approximated via MATLAB's gradient() routine. Trajectories are
1145 integrated from the gradient via MATLAB's streamline(), which uses the forward Euler method.

1146 In the upper panel of **Fig. 6e**, circuit baseline points are shown for each increment of Euler's
1147 method. The bottom panel shows the trajectories of 20 randomly selected points on the [0, 5]
1148 arbitrary units range for sSPN and FSI.

1149 In **Fig. 8g**, starting points are selected to form a 5 by 5 by 5 grid incremented along sSPN, LHb,
1150 and daSNC axes. At each point in a trajectory line, the probability a dimension is used to form
1151 decision-space is calculated via eq. (2). Then, during plotting, these calculated probabilities are
1152 interpolated using MATLAB's patch() routine.

1153 In **Extended Data Fig. 8a**, the gradient is plotted using MATLAB's streamslice(). Then the
1154 trajectories of five randomly selected are plotted.

1155 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/sSPN_DA_LH_trajec_tories.m), see
1156 [https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/sSPN DA LH traje](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/sSPN_DA_LH_trajec_tories.m)
1157 [ctories.m](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/sSPN_DA_LH_trajec_tories.m) and
1158 [https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/sSNC DA LH traje](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/sSNC_DA_LH_trajec_tories_examples2.m)
1159 [ctories_examples2.m](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/sSNC_DA_LH_trajec_tories_examples2.m)

1160

1161 **Effect of altered advantage score on future trials.**

1162 In **Extended Data Fig. 8b,c**, we examine the effect of a change to advantage score_{*l*} in eq. (19) as
1163 a modeled task is being performed.

1164 The circuit adjusts over 100 trials. At the beginning, advantage score is set to 1 (dimensionless
1165 coefficient) for the non-D decision-space and 0 for every other decision-space. Over the first 20
1166 and the last 10 time-steps (between the dashed lines on the plots), advantage score is
1167 incremented for the 4D decision-space but not others. Over time steps 21-90, advantage score is
1168 incremented for the non-D decision-space.

1169 In the plot, the value of each decision-space is divided by the total value of all decision-spaces to
1170 form a ratio.

1171 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/changing_space_value_between_trials.m), see
1172 [https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/changing_space va](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/changing_space_value_between_trials.m)
1173 [lue_between_trials.m](https://github.com/dirkbeck/DM_space_model/blob/main/circuit_trajectories/changing_space_value_between_trials.m).

1174

1175

1176 ***Rationale for the computational framework.***

1177 During the formation of our computational model, we considered several alternative modeling
1178 techniques, including neural networks, Hidden Markov Models, Bayesian methods, State Space
1179 Models, biophysics models, drift diffusion models, and others.

1180 Here, we outline justifications for the modeling methods we chose and suggest other modeling
1181 techniques that may achieve similar results.

1182

1183 **Modeling choices: dimensionality reduction.**

1184 We model the decision-making axes used to make choices (decision-dimensions) as the principal
1185 components of cortical data to link the processes of the circuit to operations commonly performed
1186 in data science. The decision-space model could easily be modified in a way that would preserve
1187 its concept, for example by replacing the principal components with the independent
1188 components¹¹⁴ of cortical data. However, modifications may come at the cost of computational
1189 convenience or interpretability.

1190

1191 **Modeling choices: choice from physiology.**

1192 We sought to derive choice and deliberation time of an arbitrary number of potential actions. Drift
1193 diffusion models have been successful in other work involving the Basal Ganglia¹¹⁵, but classically
1194 only model two possible outcomes, although extensions have been made for the multi-outcome
1195 case. We designed our model to have a similar framework to drift diffusion models but be suited
1196 to an unlimited number of possible actions. Our model successfully reproduces choice in the T-
1197 maze task (**Extended Data Figs. 2b,c**). Our goal could also be achieved through models of
1198 interacting populations¹¹⁶, though in our objective, we are more concerned with choice outcomes
1199 (choice, deliberation time, deliberation time distribution) than neural recruitment to produce it.
1200 Alternatively, we might find success by treating choice as a Bayesian process arising from circuit
1201 activity¹¹⁷ or through an intermediate layer such as in a Hidden Markov Model¹¹⁸, though
1202 deliberation time is not commonly derived using these classes of models.

1203 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m), see
1204 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m)
1205 [Counts/Neural%20Network/newDirkCode.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/newDirkCode.m) (**Extended Data**
1206 **Fig. 2b**) and
1207 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/newDirkCode.m)
1208 [Counts/Neural%20Network/newDirkCode.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/newDirkCode.m) **Extended Data Fig. 2c)**

1209

1210 **Modeling choices: physiological connections.**

1211 We modeled the overall activities of circuit elements using relative firing rates because it achieved
1212 our goal of linking the overall activities of circuit brain regions. While models that model the timing
1213 of neuron spikes have been used to precisely describe connections in portions of the circuit^{119,120},
1214 the decision-space conceptual model does not require their added granularity.

1215

1216 **Reasoning behind the FSI model.**

1217 In eq. (1), scaling of cortical data serves the important functional role of normalizing x_P so that
1218 the circuit can make sense of data coded across the wide range of firing rates that are observed
1219 in the cortex¹²¹ (**Extended Data Fig. 1a**). Previous anatomical work and physiological analysis
1220 has shown that many cortical neurons synapse to one FSI^{121,122}. The cortical to FSI connection is
1221 excitatory¹²³. This would suggest that FSI surveys the cumulative activity of cortex. Strengthening
1222 this hypothesis, physiological analysis of connected FSI and cortical neurons in the current work
1223 shows that FSI activity scales linearly with cortical activity^{10,124} (see **Extended Data Fig. 3k,l**).

1224 In the model, the parameter a_{FSI} is related to the strength of connection between cortex and FSI.
1225 The parameter b_{FSI} is related to firing rate of FSI when $x_P = 0$.

1226 For the FSI and SPN relationship, anatomical and physiological work has shown an inhibitory
1227 effect of FSI on SPN¹²⁵. The algebraic operator that best represents this inhibition is less clear: it
1228 could be thought of as a subtraction or as a division depending on the experimental evidence
1229 used to model^{126,127}.

1230 A subtraction possibility:

1231

1232 (38) $s_{\text{sSPN}}(a_{\text{FSI}}) = x_P - a_{\text{FSI}}$

1233

1234 A division possibility:

1235

1236 (39) $s_{\text{sSPN}}(a_{\text{FSI}}) = \frac{x_P}{a_{\text{FSI}}}$

1237

1238 where:

- 1239 • a_{FSI} is the weight of cortex→FSI connection (dimensionless)
1240 • x_P is the activities of the cortical neurons in a given pathway P (activity arb. u.)

1241 The analytic relationship used here leads to a convenient interpretation from the perspective of
1242 data processing. It can also be thought of as approximating subtraction or division depending on
1243 the scale of a_{FSI} . Below, we show a series approximations of eq. (1) as a function of connection
1244 strength from cortex, with input from cortex and other parameters fixed.

1245

1246 Substitution in terms of a_{FSI} :

1247

1248 (40)
$$s_{\text{sSPN}}(a_{\text{FSI}}) = \frac{1}{a_{\text{FSI}} \cdot \|\mathbf{x}_P\|_2 + b_{\text{FSI}}} \mathbf{x}_P \mathbf{W} + b_{\text{sSPN}}$$

1249

1250 Truncated Taylor series at $a_{\text{FSI}}=0$:

1251

1252 (41)
$$s_{\text{sSPN}}(a_{\text{FSI}}) = b_{\text{sSPN}} + \frac{\mathbf{x}_P \mathbf{W}}{b_{\text{FSI}}} - \frac{\|\mathbf{x}_P\|_2 \mathbf{x}_P \mathbf{W}}{b_{\text{FSI}}^2} \cdot a_{\text{FSI}} + \mathcal{O}(a_{\text{FSI}}^2)$$

1253

1254 Truncated Laurent series at $a_{\text{FSI}} = \infty$:

1255

1256 (42)
$$s_{\text{sSPN}}(a_{\text{FSI}}) = b_{\text{sSPN}} + \frac{\mathbf{x}_P \mathbf{W}}{\|\mathbf{x}_P\|_2} \cdot \frac{1}{a_{\text{FSI}}} - \mathcal{O}\left(\frac{1}{a_{\text{FSI}}^2}\right)$$

1257

1258 Thus, when FSI is weakly connected to cortex, the formula somewhat resembles a subtractive
1259 operation, and when FSI is strongly connected to cortex, the formula somewhat resembles a
1260 division operation. The ratio between the a_{FSI} and b_{FSI} parameters is important here (the first

1261 series, before truncation, converges when $\frac{|b_{\text{FSI}}|}{a_{\text{FSI}}} > \|\mathbf{x}_P\|_2$ and the second, before truncation, when

1262
$$\frac{|b_{\text{FSI}}|}{a_{\text{FSI}}} < \|\mathbf{x}_P\|_2$$
.

1263

1264 ***Inferring decision-space from SPN activity and choice.***

1265 The decision-space can be inferred from environmental or experimental inputs in conjunction with
1266 decision-making data (**Extended Data Figs. 1q,r**). The method here requires that many decision-
1267 making experiments have been run with a similar apparatus but different parameters (for instance,
1268 light level), and that average sSPN activity has been measured during the decisions. The
1269 parameter data is stored in a matrix $\mathbf{X} \in \mathbb{R}^{n \times p}$, where n here is a separate trial with separate
1270 inputs (rather than different inputs across time steps, as in the description of **Instance 1**) and p

1271 is the number of features of the experiment that may be encoded by cortex, for instance
1272 temperature, music volume, or light level (similar to the description in **Instance 1**).

1273 The process involves three steps:

1274 **Labeling sessions.**

1275 Recorded decisions are labeled using attributes of the process by which the decision was made.
1276 This might be achieved in a rodent task that measures response to music volume, for instance,
1277 by clustering sessions based on heart rate and distance traveled.

1278 **Constraints based on SPN activity.**

1279 The sessions are split by label. \mathbf{X} is standardized such that each column has a mean of 0 and
1280 standard deviation 1. Then a linear regression is run on each labeled subset \mathbf{X}_l to find coefficients
1281 \mathbf{b}_l that map those observations to predicted SPN activities (averaged across SPN decision-
1282 dimensions) $\hat{\mathbf{y}}_l$ for each session in the subset (here, the subscript l is used to indicate all elements
1283 of the subset):

1284

1285 (43) $\hat{\mathbf{y}}_l = \mathbf{X}_l \mathbf{b}_l + b_0$

1286

1287 where:

- 1288
- 1289 • $\hat{\mathbf{y}}_l$ is predicted SPN activities
 - 1290 • \mathbf{X}_l is a subset of experimental parameter data (see *Labeled sessions*) corresponding to
1291 one label
 - 1292 • \mathbf{b}_l and b_0 are the linear regression coefficients that map the experimental parameters (see
1293 **Labeled sessions**) to sSPN activity

1294 From the calculated \mathbf{b}_l , we can guess the principal axis dimensions that make up decision-space
1295 $\mathbf{w}_1, \mathbf{w}_2, \dots, \mathbf{w}_q$ and the presence of each decision-dimension $e_{li} \in \{0, 1\}$ in each labeled
1296 subset. During this process, we consider \mathbf{b}_l as the sum of the dimensions in decision-space in the
1297 subset:

1298

1299 (44) $\mathbf{b}_l = \sum_{i=1}^q e_{li} \mathbf{w}_i$

1300

1301 Using this framework, we can form a rule which we can use to assign labels to decision-
1302 dimensions and hypothesize w_1, w_2, \dots, w_q :

1303 If b_A has high correlation with b_B , then one of b_A or b_B must correspond to a higher-
1304 dimensional decision-space that also includes the dimensions of the other.

1305 For example, we might have data with labels A, B, C, and D and corresponding b_A, b_B, b_C, b_D ,
1306 where b_A is correlated with b_D , b_B is correlated with b_D , and the other possible pairs uncorrelated.
1307 It follows from the rule above that b_D is at least a two-dimensional decision-space including
1308 dimensions from b_A and b_B , and that b_A and b_B are at least one-dimensional decision-spaces.
1309 So, we would hypothesize that there are two SPN-encoded decision-dimensions used during the
1310 decision, w_1 and w_2 , and that subsets A and D use w_1 , subsets B and D use w_2 , and subset C
1311 does not use either.

1312 The logic to construct constraints I and II are as follows. When $e_{l1} = e_{l2} = \dots = e_{lq} = 0$ (i.e. a non-D
1313 decision-space), $\hat{y}_l = b_0$. The coefficients assigned to the non-D decision-space $b_{l: 0D \text{ space}}$ should
1314 have low correlation with any of the axes w_1, w_2, \dots, w_q . Therefore, it is expected that we find one
1315 b_l that has low correlation with the other $b_{l'}$, and we can label this $b_{l: 0D \text{ space}}$. Further, when e_{li} for
1316 one i is equal to 1 and for all other i is equal to 0 (i.e. a 1D decision-space), $\hat{y}_l = w_{i \text{ in space}} + b_0$.
1317 This decision-space will have high correlation with $w_{i \text{ in space}}$ but low correlation with other w_i .
1318 Therefore, it is expected that we find several $b_{l: \text{dim } i \text{ space}}$ that are not correlated with one another,
1319 or $b_{l: 0D \text{ space}}$, but may be related through the multi-dimensional decision-spaces in C. Finally, when
1320 e_{li} is equal to 1 for multiple i , b_l is calculated as a sum per eq. (44). Therefore, it is expected that
1321 some $b_{l: \text{dim } i \cap \text{dim } j \text{ space}}$ are linear combinations of $b_{l: \text{dim } i \text{ space}}$ and $b_{l: \text{dim } j \text{ space}}$.

1322 The example shown in **Extended Data Fig. 1r** uses simulated data with 2 experimentally
1323 observed features (for instance, temperature and music volume) and 100 observations. X was
1324 constructed as a matrix of i.i.d. Gaussian variables with mean 0 and standard deviation 1. The
1325 ground-truth principal component matrix W was constructed as a 2x2 matrix of i.i.d. Gaussian
1326 variables with mean 0 and standard deviation 1. Then, for each of the 100 observations, a
1327 decision-space was randomly assigned in a reference dataset. Each decision-dimension for each
1328 observation was treated as an i.i.d. uniform variable, and if the variable corresponding to the
1329 observation and the decision-dimension exceeded a value (here, 0.5), then the dimension was
1330 considered as incorporated in decision-space. The randomly generated decision-spaces were
1331 each assigned their own label. Then a simulated SPN activity was created for each of the 100
1332 observations was created by multiplying the ground-truth W by the decision-space used in each
1333 observation, similar to in eq. (1). i.i.d. Gaussian noise (mean 0, standard deviation 0.5) was then
1334 added to create simulated SPN activity observations. Using this simulated data, we ran a linear
1335 regression for each labeled subset via MATLAB's fitlm() routine. The linear regression fits are
1336 plotted as surfaces in **Extended Data Fig. 1r**. The slopes, with respect to temperature and music
1337 volume, were, for label A, -0.15 and 0.48, respectively; for label B, -437.90 and -9.72, respectively;
1338 for label C, -9.01 and -274.51 respectively; and for label D, -155.45 and -199.83. Slopes for label
1339 are relatively small, so it is assigned to "decision-space not formed" (matching the reference

1340 dataset). Of the remaining labels, label D is closer to an additive combination of labels B and C
1341 than other permutations, so label D is assigned the “2D decision-space” (matching the reference
1342 dataset), while labels B and C are each considered 1D decision-spaces (matching the reference
1343 dataset).

1344 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality_from_SPN_activity.m), see
1345 [https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality from](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality_from_SPN_activity.m)
1346 [SPN activity.m](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality_from_SPN_activity.m)

1347

1348 **Tests using choice.**

1349 We can then combine the constraints in Step 2, developed using SPN activity, with an analysis of
1350 choice given the hypothesized SPN-encoded decision-dimensions. In Step 2, a set of
1351 w_1, w_2, \dots, w_q are hypothesized. Here, choice at different levels of those w_i are compared across
1352 the labeled subsets. The hypothesis in Step 2 is supported if choice, for each labeled subset, is
1353 correlated with the decision-dimensions hypothesized to be used to form decision-space but not
1354 correlated with the decision-dimensions hypothesized not to be used to form decision-space.

1355 An example is shown in **Extended Data Fig. 1r**. For the case where decision-space is not formed,
1356 choices do not correlate with any hypothesized SPN-encoded decision-dimension. For a 1D
1357 decision-space, choices correlate with one hypothesized SPN-encoded decision-dimension. For
1358 a 2D decision-space, choices correlate with two hypothesized SPN-encoded decision-
1359 dimensions.

1360 In the plotted examples, we plot simulated choices in each of the four decision-spaces used in
1361 the analysis. Choices are simulated from reference dataset (i.e. absent noise added during
1362 simulation) average sSPN activities by session y by treating
1363 $Z = \frac{1}{1 + \exp(-y + \text{i.i.d. Gaussian noise})}$ as a random variable, where $Z < 0.5$ corresponds to a “turn
1364 left” action and $Z \geq 0.5$ to a “turn right” action. The threshold of 0.5 is chosen because it represents
1365 the expected value of Z at average sSPN activity ($y=0$). In the plots, we interpolate possible
1366 subject values from choice at different combinations of the two decision-dimensions w_1 and w_2 ,
1367 as derived in Step 2. For each action for each labeled subset, a logistic regression is used to
1368 convert actions to value of action across the grid. As expected, observations of label A, assigned
1369 to “decision-space not formed” have little correlation with either of the putative decision-
1370 dimensions derived in Step 2; observations of labels B and C, assigned to 1D decision-spaces,
1371 are correlated with one putative decision-dimension but not the other; and observations of label
1372 D, assigned to the “2D decision-space,” are correlated with both.

1373 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality_from_SPN_activity.m), see
1374 [https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality from](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality_from_SPN_activity.m)
1375 [SPN activity.m](https://github.com/dirkbeck/DM_space_model/blob/main/model_overview/dimensionality_from_SPN_activity.m)

1376

1377 **Testing the Model Through Analysis of Neural Data.**

1378 As a further test of the decision-space model, we examined the relationships between behavior
1379 and neural activity in tasks that required different reward versus cost dimensions. The analysis,
1380 new to the current work, was performed using the Corticostriosomal Circuit Stress Experiment
1381 database (published with Friedman et al., 2017). We found more functionally connected sSPN
1382 and mSPN in tasks that were difficult. We then analyzed cortex, FSI, sSPN, and mSPN during
1383 these tasks and found evidence of dimensionality reduction from cortical neurons to SPNs.

1384

1385 **Defining decision difficulty by task.**

1386 We defined decision difficulty through deliberation time, calculated as the time between when the
1387 door opened during the T-maze task and when the animal made a movement between one end
1388 of the maze or the other. Deliberation time distributions were analyzed for each trial group (for
1389 control and stress: cost-benefit cost, benefit-benefit, cost-cost, non-conflict cost-benefit).
1390 Skewness was calculated using MATLAB's skewness() routine. Example distributions are shown
1391 in **Extended Data Figs. 2b, 3a,b** (6 animals, 35 sessions) and summaries across groups in
1392 **Extended Data Figs. 2d, 3c,d** (14 rats, 249 sessions).

1393 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m), see
1394 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m)
1395 [Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m) (**Extended Data**
1396 **Fig. 2b**) and
1397 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/createSkewnessBarChartOfTRAndCBAcrossControlAndStress2.m)
1398 [Counts/Pattern%20Analysis/createSkewnessBarChartOfTRAndCBAcrossControlAndStress2.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/createSkewnessBarChartOfTRAndCBAcrossControlAndStress2.m)
1399 (**Extended Data Fig. 2d**)

1400

1401 **Fitting the modeled deliberation times.**

1402 To replicate the deliberation time distributions with a computational model, we leveraged a
1403 diffusion model where two functions would both start at zero and would continue towards either a
1404 positive or negative pre-defined threshold that represented either performing an action (positive
1405 threshold) or not performing an action (negative threshold). The first threshold that was reached
1406 by either function was which decision we considered as selected. The x-axis was the progression
1407 of time as the functions ran. The deliberation time for this model was the amount of time (in
1408 seconds) it took for the first function to reach its threshold. To match the experimental distribution
1409 times analyzed in **Extended Data Fig. 2b**, we ran the drift diffusion process adjusting drift rate,
1410 the thresholds, and noise until the modeled deliberation time distribution had a similar median
1411 and skew to experimental data from **Extended Data Fig. 2c**
1412 (<https://doi.org/10.7910/DVN/SMKW0I>). An additional 1.5 seconds was uniformly added to
1413 modeled distribution times.

1414 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m), see
1415 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m)
1416 [Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Neural%20Network/createHistogramsByTaskTypeOrConcentration.m).

1417

1418 **Connected SPNs through cross-correlation.**

1419 We used the Corticostriosomal Circuit Stress Experiment database to identify sSPN and mSPN
1420 among recorded neurons in the striatum. For details, see the Supplemental Materials & Methods
1421 of Friedman et al. (2017). 14785 cells across 14 control animals were analyzed. The total number
1422 of identified striosomal and matrix neuron per task: NCB = non-conflict cost-benefit (sSPNs = 14,
1423 mSPNs = 260), CC = cost-cost (sSPNs =46 , mSPNs = 400), CBC = cost-benefit conflict (sSPNs
1424 = 84, mSPNs =717), BB = benefit-benefit easy (sSPNs = 50, mSPNs =515 , chocolate milk
1425 concentration <50), BB = benefit-benefit difficult (sSPNs =33, mSPNs = 731, chocolate milk
1426 concentration >=50).

1427 We binned the firing rates of sSPN and mSPN during the -3s to 3s window across all tasks into
1428 1-5 bins. We used these firing rates to determine cross-correlation (MATLAB's `xcorr()`) between
1429 sSPN and mSPN recorded in the same session. Correlated pairs were defined as paired sSPN
1430 and mSPN that had a linear regression fit with correlation squared (MATLAB's `corrcoef()`) > 0.5
1431 and significance $p < 0.04$. To obtain the percentage of significantly correlated neurons, we counted
1432 the number of pairs that met the threshold for correlation and divided by the total number of
1433 identified pairs. Examples are plotted in **Extended Data Figs. 2e,f** and counts in **Extended Data**
1434 **Fig. 2g**.

1435 To determine significance threshold for the counts of correlated pairs, we shuffled the sSPN and
1436 mSPN pairs across the database. We then performed the process above on the shuffled data.
1437 Using these shuffled pairs, we formed a distribution of correlations that might happen by chance.
1438 The threshold of significance was set to the 3 standard deviation mark among this distribution of
1439 shuffled pairs.

1440 To produce **Extended Data Figs. 2e,f**, first follow the steps in `run_me.m` to generate
1441 `'pairsTableControl.mat'`, `'pairsTableStress.mat'`, and `'pairsTableStress2.mat'` are first generated.

1442 Then run the following lines of code in MATLAB:

```
1443 examplePairedNeuronPLot('twdb_control', 'PLSvsFSI', 54); % Figure S2E  
1444 examplePairedNeuronPLot('twdb_stress', 'PLSvsFSI', 32); % Figure S2F
```

1445 For the code that calls the figure creation in **Extended Data Fig. 2g**, see
1446 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Fig7A_triplet-example/updated_cross_correlation.m)
1447 [Counts/Fig7A_triplet-example/updated_cross_correlation.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Fig7A_triplet-example/updated_cross_correlation.m)

1448 The fitting occurs in:
1449 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Fig7A_triplet-example/matrix_strio_plot_dynamics.m)
1450 [Counts/Fig7A_triplet-example/matrix_strio_plot_dynamics.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Fig7A_triplet-example/matrix_strio_plot_dynamics.m)

1451

1452 **Connected SPNs through Granger causality.**

1453 sSPN and mSPN pairs were identified similarly to the previous section. 14785 cells across 14
1454 control animals were analyzed and 25758 cells across 9 stress animals. The total identified
1455 number of striosomal and matrix cells for each of the tasks are the following: Control CC = cost-
1456 cost (sSPNs =46 , mSPNs = 400), Control BB = benefit-benefit (sSPNs =83 , mSPNs = 1246),
1457 Control CBC = cost-benefit conflict (sSPNs = 84, mSPNs =717), Stress CBC = cost-benefit conflict
1458 (sSPNs =41 , mSPNs =898), Stress BB = benefit-benefit (sSPNs = 156, mSPNs = 2813).

1459 Then firing rates were determined over the span of the session by binning each trial into bins of
1460 100ms. Granger causality (MATLAB's gctest()) was run on these sSPN and mSPN firing rate pairs
1461 to determine whether each pair was functionally connected. In control animals, 92 connected
1462 pairs were identified for the cost-benefit conflict task, 77 connected pairs for the cost-cost task, 1
1463 connected pair for the non-conflict cost-benefit task, and 116 pairs for the benefit-benefit task. In
1464 stress animals, 110 connected pairs were identified for the cost-benefit conflict task and 292
1465 connected pairs for the benefit-benefit task.

1466 Next, for each of the trials with a functionally connected sSPN and mSPN pair, the class of motif
1467 was determined as either sSPN excited / mSPN excited, sSPN excited / mSPN inhibited, sSPN
1468 inhibited / mSPN excited, or sSPN inhibited / mSPN inhibited. These classes were formed by
1469 identifying whether, separately, the neurons were excited, inhibited, or neither in each of 5 blocks
1470 per each trial ([-15s, -3s], [-3s 0s], [0s 2.5s], [2.5s, 4.5s], [4.5s 20s]). A motif was counted if in a
1471 certain block each neuron was either excited or inhibited.

1472 Excited or inhibited classifications were determined through inter-spike interval analysis, plotted
1473 in **Extended Data Figs. 2h-j**. The median inter-spike interval for each neuron across the full trial
1474 was calculated. A neuron was considered inhibited during the periods of the trial when inter-spike
1475 exceeded median. Conversely, a neuron was considered inhibited during periods when inter-spike
1476 interval fell below median. Excited blocks were defined as blocks where excitation time exceeded
1477 inhibition time inhibited by 10%. Inhibited blocks were defined, oppositely, as blocks where
1478 inhibition time exceeded excitation time by 10%. Blocks that reached neither threshold were not
1479 classified.

1480 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/plotBins.m), see
1481 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/plotBins.m)
1482 [Counts/Pattern%20Analysis/plotBins.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/plotBins.m).

1483 Patterns were counted across the 5 bins and added across trials within the same group (e.g.
1484 control cost-benefit conflict). The total count, as plotted in **Fig. 2e**, was divided by the number of
1485 trials to form an average number of functionally connected neurons across the 5 bins of the trial.

1486 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/allMaps/Maps%20By%20Task%20Type/createLinearPatternCountGraphsByTaskType.m), see
1487 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/allMaps/Maps%20By%20Task%20Type/createLinearPatternCount)
1488 [Counts/Pattern%20Analysis/allMaps/Maps%20By%20Task%20Type/createLinearPatternCount](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/allMaps/Maps%20By%20Task%20Type/createLinearPatternCount)
1489 [GraphsByTaskType.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/allMaps/Maps%20By%20Task%20Type/createLinearPatternCountGraphsByTaskType.m).

1490 Significance was determined similarly to the section above. Pairs of neurons, not necessarily
1491 functionally connected, were shuffled. From a shuffled distribution, the 3 standard deviation mark
1492 was identified and considered to be the threshold of significance.

1493 For [code](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/createRandomPatterns.m), see
1494 [https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/createRandomPatterns.m)
1495 [Counts/Pattern%20Analysis/createRandomPatterns.m](https://github.com/dirkbeck/DM_space_model/blob/main/Cross%20Correlation%20Pattern%20Counts/Pattern%20Analysis/createRandomPatterns.m)

1496

1497 **Analyzing neural dimensionality reduction.**

1498 In the analysis plotted in **Fig. 2f**, using data from the Corticostriosomal Circuit Stress Experiment
1499 database, we analyzed firing rates of 1) PL neurons that project to striatum (i.e. sSPN-projecting
1500 cortex, 221 sessions, 2-47 neurons per session), 2) FSIs (96 sessions, 2-12 neurons per session),
1501 3) sSPNs (27 sessions, 2-9 neurons per session), and 4) mSPN (13 sessions, 2-6 neurons per
1502 session). For methods of classification see Friedman et al. (2017). Spike data was converted to
1503 firing rates by separating the spikes into 5-10 bins.

1504 Covariance between the neurons was determined from the firing rates of simultaneously recorded
1505 neurons over time. For each trial, the effective correlation¹³⁸
1506 was calculated from the activities of the p neurons over time X :

1507

$$1508 \quad (45) \quad \text{effective correlation} = 1 - \|\text{Corr}(X)\|^{1/p}$$

1509

1510 Effective correlations were then averaged across trials. Confidence intervals were determined
1511 from standard error between the sessions.

1512 Code is in the directory
1513 https://github.com/dirkbeck/DM_space_model/tree/main/neuron_pair_analysis.

1514 neuronSynchronyPlot.m generates the plot, which takes input files 'sessionDataOf....mat'.

1515 These input mat files are generated by the 'covAndBinCtMatrixOfNeuronsFromSameSession.m'
1516 function which takes input files 'sameSession....mat'.

1517 These input files are generated by 'extractNeuronsFromSameSession.m' function.

1518

1519 **Changes to choice after adding cost to a reward offer.**

1520 In the analysis plotted in **Extended Data Fig. 3j**, we sought to define choice patterns before and
1521 after stress when a small cost was added to a reward offer. To do this, we analyzed choice data
1522 from the CBC task before and after stress (i.e. reward and a small cost) and in the BB task before
1523 after stress (i.e. only reward). We recorded the approach percentage across sessions and then
1524 averaged these between groups. Data from 17 rodents across 38 tasks is used for Control CBC,
1525 data from 13 rodents across 24 tasks for Stress CBC, data from 23 rodents across 114 tasks for
1526 Control BB, and data from 14 rodents across 116 tasks for Stress BB.

1527 For data, see
1528 https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/experimental_data_analysis_choice_before_after_stress.xlsx.

1530

1531 **Analyzed cortex-FSI connectivity.**

1532 Using data from the Corticostriosomal Circuit Stress Experiment database (published with
1533 Friedman et al. (2017)), firing rates and striatum-projecting prelimbic cortex neurons (i.e. sSPN-
1534 projecting cortex) and FSI were analyzed. For details regarding neuron classification, see
1535 Friedman et al. (2017). Spike data was converted to firing rates by separating data into 5-10 bins.
1536 A linear regression of the form $a \cdot x + b$ was fit through the firing rates. Examples are plotted in
1537 **Extended Data Figs. 3k,l** and averages of the square of Pearson correlation coefficient across
1538 neuron pairs and the a slope parameter from the regression fit are plotted in **Extended Data**
1539 **Figs. 3o,p**. 78 neuron pairs across 7 rodents were analyzed before stress and 37 neuron pairs
1540 were analyzed across 4 rodents after stress.

1541 Code is in the directory
1542 https://github.com/dirkbeck/DM_space_model/tree/main/neuron_pair_analysis.

1543 To produce **Extended Data Figs. 3k,l**, go to the directory
1544 https://github.com/dirkbeck/DM_space_model/tree/main/neuron_pair_analysis and run
1545 `examplePairedNeuronPLot('twdb_control', 'PLSvsFSI', 54)`,
1546 `examplePairedNeuronPLot('twdb_stress', 'PLSvsFSI', 32)`, respectively.

1547 To produce **Extended Data Figs. 3o,p**, go to the directory
1548 https://github.com/dirkbeck/DM_space_model/tree/main/neuron_pair_analysis and run
1549 `plotFitParamOfNeuronTriplets.m`.

1550

1551 **Modeled cortex-FSI connectivity after stress.**

1552 Connected cortical neurons and FSI show increased correlation and reduced slopes between
1553 their firing rates after stress (**Extended Data Figs. 3k,l,o,p**). To understand how this impacts
1554 SPNs, we modeled two changes to the cortex→FSI connectivity that might produce the
1555 experimental results (**Extended Data Figs. 3q,r**). A first factor, connection weight w_i , measured
1556 the strength of connection between the i th connected cortical neuron and the FSI, that is, how
1557 strongly FSI would respond to an increase in activity in the connected cortical neuron. A second
1558 factor, number of connections c , measured the number of connected cortical neurons to the FSI.

1559 We solved for correlation between the neurons and slope using identities that link covariance,
1560 correlation, and slope. This process assumes that FSI receives input only from the cortex.

1561

1562 (46) $\text{correlation}(\text{cortex 1, FSI}) = \frac{\text{cov}(\text{cortex 1, FSI})}{\sqrt{\text{var}(\text{cortex 1}) \cdot \text{var}(\text{FSI})}}$

1563

1564 (47) $\text{slope}(\text{cortex 1, FSI}) = \frac{\text{cov}(\text{cortex 1, FSI})}{\text{var}(\text{FSI})}$

1565

1566 (48) $\text{cov}(\text{cortex 1, FSI}) = w_1 \text{var}(\text{cortex 1}) + \sum_{i=2}^c w_i \cdot \text{cov}(\text{cortex 1, cortex } i)$

1567

1568 (49) $\text{var}(\text{FSI}) = \sum_{i=1}^c w_i^2 \text{var}(\text{cortex } i) + \sum_{i=1}^c \sum_{\substack{j=1 \\ j \neq i}}^c w_i w_j \text{cov}(\text{cortex } i, \text{cortex } j)$

1569

1570 For simplicity, we assumed in our analysis that variance is equal across cortical neurons projecting
 1571 to the FSI (i.e. $\text{var}(\text{cortex 1}) = \text{var}(\text{cortex 2}) = \dots = \text{var}(\text{cortex } c)$) and that the covariance between those
 1572 neurons is equal (i.e. $\text{cov}(\text{cortex 1, cortex } i) = \text{cov}(\text{cortex 1, cortex 2}) = \text{cov}(\text{cortex 1, cortex 3}) = \dots = \text{cov}(\text{cortex 1, cortex } c)$). So, in
 1573 the analysis plotted in **Extended Data Figs. 3q,r**, we substitute uniform variance and covariance
 1574 to obtain:
 1575

1576

1577 (50) $\text{correlation}(\text{cortex 1, FSI}) = \sqrt{\frac{\text{var}(\text{cortex 1}) + (c - 1) \cdot \text{cov}(\text{cortex 1, cortex } i)}{c \cdot \text{var}(\text{cortex 1})}}$

1578

1579 (51) $\text{slope}(\text{cortex 1, FSI}) = \frac{1}{cw}$

1580

1581 where:

- 1582 • c is the number of cortex neurons connected to each FSI
 1583 • w is the weight of each cortex→FSI connection

1584 Thus, changes in strength of connection may be more likely to affect slope, while changes in the
 1585 quantity of connections, the covariance between cortical neurons, and the variance of cortical

1586 neurons may also affect the cortex to FSI correlation. In stress, correlation and slope are both
1587 larger, suggesting reduction in quantity of cortex to FSI connections.

1588 For [https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/ctx_to_FSI_sync](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/ctx_to_FSI_sync_hrony_analysis.m) see
1589 [hrony_analysis.m](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/ctx_to_FSI_sync_hrony_analysis.m).
1590

1591

1592 **Simulation illustrating the theoretical change.**

1593 We then conducted a simulation to examine the case where cortical data and cortex to FSI
1594 connectivities were less uniform. To do this, we constructed a network with random unit normal
1595 connection weights from cortex to FSI. Then we randomly lesioned all but several of the
1596 connections to reflect the sparsity of the brain. The connection from the first cortical neuron to the
1597 FSI was always preserved.

1598 In each of ten simulations, a cortical input to sSPN was generated as a random unit normal 100x1
1599 vector. Activity of the first cortical neuron and the FSI was recorded. These are plotted in
1600 **Extended Data Figs. 3m,n** along with a linear regression fit.

1601 For [https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/ctx_to_FSI_sync](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/ctx_to_FSI_sync_hrony_analysis.m) see
1602 [hrony_analysis.m](https://github.com/dirkbeck/DM_space_model/blob/main/disorder_hypotheses/ctx_to_FSI_sync_hrony_analysis.m).
1603

1604

1605 **Supplemental References**

1606

1607 95. Lévesque, M. & Parent, A. The striatofugal fiber system in primates: A reevaluation of its
1608 organization based on single-axon tracing studies. *Proc. Natl. Acad. Sci. U.S.A.* **102**,
1609 11888–11893 (2005).

1610 96. Bevan, M. D., Bolam, J. P. & Crossman, A. R. Convergent Synaptic Input From the
1611 Neostriatum and the Subthalamus Onto Identified Nigrothalamic Neurons in the Rat. *Eur J*
1612 *of Neuroscience* **6**, 320–334 (1994).

1613 97. Hajós, M. & Greenfield, S. A. Synaptic connections between pars compacta and pars
1614 reticulata neurones: electrophysiological evidence for functional modules within the
1615 substantia nigra. *Brain Research* **660**, 216–224 (1994).

- 1616 98. Ragsdale, C. W. & Graybiel, A. M. Fibers from the basolateral nucleus of the amygdala
1617 selectively innervate striosomes in the caudate nucleus of the cat. *J of Comparative*
1618 *Neurology* **269**, 506–522 (1988).
- 1619 99. Fujiyama, F., Unzai, T. & Karube, F. Thalamostriatal projections and striosome-matrix
1620 compartments. *Neurochem Int* **125**, 67–73 (2019).
- 1621 100. Ragsdale, C. W. & Graybiel, A. M. Compartmental organization of the thalamostriatal
1622 connection in the cat. *J of Comparative Neurology* **311**, 134–167 (1991).
- 1623 101. Unzai, T., Kuramoto, E., Kaneko, T. & Fujiyama, F. Quantitative Analyses of the Projection
1624 of Individual Neurons from the Midline Thalamic Nuclei to the Striosome and Matrix
1625 Compartments of the Rat Striatum. *Cereb Cortex* **27**, 1164–1181 (2017).
- 1626 102. Martínez-Selva, J. M., Sánchez-Navarro, J. P., Bechara, A. & Román, F. [Brain
1627 mechanisms involved in decision-making]. *Rev Neurol* **42**, 411–418 (2006).
- 1628 103. Zhou, J. *et al.* Evolving schema representations in orbitofrontal ensembles during learning.
1629 *Nature* **590**, 606–611 (2021).
- 1630 104. Hamid, A. A. *et al.* Mesolimbic dopamine signals the value of work. *Nat. Neurosci.* **19**, 117–
1631 26 (2016).
- 1632 105. Schultz, W. Dopamine reward prediction-error signalling: a two-component response. *Nat*
1633 *Rev Neurosci* **17**, 183–195 (2016).
- 1634 106. Assous, M. & Tepper, J. M. Excitatory extrinsic afferents to striatal interneurons and
1635 interactions with striatal microcircuitry. *Eur J of Neuroscience* **49**, 593–603 (2019).
- 1636 107. Ho, T. S. Y. & Lee, S. Term Structure Movements and Pricing Interest Rate Contingent
1637 Claims. *The Journal of Finance* **41**, 1011–1029 (1986).
- 1638 108. Bergman, H. *et al.* Physiological aspects of information processing in the basal ganglia of
1639 normal and parkinsonian primates. *Trends in Neurosciences* **21**, 32–38 (1998).

- 1640 109. Jhou, T. C. The rostromedial tegmental (RMTg) “brake” on dopamine and behavior: A
1641 decade of progress but also much unfinished work. *Neuropharmacology* **198**, 108763
1642 (2021).
- 1643 110. Baker, P. M., Rao, Y., Rivera, Z. M. G., Garcia, E. M. & Mizumori, S. J. Y. Selective
1644 Functional Interaction Between the Lateral Habenula and Hippocampus During Different
1645 Tests of Response Flexibility. *Front. Mol. Neurosci.* **12**, 245 (2019).
- 1646 111. Nielson, H. C. & McIver, A. H. Cold stress and habenular lesion effects on rat behaviors.
1647 *Journal of Applied Physiology* **21**, 655–660 (1966).
- 1648 112. Ilango, A. *et al.* Similar Roles of Substantia Nigra and Ventral Tegmental Dopamine
1649 Neurons in Reward and Aversion. *J. Neurosci.* **34**, 817–822 (2014).
- 1650 113. Shabel, S. J., Proulx, C. D., Trias, A., Murphy, R. T. & Malinow, R. Input to the lateral
1651 habenula from the basal ganglia is excitatory, aversive, and suppressed by serotonin.
1652 *Neuron* **74**, 475–81 (2012).
- 1653 114. Hyvärinen, A. Independent component analysis: recent advances. *Phil. Trans. R. Soc. A.*
1654 **371**, 20110534 (2013).
- 1655 115. Gupta, A. *et al.* Neural Substrates of the Drift-Diffusion Model in Brain Disorders. *Front.*
1656 *Comput. Neurosci.* **15**, 678232 (2022).
- 1657 116. Murray, J. D. Models for Interacting Populations. in *Mathematical Biology* (ed. Murray, J.
1658 D.) vol. 17 79–118 (Springer New York, New York, NY, 1993).
- 1659 117. Wager, T. D. *et al.* A Bayesian Model of Category-Specific Emotional Brain Responses.
1660 *PLoS Comput Biol* **11**, e1004066 (2015).
- 1661 118. Friedman, A., Keselman, M. D., Gibb, L. G. & Graybiel, A. M. A multistage mathematical
1662 approach to automated clustering of high-dimensional noisy data. *Proc Natl Acad Sci U S*
1663 *A* **112**, 4477–4482 (2015).
- 1664 119. Abeles, M., Hayon, G. & Lehmann, D. Modeling Compositionality by Dynamic Binding of
1665 Synfire Chains. *J Comput Neurosci* **17**, 179–201 (2004).

1666 120. Hayon, G., Abeles, M. & Lehmann, D. A Model for Representing the Dynamics of a System
1667 of Synfire Chains. *J Comput Neurosci* **18**, 41–53 (2005).

1668 121. Berke, J. D. Functional properties of striatal fast-spiking interneurons. *Frontiers in systems*
1669 *neuroscience* **5**, 45 (2011).

1670 122. McKeon, P. N., Bunce, G. W., Patton, M. H., Chen, R. & Mathur, B. N. Cortical control of
1671 striatal fast-spiking interneuron synchrony. *The Journal of Physiology* **600**, 2189–2202
1672 (2022).

1673 123. Sciamanna, G., Ponterio, G., Mandolesi, G., Bonsi, P. & Pisani, A. Optogenetic stimulation
1674 reveals distinct modulatory properties of thalamostriatal vs corticostriatal glutamatergic
1675 inputs to fast-spiking interneurons. *Sci Rep* **5**, 16742 (2015).

1676 124. Peters, A. J., Fabre, J. M. J., Steinmetz, N. A., Harris, K. D. & Carandini, M. Striatal activity
1677 topographically reflects cortical activity. *Nature* **591**, 420–425 (2021).

1678 125. Plenz, D. & Kitai, S. T. Up and Down States in Striatal Medium Spiny Neurons
1679 Simultaneously Recorded with Spontaneous Activity in Fast-Spiking Interneurons Studied
1680 in Cortex–Striatum–Substantia Nigra Organotypic Cultures. *J. Neurosci.* **18**, 266–283
1681 (1998).

1682 126. Humphries, M. D., Wood, R. & Gurney, K. Reconstructing the Three-Dimensional
1683 GABAergic Microcircuit of the Striatum. *PLoS Comput Biol* **6**, e1001011 (2010).

1684 127. Liénard, J. & Girard, B. A biologically constrained model of the whole basal ganglia
1685 addressing the paradoxes of connections and selection. *J Comput Neurosci* **36**, 445–468
1686 (2014).

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KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Corticostriosomal Circuit Stress Experiment	Friedman et al. (2017)	https://data.mendeley.com/datasets/z9jd8xhj84/1
A decision-space model explains context-specific decision-making	This paper	https://doi.org/10.7910/DVN/SMKW01
Overview of the model	This paper	https://github.com/dirkbeck/DM_space_model/tree/main/model_overview
Tests of the model	This paper	https://github.com/dirkbeck/DM_space_model/tree/main/model_tests
Disorder hypotheses	This paper	https://github.com/dirkbeck/DM_space_model/tree/main/disorder_hypotheses
Instances 2 (sparse connectivity) and 3 (dynamics)	This paper	https://github.com/dirkbeck/DM_space_model/tree/main/dynamic_model_and_neural_net
Day to day differences and disorder comorbidity	This paper	https://github.com/dirkbeck/DM_space_model/tree/main/day_to_day_space_sampling
Circuit adjustment between trials	This paper	https://github.com/dirkbeck/DM_space_model/tree/main/circuit_trajectories
Analysis of the correlation between cortical neurons, FSIs, sSPNs, and mSPNs during decision-making	This paper	https://github.com/dirkbeck/DM_space_

		model/tree/main/neuron_pair_analysis
Analysis of the functional connectivity of sSPNs and mSPNs during decision-making	This paper	https://github.com/dirkbeck/DM_space_model/tree/main/Cross%20Correlation%20Pattern%20Counts
Software and algorithms		
MATLAB R2021a	Mathworks	https://www.mathworks.com/products/matlab.html