

# **Coding of behaviorally relevant and irrelevant cue features in the nucleus accumbens**

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**1 Abstract**

**2 to do**

**3 Significance Statement (120 words)**

**4 to do**

## 5 Introduction

6 Theories of nucleus accumbens (NAc) function generally agree that this brain structure contributes to moti-  
7 vated behavior, with some emphasizing a role in learning from reward prediction errors (Joel, Doya, Schultz;  
8 see also the addiction literature on the effects of drug rewards; Nestler, Kalivas; Carelli) and others a role  
9 in the modulation of ongoing behavior through stimuli associated with motivationally relevant outcomes  
10 (invigorating, directing; Nicola, Floresco, Salamone). These proposals echo similar ideas on the functions  
11 of the neuromodulator dopamine (Schultz, Berridge, Maia/Frank, Cools), with which NAc is tightly linked  
12 functionally as well as anatomically (Haber, Sesack, something more recent).

13 Much of our understanding of NAc function comes from studies of how cues that predict motivationally  
14 relevant outcomes (e.g. reward) influence behavior and neural activity in the NAc. Task designs that associate  
15 such cues with rewarding outcomes provide a convenient access point eliciting conditioned responses such  
16 as sign-tracking and goal-tracking (Robinson), pavlovian-instrumental transfer (Balleine) and response vigor  
17 (Niv; McGinty) which tend to be affected by NAc manipulations (Flagel, Balleine, Chang; although not  
18 always straightforwardly: Hauber, Chang). Similarly, analysis of reward prediction errors typically proceeds  
19 by establishing an association between a cue and subsequent reward, with NAc responses transferring from  
20 outcome to the cue with learning (Schultz, Schoenbaum, Carelli). WHAT ABOUT HUMAN WORK

21 Surprisingly, although substantial work has been done on the coding of outcomes predicted by such cues  
22 (e.g. reward value; Hollerman/Schultz, Roesch, Day; reward identity; Cooch), much less is known about  
23 how reward-predictive cues themselves are encoded in the NAc (Hayden from primate realm). This is an  
24 important issue for at least two reasons. First, in reinforcement learning, motivationally relevant outcomes  
25 are typically temporally delayed relative to the cues that predict them. In order to solve the problem of  
26 assigning credit (or blame) across such temporal gaps, some trace of preceding activity needs to be main-  
27 tained (Maia?). Since NAc is a primary target of DA signals interpretable as RPEs, its activity trace will help  
28 determine what can be learned when RPEs arrive.

29 Second, for ongoing behavior, the relevance of cues typically depends on context. In experimental settings,  
30 context may include the identity of a preceding cue (occasion setter, Holland, Kesner), spatial or configural  
31 arrangements (Good/Honey, Eichenbaum), and unsignaled rules as occurs in set shifting and other cognitive  
32 control tasks (CITE). In such situations, the question arises how selective, context-dependent processing of  
33 reward-predictive cues is implemented. For instance, is there a gate prior to NAc, or are all cues represented  
34 in NAc but their current values dynamically updated (FitzGerald; WHAT ARE SOME THEORETICAL  
35 POSITIONS ON THIS)?

36 Thus, both from a learning and a flexible performance perspective, it is of interest to determine how cue  
37 identity is represented in the brain, with NAc of particular interest given its anatomical and functional posi-  
38 tion at the center of motivational systems. We sought to determine whether cue identity is represented in the  
39 NAc, and if various cue features are represented alongside other motivationally relevant variables, such as  
40 cue value (Figure 1). To address this question, we designed an experiment in which multiple, distinct sets of  
41 cues predicted the same outcome. We recorded the activity of NAc neurons as rats performed this task.

42 [Figure 1 about here.]

## 43 Methods

### 44 Subjects:

45 Adult male Long-Evans rats ( $n = 4$ , Charles River, Saint Constant, QC) were used as subjects. Rats were in-  
46 dividually housed with a 12/12-h light-dark cycle, and tested during the light cycle. Rats were food deprived  
47 to 85-90% of their free feeding weight (weight at time of implantation was 440 - 470 g), and water restricted  
48 4-6 hours before testing. All experimental procedures were approved by the the University of Waterloo An-

49 imal Care Committee (protocol# 11-06) and carried out in accordance with Canadian Council for Animal  
50 Care (CCAC) guidelines.

51 **Overall timeline:**

52 Each subject was first handled for seven days where they were exposed to the running room, the sucrose  
53 solution, and the click of the valves upon approach to the receptacles. They were then shaped to run on the  
54 task for seven days where they were restricted to running in the clockwise direction by presenting a physical  
55 barrier to running counterclockwise. Rats underwent hyperdrive implantation after showing discrimination  
56 of approach behavior for rewarded and unrewarded cues for three consecutive days according to a chi square  
57 test. Rats were allowed to recover for a minimum of five days before being retrained on the task, and  
58 recording began once performance returned to pre-surgery levels. Upon completion of recording, animals  
59 were sacrificed and recording sites were histologically confirmed.

60 **Behavioral task and training:**

61 Rats were trained to run clockwise on an elevated, square-shaped track (100x100 cm) containing four possi-  
62 ble reward locations (Figure 2). Rats initiated a trial by running down the length of an arm, and triggering a  
63 photobeam located 24 cm from the start of each arm. Upon trial initiation, a cue was presented that signaled  
64 the presence or absence of a 12% sucrose water reward (0.1 mL) at the upcoming site. A trial was classified  
65 as an approach trial if the rat turned left at the decision point and made a nosepoke at the reward receptacle  
66 (40 cm from the decision point), while trials were classified as a skip trial if the rat instead turned right at the  
67 decision point and triggered the photobeam to initiate the following trial. There was a 1 second delay from  
68 a rewarded nosepoke and reward delivery. Each day rats were trained in both a light and sound block for  
69 100 trials each. Within a block, one cue signaled reward was available on that trial, while the other signaled  
70 reward was not available. Light block cues were a flashing white light, and a constant yellow light. Sound  
71 block cues were a 2 kHz sine wave and a 8 kHz sine wave whose amplitude was modulated from 0 to maxi-

72 mum by a 2 Hz sine wave. Reward-cue associations were counterbalanced across rats. Cue presentation was  
73 pseudorandomized so that the same cue could not be presented more than twice in a row. Block order within  
74 each day was also pseudorandomized, such that the rat could not start with the block within a session more  
75 than two days in a row. Each training or testing day consisted of a 5 minute pre-session period on a pedestal,  
76 followed by the first block, then the second block, then a 5 minute post-session period on the pedestal. Ac-  
77 curacy was determined by the proportion of trials a rat approached each cue. Perfect performance would be  
78 100% approach on approach trials (reward available), and 0% approach on skip trials (no reward available).  
79 Trial length was determined by measuring the length of time from cue onset until nosepoke or the start of the  
80 following trial. Rats were trained daily until they could distinguish between the rewarded and unrewarded  
81 cues for both light and sound blocks for three consecutive days according to a chi-square test, at which point  
82 they underwent surgery.

[Figure 2 about here.]

84 **Surgery:**

85 Surgical procedures were as described previously (Malhotra et al., 2015). Briefly, animals were anesthetized  
86 with isoflurane, induced with 5% in medical grade oxygen and maintained at 2% throughout the surgery  
87 (0.8 L/min). Rats were then chronically implanted with a hyperdrive consisting of 16 independently drivable  
88 tetrodes, either all 16 targeted for the right NAc (AP +1.4 mm and ML +1.6 mm, relative to bregma; Paxinos  
89 and Watson, 2005), or 12 in the right NAc and 4 targeted at the mPFC (AP +3.0 mm and ML +0.6 mm,  
90 relative to bregma; only data from NAc tetrodes were analyzed). Following surgery, all animals were given  
91 a least five days to recover and lower tetrodes to the target (DV -6.0 mm) before being reintroduced to the  
92 behavioral task.

## 93 Data acquisition and preprocessing:

94 After recovery, rats were placed back on the task for recording. NAc signals were acquired at 20 kHz with  
95 a RHA2132 v0810 preamplifier (Intan) and a KJE-1001/KJD-1000 data acquisition system (Amplipex).  
96 Signals were referenced against a tetrode placed in the corpus callosum above the NAc.

97 Candidate spikes for sorting into putative single units were obtained by band-pass filtering the data between  
98 600-9000 Hz, thresholding and aligning the peaks (UltraMegaSort2k, Hull et al., 2011). Spike waveforms  
99 were then clustered with KlustaKwik using energy and the first derivative of energy as features (peak, valley,  
100 peak index, wave PC1, time were used as extra features, does this need to be included?), and manually  
101 sorted into units (MClust 3.5, A.D. Redish et al.). Isolated units containing a minimum of 200 spikes within  
102 a session were included for subsequent analysis. Units were classified as high firing neurons if they had high  
103 tonic firing rates marked by an absence of interspike intervals (ISIs) > 2 s, while medium spiny neurons had  
104 a combination of ISIs > 2 s and phasic activity with shorter ISIs (Barnes 2005, Atallah 2014).

105 **Data analysis:**

106 Average firing rates for a session were generated for the 1 s preceding cue-onset, and the 1 s following cue-  
107 onset. Single units were considered to be cue-responsive if both the mean firing rate difference between pre-  
108 and post-cue onset was within the lower or upper 2.5% of a shuffled distribution, and a Wilcoxon signed-  
109 rank test comparing pre- and post-cue firing was  $p < .01$ . Units were classified as having either an excitatory  
110 or inhibitory response if the post-cue activity was higher or lower than the pre-cue activity, respectively. A  
111 stepwise general linear model (GLM) was then fit to cue-responsive units using cue modality, cue location,  
112 cue outcome, approach behavior, trial length, trial number, and trial history as potential predictors. Units  
113 were classified as being modulated by a given task parameter if addition of the parameter significantly im-  
114 proved the model fit using deviance as the criterion ( $p < .01$ ). Perievent time histograms (PETHs) were  
115 generated by smoothing firing rates with a gaussian kernel. To align the data in the heat plots, firing rates of  
116 each units were z-scored then ordered by location of their peak firing rate. All analyses were completed in  
117 MATLAB R2015a, and the code is available on GitHub.

<sup>118</sup> **Histology:**

<sup>119</sup> Upon completion of the experiment, rats were anesthetized with 5% isoflurane, then asphyxiated with carbon  
<sup>120</sup> dioxide. Transcardial perfusions were performed, and brains were fixed and removed. Brains were sliced in  
<sup>121</sup> 50 um coronal sections and stained with thionin. Slices were visualized under light microscopy, and tetrode  
<sup>122</sup> placement was determined (Figure 3).

<sup>123</sup> [Figure 3 about here.]

<sup>124</sup> **Results**

<sup>125</sup> **Behavior**

<sup>126</sup> Rats were trained to discriminate between cues signalling the availability and absence of reward on a square  
<sup>127</sup> track with four identical arms. An example learning curve is seen in Figure 4A,B. All four rats learned to  
<sup>128</sup> discriminate between the rewarded and unrewarded cue for both the light and sound blocks as determined  
<sup>129</sup> by reaching significance ( $p < .05$ ) on a daily chi-square test comparing approach behavior for rewarded and  
<sup>130</sup> unrewarded cues for each block, for at least three consecutive days. Additionally, all four trial types had  
<sup>131</sup> relatively similar trial lengths (Figure 4C,D).

<sup>132</sup> [Figure 4 about here.]

<sup>133</sup> **NAc neurons encode behaviorally relevant and irrelevant cue features**

<sup>134</sup> **General responses to cue:**

<sup>135</sup> A total of 443 units were recorded in the NAc from 4 rats over 57 sessions. The activity of 171 (39%) of  
<sup>136</sup> these was modulated by the cue, with more units showing a decrease in firing ( $n = 124$ ) than an increase  
<sup>137</sup> ( $n = 47$ ) around the time of the cue (Table 1). Within this group, 32 were classified as HFNs, while 139  
<sup>138</sup> were classified as SPNs. Fitting a GLM to each unit revealed that a variety of task parameters accounted  
<sup>139</sup> for a significant portion of firing rate variance in NAc cue-modulated units (Figure 6). Notably, there were  
<sup>140</sup> units that discriminated between whether the rat was performing in the light or sound block, which arm the  
<sup>141</sup> rat was currently on, and whether the rat was engaged in a rewarded or unrewarded trial (Figure 5A-F).  
<sup>142</sup> Interactions between multiple cue features appeared as significant predictors of firing rate variance for x %  
<sup>143</sup> units, although this effect was relatively modest (Figure 5G,H).

<sup>144</sup> [Figure 5 about here.]

<sup>145</sup> [Figure 6 about here.]

<sup>146</sup> **Population level responses:**

<sup>147</sup> To get a better sense of how cue information was encoded at the population level, firing activity was nor-  
<sup>148</sup> malized then averaged for each cell whose firing rate was modulated by a given cue feature. Plotting these  
<sup>149</sup> averages aligned to cue-onset revealed that as a population, units whose activity was modulated by cue  
<sup>150</sup> modality showed a difference in firing rate across blocks that extended beyond the transient response to the  
<sup>151</sup> cue (Figure 7A,B). Additionally, units whom had exhibited a decrease in firing in response to the cue and  
<sup>152</sup> whose activity was modulated by cue outcome, showed a sustained response that extended beyond cue-onset

153 (Figure 7F).

154

[Figure 7 about here.]

155 **NAc units segment the task:**

156 It has been shown that NAc neurons are not silent outside of key task events. To look at the distribution of  
157 responses across the entire task, we z-scored the firing rate of each unit and plotted the normalized firing rates  
158 of all units aligned to cue-onset and according to peak firing rate. We did this separately for both the light  
159 and sound blocks, and found a nearly uniform distribution of firing fields in task space that was not limited  
160 to alignment to the cue (Figure 8). Furthermore, to see if this population level activity was similar across  
161 blocks, we also organized firing during the sound blocks according to the ordering derived from the light  
162 blocks. This revealed, that the overall firing was qualitatively different across the two blocks. Additionally,  
163 given that the majority of our units showed an inhibitory response to the cue, we also plotted the firing rates  
164 according to the lowest time in firing. This process was repeated for cue location and cue outcome, with  
165 similar results.

166

[Figure 8 about here.]

167 **Encoding of cue features is not limited to cue-onset:**

168 In order to be useful for learning, a trace of the cue must be maintained until the outcome. Fitting a GLM  
169 to firing rates at the time of a nosepoke response showed that a variety of units still discriminated firing  
170 according to various cue features (Figures 9, 10). Furthermore, aligning normalized peak firing rates to  
171 nosepoke onset, revealed a clustering of responses around reward receipt (Figure 11).

172

[Figure 9 about here.]

173

[Figure 10 about here.]

174

[Figure 11 about here.]

175 **Discussion**

176 The present study found evidence for coding of multiple identifying features of motivationally relevant stim-  
177 uli; the sensory modality of the presented cue, as well as its physical location within the track. Furthermore,  
178 this coding was both independent, and intermixed with coding for the associated outcome of the cue as well  
179 as motivational vigor, measured by time to complete the trial. At the population level, a tiling of task struc-  
180 ture was observed such that all points within our analyzed task space was accounted for by the ordered peak  
181 firing rates of all cells, and this tiling differed between blocks where sound or light cues were presented.  
182 Cells that discriminated across blocks were not simply due to drifting of the signal across trials, as cells that  
183 showed a drift in firing between the first and second half within a block were excluded from the analysis.  
184 Furthermore, even though actions were stereotyped during correct trials, such that the rat always turned left  
185 at the decision point to approach for reward, and right to skip the receptacle and initiate the next trial, cells  
186 that were modulated by the expected value of the cue maintained their specific firing patterns even during  
187 error trials where the rat turned left after presentation of the unrewarded cue, suggesting that these signals  
188 did not represent action values. Additionally, NAc signals have been shown to be modulated by response  
189 vigor, to detangle this from our results we included the trial length as a predictor in our GLMs, and found  
190 cells with correlates independent of trial length.

191 **Cue modality:**

192 Our finding that ventral striatal units can discriminate between cues from different sensory modalities ex-  
193 pands upon an extensive literature examining neural correlates of conditioned stimuli. Perhaps the most  
194 comparable work in rodents comes from a study that found distinct coding for an odor when it predicted  
195 separate but equally valued rewards (Cooch). The present work is complementary to this as it shows that  
196 ventral striatal cells have representations of identifiable aspects of the cue itself, in addition to the reward  
197 it predicts. Another study paired separate cues with appetitive or aversive outcomes, and found separate  
198 populations of cells that encode each cue, with many switching selectivity after reversal of the associations  
199 between the cues and outcomes, providing evidence that the NAc encodes the biological significance of  
200 stimuli. Once again, our study was different as we recorded neural responses to distinct cues encoding the  
201 same anticipated outcome, suggesting that even when the biological relevance of these stimuli is similar, the  
202 NAc dissociates their representations at the level of the single-unit (Setlow). Another possibility is that these  
203 modality specific cells were encoding the context, rule, or sequence within a session as some cells responded  
204 similar for both rewarded and unrewarded cues within a block. This interpretation is in alignment with a  
205 recent paper from the primate realm that recorded ventral striatal responses during the Wisconsin Card Sort-  
206 ing Task (WCST), a common set-shifting task used in both the laboratory and clinic, and found cells that  
207 preferred firing to stimuli when a certain rule, or rule category was currently active (Sleazeer). Indeed, an  
208 encoding of the current strategy could be an explanation as to why differentially tiling of task structure was  
209 observed across blocks in the current study. Further support for a modulation of NAc responses by strategy  
210 comes from an fMRI study that examined BOLD levels during a set-shifting task (FitzGerald et al., 2014). In  
211 this task, participants learned two sets of stimuli-reward contingencies, a visual set and auditory set. During  
212 testing they were presented with both simultaneously, and the stimulus dimension that was relevant was peri-  
213 odically shifted between the two. Here, they found that bilateral NAc activity reflected value representations  
214 of whatever the currently relevant stimulus dimension was, and not the irrelevant stimulus. The current find-  
215 ing of separate, but overlapping, populations of cells encoding cue modality and expected value, suggests  
216 that the fMRI finding is generated by the combined activity of several different functional cell types.

217 A caveat of the current study is that rats were never presented with both sets of cues simultaneously, and

thus never had to switch strategies, although extrapolating the data from the primate study, suggests that the activity of the cue modality cells would be modulated by relevance. Keeping along this theme, the current data set is unable to identify precisely what the modality-sensitive neurons were encoding, that is were they tracking representations of stimulus identity, a preferred context, or even a macroscale representation of progress through the session. Furthermore, their relevance for ongoing behavior is also uncertain. Nucleus accumbens core lesions have been shown to impair shifting between different behavioral strategies, and it is possible that selectively silencing the cells that prefer responding for a given modality or rule would impair performance when the animal is required to use that information, or artificial enhancement of those cells would cause them to use the rule when it is the inappropriate strategy.

**Encoding of position:**

Our finding that cue-evoked activity was modulated by cue location sides with some of the literature (Lavoie, 1994; Tabuchi, 2000; Strait, 2016). An alternative explanation for a pure spatial representation, is that these are task segmentation correlates, keeping track of where in the task the rat is. A previous non-human primate paper has shown that when reward is contingent upon completion of a series of trials, separate populations of NAc neurons signal the start of a schedule, subsequent trials in the schedule, and the first trial in extended schedules (Shidara et al., 1998). This signalling of position within a sequence has been observed in subsequent studies, and it is possible that the our rats were keeping track of which specific arm they were in as part of a sequence of arms, and not just strictly a spatial representation (Mulder, 2004 and 2005; Khamassi et al., 2008; Berke, 2009). Also, given that our task is pseudo-random, it is possible that the rats learned which cue to anticipate, and the neural activity could reflect this. However, this is unlikely as including a previous trial variable in the analysis did not explain a significant amount of firing rate variance in response to the cue for the vast majority of cells..

**Mixed selectivity:**

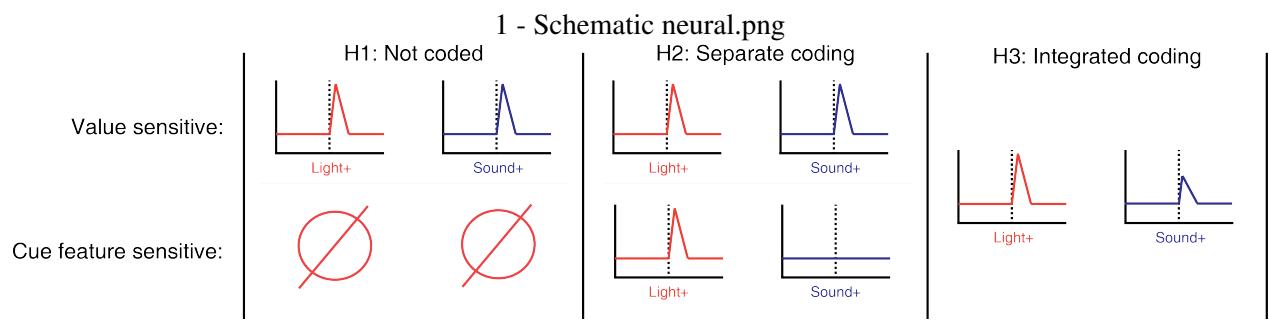
241 Several other papers have reported unit profiles that integrate different task-related variables. These papers  
242 report integrated coding between expected value and subsequent motor responses, expected value and iden-  
243 tity of a reward, and a combination of spatial-, movement-, and reward-related features (Roesch, Lavoie,  
244 Cooch). However, our study is the first to show mixed selectivity among identifying features of a cue and  
245 expected outcome or behavior. The presence of mixed selectivity responses confers a larger number of input-  
246 output relationships that are available to a given neuron. A possible functional consequence of this attribute  
247 of NAc units, is the combination and transformation of various motivationally relevant features into a sig-  
248 nal informing downstream decoders such as the ventral pallidum about appropriate behaviors in obtaining  
249 motivationally relevant goals and biasing action selection towards these behaviors. Mixed selectivity in the  
250 NAc could be a consequence of synaptic integration from a variety of anatomically distinct inputs, as seen  
251 in experiments examining the convergence of various NAc afferents at the level of synaptic transmission and  
252 stimulation-induced firing (Goto and Grace 2008). In one such experiment it was shown that NAc cells that  
253 responded to stimulation of either the fornix, amygdala, or PFC, typically responded to stimulation from all  
254 inputs (ODonnell and Grace, 1995). Furthermore, an interaction between these inputs was observed such  
255 that PFC stimulation failed to elicit spiking in the NAc neurons unless they were in a depolarized UP-state, a  
256 state induced by hippocampal stimulation and was dependent on an intact fornix. Hippocampal-induced sup-  
257 pression of other inputs has also been observed for the BLA (Mulder et al., 1998). Recently, it has also been  
258 shown that train stimulation of PFC afferents reduces hippocampal-evoked NAc responses, suggesting that  
259 there is competition between various inputs (Calhoon and ODonnell, 2013). These studies suggest that the  
260 integration of the variables we saw could be the result of this gating observed in behaviorally-independent  
261 preparations. However, given that we did not systematically manipulate these various limbic and cortical  
262 afferents, comments on the anatomical origins of the observed mixed selectivity responses are speculative at  
263 this point.

264 Integrating cue identity and value, as seen in the present study, could be one neural instantiation of how  
265 value is associated with the appropriate predictive stimuli (credit assignment), keeping in mind that value  
266 encoding is distributed, redundantly in some aspects, across various structures (Hayden Nat Neuro opinion).

267 Indeed, lesions of the NAc impair the ability to learn changes in reward value or identity in an unblocking  
268 experiment, as well as disrupting dopamine RPEs generated by modification of timing of reward (McDannald  
269 2011, Takahashi 2016). Would be interesting to see if uncoupling the integrated coding of stimulus features  
270 and predictive properties of a cue has an effect on the ability of a rat to use reward-predictive cues to pursue  
271 the associated reward.

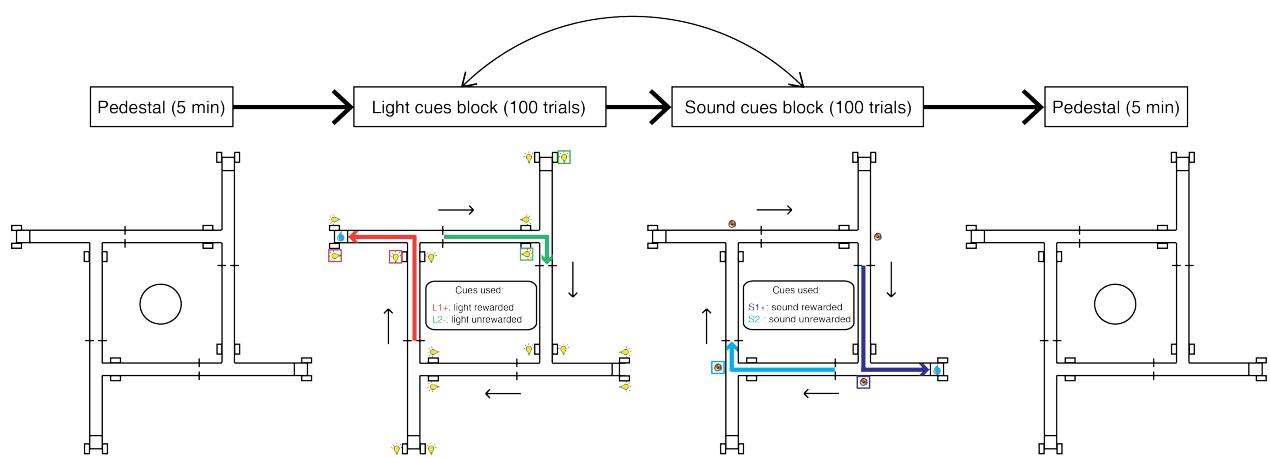
272 **Tiling of task structure:**

273 Additionally, we found that the population of recorded units had a relatively uniform distribution of firing  
274 fields within our task space, similar to what has been reported previously (Shidara, 1998; Berke, 2009;  
275 Lansink, 2012). Uniquely, we found that this representation differed according to whether the rat was cur-  
276 rently engaged in the light or sound block, suggesting that this could be a possible neural correlate for  
277 encoding the currently relevant strategy in the NAc. During progress through a predictable trial series, neu-  
278 rons represented state value of cue (Shidara 1998). Single-unit responses allowed the monkey to know how  
279 it was progressing throughout the task. Likewise, the tiling we saw could be a consequence of upstream cor-  
280 tical or limbic inputs informing the striatum of the current task rules. Another possibility is that the NAc not  
281 only pays attention to progress throughout a task within a trial, but also higher-order task information, like  
282 blocks. Cue location was a behaviorally irrelevant variable in the current experiment, but it is possible that  
283 if this tiling is dependent on hippocampal input, or related to a state value representation, that making cue  
284 location a relevant variable by adding positional contingencies such as only alternating arms are rewarded  
285 in one block, would result in a further separation of the mapping within a block between the rewarded and  
286 unrewarded arms. Furthermore, dopamine levels in the NAc fluctuate through a trial, and it is possible that  
287 the observed tiling could be a NAc-representation of state value related to this temporally evolving dopamine  
288 signal. Future experiments should monitor this mapping of task structure during the application of dopamine  
289 antagonists. Finally, the presence of functional correlates not evident when looking at single-unit responses  
290 time-locked to salient task events emphasizes the need to employ ensemble level analyses across all aspects  
291 of a task.



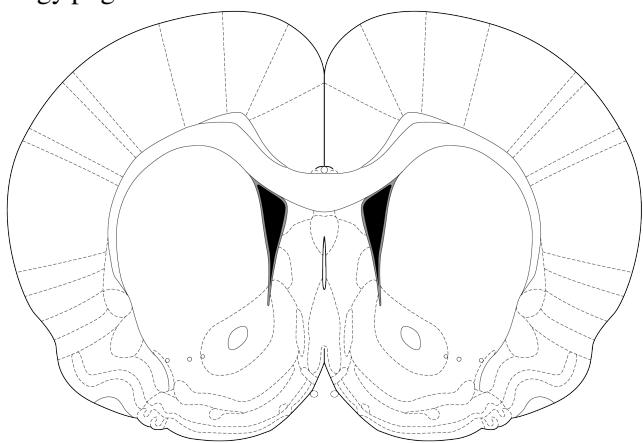
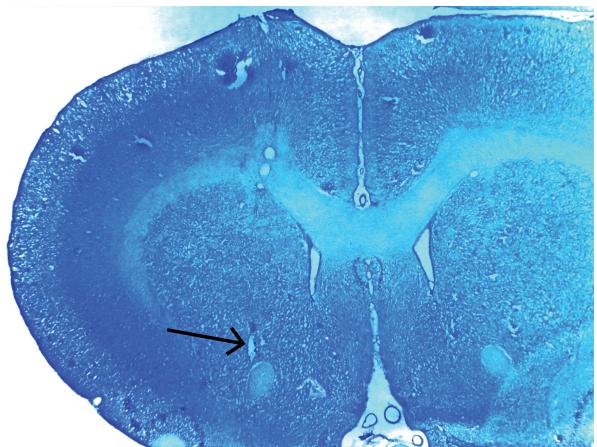
**Figure 1: Neural schematic**

2 - Schematic task.png  
Block order counterbalanced across sessions



**Figure 2:** Task schematic

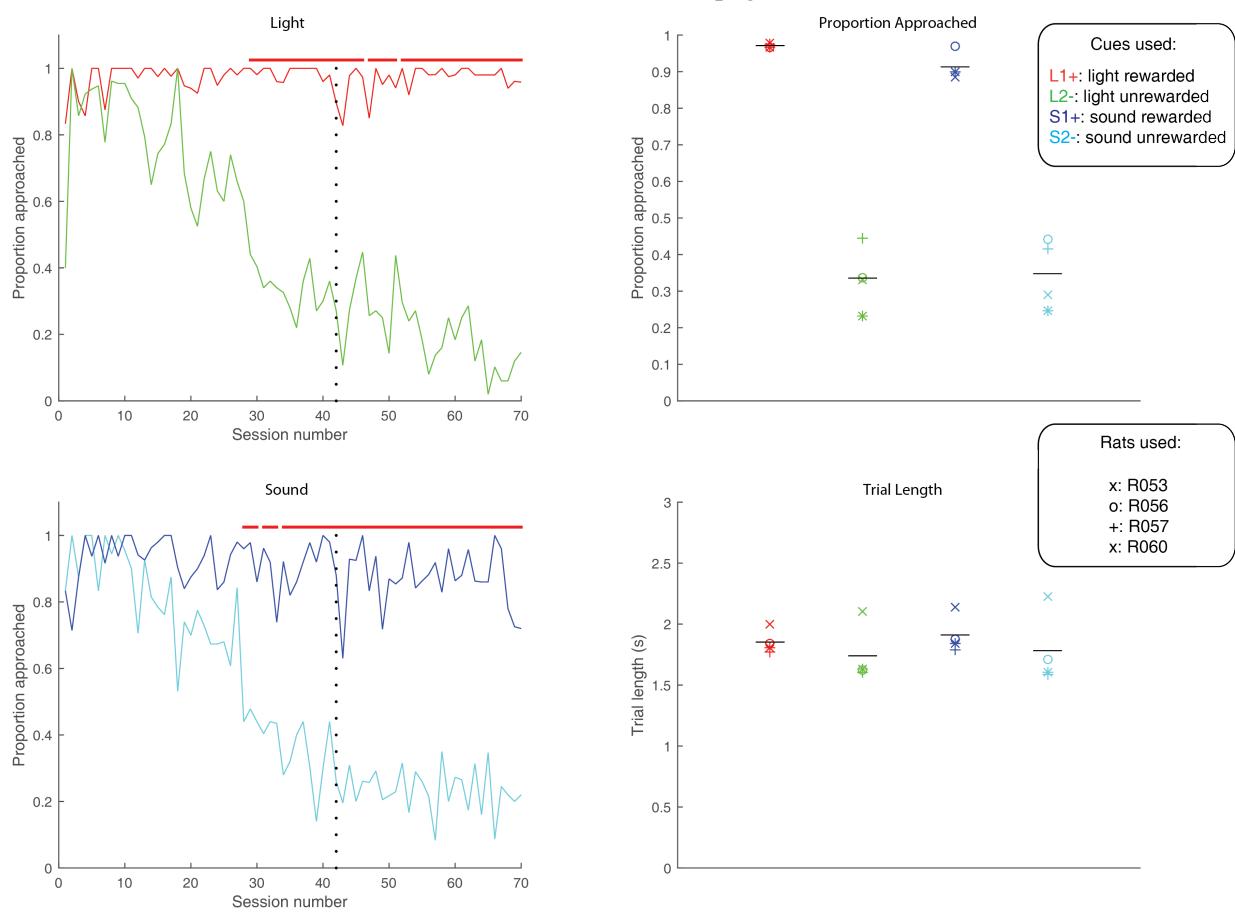
3 - Histology.png



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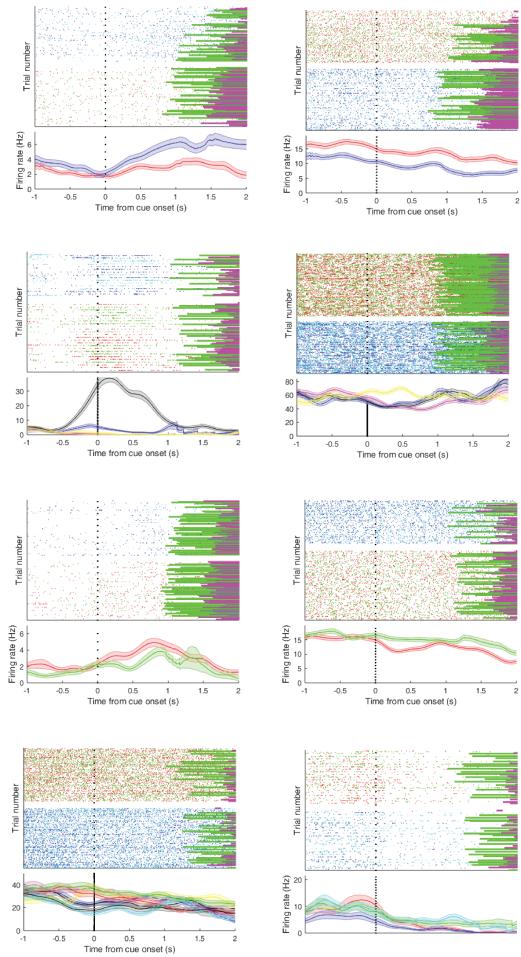
**Figure 3: Histology**

4 - Behavioral results.png



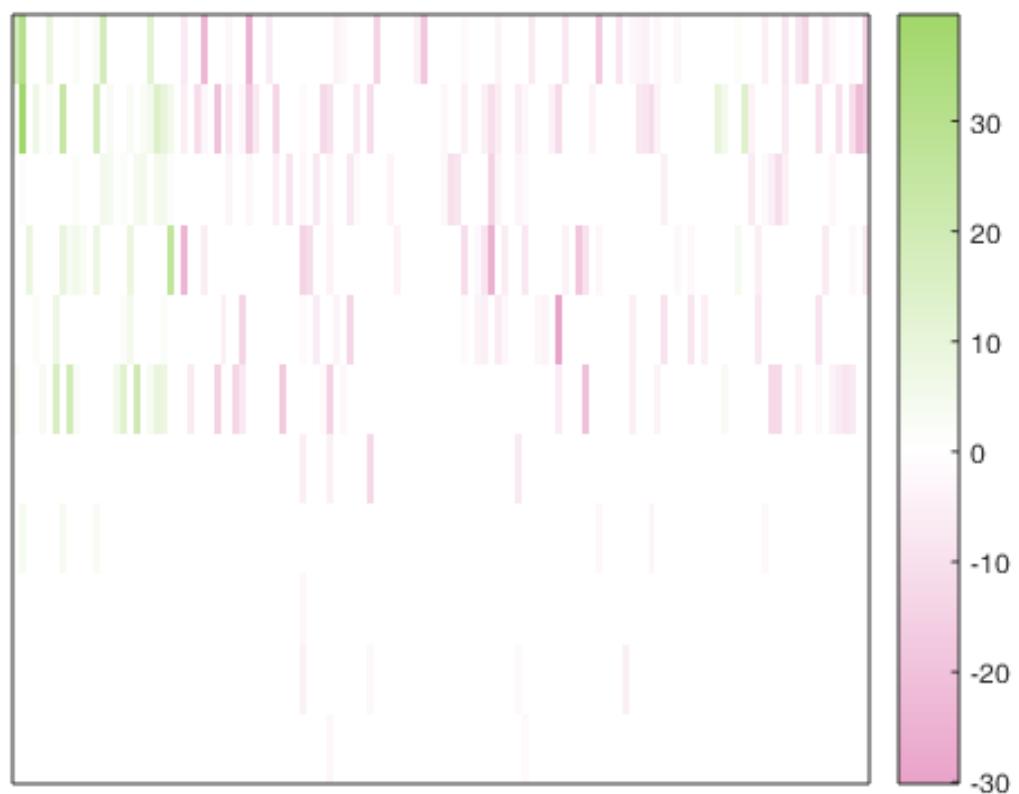
**Figure 4: Behavioral results**

5 - Neural examples.png



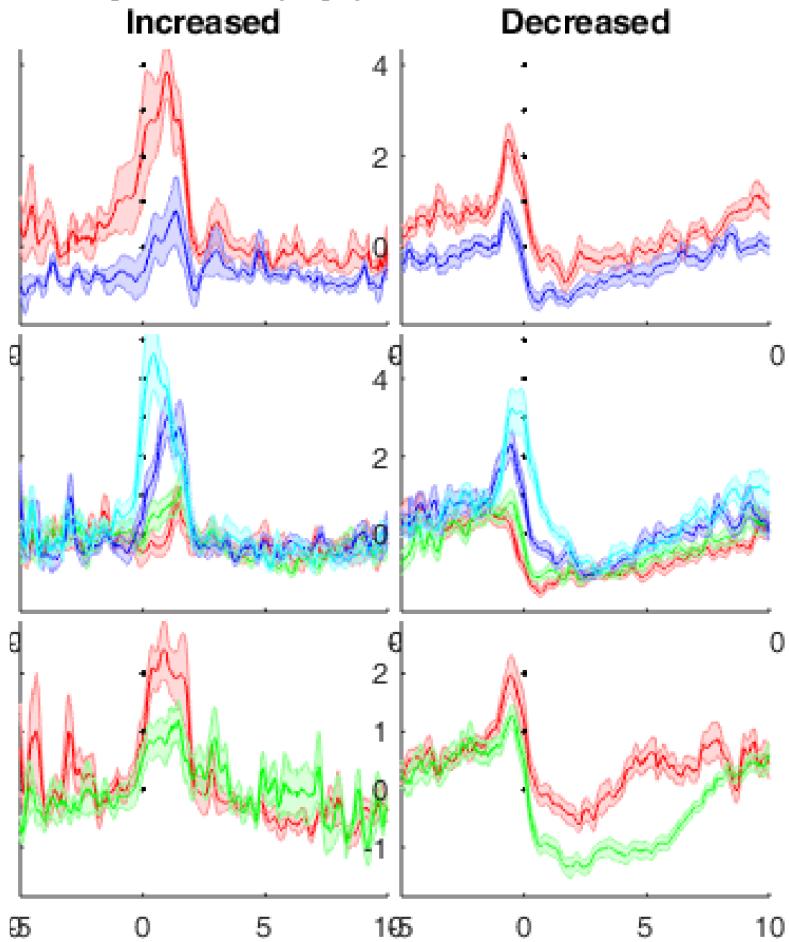
**Figure 5:** Neural examples

6 - GLM matrix.png



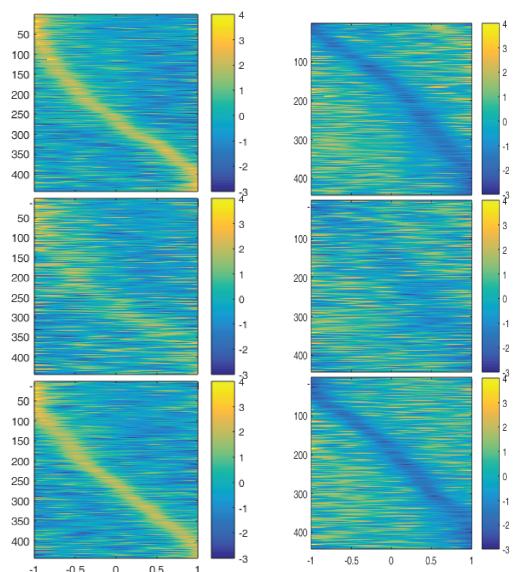
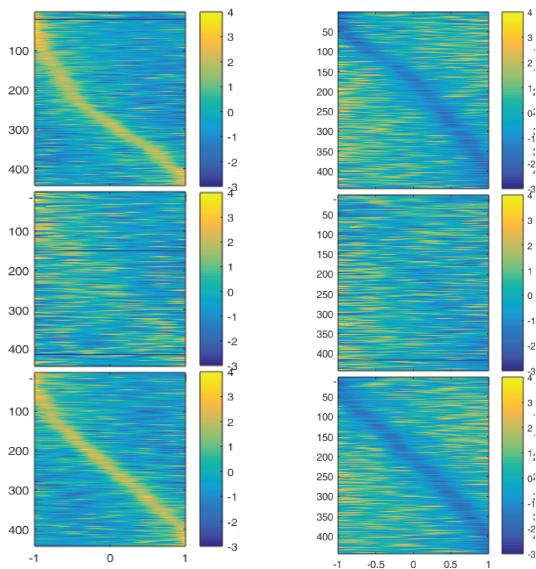
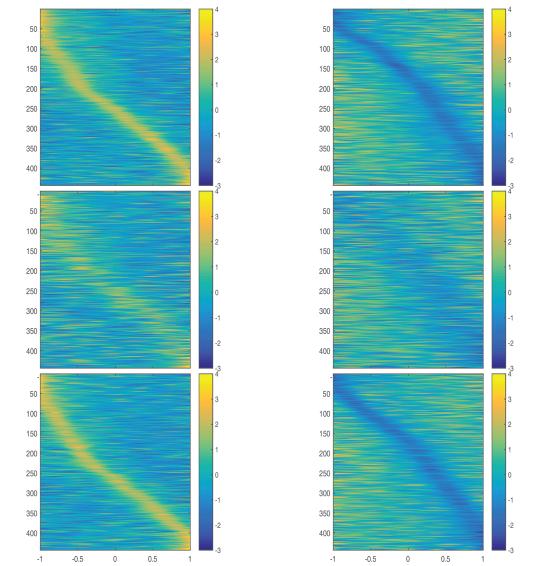
**Figure 6:** GLM matrix

7 - Population averages.png



**Figure 7:** Population averages

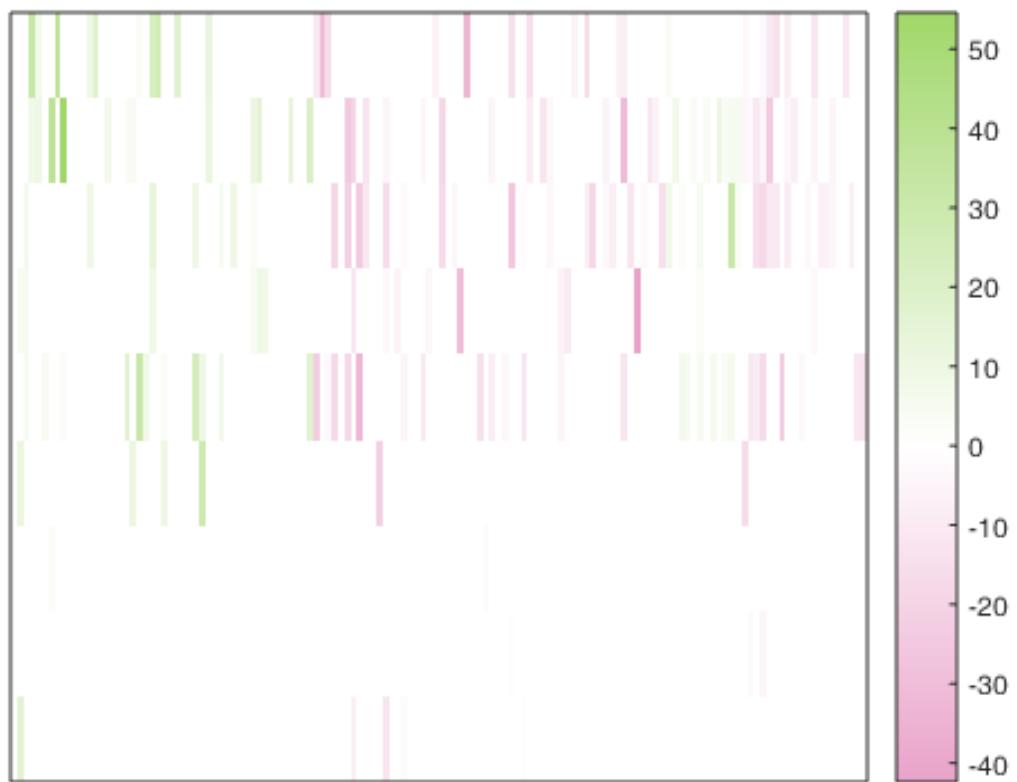
8 - Task tiling.png



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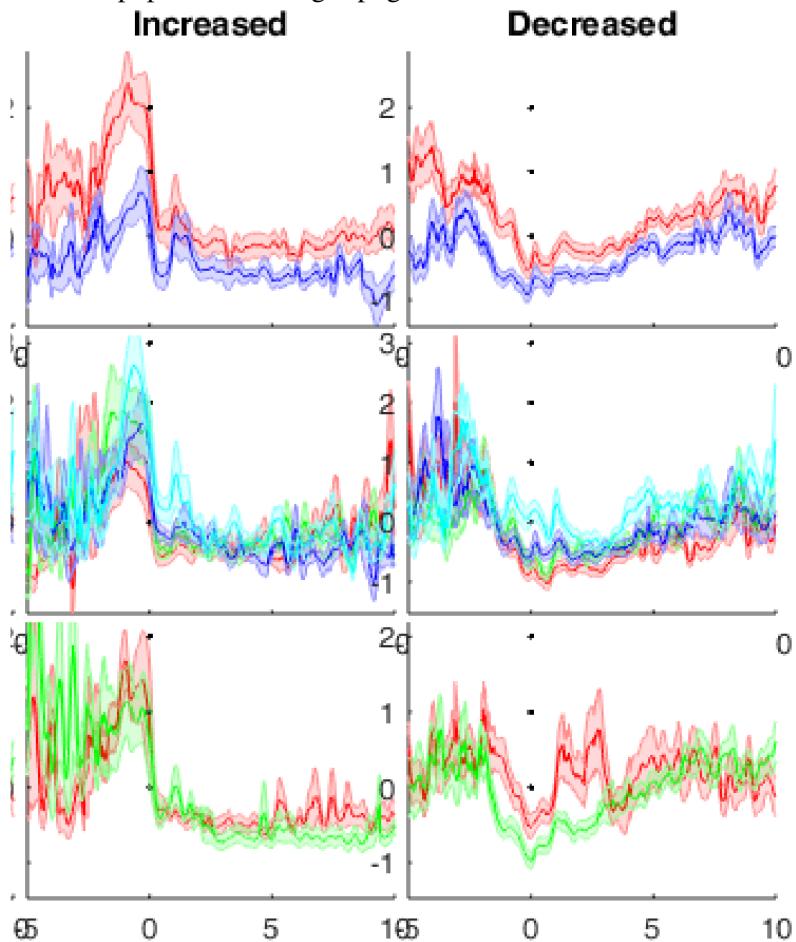
Figure 8: Task tiling

9 - NP GLM matrix.png



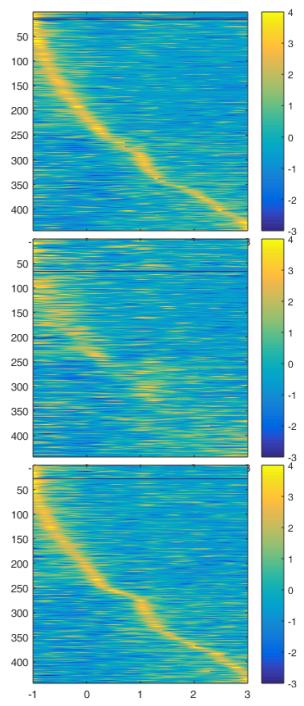
**Figure 9:** NP GLM matrix

10 - NP population averages.png



**Figure 10:** NP population averages

11 - NP task tiling.png



**Figure 11:** NP task tiling