Shared roles of dorsal and subgenual anterior cingulate cortices in economic decisions

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ABSTRACT

Theories of dorsal anterior cingulate cortex (dACC) function generally emphasize its cognitive and regulatory functions while theories of subgenual ACC (sgACC) emphasize its emotional, limbic, and arousal-related roles. But how different are these areas when compared in the same task? We recorded neuronal responses in both regions in macaques in a task with cognitive and limbic aspects, a token gambling task. Using tokens allowed us to compare responses to wins and losses. Both regions phasically encoded several important economic variables in similar ways; these included offered values, remembered values, attended values, and obtained values, and number of current tokens. Signal-to-noise ratio in sgACC was substantially lower than in dACC, and sgACC neurons responded more strongly to losses and in anticipation of large rewards. These results highlight the common economic functions of the anterior cingulum and suggest different functional emphases between regions, rather than a strict cognitive vs. emotional division.

INTRODUCTION

The cingulum is a large structure on the medial wall encircling the corpus callosum in the saggital plane. The portion rostral to the central sulcus, the anterior cingulate cortex (ACC), is important for almost every aspect of cognition and its malfunction is associated with several psychiatric diseases (Bush et al., 1999; Heilbronner & Hayden, 2016; Paus, 2001; Rushworth et al., 2012; Shenhav et al., 2013). A great deal of evidence indicates that the ACC can be functionally subdivided into at least two portions, a dorsal (dACC) and subgenual (sgACC) one. These portions are associated with different cytoarchitectonics, connectivity patterns, patterns of hemodynamic activation, and lesion effects (Bush et al., 2000; Vogt et al., 1995). Nonetheless, a direct comparison of their function at the single-neuron level has never been made.

Theories of dACC generally emphasize its cognitive and regulatory roles rather than limbic and emotional ones. Cognitive functions associated with dACC include error- and conflict-monitoring, allocation of control, task-switching and regulation of strategy (Allman et al., 2001; Amiez et al., 2005; Carter et al., 2007; Kerns et al., 2004; Neubert et al., 2015; Procyk et al., 2000; Quilodran et al., 2008; Rushworth et al., 2002; Shenhav et al., 2013). In contrast, theories of sgACC emphasize its limbic, emotional, and arousal-related roles and not its cognitive function. These functions include emotional processing, mood-changes, sleep, and potentially a role in depression (Botteron et al., 2002; Coryell et al., 2005; Drevets et al., 1997; George et al., 2006; Johansen-Berg et al., 2008; Rolls et al., 2003). Some evidence suggests that these regions have negatively correlated activity patterns (Bush et al., 2000), consistent with the idea they inhibit each other. These

63 differences have led to the theory that these two regions play antagonistic roles in
64 cognition (Bush et al., 2000).

65 Nonetheless, there are reasons to believe that dACC and sgACC play overlapping
66 roles in cognition. Both are associated with monitoring and anticipation of reward (which
67 itself has both cognitive and limbic aspects.) The role of the dorsal portion of ACC in
68 reward representation is well-established (Heilbronner and Hayden, 2016). Although
69 single-unit studies in the subgenual portion have been relatively few, some of these
70 studies also implicate this region in reward processing and representation (Monosov &
71 Hikosaka, 2012; Rudebeck et al., 2014; similar findings were reported in Amemori &
72 Graybiel, 2012, who recorded in the adjacent pregenual cingulate). More broadly, both
73 regions have been implicated in pain processing (Derbyshire et al., 1998; Vogt et al.,
74 1992), depression (Cotter et al., 2001; Mayberg et al., 1997), addiction (Forman et al.,
75 2004; Goldstein et al., 2007), OCD (Graybiel & Rauch, 2000), and other psychiatric
76 disorders (Blumberg et al., 2000; Bouras et al., 2001; Drevets et al., 1997; Drevets et al.,
77 2008; Ongur, Drevets & Price, 1998). Nonetheless, our ability to compare these regions
78 is limited by the paucity of direct comparisons of their function.

79 Here we compared the responses of these two regions in a single gambling task.
80 We sought to understand their relative contributions within a single task that was
81 complex and engaging, and had both limbic and cognitive aspects. Among economic
82 choice tasks, gambling is particularly useful because it is well-characterized
83 mathematically, preferences are stable, and it involves both reward and
84 monitoring/adjustment processes (Heilbronner and Hayden, 2013; Heilbronner &
85 Hayden, 2015). Furthermore, we have a foundational understanding of the neuroscience

of risky choice, including recordings in dACC, although not in sgACC (Blanchard and Hayden, 2014; Hayden et al., 2011; Hosokawa et al., 2013; Kennerley et al., 2009; Procyk et al., 2000). To directly compare coding of gain and loss, we added a new feature to our task. On each trial, monkeys gambled for gain or loss of tokens; collection of 6 tokens produced a jackpot reward (cf. Seo & Lee, 2007). This feature allowed for direct comparison of two reward signs in a single modality (thus controlling for sensory features that, say, an air puff or hypertonic solution would not). This manipulation also allowed us to explore responses to secondary reinforcers—which has not been done in sgACC.

These two cingulate regions exhibited strikingly similar patterns of activity in our study. Both encoded several economic variables and did so in similar ways. Specifically, we found encoding of the values of offers (attended and remembered), outcomes, and number of tokens accumulated. Both regions used an attentionally-aligned, as opposed to labeled line, coding scheme for values. We also confirmed earlier results showing encoding of positions of offered and chosen options (Strait et al., 2016). We found no measurable differences in response latency. This is not to say the regions were identical: two major differences stood out. First, task-relevant coding was more frequent in dACC and signal-to-noise was roughly three times greater. Second, neurons in dACC were biased towards higher firing for gamble wins, while neurons in sgACC were biased towards higher firing for losses. There was also a positive bias at the single neuron level in anticipation of large, primary rewards in sgACC; no corresponding bias occurred in dACC. These data suggest that dACC and sgACC play overlapping roles in economic

decisions albeit with different emphases, but do not have antagonistic roles or strong cognitive / emotional specialization.

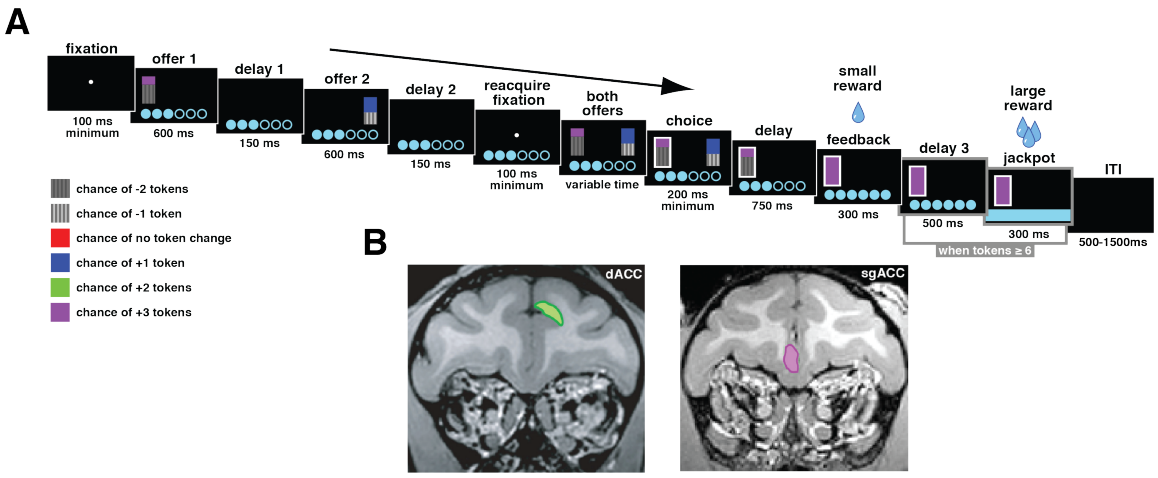

Figure 1: ***A:*** *Example trial from token-gambling task. Offers were presented asynchronously, and the side the first offer appeared on was counterbalanced across trials. Each gamble offered one of two outcomes (indicated by the colors of the bars) at a certain probability (indicated by their heights).* ***B:*** *Regions of interest (for exact coordinates, see Methods).*

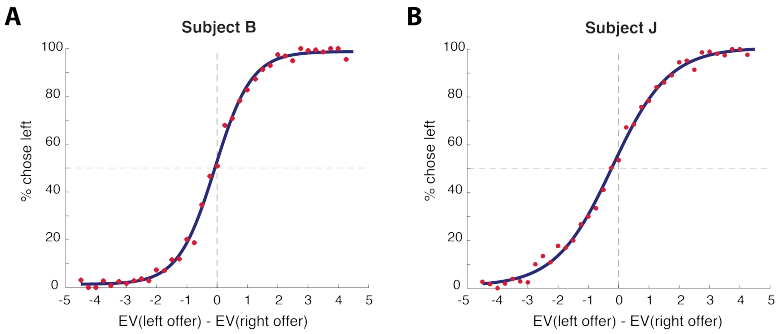

Figure 2: *Behavior for each subject, fit to a sigmoid function. Subjects choose the left option more often as its value increases. EV: expected value of gamble.*

RESULTS

Behavior

Two monkeys performed a token-gambling task. On each trial, monkeys chose between two options presented asynchronously that differed in three dimensions: win amount, loss amount, and probability of win (Figure 1A). Both monkeys showed behavior consistent with task understanding (Figure 2). Specifically, both subjects preferred the option with the greater expected value (subject B: 80.3%; subject J: 75.1%; both $P < 0.0001$; two-sided binomial test), and were sensitive to the three parameters that defined each gamble (See Table 1). Subjects were more sensitive to win amount than to loss amount, consistent with the idea that they focus on the win (Hayden & Platt, 2007; Hayden et al., 2008). Monkeys showed weak side and order biases (rightward choice: 51.0% in subject B; 47.4% in subject J; chose second: 52.5% in subject B; 55.6% in subject J.)

Monkeys were risk-seeking, consistent with earlier studies (Hayden et al., 2008; Hayden & Platt, 2007; McCoy & Platt, 2005). To assess risk-seeking, we fit a utility curve distortion parameter to subjects' behavior in each session (Lak et al., 2014; Yamada et al., 2013). This parameter, α, was always greater than 1 in both subjects (B: $\alpha = 1.61$ ($n = 66$ sessions); subject J: 1.81 ($n = 74$ sessions); both greater than 1 at $P < 0.0001$; one-sample t-test over sessions). Subjects' behavior was modestly influenced by the number of current tokens: accuracy improved as tokens increased (subject B: $\beta = 0.027$, $P = 0.0012$; subject J: $\beta = 0.078$, $P < 0.0001$; logistic regression of accuracy against tokens acquired).

Regressor	Subject B	Subject J
Win amount, left offer	1.2302 ($P < 0.0001$)	1.0097 ($P < 0.0001$)
Loss amount, left offer	0.4063 ($P < 0.0001$)	0.2451 ($P < 0.0001$)
Probability of win, left offer	3.3828 ($P < 0.0001$)	3.1745 ($P < 0.0001$)
Win amount, right offer	-1.1577 ($P < 0.0001$)	-1.1390 ($P < 0.0001$)
Loss amount, right offer	-0.3449 ($P < 0.0001$)	-0.1937 ($P < 0.0001$)
Probability of loss, right-offer	-4.1934 ($P < 0.0001$)	-3.5026 ($P < 0.0001$)
Intercept	-0.2893 ($P < 0.0001$)	0.6177 ($P < 0.0001$)

Table 1: *Regression coefficients from a logistic regression model of choice (left = 1, right = 0) against the variables in the regressor column. A 'loss' within a gamble was always less than or equal to the win outcome of that gamble. Note that losses included negative outcomes. Overall, the expected value of the win-portion of a gamble influenced behavior more than the value of a loss did in both subjects.*

Variance explained by task variables is higher in dACC than in sgACC

Responses to task variables were attenuated in sgACC neurons compared to dACC neurons. To quantify this difference, we regressed average firing rate in a sliding 500 ms window against eight task-relevant variables (see Methods). We then computed the average fraction of variance in firing rates explained by this model for each neuron in each brain region over the entire trial. We next compared these measures across regions, where neurons were the unit of analysis. Task-relevant variables explained over three times as much variance in dACC than in sgACC neurons (average adjusted R^2 over all neurons: dACC: 0.0093; sgACC: 0.0025; $T = 4.94$, $P < 0.0001$; two-sample t-test). Thus, variance explained was between 3 and 4 times greater in dACC than in sgACC.

166

Variable	dACC (t-statistic)	sgACC (t-statistic)
Offer 1 value (attended)	0.64 (P = 0.53)	1.67 (P = 0.098)
Offer 1 value (remembered)	-0.26 (P = 0.79)	-0.47 (P = 0.64)
Offer 2 value (attended)	0.95 (P = 0.34)	0.97 (P = 0.33)
Chosen value	-1.47 (P = 0.14)	**-2.31 (P = 0.022)**
Unchosen value	**2.70 (P = 0.0078)**	1.73 (P = 0.085)
Outcome	**2.35 (P = 0.02)**	**-2.85 (P = 0.0050)**
Number of tokens	1.42 (P = 0.16)	0.15 (P = 0.88)
Jackpot	0.092 (P = 0.93)	**4.47 (P < 0.0001)**

167 ***Table 2:*** *Assessment of biases in tuning in the overall population. We performed this*
168 *analysis running a one-sample t-test on the regression coefficients corresponding to each*
169 *variable obtained from a multiple linear regression (see Methods).*
170

Variable	dACC (% positive)	sgACC (% positive)
Offer 1 value (attended)	57.6% (n = 19/33, P = 0.49)	66.7% (n = 12/18, P = 0.24)
Offer 1 value (remembered)	56.0% (n = 14/25, P = 0.69)	41.7% (n = 5/12, P = 0.77)
Offer 2 value (attended)	50.0% (n = 9/18, P = 1)	57.1% (n = 8/14, P = 0.79)
Chosen value	**20% (n = 4/20, P = 0.012)**	22.2% (n = 2/9, P = 0.18)
Unchosen value	**100% (n = 12/12, P = 0.0005)**	50.0% (n = 3/6, P = 1.0)
Outcome	**71.0% (n = 22/36, P = 0.029)**	31.6% (n = 6/19, P = 0.17)
Number of tokens	60.0% (n = 27/49, P = 0.23)	58.3% (n = 14/31, P = 0.54)
Jackpot	54.3% (n = 19/35, P = 0.74)	70.6% (n = 12/17, P = 0.14)

171 ***Table 3:*** *Assessment of biases in frequency of coding in the tuned population. We*
172 *determine whether the fraction of positively tuned neurons (of the tuned population only)*
173 *is significantly larger than chance (50%), using a two-sided binomial test.*
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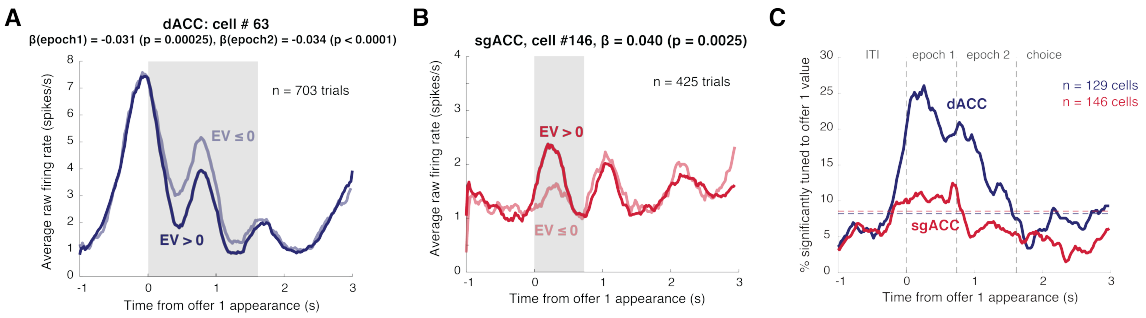

Figure 3: *Neural responses to the value of offer 1.* ***A:*** *Responses of one dACC neuron with increasing firing rate in response to smaller values of offer 1 in both the first and second epochs. Shaded regions are epochs of interest with significant modulation.* ***B:*** *Responses of one sgACC neuron with increasing firing rates in response to larger values of offer 1 in the first epoch.* ***C:*** *Proportion of neurons selective for the value of offer 1 in both regions throughout the course of the trial. This fraction was computed by regressing firing rate over a 500 ms sliding window against the expected value of the first offer, along with other task-relevant variables (see Methods). The blue and red horizontal lines indicate the percentage of neurons we would expect to see by chance (as determined by a two-sided binomial test, according to the number of neurons in each area) for dACC and sgACC, respectively.*

Neurons in both regions encode offered values

Responses of two neurons (one in dACC and one in sgACC) are shown in Figure 3. Both of these neurons' firing rates were correlated with the expected value of the first offer while it was displayed on the screen (epoch 1). The firing rate of the dACC neuron was also affected by the expected value of the first offer when the second offer appeared (epoch 2). This was not the case for the sgACC neuron.

Significant proportions of neurons in both regions encoded the value of the first offer in the 500 ms epoch starting 100 ms after that offer appeared. Note that we chose this epoch for another study and use it here to allow comparability across datasets (Strait et al., 2014; Strait et al., 2015).

We found that responses of 25.6% (n = 33/129) of neurons in dACC and 12.3% (n = 18/146) in sgACC were affected by the value of offer 1 during epoch 1. Both proportions are greater than chance (dACC: $P < 0.0001$; sgACC: $P = 0.0004$; two-sided binomial test). Figure 3C shows the fraction of neurons whose firing rates were modulated by offer 1 value through time. There was no measured bias towards a positive direction in either area (see Table 3). The average regression weight across all neurons, another measure of directionality of effect, was not different from zero in either area, indicating no bias in the overall populations (see Table 2).

Neurons in both regions integrate gamble probability and stakes

The mathematical expected value of a gamble in our task – and its subjective value – depend on three factors: the probability of the win, the win amount, and the loss amount. We wanted to know whether the individual components of a gamble are integrated into a single general value signal, or represented as separate attributes.

We explored whether probability and stakes were integrated in the first epoch of the trial, when only the first gamble had been displayed. We compared regression weights for neuronal responses to the first offer against the magnitude and probability of a win and the magnitude of loss, in one multivariate regression, while controlling for other variables that significantly explained firing rate for this neuron in this epoch (see Methods for further detail).

Regression coefficients corresponding to win-magnitude and win-probability were positively correlated, supporting the hypothesis that these parameters are integrated This correlation is observed in both cingulate regions (dACC: $r = 0.63$, $P < 0.0001$;

sgACC: r = 0.31, P = 0.0001; Pearson correlation coefficient of signed regression coefficients). The absolute values of these coefficients were also positively correlated, indicating that these variables were encoded by a single population of neurons rather than two distinct ones — further supporting the integration hypothesis (dACC: r = 0.59, P < 0.0001; sgACC: r = 0.56, P < 0.0001). We previously reported similar findings in the ventromedial prefrontal cortex (vmPFC) and the ventral striatum (VS, Strait et al., 2015). These results suggest that all four regions carry integrated value signals.

Win and loss magnitudes were also integrated in both areas (dACC: r = 0.34, P = 0.0001; sgACC: r = 0.36, P < 0.0001; Pearson correlation coefficient of signed regression coefficients). While these variables were represented in overlapping populations in sgACC (r = 0.30, P = 0.0003; Pearson correlation coefficient of unsigned regression coefficients), this relationship does not achieve significance in dACC (r = 0.17, P = 0.053).

Neurons in both regions encode remembered values

We examined whether firing rates reflected the value of the first offer while the second offer was presented (epoch 2, 500 ms epoch starting 100 ms after the second offer appeared,). We saw encoding of offer 1 in this epoch in dACC (19.4% of neurons, n = 25/129, P < 0.0001; two-sided binomial test), but it failed to reach significance in sgACC (8.22%, n = 12/146, P = 0.084). Since task-relevant signals were generally attenuated in sgACC, and the percentage of tuned neurons we saw failed to reach significance by one neuron, we repeated this analysis in an earlier 500 ms epoch, starting immediately when the second offer appeared. The fraction of neurons tuned to the value of offer 1 in this

244 epoch does achieve significance (11.0%, n = 16/146, P = 0.0028; two-sided binomial
245 test). This proportion is still significant when correcting for multiple comparisons (i.e. at
246 $P < 0.025$). This finding suggests that sgACC may, in fact, carry a memory signal,
247 although one that is more attenuated and less reliable than that in dACC. There was no
248 bias in tuning in either brain region (see Table 3), nor was there any bias in the regression
249 coefficients of the overall populations (see Table 2).

250 We next investigated the relationship between the pattern of tuning for attended
251 and remembered offers. Was offer 1 encoded in similar tuning formats as it moved from
252 the retina to working memory? And were the putative working memory neurons, which
253 carried the value of offer 1 in the second epoch, the same ones that encoded it when it
254 was first presented—in the first epoch? The answers to both questions is yes for dACC,
255 but we cannot draw conclusions from our results in sgACC. We computed regression
256 weights for the expected value of offer 1 in epoch 1 (when it was present on the screen)
257 and for the same option in epoch 2 (when it was remembered), while controlling for other
258 task variables that best explained each neuron's response (see Methods). These values
259 were positively correlated in dACC ($r = 0.32$, $P = 0.0002$; Pearson correlation coefficient
260 of signed regression coefficients), indicating a preservation of coding format as
261 information was transferred from an active to a remembered storage buffer. The absolute
262 regression coefficients were also positively correlated ($r = 0.44$, $P < 0.0001$), suggesting
263 these variables were encoded by a single task-sensitive population, rather than memory
264 and active-buffer neurons (consistent with vmPFC and VS; Strait et al., 2015).

265 We cannot draw any strong conclusions from results in sgACC. There was no
266 significant correlation between these variables: neither one indicating preservation of

format (r = 0.090, P = 0.28; Pearson correlation of signed regression coefficients), nor one indicating that this signal was carried by the same population (r = 0.0380, P = 0.65; Pearson correlation of unsigned regression coefficients). Results were similar in the slightly earlier 500 ms epoch we used earlier (preservation of format: r = 0.15, P = 0.079; overlapping populations: r = 0.063, P = 0.45). It is difficult to draw conclusions from the absence of this correlation, as it could be due to weaker signal-to-noise ratio in this region. We therefore performed a cross-validation procedure similar to that in Blanchard et al. (2015), and found that our signal in the epochs of interest was not strong enough to detect correlations (see Methods). The failure of this procedure suggests that we could not detect this effect with our data, even if it existed. We therefore draw no conclusions from this null result.

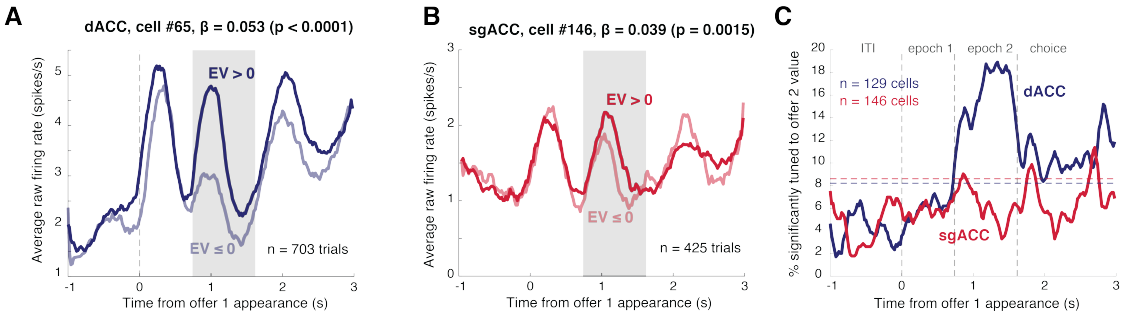

Figure 4: *Neural responses to the value of offer 2.* ***A:*** *Responses of one dACC neuron whose firing rate increased in response to larger values of offer 2.* ***B:*** *Responses of one sgACC neuron whose firing rate increased in response to larger values of offer 2.* ***C:*** *Percentage of neurons tuned to the value of the second offer in both regions over the course of the trial. A 500 ms sliding window was used to compute these values at each point of the trial. The blue and red horizontal lines indicate the percentage of neurons we would expect to see tuned by chance (as determined by a two-sided binomial test, according to the number of neurons in each area) for dACC and sgACC, respectively.*

290 **Simultaneous encoding of both offer values**

291 We next explored the effects of the second offer value on firing rates during
292 epoch 2. Figure 4 shows two example neurons, one from dACC and one from sgACC,
293 whose firing rates increased in response to the second offer. A significant proportion of
294 neurons in both regions encoded the value of the second offer when it appeared (dACC:
295 14.0%, n = 18/129; sgACC: 9.59%, n = 14/146). Both proportions exceed what we would
296 predict by chance (dACC: P = 0.0001; sgACC: P = 0.016; two-sided binomial test).
297 There was no significant bias in tuning in either area (Table 3), and the average
298 coefficient of offer 2 value over the entire population was also not biased in either brain
299 region (Table 2). Figure 4C shows how the fraction of neurons responsive to offer 2
300 changed over the course of the trial.
301
302 **Attentionally-aligned coding scheme for offer values**

303 Do cingulate regions encode all attended offers similarly, using the same
304 population? Our previous studies of vmPFC and VS indicate that value coding in these
305 regions is attentionally-aligned – that is, they encode the value of the attended offer in a
306 conserved attended format (by format, we mean tuning strength and sign, and identity of
307 neurons; Strait et al., 2015; Akaishi & Hayden, 2016; Rich & Wallis, 2016).). This
308 framework differs from a labeled-line format, in which a specialized set of neurons
309 encodes the value of each offer respectively (e.g. Hunt et al., 2015). To test this, we
310 compared the regression coefficients associated with the first offer in the first epoch to
311 those associated with the second offer in the second epoch.

Our data support the attentional alignment hypothesis. Specifically, coding direction for both offers was consistent in both areas (dACC: $r = 0.51$, $P < 0.0001$; sgACC: $r = 0.26$, $P = 0.0013$; Pearson correlation test of signed coefficients). Second, both regions made use of a consistent set of neurons for the two offers (dACC: $r = 0.45$, $P < 0.0001$; sgACC: $r = 0.32$, $P = 0.0001$; Pearson correlation test of unsigned coefficients).

Beta anti-correlation in dACC: a putative signature of comparison through mutual inhibition

One putative neural signature of the comparative process is an anti-correlation between regression coefficients for the values of the two offers while they are being compared (Strait et al., 2014). This anti-correlation indicates that the two offers modulate neuronal activity in opposing directions, and that the ensemble of neurons effectively subtracts their values. We observed this pattern in dACC during the second epoch—when both offers had been presented ($r = -0.17$, $P = 0.050$; Pearson correlation coefficient of signed regression coefficients), suggesting that this area is involved in comparing the two offers. We found no significant correlation in sgACC ($r = -0.077$, $P = 0.35$). It is difficult to interpret the lack of a significant correlation as the absence of a comparison signal in light of our weak signal-to-noise ratio, and due to the failure of the cross-validation procedure (see Methods).

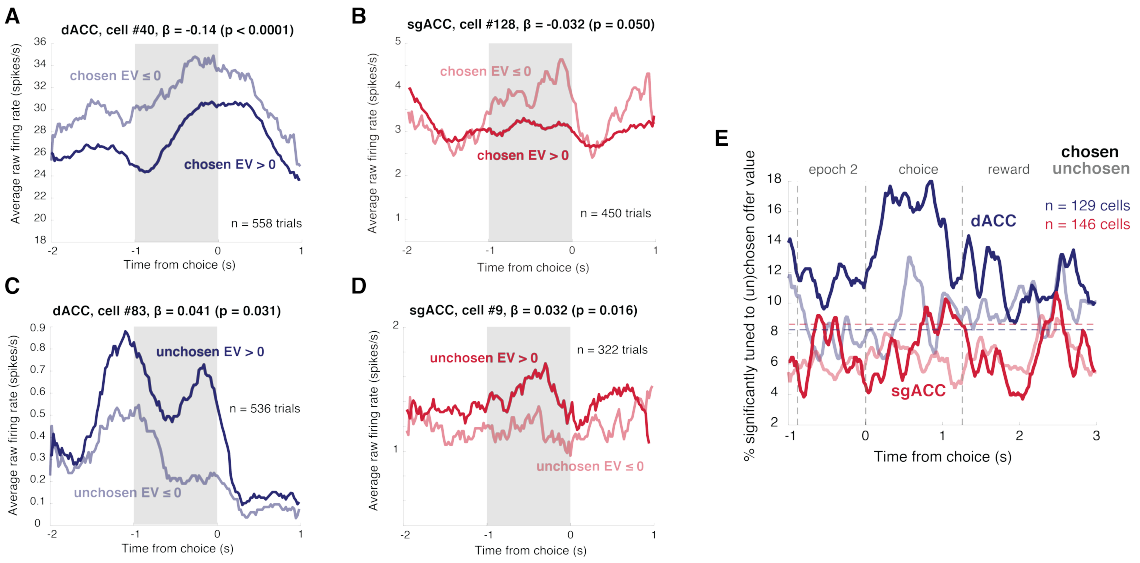

Figure 5: *Neural responses to the values of the chosen and unchosen offers.* ***A:*** *Responses of dACC neuron whose firing rate was negatively modulated by the value of the chosen offer. This pattern is typical of neurons in this region (see text and Tables 2 and 3).* ***B:*** *Responses of sgACC neuron whose firing rate was negatively modulated by the value of the chosen offer.* ***C:*** *Responses of dACC neuron whose firing rate was positively modulated by the value of the unchosen offer. This pattern is typical of neurons in this region (see text and Tables 2 and 3).* ***D:*** *Responses of sgACC neuron whose firing rate was positively modulated by the value of the unchosen offer.* ***E:*** *Percentage of neurons tuned to the values of the chosen and unchosen offer values in both cingulate regions throughout the course of the trial. Percentages were computed using a 500 ms sliding window, using a regression analysis (see Methods for details). The blue and red horizontal lines indicate the percentage of neurons we would expect to see tuned by chance (as determined by a two-sided binomial test, according to the number of neurons in each area) for dACC and sgACC, respectively.*

Encoding of chosen and unchosen value signals in both regions

We examined selectivity for chosen and unchosen offer values in the 1-second epoch ending with the saccade that indicated the subject's choice. We chose this epoch to capture any correlates of the choice process that arose when the second offer was presented (presumably when the comparison was made), and when the subject had to indicate his choice.

Figure 5 shows four neurons whose firing rates were affected by the values of the chosen and unchosen offer values in both brain regions. Significant proportions of such neurons were found in dACC, but not in sgACC. 15.5% (n = 20/129) of dACC responded to the chosen value (two-sided binomial test: $P < 0.0001$), and 9.30% (n = 12/129) responded to the unchosen value ($P = 0.030$). The proportion of neurons encoding chosen value was greater than the proportion encoding unchosen value ($P = 0.018$; two-sided binomial test). However, encoding of chosen value was not stronger than encoding of unchosen value when the tuning coefficients of all neurons in the population were compared ($T = 1.67$, $P = 0.097$; unpaired two-sample t-test of absolute regression coefficients). There was more overlap than expected by chance between these populations ($r = 0.22$, $P = 0.013$; Pearson correlation of unsigned regression coefficients). Figure 5E shows the change in these fractions as the choice was made.

There was a bias towards negative tuning for the chosen value in the tuned population (n = 16/20 negatively tuned, $P = 0.012$; two-sided binomial test), but not in the regression coefficients of the overall population (Table 2). We found a bias towards positive tuning for the unchosen value: both in the tuned population (n = 12/12 positively tuned; $P = 0.0005$; two-sided binomial test), and in the overall population ($T = 2.70$, $P = 0.0078$; one-sample t-test).

No significant proportion of neurons encoding chosen (6.16%, n = 9/146, $P = 0.57$; two-sided binomial test) or unchosen (4.11%, n = 6/146, $P = 0.71$) offer values was found in sgACC. However, the overall population was negatively biased towards encoding of the chosen value ($T = -2.31$, $P = 0.022$; one-sample t-test), and exhibited a

positive trend in encoding the unchosen value (Table 2), echoing the patterns we see in dACC, albeit attenuated.

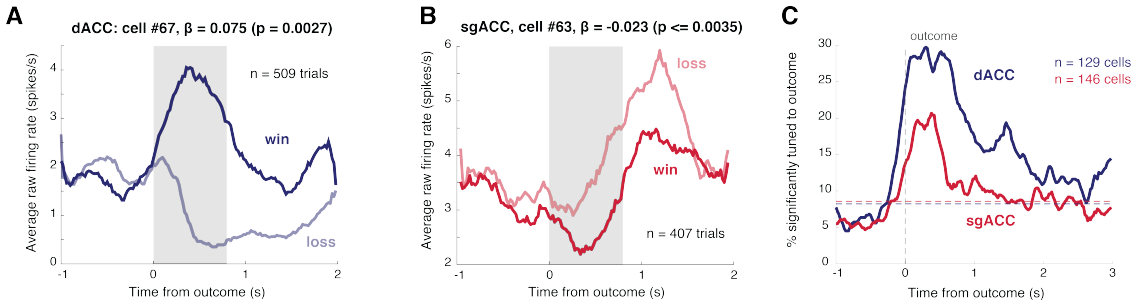

Figure 6: *Neural responses to outcomes in both regions.* ***A:*** *Responses of dACC neuron with increasing firing rate in response to wins. There was a bias towards this pattern in the dACC population (see text and Table 2).* ***B:*** *sgACC neuron with increasing firing rate in response to losses. There was a bias towards this pattern in the sgACC population (see text and Table 2).* ***C:*** *Percentage of neurons in both regions tuned to the outcome of a trial throughout the course of a trial, using a 500 ms sliding window. The blue and red horizontal lines indicate the percentage of neurons we would expect to see tuned by chance (as determined by a two-sided binomial test, according to the number of neurons in each area) for dACC and sgACC, respectively.*

Encoding of gamble outcomes

We examined selectivity for gamble outcomes during the 800 ms reward epoch that began with the reveal of the outcome and extended into the intertrial interval (see Figure 1). Recall that outcomes in this task were tokens, not juice rewards. Figure 6 shows responses of two example neurons, one from each region, selective for outcome amount. We excluded jackpot trials from this analysis so that liquid reward was matched in all cases; the only difference was tokens given or taken. 24.03% (n = 31/129) of neurons in dACC and 13.0% (n = 19/146) of neurons in sgACC encoded the outcome of a trial. Both of these proportions are significant ($P < 0.0001$ in dACC and $P = 0.0001$ in sgACC; two-sided binomial test). Figure 6C shows the peak of these fractions in the

outcome epoch. These are the first demonstration of sgACC selectivity to gains or losses of secondary reinforcers.

Neurons in dACC showed a positive bias in outcome encoding. Specifically, the majority of tuned neurons were positively tuned for outcome (71.0% positively tuned, n = 22/36, P = 0.029; two-sided binomial test). There was also a positive bias in regression coefficients in the overall population (T = 2.35, P = 0.02; one-sample t-test). In sgACC, neurons in the overall population were negatively tuned to outcomes (T = -2.85, P = 0.0050; one-sample t-test), although this bias in the overall population's regression weights was not significant in the tuned population (Table 3).

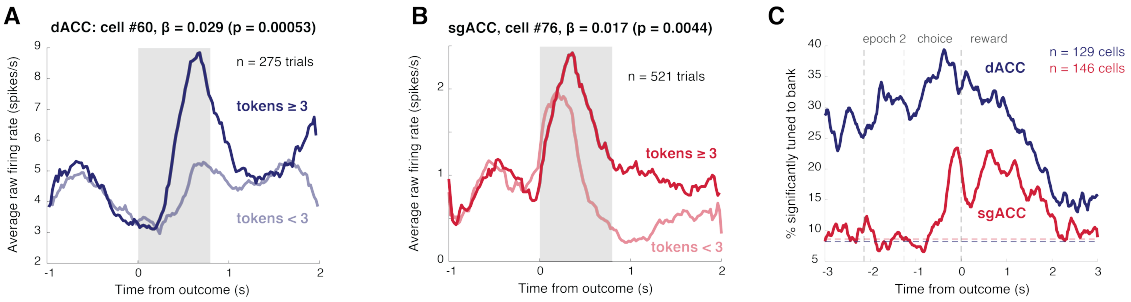

Figure 7: *Neural responses to the number of tokens accumulated at the beginning of the trial.* ***A:*** *Responses of dACC neuron that increased its firing rate as subjects accumulated more tokens.* ***B:*** *Responses of sgACC neuron that increased its firing rate as subjects accumulated more tokens.* ***C:*** *Percentage of neurons in each area tuned to the number of tokens accumulated throughout the course of the trial. All percentages were computed using a 500 ms window (see Methods). The blue and red lines indicate the percentage of neurons we would expect to see tuned by chance (as determined by a two-sided binomial test, according to the number of neurons in each area) for dACC and sgACC, respectively.*

Both regions encode current number of tokens

In our task, the number of tokens provided a measure of progress towards the jackpot reward. As noted, performance improved modestly with number of tokens. We

hypothesized that this variable would affect neuronal responses in both cingulate areas. Figure 7 shows two neurons (one in dACC, the other in sgACC) whose responses were modulated by the number of tokens acquired during the 800 ms reward epoch. 34.9% (n = 45/129) in dACC and 16.4% in sgACC (n = 24/146) significantly represented this variable in that epoch. Both of these fractions are significant ($P < 0.0001$ in both regions; two-sided binomial test). Figure 7C shows the change in this fraction throughout the trial. There was no bias in tuning in either brain region: neither within the tuned population (Table 3), nor in the overall population's regression coefficients (Table 2).

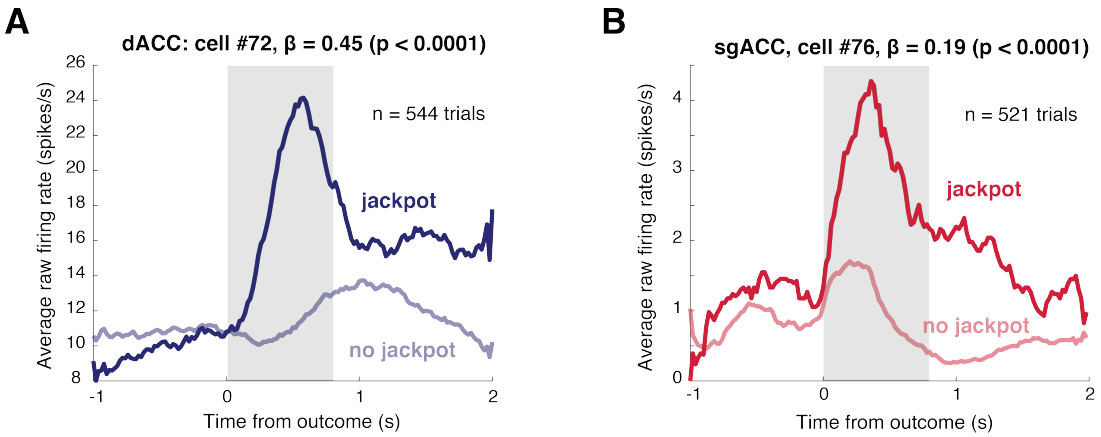

Figure 8: *Neural responses to the anticipation of a large liquid reward (jackpot).* ***A:*** *Responses of dACC neuron with increasing firing rate before jackpot rewards.* ***B:*** *Responses of sgACC neuron with increasing firing rate before jackpot rewards. There was a bias towards this response profile in the sgACC population (see text and Table 2).*

Neurons in both regions carry reward anticipation signals

We quantified neural responses to anticipation of jackpots by comparing them to responses on standard trials. Figure 8 shows two example neurons—one from each region—with activity that varied with anticipation of a jackpot reward. Significant proportions of such neurons were found in both regions (27.3% in dACC, n = 35/129, P <

0.0001; 11.6% in sgACC, n = 17/146, P = 0.0011; two-sided binomial test). We saw no bias in positive or negative tuning in dACC: neither in the tuned population (Table 3), nor in the population overall (Table 2). However, there was a positive bias in sgACC in the overall population (T = 4.47, P < 0.0001; one-sample t-test), although not significantly in the tuned population (Table 3).

Neurons in both regions carry spatial signals

We previously showed coding for two task variables, spatial position of offer and chosen option, in both dACC and sgACC (Strait et al., 2016). The sgACC data used in that study (n = 112 neurons) were augmented with additional neurons collected in the same animals in the same task (n = 34 additional neurons; total of 146 neurons). We still find these effects in the larger dataset. (Note that for consistency with the other analyses in this manuscript, we used a *multiple* linear regression analysis, see Methods). Specifically, sgACC encoded the position of the offer during the first offer epoch (n = 14/146 neurons, P = 0.016; two-sided binomial test), and the position of the chosen option during the post-choice epoch (n = 20/146 neurons, P < 0.0001). Results remained qualitatively similar in dACC with our new analyses. We see a significant proportion of neurons tuned to the side of the first offer in the first epoch (n = 20/129 neurons, P < 0.0001), and to the side of the chosen offer in the post-choice epoch (n = 30/129 neurons, P < 0.0001).

No significant difference in latency of encoding chosen side between regions

We investigated latency differences between dACC and sgACC. We were particularly interested in encoding of the chosen side, since this variable defined the action ultimately taken to indicate the subject's decision. Conventional latency analyses may be confounded due to the difference in signal-to-noise ratio between regions. This problem is especially acute when these differences are large, as they are in our sgACC and dACC datasets. In our data, signals are likely to achieve significance sooner in dACC, simply because they are stronger than in sgACC.

To avoid this confound, we developed a new procedure to control for signal-to-noise differences. We added Poisson distributed noise to our dACC dataset (mean = mean firing rate of each cell), and tested the proportion of variance explained in this new whitened dataset. If signal-to-noise in the reward epoch (when both regions were most responsive) was within 1.5% of that in sgACC, we included this dataset in our analyses. We generated 500 datasets in this manner, then performed a latency analysis the same as in Strait et al. (2015), with the slight modification that we used a multiple regression model instead of a t-test to determine when neurons first responded significantly to chosen side (this analysis takes into account neuronal responses to other variables, and is therefore more robust). We used this manipulation to account for the variance explained by other task-variables (listed in Methods). Even using this more sensitive measure and better-controlled analysis, we failed to see a significant difference between latencies across regions (t-test across regions significant for 1/500 datasets, $P = 0.998$).

DISCUSSION

We examined responses of neurons in two cingulate regions, dACC and sgACC, in a token gambling task. Both areas encoded several task variables, including values of attended and remembered offers, outcomes, current token number, and, confirming an earlier study, position of offered and chosen options. Neuronal response latencies were similar in both areas. We observed two major differences between the regions: first, the task-related signal-to-noise was consistently greater in dACC than in sgACC. Second, we observed some differences in the average direction of value tuning: sgACC shows a negative bias to outcomes while dACC shows a positive one, and, prior to jackpots, sgACC shows a positive bias in activation, while dACC shows no consistent pattern. Overall, these results point to a broad functional overlap between dACC and sgACC, with differences more in emphasis than in major functional role.

Studies of functional neuroanatomy often focus on identifying each area's unique specialization, but there are other important questions about brain regions—such as: which regions subserve a given brain function? One mental operation may be implemented by similar computations occurring simultaneously in multiple brain areas (Behrmann & Plaut, 2013; Cisek & Kalaska, 2010; Cisek, 2012; Farah, 1994; McClelland & Rumelhart, 1986). Our data suggest that risky economic choice may be mediated by computations occurring in both dACC and sgACC, and, given our earlier data, across vmPFC and VS as well (Strait et al., 2014; Strait et al., 2015). While these regions may, in principle, compute similar variables for distinct purposes, it is more parsimonious to assume, without strong evidence to the contrary, that they play similar roles.

By way of analogy, an earlier generation of scholars proposed that early and mid-level visual areas are specialized for specific aspects of form (Zeki, 1978), and that V4 is specialized for color (Essen & Zeki, 1978; Zeki, 1977; Zeki, 1980). Subsequent work disproved this idea and demonstrated that its role in color processing is not very different from those of adjacent areas (Schein et al., 1982; Motter, 1994; Van Essen & Maunsell, 1983). Its properties are similar to (but slightly more complex than) its afferent V2 and similar to (but slightly less complex than) its efferent PIT (Desimone & Schein, 1987; Desimone et al., 1985; Desimone & Duncan, 1995; Hayden & Gallant, 2013; Mirabella et al., 2007). It would be a mistake to look for color vision in any one brain region: it depends on the distributed and coordinated action of several brain regions, all of which perform many other computations unrelated to color (Desimone & Duncan, 1995; Lennie, 1998). We suspect that the same principles apply to economic choice; it reflects qualitatively similar, although quantitatively different, repeated simple computations occurring in parallel across multiple prefrontal and striatal regions (and possibly others as well). These results thus argue against a strong functional dichotomy between the two regions. For example, Bush et al. (2000) argue that the dorsal cognitive region is functionally distinct from the subgenual affective region and they may even inhibit each other. We see no evidence for a cognitive/limbic split, nor of mutual inhibition between these two regions. Clearly, other studies, using other methods, do see evidence for such a split; further work will be required to reconcile these contradictions.

At the same time, the differences we observe between dACC and sgACC argue against a mass action view of brain function. The differences we see are consistent with results of both neuroimaging and lesion studies supporting some functional difference

between the areas, and with the neuroanatomy, which shows different patterns of connectivity (Heilbronner & Haber, 2014 Vogt et al., 1995). The difference in signal-to-noise is particularly intriguing. It may reflect a greater selectivity for choice tasks in the dorsal region; presumably there are other tasks that would drive sgACC more effectively than dACC (however, we would expect these differences to be quantitative, not qualitative). Another possibility is that economic decision-making, while distributed, has a fan-in structure and that dACC, which is presumably later in the hierarchy, has a more concentrated and thus stronger set of task signals.

Our findings generally confirm and extend the existing literature on sgACC. Monosov & Hikosaka (2012), like us, find a bias towards encoding of negative outcomes in area 25. We show that this finding extends to secondary (token) reinforcers. They report no encoding of probability, and thus of integrated value; our finding of integrated value encoding thus suggests that sgACC may play a more direct economic role, especially in decision-making tasks. Amemori & Graybiel (2012) recorded in pregenual cingulum, in a region that is rostral to our region, but has a small overlap (see Methods). They found a subzone, which may overlap with our subgenual recording site, biased towards negative encodings. Our high fraction of subgenual neurons encoding upcoming large rewards (jackpots) provide confirmation for the idea, proposed by Rudebeck and colleagues (2014), that sgACC serves to sustain autonomic arousal in anticipation of a reward. The phasic, task-relevant signals in sgACC, and its direct role in reward-processing and anticipation, suggest that the role for subgenual neurons extends beyond the control of basic arousal functions like sleep (Rolls et al., 2003). Our findings also cohere with the findings relating activity in sgACC to negative affect and depression.

Overactivity in this region correlates with depressive symptoms (Drevets, 2002; Mayberg et al., 2000) and with transient sadness in healthy subjects (Mayberg et al., 1999); chronic stimulation of sgACC can alleviate the symptoms of depression (Mayberg et al., 2005). Negative mood inducing stimuli tend to activate sgACC (George et al., 1995; Mayberg et al., 1997; Mayberg et al., 1999), and structural abnormalities in sgACC correlate with mood disorders (Botteron et al., 2002; Coryell et al., 2005; Drevets et al., 1997).

These findings also have implications for our understanding of dACC as well. The role of dACC in economic choice remains disputed. Some research indicates that it serves as the site of choice (Rangel & Hare, 2010); our work confirms this idea but, in the broader context of data from other studies, suggests it does not play a unique role. Other research suggests that dACC plays a specifically post-decisional role, in part because it preferentially encodes the value of unchosen options (Blanchard & Hayden, 2014; Boorman et al., 2011; Rushworth et al., 2012; Hayden et al., 2009). Our results here suggest that dACC may encode predecisional variables: the values of both chosen and unchosen options – at least before the decision is made. Other work links dACC to persistence – that is, in maintenance of value encoding until the time of reward to allow stable behavior (Hillman & Bilkey, 2013, Chudasama et al., 2013; Picton et al., 2007; Blanchard et al., 2015; Shidara and Richmond, 2002). While we did not use a persistence task, our results do endorse the idea that dACC serves to encode prospective rewards, suggesting that it does serve this function although not necessarily purely for the purpose of persistence.

Overall, these results invite speculation on whether one can ascribe a single integrated role for the cingulum (Hayden & Platt, 2009). On one hand, the broad overlap

581 between dACC and sgACC that we see suggests it may have a general economic role. On
582 the other, our findings in a similar task in vmPFC and VS suggest this role may not be
583 unique to the cingulate cortex (Strait et al., 2014; Strait et al., 2015). Our results also have
584 some similarity to findings from the posterior cingulate cortex. Neural responses in that
585 region are associated with several economic variables, including offer and outcome
586 variables, as well as learning and control variables (Dean & Platt, 2003; Hayden et al,
587 2009; Heilbronner & Platt, 2013; McCoy et al., 2003; Heilbronner et al., 2011). Neurons
588 in sgACC tend to have poorer signal-to-noise than dACC, much like neurons in PCC
589 (Hayden et al., 2008), suggesting they may have some affinity. Still, we consider the
590 question of whether there is a general and unique function for the cingulum to be
591 unanswered.
592
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MATERIALS AND METHODS

Some of the data for both dACC and sgACC recordings were published (Strait et al., 2016); all analyses presented here are new.

Surgical Procedures

All procedures were approved by the University Committee on Animal Resources at the University of Rochester and were designed and conducted in compliance with the Public Health Service's Guide for the Care and Use of Animals. Two male rhesus macaques (*Macaca mulatta*: subject B age 5y. 7mo.; subject J age 6y. 7mo.) served as subjects. A small prosthesis for holding the head was used. Animals were habituated to laboratory conditions and then trained to perform oculomotor tasks for liquid reward. A Cilux recording chamber (Crist Instruments) was placed over the dACC. Position was verified by magnetic resonance imaging with the aid of a Brainsight system (Rogue Research Inc.). Animals received appropriate analgesics and antibiotics after all procedures. Throughout both behavioral and physiological recording sessions, the chamber was kept sterile with regular antibiotic washes and sealed with sterile caps. All recordings were performed during the animals' light cycle between 8am and 5pm.

Recording Site

We approached dACC through a standard recording grid (Crist Instruments). We defined dACC according to the Paxinos atlas (Paxinos et al., 2000). Roughly, we recorded from a ROI lying within the coronal planes situated between 29.50 and 34.50 mm rostral to interaural plane, the horizontal planes situated between 4.12 to 7.52 mm

627 from the brain's dorsal surface, and the sagittal planes between 0 and 5.24 mm from
628 medial wall. Our recordings were made from a central region within this zone. We
629 confirmed recording location before each recording session using our Brainsight system
630 with structural magnetic resonance images taken before the experiment. Neuroimaging
631 was performed at the Rochester Center for Brain Imaging, on a Siemens 3T
632 MAGNETOM Trio Tim using 0.5 mm voxels. We confirmed recording locations by
633 listening for characteristic sounds of white and gray matter during recording, which in all
634 cases matched the loci indicated by the Brainsight system.
635 We approached sgACC using similar equipment, in a similar manner. We defined
636 sgACC as lying within the coronal planes situated between 24 and 36 mm rostral to
637 interaural plane, the horizontal planes situated between 17.33 to 25.12 mm from the
638 brain's dorsal surface, and the sagittal planes between 0 and 5.38 mm from the medial
639 wall. Our recordings were made from a central region within this zone. We again confirm
640 recording locations using structural magnetic resonance images, Brainsight, and listening
641 to characteristic sounds of white and gray matter. These regions correspond to area 25 as
642 identified by Paxinos (n = 118 neurons) and also to the most caudal portion of area 32 (n
643 = 28 neurons).
644
645 **Electrophysiological Techniques**
646 Single electrodes (Frederick Haer & Co., impedance range 0.8 to 4 MU) were
647 lowered using a microdrive (NAN Instruments) until waveforms of between one and
648 three neuron(s) were isolated. Individual action potentials were isolated on a Plexon
649 system (Plexon, Inc.). Neurons were selected for study solely on the basis of the quality

of isolation; we never pre-selected based on task-related response properties. All collected neurons for which we managed to obtain at least 250 trials were analyzed.

Eye Tracking and Reward Delivery

Eye position was sampled at 1,000 Hz by an infrared eye-monitoring camera system (SR Research). Stimuli were controlled by a computer running Matlab (Mathworks) with Psychtoolbox (Brainard,1997) and Eyelink Toolbox (Cornelissen et al., 2002). Visual stimuli were colored rectangles on a computer monitor placed 57 cm from the animal and centered on its eyes (Figure 1A). A standard solenoid valve controlled the duration of juice delivery. The relationship between solenoid open time and juice volume was established and confirmed before, during, and after recording.

Behavioral Task

Monkeys performed a two-option gambling task. The task was similar to one we have used previously (Strait et al., 2014; Strait et al., 2015), with two major differences: (1) monkeys gambled for virtual tokens—rather than liquid—rewards, and (2) outcomes could be losses as well as wins.

Two offers were presented on each trial. Each offer was represented by a rectangle 300 pixels tall and 80 pixels wide (11.35° of visual angle tall and 4.08° of visual angle wide). 20% of options were safe (100% probability of either 0 or 1 token), while the remaining 80% were gambles. Safe offers were entirely red (0 tokens) or blue (1 token). The size of each portion indicated the probability of the respective reward. Each gamble rectangle was divided horizontally into a top and bottom portion, each colored according to the

673 token reward offered. Gamble offers were thus defined by three parameters: two possible
674 token outcomes, and probability of the top outcome (the probability of the bottom was
675 strictly determined by the probability of the top). The top outcome was 10%, 30%, 50%,
676 70% or 90% likely.

677 Six initially unfilled circles arranged horizontally at the bottom of the screen
678 indicated the number of tokens to be collected before the subject obtained a liquid
679 reward. These circles were filled appropriately at the end of each trial, according to the
680 outcome of that trial. When 6 or more tokens were collected, the tokens were covered
681 with a solid rectangle while a liquid reward was delivered. Tokens beyond 6 did not carry
682 over, nor could number of tokens fall below zero.

683 On each trial, one offer appeared on the left side of the screen and the other
684 appeared on the right. Offers were separated from the fixation point by 550 pixels (27.53°
685 of visual angle). The side of the first offer (left and right) was randomized by trial. Each
686 offer appeared for 600 ms and was followed by a 150 ms blank period. Monkeys were
687 free to fixate upon the offers when they appeared (and in our observations almost always
688 did so). After the offers were presented separately, a central fixation spot appeared and
689 the monkey fixated on it for 100 ms. Following this, both offers appeared simultaneously
690 and the animal indicated its choice by shifting gaze to its preferred offer and maintaining
691 fixation on it for 200 ms. Failure to maintain gaze for 200 ms did not lead to the end of
692 the trial, but instead returned the monkey to a choice state; thus, monkeys were free to
693 change their mind if they did so within 200 ms (although in our observations, they
694 seldom did so). A successful 200 ms fixation was followed by a 750 ms delay, after
695 which the gamble was resolved and a small reward (100 μL) was delivered—regardless

of the outcome of the gamble—to sustain motivation. This small reward was delivered within a 300 ms window. If 6 tokens were collected, a delay of 500 ms was followed by a large liquid reward (300 μL) within a 300 ms window, followed by a random inter-trial interval (ITI) between 0.5 and 1.5 s. If 6 tokens were not collected, subjects proceeded immediately to the ITI.

Each gamble included at least one positive or zero-outcome, ensuring that every gamble carried the possibility of a win. This decreased the number of trivial choices presented to subjects, and maintained motivation.

Statistical Methods

PSTHs were constructed by aligning spike rasters to the task event of interest (offer 1 appearance, choice or feedback) and averaging firing rates across multiple trials. Firing rates were calculated in 20 ms bins but were generally analyzed in longer (500-1000 ms) epochs. Plots were generated in Matlab, and use the Matlab function *smooth* with a smoothing factor of 20.

Firing rates were **normalized** by subtracting the mean and dividing by the standard deviation of the entire neuron's psth.

We test for significant tuning and assess variance explained using a **multiple linear regression**, including the following task-relevant variables: expected value of offers 1 and 2, the number of tokens collected as of the beginning of the trial, the side the first offer appeared on, conflict between offer values (defined as the absolute difference between them), the side of the chosen offer, the outcome of the trial (in tokens), and the probability of that outcome (a measure of surprise).

719 **Analysis epochs** were chosen *a priori*, before data analysis began, to reduce the
720 likelihood of p-hacking. The first and second offer epochs were defined as the 500 ms
721 epoch beginning 100 ms after the offer was presented, to account for information
722 processing time. The choice epoch was the 1-second epoch before choice was indicated
723 using an express saccade. The reward epoch was defined as the 800 ms epoch following
724 the resolution of a gamble: this was when feedback and a small liquid reward were given
725 (regardless of trial outcome), followed by a 500 ms delay (this was part or all of the
726 intertrial interval on non-jackpot trials, and a pre-jackpot delay on jackpot trials).
727 All **fractions of tuned neurons** were tested for significance using a two-sided
728 binomial test. All binomial tests throughout the manuscript were two-sided.
729 All **sliding window plots** use a sliding 500 ms window, computing the fraction of
730 tuned neurons in the population every 20 ms. Points on the plot are aligned to the start of
731 this window. Significance is assessed using a multiple linear regression including all
732 task-variables (mentioned above). Plots were smoothed using the Matlab function *smooth*
733 and a smoothing factor of 20.
734 We use **beta correlation analyses using stepwise regression** to assess whether
735 neurons represent two variables (or the same variable at different time periods) using
736 similar / orthogonal / opposing formats, in overlapping / orthogonal / distinct populations.
737 In these analyses, we first find the regression coefficients associated with the variables in
738 question, then find the Pearson correlation coefficient between these.
739 We noticed that, depending on which variables we included in the regression, the
740 results of our beta correlation analyses sometimes differed. We therefore used a stepwise
741 regression model as an objective method of determining which variables should be

included in the final regression for each individual neuron. We first include all relevant task variables, including the variables of interest, in this stepwise regression. We then perform a (non-stepwise) multiple linear regression analysis again using only the variables obtained from the previous step, as well as the variables of interest. We do this to obtain a regression coefficient corresponding to the variable of interest for each neuron, regardless of whether the coefficient for this variable achieved significance in the previous step.

The Pearson correlation coefficient between signed regression coefficients indicate whether variables were represented in a similar *format* i.e. directionality of tuning across the population. A positive correlation indicates a preservation of directionality, while a negative correlation indicates variables were represented in opposing directionality of firing rate modulation. No correlation suggests orthogonal formats, but we draw no strong conclusions from these.

Similarly, the Pearson correlation coefficient between unsigned regression coefficients indicates whether similar neuronal populations tended to be involved in encoding the two variables in question. A positive correlation indicates overlapping populations, while a negative correlation indicates separate ones. A lack of correlation suggests orthogonal populations (i.e. encoding one variable does not affect a neuron's likelihood of encoding the other variable), but we again draw no strong conclusions from this null result.

We performed a **cross-validation procedure** similar to that in Blanchard et al. (Blanchard et al., 2015) on our sgACC dataset to determine whether our signal in the first and second epochs was strong enough to detect correlations. We split trials into two

765 random sets (even and odd), and computed the regression coefficients for each individual
766 neuron in response to offer 1 value in both epochs 1 and 2. We then obtained the Pearson
767 correlation coefficient of these signed regression coefficients within each epoch. We see
768 no correlation in the epoch we analyzed for offer 1 memory signals (i.e. epoch 2: $r =$
769 0.16, $P = 0.058$, Pearson correlation coefficient). The failure of this cross-validation
770 procedure to detect a significant correlation in sgACC indicates that we did not have
771 sufficient signal in our dataset to detect correlation effects, even if they existed. This
772 procedure prevents us from drawing strong conclusions regarding the *absence* of a signal
773 in this region.
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