Prediction of economic choice by primate amygdala neurons

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The amygdala is a key structure of the brain's reward system. Existing theories view its role in decision-making as restricted to an early valuation stage that provides input to decision mechanisms in downstream brain structures. However, the extent to which the amygdala itself codes information about economic choices is unclear. Here, we report that individual neurons in the primate amygdala predict behavioral choices in an economic decision task. We recorded the activity of amygdala neurons while monkeys chose between saving liquid reward with interest and spending the accumulated reward. In addition to known value-related responses, we found that activity in a group of amygdala neurons predicted the monkeys' upcoming save–spend choices with an average accuracy of 78%. This choice-predictive activity occurred early in trials, even before information about specific actions associated with save–spend choices was available. For a substantial number of neurons, choice-differential activity was specific for free, internally generated economic choices and not observed in a control task involving forced imperative choices. A subgroup of choice-predictive neurons did not show relationships to value, movement direction, or visual stimulus features. Choice-predictive activity in some amygdala neurons was preceded by transient periods of value coding, suggesting value-to-choice transitions and resembling decision processes in other brain systems. These findings suggest that the amygdala might play an active role in economic decisions. Current views of amygdala function should be extended to incorporate a role in decision-making beyond valuation.

neurophysiology | abstract representation | subjective value | emotion

The amygdala is a key structure of the brain's reward system, and it is involved in value-guided behavior. Damage to the amygdala in humans is related to changes in decision-making under conditions of ambiguity (1) and risk (2). In monkeys and rats, amygdala lesions impair reward-related and affective behavior (3, 4). Individual amygdala neurons respond to basic rewarding and aversive stimuli (5, 6), code expectations about rewarding and aversive outcomes (7–10), and update the positive and negative values of conditioned stimuli during learning (9–11). In human imaging studies, amygdala activation is associated with basic rewards (12), decision variables (13), and decision-related emotions (14). Together, these findings suggest an important contribution of the amygdala to economic decision-making in addition to its well-known roles in emotion and fear conditioning (5, 14–19). However, the specific nature of this contribution is currently unknown.

Existing theories of the amygdala view its role in decision-making as restricted mainly to the evaluation of choice options (1, 14, 20), which may serve as input for decision mechanisms in downstream brain structures. Although this view ties in well with known amygdala functions in reward (3, 5, 21), Pavlovian learning (4, 11), and emotion (14–20), it may be premature to conclude that the role of the amygdala in decision-making is confined to the valuation stage. Crucially, the information coded by individual amygdala neurons during economic decision-making has not been systematically explored. Therefore, it is currently unclear whether information processing in the amygdala ends with the coding of values or whether its neurons also carry information about upcoming economic choices.

Here, we report that the activity of single neurons in the primate amygdala predicted behavioral choices in an economic reward–saving task. The decision task temporally dissociated the economic choice from the process of action selection, which allowed us to assess neuronal choice coding independently from action coding.

Results

Two monkeys performed in a free choice economic task (Fig. 1*A*). The animals chose between saving a liquid reward with interest for future trials and spending the already accumulated reward immediately. The increase of reward magnitude over successive save choices was determined by a geometric series (Eq. **1**),

$$x_n = b\sum_{i=0}^{n-1} q^i, \qquad [1]$$

with x_n as the reward magnitude on trial n, b as the base rate of reward magnitude, and q as the interest rate, resulting in exponential increases for higher interest rates (Fig. S1). Monkeys indicated their choices by a saccade to the visual save or spend cue. Notably, the task temporally dissociated the internal process of save vs. spend choice, which could occur before the saccade targets were presented, from the process of left vs. right action selection.

The monkeys also performed in an imperative task with the same visual cues but small dots indicating the required target choice. This imperative task was a useful control to examine the extent to which choice-related neuronal activity would also occur when choices were externally instructed. We matched the ratio of save to spend trials in the imperative task to the ratio observed in the free choice task for a given monkey and a given interest rate.

Behavioral Data. The monkeys took advantage of the nature of the reward–saving task by making more consecutive save choices with higher interest rates (Fig. 1*B*). The spend probability at any point in a save choice sequence depended on the number of preceding save choices since the last spend choice ($P < 0.003$, repeated measures ANOVA). There were also slight differences in saving between monkeys (interaction between interest rate and animal identity; $P < 0.003$, repeated measures ANOVA). To further examine these effects, we constructed an index that reflected preferences for longer save sequences (*SI Methods*). For both monkeys, this index increased with higher interest rates ($P < 0.03$, linear regression) (Fig. 1*C*). The average index across interest rates was also higher for monkey A compared with monkey B ($P = 0.005$, paired t test) (Fig. 1*C Inset*), indicating a

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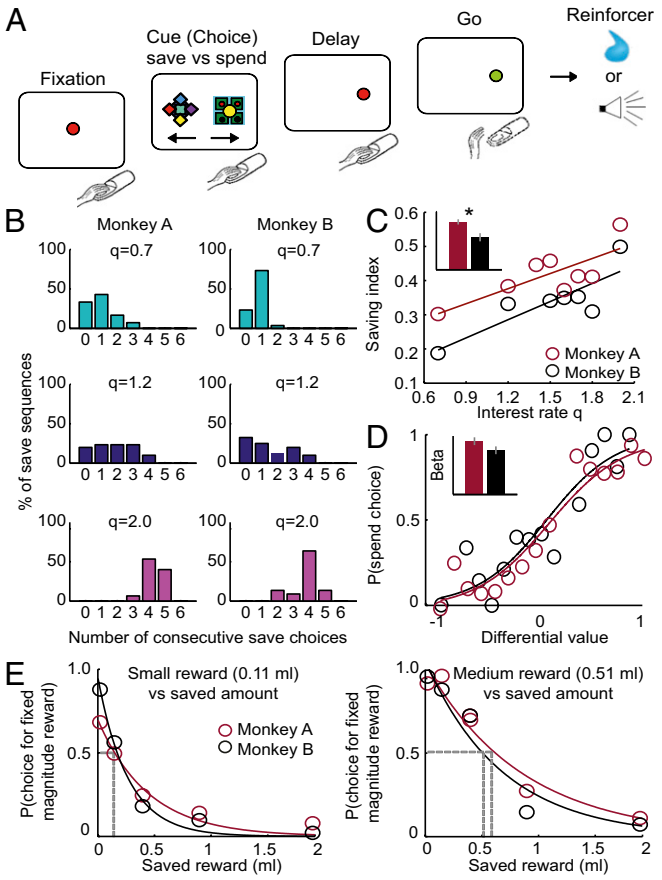

Fig. 1. Behavioral task and economic choice behavior. (*A*) Sequence of events in the free choice save–spend task. Monkeys indicated their choices with a saccade to one of two visual cues. Specific cues predicted save and spend options; different save cues indicated different interest rates. (*B*) Monkeys made more consecutive save choices with higher interest rates. Percentage of observed save sequences in six representative sessions with different interest rates (*q*). (*C*) Saving index increased as a function of interest rate (monkey A: $R^2 = 0.61$; monkey B: $R^2 = 0.71$; both $P < 0.03$, linear regression), and mean index differed between monkeys (*Inset*; $P = 0.005$, paired *t* test; error bars denote ± SEM). (*D*) Spend probability as a function of differential subjective value between save and spend options (color code is the same as in *C*, and curves represent logistic fits to choice data). *Inset* shows standardized logistic regression coefficients (both $P < 1 \times 10^{-8}$, *t* test for logistic regression coefficient; error bars denote ± SEM). (*E*) Control test with fixed reward. On random trials (in sessions with the same interest rate), monkeys chose between a fixed reward (0.11 or 0.51 mL, indicated by different cues) and the accumulated saved amount. Intersections between horizontal gray lines and choice curves (exponential fits) indicate points of subjective indifference between fixed and saved rewards.

stronger preference for saving over multiple trials. Thus, in both animals, save sequences became longer with higher interest rates, although saving behavior differed slightly between animals.

We modeled the monkeys' trial-by-trial choices with a logistic function of the differential subjective value of spending or saving on a given trial (*Methods*). Logistic regressions suggested that the differential value of spending on the present trial vs. spending on any potential subsequent trial of the same save sequence provided a good fit to the monkeys' behavior (Fig. 1*D*, Fig. S2, and Table S1). Thus, the monkeys' choices were guided by the reward value of potential future trials in a save sequence. Moreover, saving behavior was better explained by this differential value model compared with a simpler model based only on the monkeys' average choice probabilities (*SI Results*). This finding suggested that monkeys incorporated trial-by-trial variations in subjective value rather than using a simple counting strategy.

To confirm that monkeys tracked accumulated rewards over consecutive save choices, we offered them, on randomly selected control trials, a choice between the accumulated reward and fixed reward amounts, which were indicated by pretrained visual cues. Both animals consistently chose the fixed reward when it exceeded the saved magnitude (Fig. 1*E*) ($P < 0.001$, Mann–Whitney test). This result suggested that monkeys kept track of accumulated rewards over successive save trials and based their choices on this information.

Analysis of licking durations confirmed that monkeys distinguished save–spend trials in both free choice and imperative tasks even before cue appearance (Fig. S3). Furthermore, performance levels were similar for both tasks (80% and 76% correct trials in the free choice and imperative tasks, respectively). These observations suggested that monkeys anticipated save and spend choices in the imperative task.

Neuronal Activity. We recorded the activity of 329 task-related amygdala neurons and used multiple regression analysis to test for coding of the monkeys' upcoming save–spend choices before the behavioral responses (*Methods*). We included several reward value measures as regression covariates and estimated their coefficients simultaneously with choice coefficients. This method ensured that significant choice coefficients were not confounded by value coding.

The choice-related activity of the neuron shown in Fig. 2 was higher before spend choices compared with save choices ($P = 0.026$, *t* test for the save–spend coefficient) (Fig. 2 *A* and *E*). Importantly, save–spend differences occurred only in free choice and not imperative trials (Fig. 2 *B* and *F*). Multiple regression revealed that the neurons' activity was unrelated to different measures of value (Fig. 2 *C*, *E*, and *G*). The activity did not predict upcoming left or right eye movements, and it was independent of visual cue position or reaction time (Fig. 2 *D*, *G*, and *H*). Taken together, the neuron's response predicted the behavioral choice to save or spend irrespective of value, action, and other measured choice parameters.

Of 846 task-related responses in 329 neurons, 127 responses in 94 neurons (29% of the neuronal population; 50 and 44 neurons from monkeys A and B, respectively) showed choice-predictive activity (i.e., differential activity for upcoming save–spend choices as defined by a significant choice regressor) (Fig. 3*A* and Table 1). Task-related responses were defined by comparing a neuron's activity in a given task period with the neuron's activity in a control period ($P < 0.05$, Wilcoxon test) (*Methods*). In addition to choice coding, we confirmed the known value coding (8, 11, 22) in 140 amygdala neurons (43% of the neuronal population). Among the 127 choice-predictive responses, 85 responses (67%) showed no value coding, and 42 responses showed conjoint choice and value coding (Table 1). Only a few neurons showed relationships with left vs. right actions or reaction times (*SI Results*).

These data suggest that a substantial fraction of amygdala neurons carried choice-predictive information. The question arises whether these neurons genuinely coded economic choices or whether choice-predictive activity reflected differential reward expectation on save–spend trials. To address this question, we tested 156 neurons in both the free choice and imperative control tasks. If a neuron coded economic choices rather than reward expectations, its choice-predictive activity should be specific to the free choice task. Of 156 neurons tested in both tasks, 56 neurons showed choice-predictive activity during free choices. Among them, 45 neurons (80%) failed to predict choices on imperative trials ($P < 0.001$, binomial test for choice coding only in free choice vs. both tasks). In these 45 neurons, 41 responses showed higher activity on spend than save trials, and 16 responses showed the opposite pattern (Fig. 3*B*) ($P < 0.001$, two-tailed binomial test). Across all neurons tested in both tasks (not selected for choice coding), simple save–spend differences were small and mainly restricted to cue and outcome periods (Fig. 3*C*). As behavioral data showed, reward expectation was similar in free choice and imperative tasks (Fig. S3). Thus, specificity of save–

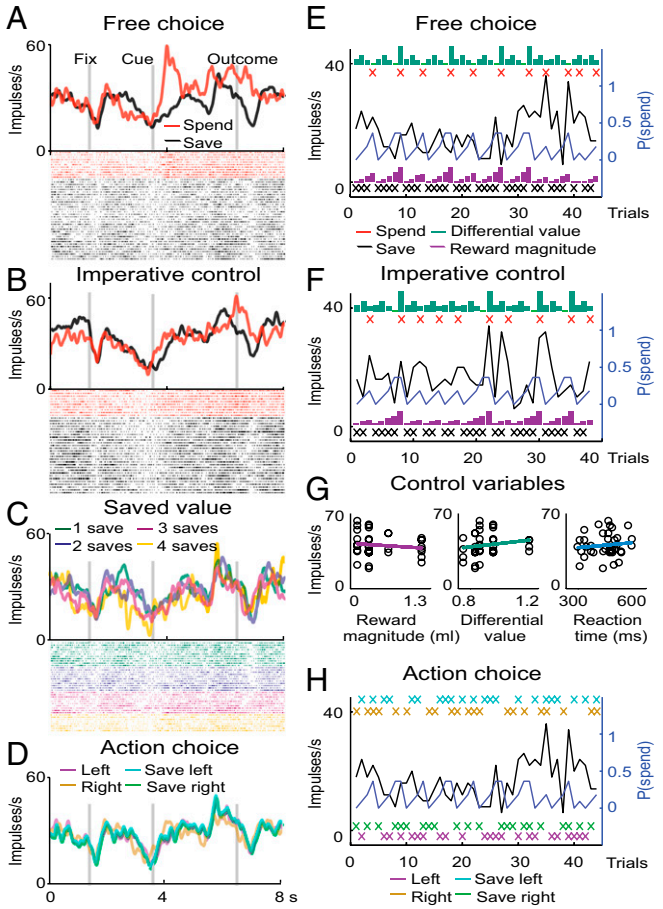

Fig. 2. Choice coding in an example amygdala neuron. (*A*) Choice-predictive activity in the free choice task. Activity time courses and raster plots for save (black) and spend (red) choices. Each line in the raster plots represents one trial; each dot represents one impulse. The regression coefficient for save–spend choice was significant ($P = 0.026$, t test) in the cue period before the behavioral response. The differential response did not reflect cue differences, as both cues appeared in all trials. (*B*) Activity in the imperative control task did not distinguish between save–spend trials. (*C*) Activity in save trials did not track accumulated reward over successive save trials (one to four saves). (*D*) Activity failed to distinguish between left/right eye movements or visual cue positions (save cue left/right). (*E*) Trial-by-trial record of activity across save–spend choices (black trace, neuronal activity in the cue period; blue trace, spend probability; black/red crosses, save–spend trials; vertical bars, value; magenta/green, reward magnitude/differential value). (*F*) Trial-by-trial record during the imperative task. (*G*) Activity did not track reward magnitude, differential value, or reaction times (all $P > 0.3$, t test on regression coefficients). (*H*) Trial-by-trial record across left–right actions and cue positions.

spend differences for free choices in these 45 neurons implied that their activity did not reflect differential reward expectation.

To examine relationships between choice-predictive activity and other decision parameters, we performed additional tests. Across choice-predictive responses, we searched for trials in which monkeys were, on average, indifferent between saving and spending. We identified 55 responses in 39 neurons in which this criterion was fulfilled [median P (spend) = 0.5; median number of successive save choices after which indifference was observed was three, depending on the interest rate]. We then tested whether neuronal activity on indifference trials tracked trial-by-trial choices. Across these 55 responses, activity was significantly higher for each neuron's preferred compared with nonpreferred choices (Fig. 3*D*) ($P < 0.001$, Wilcoxon test), despite identical choice probability and value-related decision variables. In another test, we evaluated whether choice coding remained constant over changes in interest rate. Among the 45 neurons in which choice-predictive activity was specific to the free choice but not the imperative task, 20 neurons were also tested with different interest rates. The majority of these neurons (16/20, 80%) showed a significant choice regressor, despite changed interest rate and visual save cues (Fig. S4).

A subgroup of 37 choice-predictive responses (31 neurons, 20% of neurons tested in both tasks; 16 and 15 neurons from monkeys A and B, respectively) showed the same characteristics as the neuron in Fig. 2; this subgroup predicted upcoming save–spend choices, but it failed to predict choice in imperative trials and failed to code value, action, visual stimulus position, and reaction time (Fig. 3*E*). As a useful control, less than 5% (our statistical threshold) of neurons exhibited such characteristics only in the imperative task and not in the free choice task, suggesting that this response pattern was not caused by random variability ($P < 0.001$, χ^2 test comparing proportions of such response types in both tasks). Thus, a group of amygdala neurons coded the monkeys' economic choices largely independent of value, action, and other choice parameters.

To quantify the degree to which economic choices could be predicted from neuronal activity, we used a biologically plausible classifier (23) as well as, independently, linear discriminant analysis to decode choices from trial-by-trial impulse rates. Notably, classifications used data from individual trials, which reflect the information propagated to the next downstream neuron during decision-making. We focused on those 57 responses that predicted choices in the free but not imperative task (although similar results were obtained with all 127 choice-predictive responses) (Fig. S5). On average, neuronal responses predicted save–spend choices with an accuracy of 78% (80% for the biologically plausible classifier; 76% for linear discriminant analysis) (Fig. 3*F* and Fig. S6). Combining responses, the classifier predicted choices with an accuracy of 91% ($P < 0.001$, permutation test with 1,000 iterations) (Fig. 3*F*). Increases in accuracy as responses were combined (Fig. 3*F*) indicated that neurons contributed partly independently to the prediction.

Of 45 neurons with choice coding only in the free choice task, 23 neurons were from the dorsal amygdala, 1 neuron was from the lateral amygdala, 10 neurons were from the basomedial amygdala, 9 neurons were from the basolateral amygdala, and 2 neurons were from the basoventral amygdala (Fig. 3*G* and Fig. S7). We were unable to identify systematic differences between recording sites (nonsignificant χ^2 tests); therefore, in line with previous studies (6, 24), we present the neuronal data as one set.

In perceptual decision-making, individual neurons in parietal cortex and related systems exhibit transitions from coding of decision variables to coding of perceptual choices (25, 26). Such signals are often interpreted as correlates of decision processes. To test for analogous value-to-choice transitions, we identified neurons with significant choice coding and in the same or preceding task period, significant value coding, and we examined the related temporal dynamics using sliding window regressions (*Methods*). We found 39 responses (33 neurons) in which value coding in different task periods preceded choice coding (Fig. 4). Among them, 22 responses (19 neurons) were also tested in the imperative task. None of them coded choices in imperative trials. The mean latency difference between the onset of value and choice coding was 1,741 ± 302 ms (SEM). Such responses might reflect translations from value to choice coding, resemble perceptual decision processes in other brain systems (25, 26), and match predictions from computational models of decision mechanisms (27–29).

Discussion

The present data show that the activity of individual amygdala neurons predicts behavioral choices during economic decision-making. In many neurons, choice-predictive activity occurred before information about specific behavioral responses was available to the monkeys. This finding suggested neuronal coding of the abstract economic save–spend choice rather than specific actions. For a large proportion of choice-predictive neurons that were

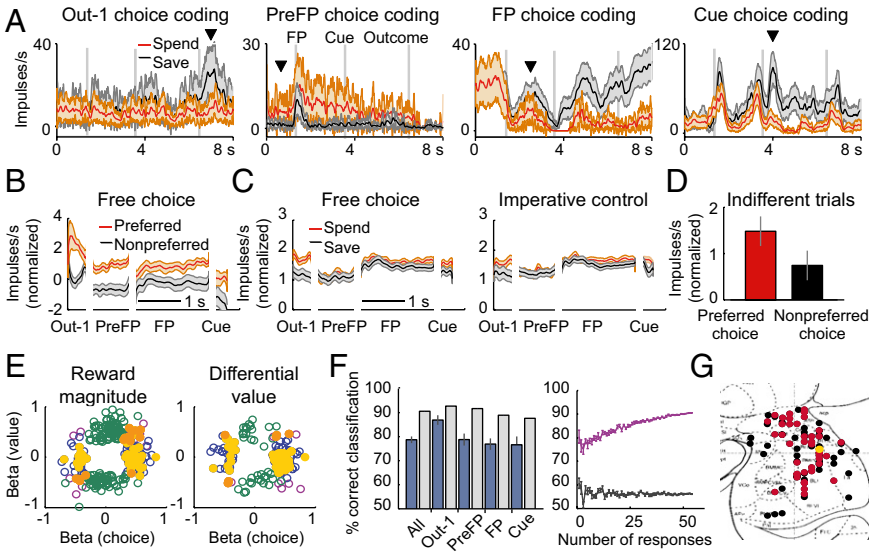

Fig. 3. Choice-predictive activity in amygdala neurons. (*A*) Four example neurons with choice-predictive activity in different task periods. Out-1 data were sorted according to choice on the next trial. Arrows indicate first period with significant choice regressor. Shaded regions indicate SEM. (*B*) Population time courses of *z*-normalized activity for 57 responses that predicted choice in the free task but not in the imperative task [Out-1 (outcome period of previous trial): $n = 8$; PreFP (before fixation spot): $n = 16$; FP (during fixation): $n = 20$; Cue (cue period): $n = 13$). (*C*) Population time courses of *z*-normalized activity for all 421 responses that were tested in both tasks (not selected for choice prediction) sorted into save–spend trials. (*D*) Mean normalized activity of 55 choice-predictive responses on trials in which monkeys were indifferent between spending and saving sorted according to trial-by-trial choice. (*E*) Relationships between choice and value coding. Standardized choice regression coefficients plotted against coefficients for reward magnitude (*Left*) and differential value (*Right*). Blue, significant choice but not value coefficients (*Left*, $n = 87$ responses; *Right*, $n = 106$ responses); green, significant value but not choice coefficients (*Left*, $n = 137$ responses; *Right*, $n = 37$ responses); magenta, significant choice and value coefficients (*Left*, $n = 36$ responses; *Right*, $n = 14$ responses); yellow, 37 responses (31 neurons) coding choice only during free choices without coding value; orange, 20 responses (14 neurons) coding choice only during free choices and coding value. (*F*) Decoding choices from neuronal activity. Accuracy (percent correct classification) of a biologically plausible classifier (23) using 57 responses with choice coding only during free choice. Blue bars, mean accuracy (±SEM) for classification based on individual responses; gray bars, accuracy for combining data across responses. Chance performance was 50%. (*Right*) Increases in accuracy (mean ± SEM) as responses were combined. Black trace, accuracy for randomly permuted data. (*G*) Histological reconstruction of recording sites. Locations of all 94 choice-predictive neurons (black symbols) and 45 neurons with choice coding only in the free choice task (red symbols) overlaid on a section from a stereotaxic atlas showing approximate amygdala subdivisions [45; the rhesus monkey brain in stereotaxic coordinates, Paxinos G, Huang XF, Toga AW, p 1, Copyright Elsevier (2000)]. Yellow symbol, example neuron from Fig. 2. Collapsing in the anterior–posterior dimension resulted in symbol overlap.

tested in both free choice and imperative tasks, choice-predictive activity was specific to free, internally generated choices. The inclusion of value covariates ensured that choice coding could not be explained in terms of reward value or related decision variables. Choice-predictive activity in a subgroup of neurons was irrespective of value, action, visual cue position, or other measured parameters. Taken together, neurons with such responses seem to code the monkeys' economic choices in a predictive manner.

A potential alternative explanation is that the choice-predictive activity might reflect differences in reward expectation, because immediate rewards were only available on spend but not save trials. However, several observations seem incompatible with this interpretation. First, in the majority of neurons tested in both tasks, choice-differential activity was not observed during the externally instructed imperative task, despite similar reward timing (although in some neurons, choice-predictive activity persisted during imperative trials). Second, reaction time and licking differences between save–spend trials, potentially reflecting differential reward expectation, were similar in both tasks (Fig. S3), and many choice-predictive neurons did not track them (*SI Results*). Third, a previous study showed that reward expectation-related activity in amygdala neurons covaried with the temporal distance

Table 1. Numbers of neurons with significant value and choice coefficients in different task periods and numbers of total significant responses summed over task periods

	Total neurons*	Total responses†	Out-1	Pre FP	FP	Cue
All						
Task-related	329	846	144	327	210	165
Value‡	140 (43%)	225 (27%)	65 (45%)	49 (15%)	67 (32%)	44 (27%)
Choice§	94 (29%)	127 (15%)	19 (13%)	27 (8%)	38 (18%)	43 (26%)
No value/value/complex¶	59/25/10	85/42/—	9/10/—	22/5/—	26/12/—	28/15/—
Imperative‖						
Task-related	156	421	76	155	104	86
Value	76 (49%)	115 (27%)	28 (37%)	25 (16%)	34 (33%)	28 (33%)
Choice	56 (36%)	73 (17%)	10 (13%)	18 (12%)	23 (22%)	22 (26%)
Free choice only**	45 (29%)	57 (14%)	8 (11%)	16 (10%)	20 (19%)	13 (15%)
No value/value/complex	31/12/2	37/20/—	3/5/—	11/5/—	13/7/—	10/3/—

*Numbers of individual neurons with significant responses in at least one task period; some neurons showed effects in multiple periods.
†Numbers of significant responses summed over task periods.
‡Significant reward magnitude or differential value coefficient.
§Significant save–spend choice coefficient.
¶Complex indicates neurons that coded choice both with and without value in different periods; it only applies for the total neurons column.
‖Neurons tested in both free choice and imperative tasks.
**Significant choice coefficients in the free choice task but not the imperative task.

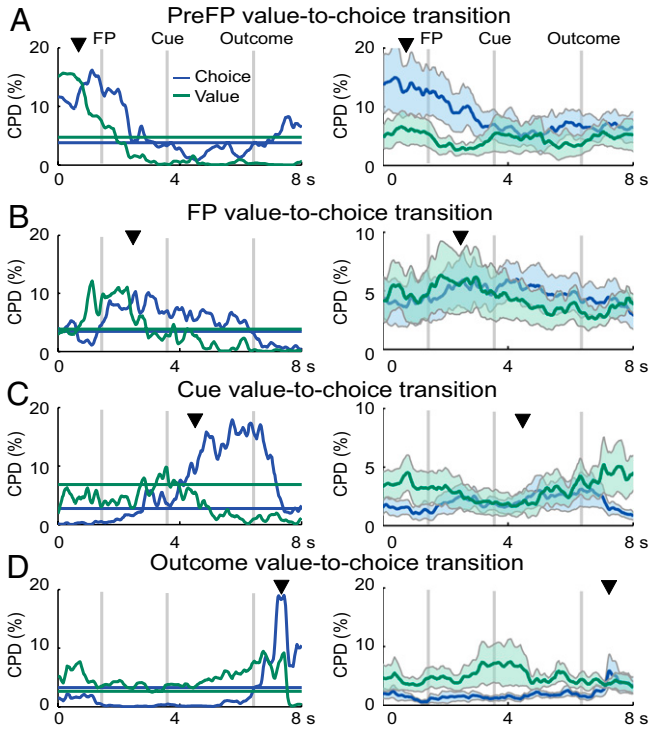

Fig. 4. Value-to-choice transitions. Four example neurons (*Left*) and related subpopulation means (*Right*; shaded regions indicate SEM) in which choice coding in a given task period was preceded by value coding. Coefficients of partial determination (CPDs) for value (green trace) and choice (blue trace) regressors from a sliding regression quantify the percent of variance in neuronal activity explained by one regressor in a multiple regression model. Arrows indicate task periods with significant choice coding. Horizontal lines indicate 3 SDs above the mean CPD obtained from randomly permuted data. Value-to-choice transitions were found in 39 responses [33 neurons; (*A*) PreFP: $n = 6$; (*B*) FP: $n = 12$; (*C*) Cue: $n = 12$; (*D*) Out-1: $n = 9$]. Value-to-choice transitions occurred within each individual response, and exact timing varied across responses; the population CPDs reflect the relative strength of value and choice coding across responses without necessarily also showing these transitions.

to reward receipt (24). By contrast, activity in many choice-predictive neurons in the present study did not covary with distance to reward (*SI Results*). Taken together, these observations argue against an explanation of choice-predictive activity solely in terms of reward expectation.

What role might neurons with choice-predictive responses serve in the context of general amygdala function? One potential role of the amygdala in decision-making might be to provide valuation signals that inform decision processes in downstream brain structures. This view fits well with current theories of amygdala function (1, 14, 20), known value coding in the amygdala in nonchoice situations (6, 11), and findings that human amygdala neurons track values during decision-making (22). Furthermore, decision impairments in humans with amygdala lesions are usually interpreted as valuation deficits based on concomitant changes in autonomic responses to decision outcomes (1, 2). A second possibility is that choice-predictive responses in the amygdala reflect the output of decision processes in other brain structures. The convergence of information about already computed decisions with value signals in the amygdala could be useful in learning processes (for example, by comparing values between expected and obtained outcomes). Conceptually similar chosen value neurons are found in the orbitofrontal cortex and striatum along with other neurons that code the value of individual choice options (30–35). However, many amygdala neurons in the present study coded information about upcoming choices without also coding their values. Indeed, supplementary analyses showed that the majority of choice-predictive responses could not be explained by these different forms of value coding (*SI Results*, Table S2).

A third and perhaps, more tantalizing possibility is that choice-predictive responses could reflect decision computations within the amygdala, which might directly instruct the selection of actions. The presently observed value-to-choice transitions could be interpreted as initial evidence for such a local decision mechanism. Current views of the role of the amygdala in fear conditioning also emphasize its potential to directly guide behavior through outputs to the striatum (17). Although this possibility could explain some of the behavioral deficits associated with amygdala lesions (1–3), it might seem inconsistent with evidence from reinforcer devaluation paradigms. In these studies, amygdala inactivation does not cause deficits in object choice after reward values have been updated, which is in contrast to inactivation of the orbitofrontal cortex (36, 37). However, the absence of behavioral deficits after inactivation does not, per se, preclude amygdala involvement in choices. For example, the amygdala might code choices in parallel with other brain systems, including the orbitofrontal cortex. Indeed, a recent study showed largely parallel value coding in amygdala and orbitofrontal cortex (10). By analogy, studies of perceptual decision-making showed parallel choice coding throughout multiple neural systems (38). Furthermore, reward structures, such as the amygdalae, consist of functionally heterogeneous neuronal populations (5, 6), and the behavioral consequences of lesions may reveal only a small part of the information processing in such brain structures. Nevertheless, a conclusive understanding of choice-predictive activity within the amygdala will require additional experimental investigation.

This discussion raises the question of whether similar coding of economic choices exists in other reward structures. The work by Padoa-Schioppa and Assad (34) described neurons in the orbitofrontal cortex that coded the chosen taste in an economic decision task. Recent observations suggest that such responses can occur early in trials before action information (39). Accordingly, chosen taste responses in the orbitofrontal cortex could potentially reflect the output of a decision mechanism for translating values into choices. However, it will be important to determine whether these responses reflect genuine economic choice coding or the expectation of specific taste rewards.

Our findings have implications for an ongoing debate about the nature of economic choice coding in the primate brain. Evidence for action-based coding of decision variables in the parietal cortex and related systems (25, 40) has led to views that economic decisions take place primarily among actions (40). By contrast, evidence for action-independent value coding in reward structures has led to the proposal that economic decisions take place in an abstract space of economic goods (34, 39). Thus, a fundamental, unresolved question is whether economic choices can exist as action-independent neuronal representations. Recent studies indicated that perceptual choice coding in parietal (41) and frontal cortices (42) and even the superior colliculus (43) can occur in an action-independent manner. Here, we extended these observations to value-based economic choices. We found choice-predictive responses before action information in the amygdala, a reward structure that is conceptually even farther upstream of action selection. The present behavioral testing with eye movements should not imply that the observed choice-related activity is specific for eye movements. As the absence of relationships to saccadic reaction times suggests, the observed activity may well occur with economic decisions involving other effector systems. Thus, taken together with previous evidence, our findings imply that abstract, action-independent neuronal representations may provide the basis for both perceptual and economic decisions.

In conclusion, our findings show that, in addition to providing value inputs to decision-making, the amygdala also codes economic choices in a predictive manner. Conceptually, choice coding in the amygdala seems to occupy an intermediate stage in neuronal information processing that is situated between valuation and action selection. Existing views of the amygdala as a pure valuation structure may, therefore, need to be extended to incorporate a more direct role in economic decisions.

Methods

Animals. Two adult male rhesus monkeys (*Macaca mulatta*) weighing 9.2 and 12.0 kg participated in the experiment. All animal procedures conformed to US National Institutes of Health Guidelines and were approved by the Home Office of the United Kingdom.

Free Choice Task. In different blocks of typically 50–100 consecutive trials, different stimuli were used as save cues to indicate different interest rates. We tested interest rates ranging from $q = 0.7$ to $q = 2.0$. Each neuron was typically tested with one or two different interest rates.

Imperative Control Task. A small visual cue was presented next to either the save or the spend cue to indicate the correct choice on each trial that was otherwise identical to a free choice trial.

Electrophysiological Recordings. We recorded the activity of single amygdala neurons from extracellular positions during task performance using standard electrophysiological techniques. We sampled activity from about 700 amygdala neurons in exploratory tests with the save–spend task, resulting in a database of 329 neurons with task-related responses that we analyzed statistically.

Data Analysis. We counted impulses in each neuron relative to different task events with fixed time windows: 1,000 ms before fixation spot (PreFP), 1,775 ms after fixation spot but before cues (FP; starting 25 ms after fixation spot onset), 300 ms after cues (Cue; starting 20 ms after cue onset), and 500 ms during the reward/outcome period of the preceding trial (Out-1; starting 50 ms after reward onset). We used the following multiple regression model to assess relationships to different variables ($P < 0.05$) (Eq. **2**):

$$Y = \beta_0 + \beta_1 SS + \beta_2 RM + \beta_3 DV + \beta_4 LR + \beta_5 SL + \beta_6 RT + \varepsilon, \quad [2]$$

with *SS* as save vs. spend choice, *RM* as the sum of objective reward magnitudes available for save and spend choices, *DV* as the subjective differential value used for behavioral modeling, *LR* as left vs. right action, *SL* as spatial cue position (save cue left vs. right), and *RT* as saccadic reaction time; β_{1-6} are corresponding regression coefficients, β_0 is the intercept, and ε is error.

Standardized regression coefficients (β values) in Figs. 1D and 3E were defined as x_i (s_i/s_y); x_i is the raw slope regression coefficient for regressor i, and s_i and s_y are the SDs of independent variable i and the dependent variable, respectively (44).

Decoding Choices from Neuronal Data. We used a leave-one-out cross-validation procedure, in which every trial was decoded based on the distribution of impulse rates from all other trials For combining data across responses, we used *z*-normalized neuronal data.

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Supporting Information

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SI Methods

Electrophysiological Recording. A head holder and a recording chamber were fixed to the skull under general anesthesia and aseptic conditions. Before neuronal recordings, we located the amygdala from bone marks on coronal and sagittal radiographs taken with a guide cannula and electrode inserted at a known coordinate in reference to the stereotaxically implanted chamber. The anteroposterior position of the amygdala was between the sphenoid bone (rostral) and the posterior clinoid process at and above the dorsoventral position of the posterior clinoid (1). We recorded activity from single amygdala neurons from extracellular positions during task performance using standard electrophysiological techniques, including online visualization and threshold discrimination of neuronal impulses on oscilloscopes. We recorded from one neuron at a time; this record permitted varied exploratory tests during early experimental phases. We aimed to record representative neuronal samples from the dorsal, lateral, and basal amygdala.

We sampled activity from about 700 amygdala neurons in exploratory tests with the save–spend task. We recorded and saved the activity of neurons that seemed to respond to at least one task event during online inspection of several trials. This procedure resulted in a database of 329 neurons with task-related responses that we analyzed statistically.

After completion of data collection, recording sites were marked with small electrolytic lesions (15–20 μA × 20–60 s). The animals received an overdose of pentobarbital sodium (90 mg/kg i.v.) and were perfused with 4% paraformaldehyde in 0.1 M phosphate buffer through the left ventricle of the heart. Recording positions were reconstructed from 50-μm-thick stereotaxically oriented coronal brain sections stained with cresyl violet. The histological reconstructions also validated the previously radiographically assessed anatomical position of the amygdala in agreement with earlier reports (1–3). Fig. S7 shows the cresyl violet-stained brain sections from monkey A for the left amygdala. For Fig. 3*G*, we collapsed recording sites from both monkeys spanning 3 mm in the anterior–posterior dimension onto the same coronal section. Because our accuracy of recording site reconstructions was likely to be lower than 1-mm resolution, recording positions with respect to individual amygdala nuclei were approximated based on a stereotaxic atlas (4) and typical anatomical landmarks.

Free Choice Task. In each trial (Fig. 1*A*), the monkey chose between saving the reward that was available on that trial, thereby increasing its magnitude by a variable interest rate, and spending the previously accumulated reward for consumption on the present trial. A natural upper limit to the length of save choice sequences was given by the total amount of liquid that each monkey was able to drink on one trial. Animals initiated trials by placing their hands on an immobile, touch-sensitive key. The trial then started with an ocular fixation spot of 1.3° of visual angle at the center of the computer monitor. Animals were required to keep their gaze on the fixation spot at the stimulus center within 2–4°. At 1,500 ms plus mean of 500 ms (truncated exponential distribution) after fixation spot onset, the two save and spend visual stimuli of 7.0° appeared on the left and right sides of the computer monitor (pseudorandomized). In different blocks of typically 40–100 consecutive trials, different stimuli were used as save cues to indicate different interest rates. Animals indicated their choice with a saccade. The chosen stimulus was then replaced by a peripheral fixation spot of 7.0° of visual angle. The monkey could make its choice as soon as the visual cues appeared. After a delay period of 1,500 ms, a color change of the peripheral fixation spot served as a go signal for the monkey to release the touch key. The release of the touch key was followed by the delivery of the reinforcer (an auditory or visual cue on save trials vs. a drop of juice reward on spend trials). Failures of key touch or fixation breaks were considered errors and resulted in trial cancellation. More than three sequential errors led to a pause in behavioral testing. Accumulated saved rewards were retained across error trials.

To provide an example of how rewards were calculated, consider a series of two successive save choices by the monkey with a base rate of reward $b = 0.11$ and interest rate $q = 1.5$. On the second trial of the choice sequence, after the first save choice, reward $R = 0.11 \times (1 + 1.5) = 0.275$ mL is given. On the third trial, after two successive save choices, reward $R = 0.11 \times (1 + 1.5 + 1.5^2) = 0.523$ mL is given.

Each neuron was typically tested with one to two different interest rates. The duration required for testing neurons with statistically sufficient numbers of trials in both tasks usually precluded using more than two interest rates.

The decision task resembled tasks used to study intertemporal decision-making, because it required choosing between immediately available rewards and future rewards of different magnitudes. However, in contrast to standard intertemporal choice tasks, temporal delays in the present task were not imposed by the experimenter but chosen by the monkeys. Thus, monkeys were free to produce save choice sequences of different lengths, which were associated with different reward magnitudes depending on the interest rate. Furthermore, longer delays invariably involved higher numbers of behavioral reactions (ocular saccades).

The collection of reproducible electrophysiological data from many individual neurons required standardized testing during stable and reproducible behavioral performance. We trained each animal for 3–4 mo before neuronal recordings with the different visual stimuli and the different interest rates (300–400 trial/d, 5 d/wk). The animals were overtrained at the time of neuronal recordings and showed no behavioral signs of additional learning.

Control Task with Fixed Reward. To test whether the monkeys kept track of the amount of reward that they had accumulated through consecutive save choices, we offered them, on randomly interspersed trials, a choice between the accumulated reward and fixed amounts indicated by pretrained visual cues.

Rewards. A computer-controlled solenoid valve delivered juice reward from a spout in front of the animal's mouth (valve opening time of 100 ms, which corresponds to 0.38 mL). For monkey A, the base rate of reward magnitude, b from Eq. 1, was set to 0.11 mL for all sessions; for monkey B, the base rate was set to 0.11 mL for one-half of the sessions and 0.13 mL for one-half of the sessions. The animal's tongue interrupted an infrared light beam below the adequately positioned spout. An optosensor monitored licking behavior with 0.5-ms resolution (STM Sensor Technology), and the summed durations of beam interruptions during specific trials and task periods provided a measure of licking.

Saving Index. To examine the relationship between saving behavior and interest rate, we constructed a save choice index separately for each monkey and interest rate as follows. First, we calculated the average relative probability of observing a save choice sequence of a specific length, where sequence lengths

varied from zero consecutive save choices to the maximal sequence length observed for a monkey. (The maximal observed sequence length was effectively the upper limit of liquid that the animal could consume on one trial, as described in *Methods*.) These probabilities were defined to sum to 1.0 across sequence lengths within a given interest rate. Thus, these relative probabilities reflect the monkey's behavioral preference for a given sequence of save choices relative to all other possible sequences for a specific interest rate. Second, we weighted (multiplied) these relative probabilities with their associated sequence lengths (i.e., with the number of successive save choices for that sequence), thereby giving higher weight to probabilities that were associated with higher sequence lengths. Third, we calculated the mean over all weighted sequence lengths for a given interest rate. This mean defined the saving index for a given interest rate, and it is plotted in Fig. 1*C* for both monkeys and all interest rates. Thus (Eq. **S1**),

$$SI_q = \frac{1}{n}\sum_{i=1}^{n} P_{i,q} L_i, \qquad \textbf{[S1]}$$

where SI_q is the saving index for a given interest rate q, n is the maximal sequence length observed for the monkey, $P_{i,q}$ is the mean (relative) probability of observing a save choice sequence of a specific save sequence length i, and L_i is the number of successive save choices required to obtain sequence length i.

Logistic Regression of Save–Spend Choices on Differential Values. To analyze monkeys' saving behavior on a trial-by-trial basis, we used logistic regression analysis. First, we reasoned that, in analogy to decision-making in other economic tasks, choices would be guided by an internally computed decision variable that is based on the subjective values that monkeys' assigned to the different choice options. To construct a measure of subjective value in the save–spend task, we used the monkeys' relative probabilities of producing save sequences of specific lengths (as described in the preceding paragraph) and weighted (i.e., multiplied) them by the corresponding objective reward magnitude in milliliters that would be available from spending at that point of a save sequence. For both monkeys and all interest rates, this calculation produced a subjective weighting of the objective reward magnitude according to monkeys' behaviorally observed preferences for different save sequence lengths. Thus, the subjective value SV for spending at a given point i in a save sequence for a given interest q was defined as (Eq. **S2**)

$$SV_i = P_i M_i, \qquad \textbf{[S2]}$$

where P_i is the mean (relative) probability of observing a save choice sequence of a specific save sequence length i, and M_i is the objective reward magnitude in milliliters of juice at that point in the save sequence (the task description is discussed above). To obtain unbiased estimates of these subjective values that could be used as regressors for both behavioral choices and neural data, we used one-half of the behavioral data in each monkey (i.e., one-half of the experimental sessions for a given interest rate) to estimate the subjective values, and we used the other half for subsequent analysis. We then used these subjective values to construct a decision variable to model the monkeys' trial-by-trial choices.

The decision variable differential value plotted in Fig. 1*D* and Fig. S2 was constructed in analogy to decision variables commonly used in studies of intertemporal decision-making. It was defined as the difference between the subjective value for choosing to spend on the present trial and the mean subjective value for choosing to spend on any potential subsequent trial of the same save sequence (where the upper limit of potential future trials was given by the maximal observed sequence length for the monkey). For example, if the monkey was in the fourth trial of a save sequence (after having made three consecutive save choices), the differential value for the present trial would be calculated as the difference between the subjective value for spending on the fourth trial of a save sequence and the mean of the subjective values for spending on any of the potential next five trials (with nine consecutive save choices being the observed maximal number of consecutive save choices for the monkey). Thus, the differential subjective value DV on a given trial n for a given interest rate was calculated as (Eq. **S3**)

$$DV_n = SV_n - \frac{1}{m}\sum_{i=n+1}^{m} SV_i, \qquad \textbf{[S3]}$$

where SV_n is the subjective value of choosing to spend on trial n, and the term in the subtrahend reflects the average subjective value of choosing to spend on any of the potential subsequent trials i of the same save sequence, with m defining the upper limit of the save sequence (given by the maximal observed sequence length for the monkey). We used logistic regression analysis to model the monkeys' choices based on this decision variable. The dependent variable was a binary indicator function denoting whether the monkey made a save or spend choice on a given trial. The independent variable was the differential value for the corresponding trial as defined above. The main purpose of this analysis was to test whether the differential value provided an adequate approximation of the decision variables that guided the monkeys' choices to inform our analysis of the neuronal data. The results of this analysis are summarized in Fig. 1*D*, Fig. S2, and Table S1. We found that this differential value (i.e., a decision variable that incorporated the average subjective value of potential future trials in a sequence) provided a better fit than a comparable decision variable that incorporated only the subjective value of choosing to spend on the next trial. Moreover, a differential value based on subjective values provided a better fit compared with decision variables based only on objective reward magnitudes or choice probabilities.

Data Analysis. We counted neuronal impulses in each neuron on correct trials relative to different task events with time windows that were fixed across all neurons: 1,000 ms before fixation spot (PreFP), 1,775 ms after fixation spot but before cues (FP; starting 25 ms after fixation spot onset), 300 ms after cues (Cue; starting 20 ms after cue onset), and 500 ms during the reward/outcome period of the preceding trial (Out-1; starting 50 ms after reward onset). We first identified task-related responses by comparing activity in the FP, Cue, and Out-1 periods with a control period (PreFP) using the Wilcoxon test ($P < 0.05$). Because the PreFP period served as the control period, we did not select for task-relatedness in this period and included all neurons with observed impulses in the analysis. We then used the following multiple regression model to assess relationships to trial-by-trial save–spend choices, different measures of reward value, left–right actions, left–right cue positions, and saccadic reaction times ($P < 0.05$) (Eq. **S4**):

$$Y = \beta_0 + \beta_1 SS + \beta_2 RM + \beta_3 DV + \beta_4 LR + \beta_5 SL + \beta_6 RT + \varepsilon, \qquad \textbf{[S4]}$$

with SS as the save vs. spend choice, RM as the sum of objective reward magnitudes available for save and spend choices, DV as the subjective differential value used for behavioral modeling, LR as left vs. right action, SL as spatial cue position (save cue left vs. right), and RT as saccadic reaction time; β_{1-6} are corresponding regression coefficients, β_0 is the intercept, and ε is error. On average, intercorrelations between these regressors

were low (Table S2). Because reward magnitudes for both save and spend choices increased monotonically over save trials, different potential reward magnitude regressors (e.g., sum of reward magnitudes and chosen/not chosen reward magnitude) were highly correlated and produced similar results. The same model was used to analyze responses in the imperative task.

Standardized regression coefficients (β values) in Figs. 1*D* and 3*E* were defined as x_i (s_i/s_y); x_i is the raw slope regression coefficient for regressor i, and s_i and s_y are the SDs of independent variable i and the dependent variable, respectively (5).

Decoding of Choices from Neuronal Data. Here, we provide more details about the decoding analysis. We used a biologically plausible classifier to decode choices from neuronal data on a trial-by-trial basis (6). The decoding procedure used by the classifier was based on a nearest neighbor algorithm. The neuronal activity measured in impulses per second on a single trial in an individual neuron was used as input to the classifier. For each individual neuron, every trial was represented in the space spanned by the distribution of its impulse rates on save and spend choice trials and decoded by assigning it to the class of its nearest neighbor using the Euclidean distance (6). This type of classification is biologically plausible in that a real downstream neuron could perform the classification in a similar way by comparing the input on a given trial with a stored vector of synaptic weights (7). We used a leave-one-out cross-validation procedure, in which every trial was decoded based on the distribution of impulse rates from all other trials. To investigate population coding of choices, we considered neurons as simultaneously recorded in the sense that the trial-specific responses of all neurons were grouped together and that decoding proceeded using the cross-validation procedure just described (6). Classification performance was measured as the percentage of correctly decoded individual trials, which we averaged across responses. We repeated the analysis using linear discriminant analysis, which also used leave-one out cross-validation procedures. To produce the graphs in Fig. 3*F* and Fig. S5, we randomly selected a given number of responses at each step and then determined the percentage correct. For each step, this procedure was repeated 10 times. We used a permutation test with 1,000 iterations to define statistical significance of the classification. Statistical significance was defined as the probability that the observed percentage correct was below a given percentile of the probability distribution of classification results based on randomly shuffled data.

Sliding Window Regression Analysis. We used sliding window multiple regression analysis (using the regression model described above) with a 200-ms window, and then, we moved the window in steps of 25 ms across each trial. Coefficients of partial determination (CPDs) (5) were defined as (Eq. **S5**),

$$\mathrm{CPD}(\mathrm{X_i}) = [\mathrm{SSE}(\mathrm{X_{-i}}) - \mathrm{SSE}(\mathrm{X_{-i}}, \mathrm{X_i})]/\mathrm{SSE}(\mathrm{X_{-i}}), \qquad \textbf{[S5]}$$

with SSE(X) indicating the sum of squared errors in a regression model that includes a set of regressors X, and $\mathrm{X_{-i}}$ indicating the set of regressors that includes all regressors except $\mathrm{X_i}$. Using methods from previous studies (5), latencies of choice and value coding were defined as the first window in which a CPD was 3 SDs above the mean CPD obtained from a permutation test (1,000 iterations) for three consecutive steps.

SI Results

Licking Durations. We measured anticipatory licking durations on save and spend trials before the cues were presented (Fig. S3). In the free choice task, significant differences in licking durations between save and spend trials would likely indicate a difference in reward expectation between these trials, because immediate rewards were only delivered if the monkeys chose to spend. Indeed, for both monkeys, licking times were significantly different between save and spend trials in the free choice task, despite individual differences between animals (both $P < 0.001$, Mann–Whitney test). We also examined licking durations in the imperative control task before cue appearance on every trial. If licking durations in the imperative task also differed between save and spend trials, even before cue appearance, this result might indicate that the monkeys anticipated these trial types, similar to the free choice task. Indeed, for both monkeys, licking times in the imperative task were significantly different between save and spend trials (both $P < 0.001$, Mann–Whitney test). No significant differences in licking patterns were found between the free choice and imperative tasks. Fig. S3 shows this pattern of licking durations for monkey A.

Reaction Times. We analyzed the reaction times of the saccades with which monkeys indicated their choices on save and spend trials. This analysis helped to test whether choice-differential neuronal activity could be explained by task difficulty as measured with reaction times (Fig. S3). For both monkeys, saccadic reaction times were longer on save compared with spend trials in both the free choice task ($P < 0.001$, Mann–Whitney test) and the imperative control task ($P < 0.001$, Mann–Whitney test). If choice-differential neuronal activity reflected differences in task difficulty between save and spend trials [or any secondary variable resulting from differences in task difficulty (for example, differential attention or arousal levels) on save vs. spend trials], then neuronal activity should differ between save and spend trials on both the free choice task and the imperative task. By contrast, as reported in the text, neuronal responses showed differences between these trial types only in the free choice task and not in the imperative task. These observations would argue against an explanation of our effects in terms of task difficulty.

Comparison of Behavioral Models. We evaluated whether monkeys' choices were better explained by the differential subjective value model compared with a simpler model that only incorporated the monkeys' average choice probabilities for different save sequences. If choices were explained by a model based solely on the monkeys' save sequence distributions, this finding might suggest that the animals developed a simple counting strategy and did not incorporate trial-by-trial changes in differential subjective value. To test this directly, we compared a logistic regression model that incorporated only the monkey's choice probabilities with one that also incorporated differential value as a covariate. The models were fit separately for different interest rates and the two animals. Across animals and interest rates, the differential value regressor remained significant ($P < 0.002$ in all cases), even if choice probabilities were included as an additional regressor. The same result was obtained if differential value was orthogonalized with respect to choice probabilities (i.e., the shared variance between regressors was assigned to choice probabilities) using Gram–Schmidt orthogonalization (8). This result suggested that the differential value regressor explained a significant proportion of variance not accounted for by simple choice probabilities. Indeed, a direct comparison of standardized regression coefficients showed significantly higher coefficients for differential value compared with choice probability across monkeys and interest rates ($P = 0.001$, paired t test). To test whether the differential value model provided a better fit, even if the number of model parameters was taken into account, we used the Akaike information criterion (AIC) and Bayesian information criterion (BIC), which penalize models with higher numbers of free parameters (9). AIC is defined as $-2 \ln \mathrm{L} + 2 \mathrm{k}$, in which L is the likelihood of the model, and k is the number of model parameters. BIC is defined as $-2 \ln \mathrm{L} + \mathrm{k} \ln \mathrm{N}$, in which N is the number of observations. Across animals and interest rates, AIC and BIC comparisons consistently fa-

vored the differential value model over the simpler choice probability model. Together, these results indicate that monkeys' choices were better explained by the differential value model, and thus, they were influenced by trial-by-trial variations in differential subjective value.

Anatomical Location of Recorded Neurons. Of all 94 choice-selective neurons, 45 neurons were recorded in the dorsal amygdala (Fig. 3*G*) (including central and medial nuclei; of 168 neurons in total recorded in this area), 3 neurons were recorded in the lateral amygdala (of 23 recorded neurons in this area), 20 neurons were recorded in the basomedial amygdala (of 67 recorded neurons in this area), 16 neurons were recorded in the dorsal basolateral amygdala (of 47 recorded neurons in this area), and 10 neurons were recorded in the basoventral amygdala (of 24 recorded neurons in this area). No systematic differences were found between recording sites (nonsignificant χ^2 test).

Reward Expectation. To test whether choice-predictive activity could be explained by differences in reward expectation between save and spend trials, we tested specifically for changes in neuronal activity across successive save trials. Previous studies have shown that reward expectancy-coding neurons show activity changes across trials to reward receipt (10). By contrast, many of our choice-predictive responses showed no significant value coefficients, which modeled systematic changes over successive save trials [85 of 127 choice-predictive responses (67%); 37 of 57 with choice-predictive activity in the free choice but not imperative task (65%)]. Moreover, all of our choice-predictive responses showed a significant choice regressor, although several measures of value were included as covariates in the multiple regression model. This finding suggested that choice coding in these responses cannot be explained in terms of reward value coding or related expectancy. Furthermore, the imperative control task served to explicitly control for simple reward expectation effects. In both tasks, reward expectation between save and spend trials was similar, which was indicated by patterns of differences in licking durations and saccadic reaction times (Fig. S3). By contrast, 80% of choice-predictive responses tested in both tasks failed to show significant choice coefficients in the imperative task, suggesting that choice coding in these neurons is unlikely caused by simple reward expectation.

Neuronal Coding of Value, Action, Visual Cue Features, and Reaction Times. In addition to choice coding, we confirmed the known value (reward magnitude and differential value) coding in the amygdala (3, 11–14) in 225 of 846 task-related responses (27%). Furthermore, 32 of 169 task-related responses in the Cue period (19%) were modulated by the spatial arrangement of the cues, consistent with known visual feature responses in the amygdala (11). Few neurons in the cue period showed a significant regression coefficient for left/right eye movements (15 neurons; 9%) or saccadic reaction times (10 neurons; 6%). In all other task periods, less than 5% of responses (our significance threshold) were modulated by eye movement direction, spatial cue position, or reaction time.

Control Analyses Testing for Different Forms of Value Coding. The main analysis reported in the paper identified 127 neuronal responses with significant choice coefficients. A subgroup of these responses coded choice without also coding value, which was indicated by nonsignificant coefficients for reward magnitude and differential value (Table 1). To further examine whether significant choice coefficients might be explained by other forms of value coding, we performed supplementary analyses. Previous studies found that neurons in the orbitofrontal cortex and striatum code different types of value signals (15–19), including the value of specific choice options, irrespective of whether the option is chosen (offer value or action value signals), the value of the chosen option, irrespective of its identity (chosen value signals), and the value of a specific choice option if that option is chosen (subtype of chosen value signals). We tested whether the choice-predictive responses described in the present study can be explained in terms of such value signals. We used the following three supplementary regression models. In (Eq. **S6**)

$$\text{Model S1: } Y = \beta_0 + \beta_1 SS + \beta_2 RM + \beta_3 SVspend + \beta_4 SVsave + \beta_5 LR + \beta_6 SL + \beta_7 RT + \varepsilon, \quad \textbf{[S6]}$$

SVspend is the subjective value of the spend choice option (irrespective of whether it is chosen), and *SVsave* is the subjective value of the save choice option (irrespective of whether it is chosen); all other regressors are defined as in our main regression model. This model, thus, tests for coding of offer value. In (Eq. **S7**)

$$\text{Model S2: } Y = \beta_0 + \beta_1 SS + \beta_2 RM + \beta_3 CV + \beta_4 UCV + \beta_5 LR + \beta_6 SL + \beta_7 RT + \varepsilon, \quad \textbf{[S7]}$$

CV is the subjective value of the chosen option (regardless of whether it is a save or spend choice), and *UCV* is the subjective value of the not chosen option. This model, thus, tests for coding of chosen value. In (Eq. **S8**)

$$\text{Model S3: } Y = \beta_0 + \beta_1 SS + \beta_2 RM + \beta_3 CVspend + \beta_4 CVsave + \beta_5 LR + \beta_6 SL + \beta_7 RT + \varepsilon, \quad \textbf{[S8]}$$

CVspend is the subjective value of the spend choice option only if it is chosen (taking a value of zero if it is not chosen), and *CVsave* is the subjective value of the save choice option only if it is chosen (taking a value of zero if it is not chosen). This model, thus, tests for coding of a subtype of chosen value, which combines information about the chosen value with information about the identity of the chosen option.

Model S3 is of particular interest, because coding of the chosen value for a specific option could appear very similar to coding of the categorical choice. Thus, if neuronal responses showed a significant choice regressor in this model, despite the inclusion of the chosen value covariates, this result would support our conclusion of choice coding beyond value. Using these additional regression models to estimate coefficients for choice signals simultaneously with different value signals, we found that the majority of our choice-predictive responses was not accounted for by value coding: Model S1 resulted in 110 responses (84 neurons) with significant choice coefficients (compared with 127 such responses in 94 neurons with our main regression model), model S2 resulted in 101 responses (77 neurons) with significant choice coefficients, and model 3 resulted in 106 responses (88 neurons) with significant choice coefficients. The percentages of neurons with significant choice coefficients but nonsignificant value coefficients were 56%, 68%, and 52% for models S1–S3, respectively (compared with 63% with our main regression model).

Thus, the majority of choice-predictive responses found in amygdala neurons could not be explained in terms of different types of value coding and rather, seemed to reflect the monkeys' categorical choices. We acknowledge that some choice-predictive responses could be interpreted as special types of value coding; indeed, this result may be expected from our main analysis, because some of the choice-predictive responses identified with our main regression model had both significant choice and value coefficients (Table 1).

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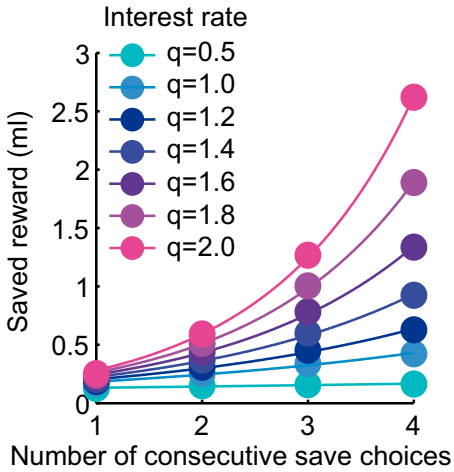

Fig. S1. Increase of reward magnitude for consecutive save choices as a function of interest rate *q*. (In this example, reward magnitude was calculated for a base volume of 0.09 mL.)

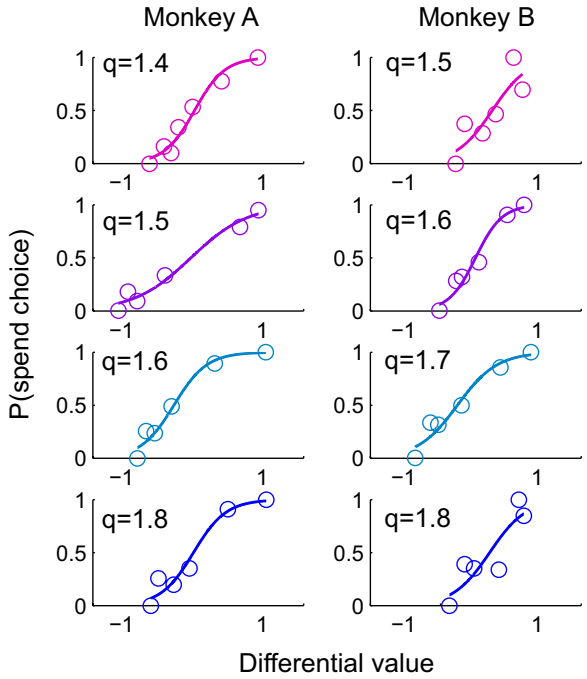

Fig. S2. Spend choice probability as a function of differential subjective value for save and spend choice options shown for different interest rates *q* (curves represent logistic fits to choice data; all logistic regressions were significant at $P < 0.001$).

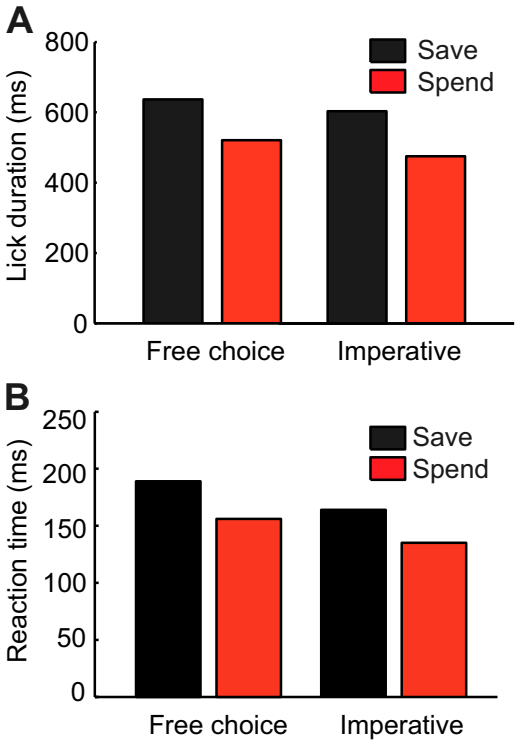

Fig. S3. Licking durations and saccadic reaction times. (*A*) Medians of anticipatory licking durations in the free choice and imperative control tasks measured before cue appearance. Significant differences were found between save and spend trials for both tasks ($P < 0.001$, Mann–Whitney test). (*B*) Medians of saccadic reaction times in the free choice and imperative control tasks. Significant differences were found between save and spend trials for both tasks ($P < 0.001$, Mann–Whitney test). Similar results were found for both monkeys.

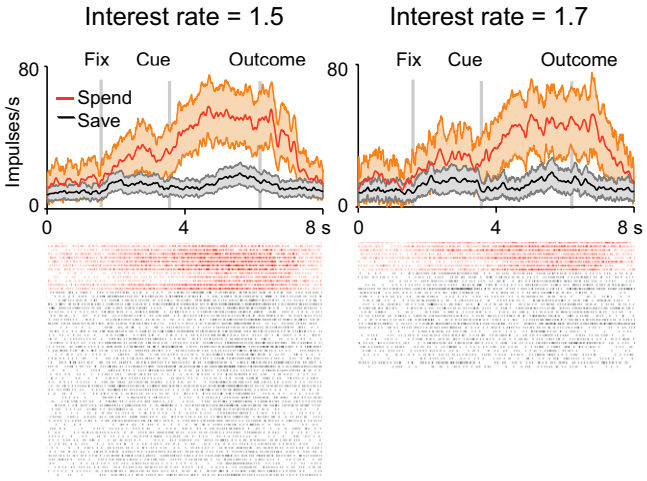

Fig. S4. Choice-predictive responses irrespective of interest rate. (*Left*) Example neuron showing a significant choice regression coefficient when tested with an interest rate of q = 1.5. (*Right*) The save–spend difference (significant choice regression coefficient) persisted when the same neuron was tested with a different interest rate of q =1.7.

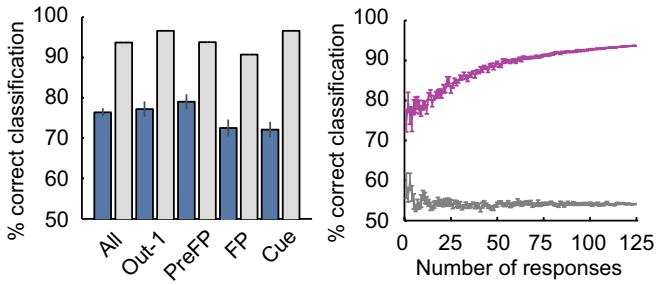

Fig. S5. (*Left*) Classification accuracy (percent correct classification ± SEM) of a biologically plausible classifier (1) decoding save–spend choices from neuronal impulse rates using all 127 choice-predictive responses. Blue bars, average accuracy for classification based on individual responses; gray bars, accuracy when data were combined across responses. Task periods: Out-1 (n = 19), PreFP (n = 27), FP (n = 38), Cue (n = 43), all periods (All; n = 127). Chance performance is 50%. (*Right*) Increase in classification accuracy (mean ± SEM) as a function of the number of responses from which data were combined (n = 127). Gray trace, classification based on randomly permuted data.

1. Quian Quiroga R, Snyder LH, Batista AP, Cui H, Andersen RA (2006) Movement intention is better predicted than attention in the posterior parietal cortex. *J Neurosci* 26(13):3615–3620.

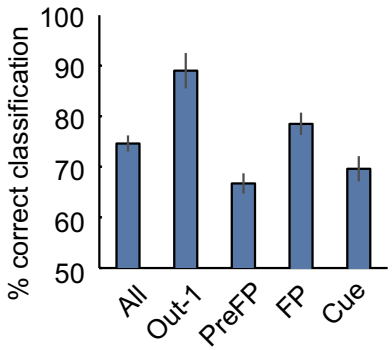

Fig. S6. Classification accuracy (percent correct classification ± SEM) of a classifier based on linear discriminant analysis using 57 choice-predictive responses. Task periods: Out-1 (n = 8), PreFP (n = 16), FP (n = 20), Cue (n = 13), All (n = 57). Chance performance is 50%.

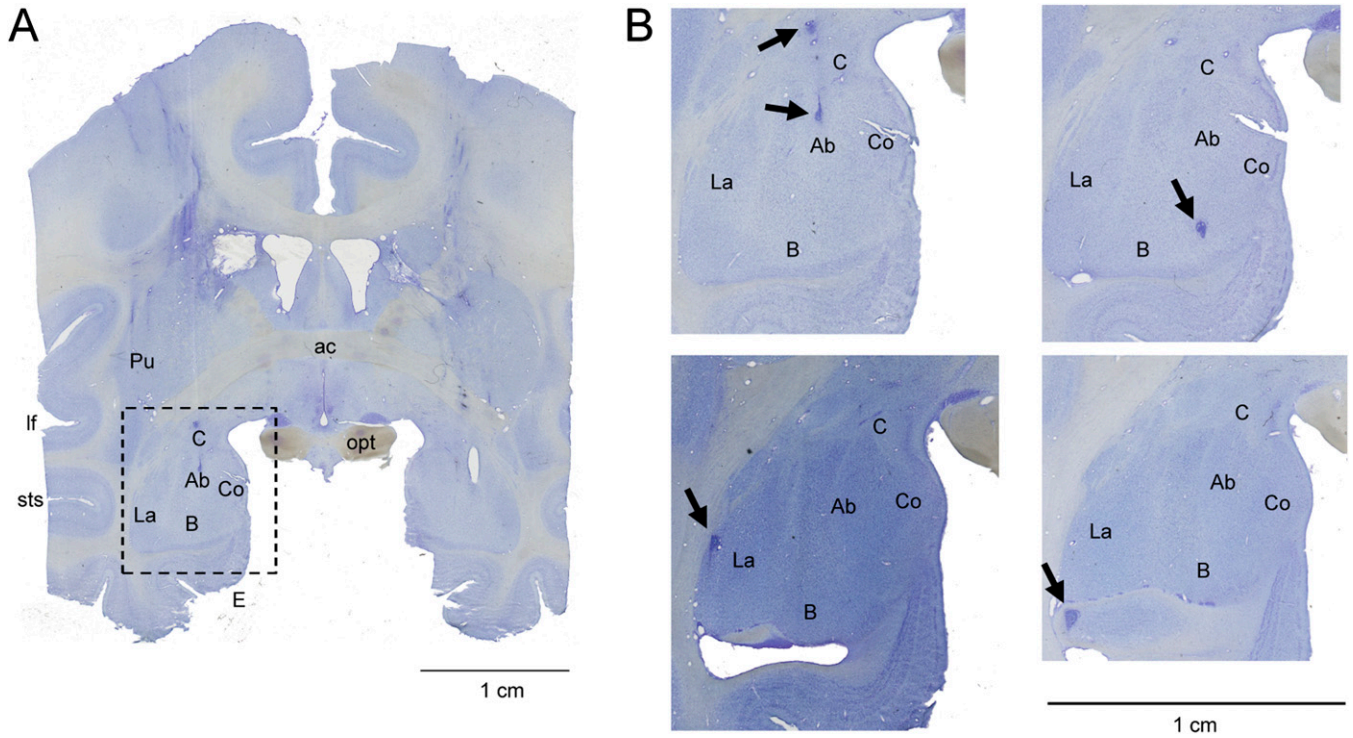

Fig. S7. Histological reconstruction of recording sites. (*A*) Photomicrograph of a cresyl violet-stained coronal section showing the amygdala and surrounding structures in monkey A. The dashed box indicates the location of the region magnified in *B*, *Upper Left*. (*B*) Arrows mark electrolytic lesions made after recordings. Lesions were placed to indicate typical recording sites in the amygdala (*Upper*) and the estimated boundaries of the amygdala (*Lower*). Location of individual nuclei were approximated based on a stereotaxic atlas (1) and typical anatomical landmarks. Ab, accessory basal nucleus; ac, anterior commissure, B, basal nucleus; C, central nucleus; Co, cortical nucleus; E, entorhinal cortex; lf, lateral fissure; La, lateral nucleus; opt, optic tract; Pu, putamen; sts: superior temporal sulcus.

1. Paxinos G, Huang X-F, Toga AW (2000) *The Rhesus Monkey Brain in Stereotaxic Coordinates* (Academic, San Diego).

Table S1. Logistic regression of save–spend choices on differential value

Regressor	Monkey A (differential value)	Monkey B (differential value)
β (SE)	1.65 (0.09)*	1.12 (0.14)*
N (trials)	3,859	2,939
χ^2	850.42†	476.84†
−2 log likelihood	3,266.33	3,086.82
Cox and Snell R^2	0.20	0.19
Nagelkerke R^2	0.30	0.21
Percent correct	83.4	76.0

χ^2 denotes result of omnibus test for significance of model coefficients.
*Significant at $P < 1 \times 10^{-8}$.
†Significant at $P < 0.001$.

Table S2. Correlations between regressors for the main multiple regression model averaged across all sessions

	SS	RM	DV	LR	SL	RT
SS	1					
RM	0.24	1				
DV	0.28	0.09	1			
LR	−0.02	−0.02	−0.03	1		
SL	0.02	−0.03	−0.03	−0.44	1	
RT	−0.24	−0.06	−0.1	0.11	0.02	1

DV, differential subjective value; LR, left–right action choice; SL, save cue left–right position; RM, reward magnitude; RT, saccadic reaction time; SS, save–spend choice.