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Categorical evidence, confidence, and urgency during probabilistic categorization

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Abstract

We used a temporally-extended categorization task to investigate the neural substrates underlying our ability to integrate information over time and across multiple stimulus features. Using model-based fMRI, we tracked the temporal evolution of two important variables as participants deliberated about impending choices: 1) categorical evidence, and 2) confidence (the total amount of evidence provided by the stimuli, irrespective of the particular category favored). Importantly, in each model, we also included a covariate which allowed us to differentiate signals related to information accumulation from other, evidence-independent functions that increased monotonically with time (such as urgency or cognitive load). We found that somatomotor regions tracked the temporal evolution of categorical evidence, while regions in both medial and lateral prefrontal cortex, inferior parietal cortex, and the striatum tracked decision confidence. As both theory and experimental work suggest that patterns of activity thought to be related to information-accumulation may reflect, in whole or in part, an interaction between sensory evidence and urgency, we additionally investigated whether urgency might modulate the slopes of the two evidence-dependent functions. We found that the slopes of both functions were likely modulated by urgency such that the difference between the high and low evidence states increased as the response deadline loomed.

Keywords

categorization; decision-making; attention; confidence; fMRI

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1 Introduction

Decision making can be characterized as a deliberative process that involves weighing noisy samples of evidence for competing hypotheses until committing to a particular choice. Real world decisions require decision-makers to flexibly optimize this process based on contextual demands. For instance, decision makers must often compromise decision accuracy in order to respond quickly, a phenomenon known as the speed-accuracy trade-off (SAT), and they must often make decisions based on uncertain evidence. For example, although the consequences of either choice might be unknown, a skier heading for a tree must commit to turn left or right within a limited period of time. To be able to make advantageous decisions in such environments, decision makers must first track the evidence for each response (the probability that each response will lead to a desirable state). Second, in order to determine whether it might be advantageous to engage in additional deliberation, make a guess based on the current evidence, or to opt-out of certain trials, decision-makers must also track their decision confidence, the probability of reaching a desirable state irrespective of a particular choice (Ding & Gold, 2010; Kepecs, Uchida, Zariwala, & Mainen, 2008; Schwartenbeck, FitzGerald, Mathys, Dolan, & Friston, 2014; Sutton & Barto, 1998). Finally, in order to minimize costs associated with deliberation and to maximize the probability of reaching a desirable state, they must flexibly modulate their decision strategies based on the time available to respond (Cisek, Puskas, & El-Murr, 2009; Hanks, Mazurek, Kiani, Hopp, & Shadlen, 2011; Reddi & Carpenter, 2000).

In the present study, we used an implementation of the weather-prediction categorization task in which probabilistic evidence for specific categories could unpredictably shift within single trials. This allowed us to identify neural signals associated with information accumulation and decision confidence, and to differentiate them from evidence-independent functions, such as urgency or cognitive load. Before describing our task and predictions in detail, we briefly describe the sequential sampling class of decision making model, which provides a useful framework for conceptualizing the temporal dynamics of decision making processes. We then describe relevant theoretical and experimental work related to the accumulation of categorical evidence and confidence. Finally, we discuss evidence-independent functions, in particular urgency, which represents a potential mechanism underlying flexible decision thresholding, and represents an important potential confound for studies designed to investigate neural mechanisms underlying the accumulation of decision evidence.

1.1 The Sequential Sampling Model Framework

Sequential sampling models (SSMs), such as the Drift Diffusion Model (Palmer, Huk, & Shadlen, 2005; Ratcliff, 1978; Smith & Ratcliff, 2004) have been particularly successful in accounting for the temporal dynamics of decision-making behavior, particularly within perceptual contexts. Within this framework, the strength of evidence modulates the speed with which a decision variable (representing accumulated evidence) diffuses towards a decision boundary. The speed with which decision-makers commits to a decision is modulated both by the strength of this evidence, and by the distance between the starting point of the accumulation process and a decision threshold. One reason the SSM framework

is attractive is that it provides a compelling characterization of neural activity observed in many regions of the brain.

1.2 Categorical Evidence

One particularly influential body of research examined perceptual decision making in the domain of motion direction judgments; this research has shown that neuronal activity in the lateral intraparietal sulcus (area LIP) in the non-human primate tracks evidence for specific behavioral responses and shows a stereotyped pattern at the time of behavioral response, consistent with a role in accumulating evidence until a decision threshold is crossed (for review, see Gold & Shadlen, 2007). Other studies with non-human primates have shown that LIP neural activity reflects learned categorical structure (Fitzgerald, Freedman, & Assad, 2011; Freedman & Assad, 2006; Swaminathan & Freedman, 2012), and that other regions, including the primary and premotor cortices, the frontal eye fields, the superior colliculus, and the caudate also appear to accumulate categorical evidence over time (Ding & Gold, 2010, 2012; Glimcher & Sparks, 1992; Thura & Cisek, 2014). Neuroimaging studies with human participants suggest that a variety of cortical regions including the pre- and primary motor cortices and inferior temporal lobe track categorical evidence (Dunovan, Tremel, & Wheeler, 2014; Gluth, Rieskamp, & Büchel, 2012; Tremel & Wheeler, 2015; Wheeler et al., 2014).

1.3. Confidence

Within the sequential sampling framework, a normative estimate of decision confidence emerges as the unsigned difference in evidence between the winning and losing response options (Kepecs et al., 2008; Pleskac & Busemeyer, 2010; Vickers & Packer, 1982). Within a biological framework, representations of confidence may be naturally derived as the unsigned difference in activity between the winning and losing category-selective neuronal pools (Insabato, Pannunzi, Rolls, & Deco, 2010; Philiastides, Biele, & Heekeren, 2010; Rolls, Grabenhorst, & Deco, 2010a, 2010b). Related signals have been observed in the orbitofrontal cortex (OFC), ventromedial prefrontal cortex (VMPFC), and dorsolateral prefrontal cortex (DLPFC) (Cohen, McClure, & Yu, 2007; De Martino et al., 2013; Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006; Padoa-Schioppa, 2011; Rolls, Grabenhorst, & Deco, 2010a, 2010b). Although subjective estimates of confidence are likely influenced by additional sources of information, bias and noise (Fetsch, Kiani, & Shadlen, 2015), this general framework provides a principled means to track the temporal evolution of confidence prior to a behavioral response; one that we adopt in the present experiment.

1.4 Urgency

The final function we review is urgency, a monotonically-increasing signal hypothesized to represent an effective mechanism to modulate decision thresholds within trials (Cisek et al., 2009; Standage, Blohm, & Dorris, 2014; Standage, Wang, & Blohm, 2014; Standage, You, Wang, & Dorris, 2011; Thura, Beauregard-Racine, Fradet, & Cisek, 2012). Previous groups have modeled urgency in two different ways. The first is via multiplicative gain modulation of the decision input, an effect predicted by theory, and one that has been observed in the neural activity of the LIP and in the pre- and primary motor cortices in the non-human primate (Cisek et al., 2009; Ditterich, 2006a, 2006b; Standage et al., 2011; Thura et al.,

2012; Thura & Cisek, 2014). The second is via an additive effect that increases baseline activity across neuronal pools (Churchland, Kiani, & Shadlen, 2008; Gluth et al., 2012; Hanks, Kiani, & Shadlen, 2014; Kira et al., 2015; Thura & Cisek, 2014). Additive effects of urgency have been observed in the neural activity of the FEF, LIP, and in the primary and premotor cortices of the non-human primate (Churchland et al., 2008; Hanks et al., 2014; Heitz & Schall, 2012; Kira et al., 2015; Thura & Cisek, 2014).

Cisek and colleagues (Cisek et al., 2009; Thura et al., 2012; see also Simen, 2012) have noted that these evidence-independent urgency signals could be easily mistaken for signals related to the accumulation of decision evidence. In a strong formulation of their theory, observed patterns of “accumulator” activity might not reflect the accumulation of decision-evidence at all, but rather gain modulation, via an urgency signal, of low-pass filtered estimates of sensory evidence. In part to differentiate signals related to information-accumulation and urgency, several recent studies have employed tasks where the evidence for, and against, specific categorical responses can be modulated within single trials (Gluth et al., 2012; Kira et al., 2015; Thura & Cisek, 2014; Wheeler et al., 2014; Yang & Shadlen, 2007). To date, only two studies have employed fMRI to do so (Gluth et al., 2012; Wheeler et al., 2014). We feel that this is important for two reasons: first, neuronal pools that accumulate information over time participate in larger decision-making networks (e.g., Lo & Wang, 2006), and second, different neural regions likely accumulate information for different purposes, even within a single task.

Wheeler et al. (2014), adapted a temporally-extended version of the weather prediction classification task used by Yang & Shadlen (2007) to compare trials in which information accumulated at different rates. They found that motor cortices were sensitive to the rate at which effector-specific evidence was presented, and that regions neighboring the occipital/temporal lobe junction and superior middle temporal gyrus were sensitive the strength of decision evidence but were insensitive to effector information. Gluth et al. (2012) used a model-based approach in conjunction with a temporally-extended, value-based decision-making task in which participants integrated evidence from multiple “+” and “-” signs in order to make advantageous financial decisions. This allowed them to identify signals tracking the value of specific choices over time (bilateral cortical motor regions) and signals that were sensitive to the prediction of reward (ventral striatum and VMPFC).

1.5 Present Study

In the present experiment, we used a temporally-extended version of the weather prediction task in which the features of an abstract amoeba stimulus were added to the display one-by-one over four discrete steps (Figure 1). Each feature was associated with a different amount of probabilistic evidence for a specific category, and participants had to integrate this information both across time and across multiple stimulus features. These characteristics capture important aspects of decisions made within high dimensional real world environments. First, real-world decision-makers often have to flexibly assign weights to information sources according to their estimated reliability, and second, they often have to consider multiple samples of noisy information to improve the accuracy of their judgments. Importantly, our experimental design allowed us to differentiate representations of

categorical evidence and confidence from signals that would be expected to increase monotonically with each trial (such as the additive urgency signal or demands associated with an increasing number of stimulus features). It also allowed us to investigate whether representations of decision evidence are multiplicatively modulated by urgency.

In line with previous research, we hypothesized that the integration of categorical evidence would recruit regions of the parietal lobe (Churchland et al., 2008; Ploran et al., 2007; Ploran, Tremel, Nelson, & Wheeler, 2011; Shadlen & Newsome, 2001; Yang & Shadlen, 2007), as well as primary and premotor regions (Gluth et al., 2012; Pastor-Bernier & Cisek, 2011; Thura & Cisek, 2014; Wheeler et al., 2014). We predicted that frontal regions, such as the VMPFC, the OFC and DLPFC would represent effector-independent decision confidence (the unsigned difference in evidence for each of the two categories; Cohen, McClure, & Yu, 2007; De Martino et al., 2013; Heekeren, Marrett, Ruff, Bandettini, & Ungerleider, 2006; Padoa-Schioppa, 2011; Rolls, Grabenhorst, & Deco, 2010a, 2010b). We also predicted that urgency would multiplicatively modulate representations of categorical evidence in cortical somatomotor regions (Thura & Cisek, 2014). Finally, although we are unaware of any experimental research investigating interactions between confidence and urgency, if category-selective neuronal pools are multiplicatively modulated by urgency, and if confidence is derived from the unsigned difference in their activity (Insabato et al., 2010; Rolls et al., 2010a), it follows that representations of confidence should also show this effect.

2 Methods

2.1 Participants

Twenty right-handed participants (mean age=24, $SD=4$; 12 female) were recruited from the Colorado State University and University of Colorado at Boulder communities. Participants were screened for history of psychiatric and neurological disorders, for current use of psychoactive medications and for exclusionary MR criteria. All participants were compensated at a rate of \$20 per hour.

2.2 Task

Participants performed a temporally-extended, binary, probabilistic categorization task (Wheeler et al., 2014; Yang & Shadlen, 2007) wherein they were instructed to categorize different amoeba (Figure 1) into one of two categories: category “A” (indicated with a left hand response) and category “B” (indicated by a right hand response). For mnemonic purposes, throughout the paper, we will refer to the categories by the response with which they were associated, “Left” and “Right”. The amoeba stimuli consisted of a black outline upon which seven different features (such as flagella, nuclei and organelles) could appear. Features could be repeated, and could appear at four different locations. Presenting the cues as features of an amoeba was chosen for several reasons. First, we thought that presenting cues as features of a single object might encourage information integration and the representation of features as aspects of a single object. Second, it provided a suitable cover story, as biological kinds are often described in terms of typical features that may occur probabilistically.

At the beginning of each trial, the black outline served as an ad hoc fixation point, and cued the beginning of each trial. The features then accumulated, one-by-one, over four discrete steps. Each feature provided a different amount of probabilistic evidence towards each category. The logLR's associated with the individual features were -2.36, -1.12, -.56, 0, .56, 1.12, and 2.36, where positive weights indicate evidence towards Category Left, and where 0 indicates no evidence towards either response. Participants were free to respond at any time during the trial, and were instructed to simply wait until they had enough information before doing so. After making a response, the features stopped accumulating, and feedback was presented. We randomized the mapping between logLR and visual feature for each participant in order to avoid possible confounds associated with visual salience. The optimal response for each trial was determined by the sign of the sum of the logLR's associated with the individual features:

$$CmLogLR_{(step4)} = \log_7 \frac{P(\text{Left}|F_1, F_2, F_3, F_4)}{P(\text{Right}|F_1, F_2, F_3, F_4)} = \sum_{i=1}^4 w_i \quad \text{eq. 1}$$

where $F_{(1-4)}$ indicate the specific features of a particular amoeba and w , the weights assigned to the individual features. Feedback was disbursed according to the corresponding probability:

$$P(\text{Left}|F_1, F_2, F_3, F_4) = \frac{7^{\sum_{i=1}^4 w_i}}{1 + 7^{\sum_{i=1}^4 w_i}} \quad \text{eq. 2}$$

where $P(\text{Right}) = 1 - P(\text{Left})$.

2.3 Training

Participants performed two training sessions that occurred on separate days. The goals of the training sessions were to teach participants about the logLR's associated with the individual features, to teach them how to integrate information across features, and to give them experience with the temporally-extended task that they would perform in the scanner. In the first training task, in order to allow participants to quickly gain experience with a large number of experimental trials, we did not use the temporally-extended paradigm described above, but instead presented all features at the same time. Through trial and error, participants first learned to categorize amoeba with one, two, three, and then all four features. Feedback was disbursed according to the probability corresponding to the sum of the individual logLR's (eq. 2). For positive feedback, the word "Correct" was presented in green for .75 seconds, and was accompanied by a pleasant tone. For negative feedback, the word "Wrong" was shown for .75 seconds in red, and was accompanied by an unpleasant tone. Participants trained until they reached an 80% accuracy criterion twice (accuracy was determined in relation to an optimal classifier making decisions based on the sign of the sum of the individual logLR's; the criterion was polled every 30 correct trials, and was reset after 35). After completing this initial training task, participants then practiced the temporally-extended paradigm that they would later perform in the scanner.

The second training session was completed on the same day as scanning. It was identical to the first with the exception that participants began the session by training with all four features, which were presented simultaneously. After reaching the 80% accuracy criterion (twice), they again practiced with the temporally-extended paradigm.

2.4 Scanning

In the scanner, the task was similar to the temporally-extended task included during the training sessions, but both the inter-feature and inter-trial intervals were jittered. The interval between each feature (and between the last step and feedback) was jittered according to a uniform distribution with a minimum of 2 seconds (to mitigate nonlinear effects associated with shorter intervals; Buckner, 1998; Friston, Mechelli, Turner, & Price, 2000), and a maximum of 4 seconds (step size= 0.5 seconds; Gluth, Rieskamp, & Büchel, 2012). The interval between each trial was jittered according to a positively-skewed truncated exponential distribution ranging from 2-9 seconds.

Participants performed the task during 3 scanner runs, each of which required 14 minutes. As participants were free to respond at any time during the trial, the number of trials per run depended on when participants made their behavioral responses (i.e., if they tended to respond quickly, each trial tended to be shorter, and there were a greater number of trials per session). Each run involved the acquisition of 420 whole brain volumes with an interleaved EPI 2D sequence (TR = 2,000 ms, TE = 25 ms, voxel size: $2.3 \times 2.3 \times 3.5$, flip angle = 75° , GRAPPA acceleration factor 2). We discarded the first 2 volumes to allow for magnetization equilibration. We also collected anatomical images using an MPAGE sequence.

3 Analyses

3.1 Preprocessing

Preprocessing involved slice-timing correction, motion correction, coregistration, high pass filtering at 128 seconds, segmentation of the anatomical images, and normalization of the structural and functional images to the MNI template. For the classical analyses, we smoothed the normalized images with a 6-mm full-width-at-half-maximum Gaussian kernel. For the Random Effects Bayesian Model Selection (RFX-BMS) procedure (described below), we used the normalized unsmoothed functional images (down-sampled to 3-mm isotropic voxels to improve computational efficiency) to calculate the log-evidence maps for each model and each participant. We smoothed the log-evidence maps with an 8-mm full-width-at-half-maximum Gaussian kernel prior to group-level analyses. All neuroimaging analyses were performed using Statistical Parametric Mapping (SPM12; Wellcome Trust Center for Neuroimaging).

3.2 Model-Based Analyses

To track the evolution of categorical evidence and confidence, and to investigate how these representations were modulated by urgency, we adopted a model-based approach. As some of these models yielded highly similar statistical maps, in order to determine which of our models best accounted for the data, we compared them using a random-effects Bayesian

model selection procedure (RFX-BMS; Rosa, Bestmann, Harrison, & Penny, 2010; Stephan, Penny, & Daunizeau, 2009). This involves three steps. First, we used a classical (restricted maximum likelihood) approach to identify voxels surviving standard statistical thresholds. Second, we generated log evidence maps ($\log P(y|m)$, the log probability of the data, y if it were generated by the model, m) for each model and each participant using a variational Bayesian approach. Third, we used a random effects analysis at the group level to calculate the protected exceedance probabilities of each model (PXP; Rigoux, Stephan, Friston, & Daunizeau, 2014; Stephan et al., 2009). This is the probability that a given model is more frequent than any of the other models tested, above and beyond chance. Although calculation of the log evidence maps is computationally intensive, the RFX-BMS approach is attractive, as it provides an intuitive metric of model fit, allows comparison of non-nested models, and has some favorable properties when compared to the Akaike Information Criterion and the Bayesian Information Criterion (Penny, 2012; Rigoux, Stephan, Friston, & Daunizeau, 2014).

For both the classical and Bayesian analyses, we assumed that neural activity associated with deliberation would continue across each jittered inter-feature interval, and so modeled each feature step with a duration equal to the difference between its onset and the onset of the following feature or the behavioral response. Such variable-duration epoch models tend to be more sensitive for paradigms involving cognitive events of variable duration than constant epoch or variable amplitude impulse models (Grinband, Wager, Lindquist, Ferrera, & Hirsch, 2008). For all models, we used the canonical double gamma hemodynamic response function. As a default, we corrected for multiple comparisons using the topological false discovery rate (initial cluster-forming threshold: $p < .001$, $q < .05$; Chumbley & Friston, 2009). However, to improve our spatial estimates concerning the evidence-independent (EI) covariate (described below), we considered the more conservative familywise error rate (FWER, $p < .05$).

3.2.1 Definition of Parametric Modulators (PM's)—As feedback was disbursed based on all evidence available at the end of the trial, it was not possible to accurately calculate cumulative logLR for earlier steps by summing the logLR's for these features (as in equation 1). Instead, we determined the values of steps 1-3 computationally, by tabulating the full permutation matrix (with replacement) and calculating the proportion that each partial feature sequence would be categorized as “Left”. As evidence for the two categories was perfectly anticorrelated, we defined confidence as the unsigned CmLogLR (Fetsch et al., 2014; Hebart et al., 2014; Rolls, Grabenhorst, & Deco, 2010). We defined urgency as a monotonically increasing signal that peaked on the 4th step (the last step where it was possible to produce a behavioral response that would lead to positive feedback). Both linear and exponential urgency functions were tested via RFX-BMS, and because we found that the exponential function provided a better fit to the neuroimaging data, we used it for all analyses described below.

To model the multiplicative effect of urgency on categorical evidence and confidence, we multiplied them by urgency. The multiplicative effect of urgency, therefore, modulated the slope of the evidence variables such that the difference between high and low evidence states increased with each step. A limitation of our design was that we could not

differentiate the additive effect of urgency from other functions that would be expected to increase during each trial (such as increasing cognitive load associated with an increasing number of stimulus features). Accordingly, throughout the paper, we will refer to the additive urgency signal as the evidence-independent (EI) covariate to emphasize that it was included in order to control for signals that were insensitive to decision evidence. Inclusion of this covariate is important, as such monotonically-increasing, but evidence-independent, signals can be easily mistaken for those associated with evidence accumulation (Simen, 2012).

To fit our models to the strategies used by individual participants, we estimated the subjective weights of evidence (sWOE) that each participant placed on the individual features (Figure 2.B). To do so in a manner robust to separation, we performed a Bayesian logistic regression analysis (prior mean = 0 for all parameters; Gelman, Jakulin, Pittau, & Su, 2008). To calculate the cumulative subjective logLR, we followed a similar procedure used to calculate cumulative normative logLR; we tabulated the full permutation matrix of beta coefficients, summed each row to determine the optimal response, and then calculated the proportion that each sequence of features would be categorized as “Left.” Calculation of the other subjective regressors also followed the process outlined for the construction of the normative regressors.

3.2.2 Classical Analyses—As mentioned, a primary focus of the present study was to differentiate signals related to information accumulation from evidence-independent functions related to urgency or cognitive load. However, we were also interested in investigating how urgency might modulate representations of decision evidence. To do so, we built four models to track the temporal evolution of CmLogLR, confidence and the EI covariate. Each model included two PM's per mean feature regressor. The first tracked decision evidence (model 1: CmLogLR; model 2: the multiplicative interaction between CmLogLR and urgency; model 3: confidence; model 4: the multiplicative interaction between confidence and urgency), while the second PM tracked the EI-covariate. We were thus able to investigate multiplicative effects of urgency via the first PM, and control for the EI covariate via the second. Importantly, in order to limit our inferences to the unique variance associated with each regressor, we did not orthogonalize them (Mumford, Poline, & Poldrack, 2015) so that any shared variance would be included in the error term rather than the first PM. Our design thus allowed us to differentiate signals related to the strength of decisional evidence (categorical evidence and confidence) from task-related signals that increased monotonically during each trial.

3.2.3 Random-Effects Bayesian Model Selection (RFX-BMS)—As there was considerable overlap between the statistical maps derived from some of the classical analyses, we conducted two RFX-BMS analyses. The first compared categorical evidence to categorical evidence multiplicatively modulated by urgency. The second compared confidence to confidence multiplicatively modulated by urgency. For each model, we included one PM per mean regressor. We limited these analyses to voxels within binary masks that included all significant voxels from the corresponding classical statistical maps. This approach allowed us to compare models within a single framework, to use RFX-BMS

to inform our interpretations of the classical statistical maps, and to limit our inferences to voxels surpassing standard statistical thresholds. In Figures 3.C, 4.C and 5.B, we thresholded each PXP map to include only voxels where the model provided the best fit. These thresholded maps allow the reader to quickly identify voxels best accounted for by each model, and to make inferences about the strength of the evidence relative to the other model tested.

4 Results

4.1 Behavioral Results

Average accuracy (determined relative to an optimal classifier making decisions based on the sign of the cumulative normative logLR on the last step) was 85% correct ($SD = 6.34\%$). Participants were fairly conservative, and showed a strong tendency to wait until they saw all features before making a behavioral response (average response step = 3.77, $SD = 0.25$). To confirm that participants used a strategy wherein they weighted the features according to their reliability rather than using a simpler strategy (e.g., counting the features belonging to each category, or considering only the most informative features; Gluck, Shohamy, & Myers, 2002), we conducted a logistic regression analyses (described above). The normalized beta weights for each participant are plotted against the normalized normative logLR in Figure 2.B. The linear pattern and close correspondence between the two sets of estimates provides evidence that participants applied weights closely resembling the normative logLR used to determine the disbursement of feedback. We additionally conducted a logistic regression analysis to investigate whether participants placed greater weights on the evidence presented in particular steps (Figure 2.C), and found no evidence of such an effect, $F(3,76) = 0.48$, $p = 0.7$; Bayes factor in favor of the null hypothesis = 8.87. Note that this latter logistic regression analysis does not provide information about the effect of the EI covariate on the cumulative logLR (the optimal representation of current evidence), but rather provides information about the weights that participants placed on the individual features in each epoch.

4.2 Neuroimaging Results

To reduce the number of models compared, we first investigated whether the normative or subjective CmLogLR provided a better fit to the neuroimaging data using RFX-BMS. Although the normative and subjective models were highly correlated and yielded similar maps, we found stronger evidence for the normative model, and report results related to these weights for all remaining neuroimaging analyses. We then compared linear and exponential functions for the EI covariate. We found stronger evidence for the exponential function, and so included this function in all models described below. Finally, we tested whether the additive effect of urgency (the EI covariate) and the multiplicative effect of urgency on the normative representations of categorical evidence and confidence were best accounted for by linear or exponential urgency functions. Here too, we found that the exponential function provided a better fit than the linear function, and report these results below.

4.2.1 Categorical Evidence (CmLogLR) and its Interaction with Urgency—

During deliberation, we found that the evidence for a left response was represented in a large contralateral region of the right pre- and post-central gyri (overlapping BA4 and BA6) extending into the right superior parietal lobe, and in the subcortical activity of left cerebellar lobules IV and V, as well as in the right posterior putamen (Figure 3.A, Table A.1). Conversely, evidence for a right response was associated with similar patterns of spatial activity in the opposite cortical and cerebellar hemispheres. The model tracking the multiplicative interaction between categorical evidence and urgency yielded highly similar statistical maps (Figure 3.B, Table A.1). To determine which model provided a better account for the data, we compared them using RFX-BMS. As shown in figure 3.C, we found that almost all voxels associated with the two maps were best fit by the function which was multiplicatively modulated by urgency (peak PXP $>.75$). If we were to assume that one of the two functions is more frequent in the population (a common assumption for model-comparison analyses), our results strongly suggest that it would be the multiplicative interaction between categorical evidence and urgency (peak unprotected exceedance probability $>.98$; compare to: Daw, Gershman, Seymour, Dayan, & Dolan, 2011; den Ouden, Daunizeau, Roiser, Friston, & Stephan, 2010). To confirm that these results were not related to the behavioral response, we repeated this analysis but considered only the parametric effects for the non-response steps (the steps during which participants made a behavioral response were included in the model, but as a covariate of no interest without parametric modulation); we again found that the model tracking the multiplicative interaction between categorical evidence and urgency was more likely.

4.2.2 Confidence and its Interaction with Urgency—We found that confidence was represented in the activity of two large clusters in the bilateral middle frontal gyri, bilateral anterior insular cortices, bilateral SMA extending to the middle-cingulate, bilateral OFC, bilateral inferior parietal cortices, bilateral putamen and cerebellar lobules 4-6 (Figure 4.A, Table A.2). The multiplicative interaction between confidence and urgency was associated with a highly similar statistical map (Figure 4.B, Table A.2). RFX-BMS analyses indicated evidence favoring the multiplicative model across all voxels. This effect was particularly strong in regions including in the bilateral SMA and inferior parietal lobes, the right middle frontal gyrus, and the right insula (peak PXP $>.99$; Figure 4.C, Table A.3).

4.2.3 The Evidence-Independent (EI) Covariate—As described above, for each of the four classical models, we included 2 PM's per mean regressor. The first PM tracked an evidence variable (categorical evidence, confidence, or the multiplicative interaction of each with urgency), and the second PM tracked evidence-independent signals that increased exponentially within each trial (Figure 1.C). A limitation of our design was that signals related to this second PM could not be ascribed to a single functional role (i.e., the additive effect of urgency could not be differentiated from other exponentially-increasing signals). Importantly, however, this design allowed us to differentiate signals that were sensitive to the strength of the decision evidence from those that were not. It also allowed us to identify activity within regions that tracked the strength of decision evidence, but also tended to increase with time (i.e., voxels that were significantly associated with both the first and second PM). Similar multiplexed signals have been previously observed in the LIP, and in

the primary and premotor cortices of the non-human primate (Churchland et al., 2008; Thura & Cisek, 2014). We describe results related to the EI covariate for two reasons. First, our results indicate that signals tracking the EI covariate could be easily mistaken for those tracking uncertainty or confidence. Second, we believe that an important goal for future research will be to characterize the functional roles of this task-related variance.

As we found strong, widespread activation associated with this regressor, we corrected for multiple comparisons using the more conservative FWER ($p < .05$). The resulting statistical map (Figure 5, Table A.4) showed particularly strong peaks in the bilateral anterior insula, SMA, bilateral ventral striatum, bilateral substantia nigra, superior colliculus, regions of the cerebellum (crus II and lobule 6), and bilateral intraparietal sulcus. The map showed a fairly high degree of overlap with that associated with the confidence signal (compare with Figure 4) in regions of the salience network, particularly in the pre-SMA and bilateral insula; activity within these regions was sensitive to strength of the decision evidence and also tended to increase with each step. The model-comparison analysis indicated that, for all of these voxels, the slope associated with these representations of confidence was modulated by urgency, such that the difference between the high and low evidence states increased exponentially during each trial (see Figure 4.C).

Notably, this analysis suggested that the bilateral IPS, regions that we predicted would be sensitive to decision evidence (Churchland et al., 2008; Ploran et al., 2007, 2011; Shadlen & Newsome, 2001; Yang & Shadlen, 2007), tracked the EI function instead. We found that this signal could be easily mistaken for confidence as, when we orthogonalized the EI covariate with respect to confidence (thus assigning shared variance to the confidence PM; see Mumford et al., 2015), the IPS appeared to track both confidence and urgency. To investigate whether the BOLD response in the IPS was sensitive to the strength of decision evidence, we conducted an RFX-BMS analysis in which we compared a full model, which included a PM tracking confidence and a PM tracking the EI function, to a reduced model, which tracked only the EI covariate. Results from this analysis provided evidence confirming that activity in the bilateral IPS was best accounted for by the EI function alone (bilateral peak PXP's $> .90$; Figure 5.B).

5 Discussion

We used a temporally-extended design to investigate how participants integrated probabilistic featural information across time in order to make advantageous decisions. Importantly, although most of the features were informative, they were not perfectly predictive. This kind of probabilistic decision-making task is common in everyday life; environmental cues often provide only incomplete information about the course of action that will lead to a desired state. In order to make advantageous decisions within such environments, decision-makers must assign weights to information sources according to a weighting scheme that approximates the relevant characteristics of the external environment (Nosofsky, Little, & James, 2012; Nosofsky, 1986; Sigala & Logothetis, 2002). In the present experiment, our goal was to investigate the neural mechanisms underlying our capacity to integrate information across stimulus features of varying reliability, and to investigate how we modulate this process based upon the time available to respond.

Specifically, our design allowed us to differentiate signals related to the temporal evolution of categorical evidence and decision confidence from other functions that increase monotonically during each trial without regards to the strength of the decision evidence. Finally, we were also able to investigate whether urgency modulated the slopes of the two evidence-dependent functions (categorical evidence and confidence).

5.1 Multi-Cue Integration and Categorization

A primary goal of our study was to examine how fundamental decision making mechanisms were adapted for categorical decision making. We utilized a multiple cue probabilistic classification task in which participants integrated information across individual features according to a weighting scheme that closely approximated the normative weights used to disburse feedback (Figure 2). Previous work provides evidence that participants sometimes use heuristic strategies based on the consideration of only the most informative features when performing the weather prediction task (Gluck et al., 2002; Meeter, Myers, Shohamy, Hopkins, & Gluck, 2006). The extensive training in our task, and the temporally-extended paradigm wherein participants were exposed not only to the uncertainty associated with the informational content of the features but also to the uncertainty about what features would compose the final stimulus, may have encouraged participants to consider each of the individual features during deliberation.

5.2 Categorical Evidence

We found that evidence supporting a specific category and its associated response was tracked by somatomotor regions including primary motor cortex, primary somatosensory cortex, posterior putamen, and cerebellum. Activity appeared to be effector specific, such that activity within cortical somatomotor regions was positively correlated with evidence towards the contralateral response, while activity within somatomotor regions of the cerebellum was positively correlated with evidence for the ipsilateral response, consistent with the crossed nature of cortical-cerebellar projections. These observations fit with an intentional framework where these decisions can be made with regards to propositions concerning potential behavioral responses (Gold & Shadlen, 2003; Shadlen, Kiani, Hanks, & Churchland, 2008). Additionally, procedural category learning mechanisms are often effector specific (Cantwell, Crossley, & Ashby, 2015; Spiering & Ashby, 2008), and similar effector-specificity was observed in the temporally-extended fMRI studies previously discussed (Gluth et al., 2012; Wheeler et al., 2014).

5.3 Confidence

We modeled confidence as the unsigned difference in evidence for each category (Ding & Gold, 2010; Hebart et al., 2014; Kepecs & Mainen, 2012; Vickers & Packer, 1982) and tracked its evolution prior to decision commitment (Gherman & Philiastides, 2014). Our confidence regressor, therefore, tracked the total amount of information accumulated from the amoeba stimulus, without regards to specific motor responses. Such a signal may play several important roles. On difficult trials, it may allow decision-makers to opt-out and choose safe bets, rather than gambling on risky choices (Gherman & Philiastides, 2014; Kepecs et al., 2008; Kiani & Shadlen, 2009). It may also allow decision-makers to wait for an appropriate amount of time for probabilistic reward (Kepecs & Mainen, 2012; Kepecs et

al., 2008; Lak et al., 2014). Additionally, in conjunction with urgency, it may provide important information regarding the value of accumulating additional decision evidence.

Within prefrontal cortex, dorsolateral, rostromedial, ventromedial and orbitofrontal cortical regions have been reported to be sensitive to confidence (Bowman, Kording, & Gottfried, 2012; De Martino et al., 2013; Heekeren, Marrett, Bandettini, & Ungerleider, 2004; Heekeren et al., 2006; Philiastides, Auksztulewicz, Heekeren, & Blankenburg, 2011; Rolls et al., 2010a; Tobler, O'Doherty, Dolan, & Schultz, 2007). These regions were also active in our study, with the notable absence of the ventromedial prefrontal cortex; due perhaps to the minimal reward and value-processing demands associated with our task (Basten, Biele, Heekeren, & Fiebach, 2010; Smith et al., 2010). Within subcortical structures, we also found that the dorsal striatum and dopaminergic midbrain also tracked confidence. These regions are also known to be sensitive to confidence (Ding & Gold, 2010; Schwartenbeck et al., 2014), to be recruited during performance of the weather prediction categorization task specifically (Poldrack, Prabhakaran, Seger, & Gabrieli, 1999; Shohamy, Myers, Kalanithi, & Gluck, 2008), and to be sensitive to categorization demands more broadly (Braunlich, Gomez-Lavin, & Seger, 2015; Lopez-Paniagua & Seger, 2011; Seger, Braunlich, Wehe, & Liu, 2015; Seger, Peterson, Cincotta, Lopez-Paniagua, & Anderson, 2010; Waldschmidt & Ashby, 2011).

Many studies have also found decisional confidence to be associated with activity in the inferior parietal lobe and in medial frontal regions, which are commonly associated with the ventral attention or salience networks. We found that these regions, as well as the bilateral anterior insular cortices also tracked decision confidence. Together, these regions are thought to play an important role in the bottom-up orienting of attention to salient external events (Buckner, Krienen, & Yeo, 2013; Ciaramelli, Grady, & Moscovitch, 2008; Medford & Critchley, 2010; Menon & Uddin, 2010; Menon, 2011; Sridharan, Levitin, & Menon, 2008). It is therefore interesting to note that these regions tracked the strength of the decisional evidence provided by the stimulus, as the salience network may play an important role in assigning attentional weights to behaviorally-relevant sources of external information. It is also interesting to note that these regions of the medial frontal cortex and bilateral anterior insula strongly overlapped with the statistical maps representing the EI covariate, indicating that activity within these regions tracked confidence and also increased exponentially during each trial.

5.4 Gain Modulation of the Evidence-Dependent Functions by Urgency

There are a number of ways that flexible adjustments to the SAT may be implemented in the brain (for full review, see Bogacz et al., 2010). One mechanism is analogous to manipulation of the decision boundary itself; through modulation of the cortico-basal ganglia circuit (the “striatal” hypothesis of the SAT). Another hypothetical mechanism underlying flexible modulation of the SAT is through modulation of baseline activity of neuronal pools involved in evidence accumulation (the “changing baseline” hypothesis). At the algorithmic level (in the sense of Marr, 1982), this has the effect of moving representations of decision evidence closer to the decision threshold. The mechanism we consider in the present paper, however, is gain-modulation of decision evidence, which has

the effect of modulating the slopes of the evidence functions so that the differences between high and low evidence states increases as a response deadline approaches. Mathematical models provide evidence that such a mechanism represents an effective way to modulate the temporal dynamics of deliberative processes (Cisek et al., 2009; Ditterich, 2006a; Niyogi & Wong-Lin, 2013; Standage et al., 2011; Standage, You, Wang, & Dorris, 2013; Thura et al., 2012), and experimental work has shown that activity in the LIP and in the pre- and primary motor cortices in the non-human primate closely resembles predictions made by these models (Ditterich, 2006a; Thura & Cisek, 2014).

Thus, we predicted that urgency would modulate the slope of the categorical evidence signal. We also predicted that the confidence signal would show this effect if categorical evidence is multiplicatively modulated by urgency and if confidence is at least partially derived from the unsigned difference in activity between category-selective neuronal pools. This framework is supported by theoretical and experimental work (e.g., Insabato et al., 2010; Rolls et al., 2010a), and by recent work demonstrating that modulation of response-specific representations in the premotor cortex can influence subjective estimates of confidence (Fleming, Maniscalco, Ko, Amendi, & Lau, 2015). Our results are in accordance with this framework, as we found that representations of both categorical evidence and confidence were best fit by the functions tracking the multiplicative effects of urgency, however, more research is needed to understand the nature and loci of this modulatory signal.

Specifically, while our task imposed a strict response deadline on the fourth step, in real-world environments, decisions about *when* to decide are often more difficult. Thus, while real world decisions often require participants to consider fine-grained differences in costs associated with deliberation and possible benefits associated with gambling on uncertain choices, our task minimized these effects and thus inflated the salience of the last step. This allowed us to model urgency as a monotonically-increasing function that peaked at this step, but it should be noted that urgency functions associated with real-world decisions are likely to be more variable. In addition, as the amount of information presented during each trial was limited to four features, accurate information accumulation required participants to temper the probabilistic information provided by each partial feature sequence (i.e., the partial sets of features shown on steps 1, 2, or 3) by the uncertainty concerning the feature(s) not yet presented during each trial. Although we modeled this effect (see Figure 1.C), it is unknown whether this aspect of the task may also have interacted with representations of the urgency function.

5.5 The Evidence-Independent (EI) Covariate

Interpretation of the EI covariate in isolation is difficult, as signals showing monotonically-ramping activity might be related to multiple functions expected to increase during each trial (e.g., urgency, or cognitive demands associated with an increasing number of features). The primary reason for including it in each model was to differentiate signals sensitive to the strength of the decision evidence from others that were evidence-independent. This is important, as signals reflecting information accumulation can be easily mistaken for those associated with decision thresholding (Cisek et al., 2009; Simen, 2012; Thura et al., 2012).

Our results suggest that the pattern of BOLD response we observed in the bilateral posteromedial portion of IPS may represent such a signal; we found that this region was insensitive to the strength of decision evidence, but positively covaried with the EI covariate. However, both previous fMRI studies that manipulated evidence for, and against, specific categories within single trials (Gluth et al., 2012; Wheeler et al., 2014) also did not identify patterns of activity in the IPS that would be consistent with an information-accumulation account. Wheeler et al., suggested that activity within these region was most consistent with an account related to cognitive effort or to time on task, while Gluth et al. noted that bilateral IPS activity at the beginning of each trial inversely correlated with decision time. Taken together, these results suggest that the univariate BOLD response in the IPS may largely reflect processes associated with decision thresholding, rather than the accumulation of decision evidence. Regardless of the function of this signal, however, these results suggest that monotonically-increasing BOLD signals previously observed in the IPS during temporally-extended decision-making tasks (e.g., Ploran et al., 2007, 2011) may be insensitive to the strength of decision evidence. Our results confirm, however, that other regions indicated in these studies, notably the right middle and inferior frontal gyri, the left cerebellar crus I, the bilateral anterior insula, the medial prefrontal cortex / pre-SMA, the inferior parietal lobe, and the caudate, are sensitive to the strength of decision evidence.

It is important to note, however, that recent studies employing multivariate pattern analyses (MVPA) have reported success in decoding categorical representations from these regions (e.g., Christophel, Hebart, & Haynes, 2012; Jeung, 2014), and individual neurons in the non-human primate homologue of the IPS (the LIP; Sereno et al., 2001), are known to track both categorical evidence and urgency (Kira et al., 2015; Yang & Shadlen, 2007). It is thus likely that these regions are sensitive to decision evidence, but that our results reflect differences between neuroimaging methods and analyses. Specifically, we suggest that the univariate BOLD response may not reflect the information accumulation processes which likely occur within these regions, but instead may reflect neuromodulatory inputs, such as urgency, that might operate broadly across neuronal populations with different stimulus tunings (Chance, Abbott, & Reyes, 2002; Douglas, Koch, Mahowald, Martin, & Suarez, 1995; Niyogi & Wong-Lin, 2013; Salinas & Abbott, 1996; Salinas & Thier, 2000; Standage et al., 2013) and are thought to represent an important driver of the cortical hemodynamic response (Logothetis, 2008).

5.6 Conclusions

Real world environments often require decision-makers to integrate information across time and across multiple information sources. To do so effectively, they must weigh different information channels according to their estimated reliability. They must also adjust the timing of their behavioral responses to maximize transient opportunities to reach desirable states. In the present study, we build on the small number of experiments that have used temporally-extended paradigms in conjunction with fMRI to track the accumulation of decision evidence during deliberation. Through use of model-based analyses, we were able to disentangle the temporal evolution of multiple task-related signals as participants deliberated about impending choices. We found that urgency likely modulated representations of categorical evidence and confidence such that the difference between high

and low evidence states tended to negatively covary with the time available to respond. We also found that the univariate signal observed in the bilateral IPS increased exponentially during each trial, but was insensitive to the strength of decision evidence, and may thus reflect a neuromodulatory effect rather than information accumulation (see also Gluth et al., 2012 & Wheeler et al., 2014). An important goal for future research will be to investigate the functional role(s) of the signal tracking the evidence-independent covariate.

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Appendix

Table A.1

Classical Results: Categorical Evidence and Categorical Evidence Modulated by Urgency. Correction for multiple comparisons was performed through consideration of the topological false discovery rate (initial cluster forming threshold: $p < .001$, $q < .05$).

Model	Size(mm ³)	x	y	z	t	BA	Region
CmLogLR(Left)							
	2434	38	-18	54	10.6	4	Precentral_R
	219	44	-20	22	6.92	48	Rolandic_Oper_R
	176	6	-18	44	5.99	23	Cingulum_Mid_R
	172	-14	-52	-18	5.7	19	Cerebelum_4_5_L
	74	32	-2	-4	4.64	48	Putamen_R
CmLogLR(Right)							
	1151	-34	-24	58	8.95	4	Precentral_L
	82	18	-50	-20	5.01	37	Cerebelum_4_5_R
CmLogLR(Left) by Urgency							
	2780	38	-18	54	11.03	4	Precentral_R
	248	44	-20	20	6.91	48	Rolandic_Oper_R
	261	6	-20	44	6.02	23	Cingulum_Mid_R
	224	-14	-52	-20	5.58	19	Cerebelum_4_5_L
	98	32	-4	-2	4.52	48	Putamen_R
CmLogLR(Right) by Urgency							
	1208	-34	-24	58	8.93	4	Precentral_L
	109	18	-50	-20	5.24	37	Cerebelum_4_5_R

Table A.2

RFX-BMS Results: CmLogLR and CmLogLR Modulated by Urgency. Each map was thresholded to included voxels where the model provided the best fit. The protected exceedance probability (PXP) provides an estimate of the probability that the model is more frequent in the population, above and beyond chance.

Model	Size(mm ³)	x	y	z	PXP	BA	Region
CmLogLR	30	48	-25	44	0.558	3	Postcentral_R
	12	42	-22	14	0.522	48	Heschl_R
CmLogLR by Urgency	784	36	-25	68	0.755	6	Precentral_R
	352	-39	-25	65	0.731	4	Precentral_L
	68	6	-22	47	0.636	23	Cingulum_Mid_R
	35	21	-52	-19	0.634	37	Cerebelum_4_5_R
	64	45	-25	26	0.624	48	SupraMarginal_R
	64	-15	-58	-22	0.62	37	Cerebelum_6_L
	31	36	-4	2	0.618	48	Putamen_R

Table A.3

Classical Results: Confidence and Confidence Modulated by Urgency. Correction for multiple comparisons was performed through consideration of the topological false discovery rate (initial cluster forming threshold: $p < .001$, $q < .05$).

Model	Size(mm ³)	x	y	z	t	BA	Region
Confidence	1016	-32	26	40	8.01	9	Frontal_Mid_L
	7901	28	-6	4	7.32	48	Putamen_R
		14	12	60	6.77	6	Supp_Motor_Area_R
		-40	8	-4	6.6	48	Insula_L
		12	-28	40	6.08	-	Cingulum_Mid_R
		-16	-26	10	5.86	-	Thalamus_L
	1106	66	-48	14	7.19	22	Temporal_Mid_R
		54	-34	40	5.9	40	SupraMarginal_R
	129	-12	22	60	7.17	8	Supp_Motor_Area_L
	173	-28	46	-8	7.11	11	Frontal_Mid_Orb_L
	1930	-50	-20	50	6.5	4	Postcentral_L
		-18	-36	64	5.37	4	Postcentral_L
	173	-50	-60	8	5.96	37	Temporal_Mid_L
	333	-62	-24	26	5.64	48	SupraMarginal_L
	747	-18	-72	-30	5.56	-	Cerebelum_Crus1_L
		-32	-42	-32	5.29	37	Cerebelum_6_L
	109	30	54	-14	5.4	11	Frontal_Mid_Orb_R

Model	Size(mm ³)	x	y	z	t	BA	Region
	163	6	-54	-18	5.16	18	Vermis_4_5
	300	-14	-78	2	5.13	18	Lingual_L
	98	12	-84	24	5.09	19	Cuneus_R
Confidence by Urgency							
	1052	-32	26	40	7.73	9	Frontal_Mid_L
	181	-28	46	-8	7.6	11	Frontal_Mid_Orb_L
	11730	-48	-60	6	7.29	37	Temporal_Mid_L
		-12	-44	68	7.01	5	Precuneus_L
		28	-6	4	6.95	48	Putamen_R
		-40	-20	46	6.89	4	Postcentral_L
		14	-28	42	6.61	-	Cingulum_Mid_R
		-30	-8	-16	6.44	20	Hippocampus_L
		14	14	60	6.25	8	Supp_Motor_Area_R
		-52	-52	46	5.89	40	Parietal_Inf_L
		20	20	-14	5.25	11	Frontal_Sup_Orb_R
	139	-10	22	60	6.49	8	Supp_Motor_Area_L
	1332	66	-18	32	6.33	2	SupraMarginal_R
		66	-48	14	6.27	22	Temporal_Mid_R
	682	16	-84	32	6.15	19	Cuneus_R
	1724	-22	-84	-38	6.14	-	Cerebelum_Crus2_L
		-8	-46	-18	5.79	19	Cerebelum_4_5_L
		6	-70	-38	5.25	-	Vermis_8
		-36	-50	-42	4.96	-	Cerebelum_7b_L

Table A.4

RFX-BMS Results: Confidence Modulated by Urgency. This model was compared to the confidence model that was not modulated by urgency. Each map was thresholded to included voxels where the model provided the best fit, and no voxels were best accounted for by the unmodulated model. The protected exceedance probability (PXP) provides an estimate of the probability that the model is more frequent in the population, above and beyond chance.

Model	Size(mm ³)	x	y	z	PXP	BA	Region
Confidence by Urgency							
	2166	3	20	44	1	32	Supp_Motor_Area_L
		-33	-64	53	0.999	7	Parietal_Sup_L
		3	-7	68	0.969	6	Supp_Motor_Area_R
		-60	-22	23	0.957	48	Postcentral_L
		-27	-10	65	0.937	6	Precentral_L
		-6	-52	59	0.936	5	Precuneus_L
		-3	-28	35	0.934	23	Cingulum_Mid_L

Model	Size(mm ³)	x	y	z	PXP	BA	Region
		-48	-67	17	0.897	39	Temporal_Mid_L
	448	45	-46	56	0.999	40	Parietal_Sup_R
		57	-52	-4	0.928	21	Temporal_Inf_R
		60	-16	38	0.87	43	Postcentral_R
	879	39	35	29	0.998	46	Frontal_Mid_R
		42	20	-4	0.997	47	Insula_R
	319	-42	29	35	0.996	45	Frontal_Mid_L
		-30	53	17	0.914	46	Frontal_Mid_L
	124	6	-79	11	0.995	17	Calcarine_R
		69	-3	-82	0.987	18	Cuneus_L
		28	30	56	0.986	11	Frontal_Sup_Orb_R
	568	-9	-73	5	0.98	17	Lingual_L
		-30	-67	-28	0.978	19	Cerebellum_Crus1_L
	468	-33	17	8	0.963	48	Insula_L
		-33	-13	-22	0.7	20	Hippocampus_L
		48	-3	23	0.952	8	Supp_Motor_Area_L
		34	9	-16	0.947	-	Thalamus_R
		45	-30	59	0.912	11	Frontal_Sup_Orb_L
		83	-12	-19	0.902	-	Thalamus_L
		19	-51	-73	0.876	37	Occipital_Mid_L
		39	57	-31	0.867	21	Temporal_Mid_R
		33	9	-49	0.832	5	Precuneus_R

Table A.5

Classical Results: The Evidence-Independent (EI) Function. Voxels included in this map represent a conjunction analysis across the four classical models tested. T-values reflect the average values across these models. Correction for multiple comparisons was performed through consideration of the familywise error rate ($p < .05$).

Model	Size(mm ³)	x	y	z	t	BA	Region
Urgency							
	430	38	22	-6	19.04	47	Insula_R
	172	-12	12	-4	14.43	25	VentralStriatum
	522	28	-64	44	14.08	7	Angular_R
	72	-26	-68	38	13.51	7	Occipital_Mid_L
	860	4	16	44	13.36	32	Cingulum_Mid_R
	63	46	14	32	13.05	44	Frontal_Inf_Oper_R
	187	-34	18	-2	12.32	47	Insula_L
	279	-28	-52	46	11.43	7	Parietal_Inf_L
	180	12	12	4	10.77	25	Caudate_R
	42	-2	6	32	10.52	24	Cingulum_Mid_L
	109	-4	-30	32	10.51	23	Cingulum_Mid_L

Model	Size(mm ³)	x	y	z	t	BA	Region
	17	46	4	38	10.4	6	Precentral_R
	44	2	-56	-36	10.39	-	Vermis_9
	98	6	-64	48	10.16	7	Precuneus_R
	31	10	28	28	9.76	32	Cingulum_Ant_R
	19	-42	0	32	9.68	6	Precentral_L
	50	-10	-72	44	9.51	7	Precuneus_L
	42	-6	-80	-26	9.49	-	Cerebelum_Crus2_L
	27	-40	-58	-36	9.45	-	Cerebelum_Crus1_L
	27	8	-70	-28	9.09	-	Vermis_7
	20	-32	-66	-30	9.05	19	Cerebelum_Crus1_L
	36	50	-42	52	8.81	40	Parietal_Inf_R
	23	48	28	28	8.73	45	Frontal_Inf_Tri_R

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Highlights

- Cortical and subcortical motor regions accumulated categorical evidence prior to commitment
- Regions of the salience and ventral attention networks tracked confidence
- Urgency modulated representations of categorical evidence and confidence

Figure 1.

A) Trial Format. In the scanner, each trial began with the presentation of the blank amoeba profile. The features (abstract organelles, nuclei and flagella, each representing different amounts of probabilistic evidence towards a right or left response) then accumulated over four steps. Feature onsets were separated by a jittered interval. Participants were free to respond at any time during the trial. After a response, feedback was disbursed according to equation 2. A series of small dots, presented below each amoeba, indicated the number of steps remaining in the trial. **B)** Although the relationship between visual feature and logLR was randomized for each participant, we illustrate one possible mapping. Positive logLR's represent evidence for a response made with the left hand. **C)** For this mapping between visual feature and logLR, we illustrate the cumulative logLR, confidence, and evidence-independent (EI) functions for one possible trial (individual logLR's = -.56, .56, -2.36, 2.36). Note that although the cumulative logLR on the fourth step can be calculated via equation 1, due to uncertainty about impending features, an optimal representation of the evidence available on the earlier steps is less than the sum of the logLR's of the individual features (see *Definition of Parametric Modulators*). We tested both exponential and linear representations for the EI function; as the exponential function provided a better fit to the neuroimaging data, we used it in each model, and also illustrate it here.

Figure 2.

Behavioral performance. **A)** For each participant, the proportion of Category Left responses is plotted across 10 bins of summed cumulative normative LogLR (equation 1). **B)** Normalized subjective weights of evidence (sWOE) vs. the normalized normative logLR used to determine the probabilistic disbursement of feedback. X-axis: normalized logLR. Y-axis: normalized sWOE derived from each participant's pattern of behavioral performance. (Grey dots represent individual subject estimates, Dark red = mean, light red = 95% confidence interval, blue = 1 SD). **C)** Influence of each step on choice. Y-axis: absolute normalized mean sWOE for each step. These analyses provide evidence that subjects tended to integrate information across features according to a weighting scheme that closely approximated the normative logLR's.

Figure 3.

Categorical Evidence. **A)** Classical results related to the categorical evidence PM. Cortical (bilateral pre- and post-central motor regions) and cerebellar (Lobules 4-5) somatomotor regions tracked the evolution of categorical evidence. Posterior regions of the right putamen, and regions of the right middle cingulate/ SMA additionally tracked evidence specifically for the Left category. **B)** Classical Results: the model tracking the multiplicative interaction between categorical evidence and urgency yielded a similar statistical map. **C)** RFX-BMS Results: Protected exceedance probability (PXP) maps for the categorical evidence models. The PXP indicates the probability that the model is more frequent in the population (relative to the other model tested), above and beyond chance (Rigoux et al., 2014). Warm colors: CmLogLR multiplicatively modulated by urgency. Cool colors: CmLogLR. This analysis provided evidence supporting the model tracking the multiplicative interaction between categorical evidence and urgency. Slight differences in the shapes of the ROI's between the classical and RFX-BMS maps are due to differences in voxel dimensions used for these analyses.

Figure 4.

Confidence. **A)** Classical results related to the confidence PM. **B)** Classical results related to the multiplicative interaction between confidence and urgency. **C)** Protected exceedance probability (PXP) maps for the confidence models (CmLogLR vs. CmLogLR multiplicatively modulated by urgency). Warm colors: confidence modulated by urgency. No voxels were best fit by the confidence function that was not modulated by urgency. These results indicate strong evidence that urgency modulated the slope of the confidence signal. Slight differences in the shapes of the ROI's between the classical and RFX-BMS maps are due to differences in voxel dimensions used for these analyses.

Figure 5.

A) The Evidence-Independent (EI) Covariate. We modeled the EI covariate as an exponentially-increasing signal that peaked on the last step. It was included as the second PM in each model, and thus modeled shifts in baseline activity without regard to decisional evidence. Voxels were selected based on a conjunction analysis across each of the four models, and the values reflect averaged t-values across these maps. To increase precision of the spatial estimates, we corrected for multiple comparisons using the voxelwise FWER ($p < .05$; note also the increased the range of the color scale). Activity in the bilateral SMA and anterior insular cortices, as well as ventral striatum, midbrain, and bilateral intraparietal sulcus positively covaried with the EI covariate. **B)** RFX-BMS analysis designed to investigate the effect of confidence in the IPS (for consistency with figures 3.C and 4.C, we illustrate all voxels included in 5.A). Warm Colors illustrate a model with 1 PM: the EI covariate. Cool Colors illustrate a model including 2 PM's: 1) Confidence multiplicatively modulated by urgency, and 2) the EI covariate. These results suggest that the univariate BOLD response in the bilateral regions of the IPS did not covary with the strength of decision evidence but instead tracked the EI covariate. As noted above, slight differences in the shapes of the ROI's between the classical and RFX-BMS maps are due to differences in voxel dimensions used for these analyses.