

# A value-based explanation for lapses in perceptual decisions

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## Abstract:

During perceptual decisions, even well-trained subjects can have a constant rate of errors independent of evidence strength, assumed to arise from inattention or motor errors. These are referred to as “lapses”, and their proper treatment is crucial for accurate estimation of perceptual parameters, however the factors influencing them remain poorly understood.

Here, we propose uncertainty-guided exploration as an underlying cause for lapses. We demonstrate that perceptual uncertainty modulates the probability of lapses both within and across modalities on a multisensory discrimination task in rats. These effects cannot be accounted for by inattention or motor error, however they are concisely explained by a normative model of uncertainty-guided exploration. Further, we show that increasing the reward for one decision over the other shifts the lapse probability towards that decision in uncertain conditions, while leaving “sure-bet” decisions unchanged, as predicted by the model.

Finally, we demonstrate that muscimol inactivations of secondary motor cortex and posterior striatum affect lapses across modalities. The inactivations are captured by subtractive changes to action value in the model, and do not affect “sure-bet” decisions. Together, our results suggest a value-based account for lapses, and that far from being a nuisance, lapses are informative about individual animals’ exploration-exploitation tradeoff.

**Keywords:** decision making; exploration; multisensory

## Introduction

Subjects trained extensively on perceptual decision-making tasks can sometimes display a constant rate of errors independent of the evidence strength, leading to imperfect asymptotic performance even on extreme stimulus strengths. Such errors are thought to arise from a failure to attend to the stimulus, or errors in executing motor actions. For this reason, they are often referred to as “lapses” and have long been viewed as a nuisance. Proper treatment of lapses is known to be crucial for accurate and unbiased estimation of

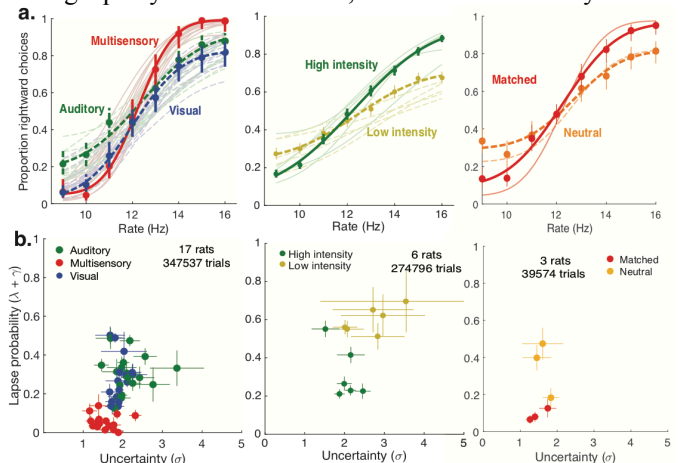
perceptual parameters (Gold & Ding, 2013; Prins, 2012), but the factors influencing them remain poorly understood.

## Results

### Perceptual uncertainty modulates lapses

Here we demonstrate that perceptual uncertainty modulates the probability of lapses and propose uncertainty-guided exploration as the underlying cause, rather than inattention or motor error. Specifically, we manipulated uncertainty on a multisensory rate discrimination task in rats using 3 strategies: 1) Presenting unisensory vs. multisensory events with matched stimulus rates, 2) Varying the signal intensity of unisensory events, 3) Presenting multisensory “neutral” trials in which visual stimulus rates were close to the category boundary and therefore uninformative.

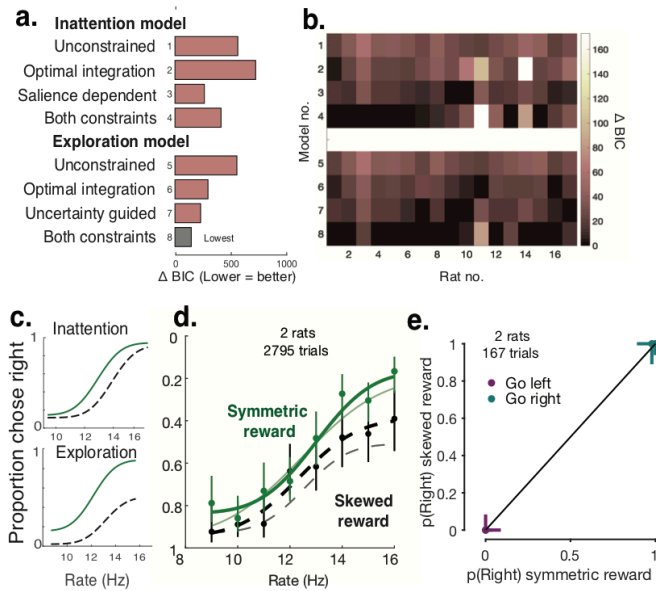
In all cases, conditions with higher uncertainty (Fig 1a dotted lines) showed an increased probability of lapses, (Fig 1b) ruling out fixed probability explanations such as motor error. Inattention was insufficient to explain the effect since multisensory “neutral” trials had increased lapses, despite being equally salient to normal, matched multisensory trials.



**Fig. 1:** a) Psychometric data. Lines: model fits. b) Lapse probability increases with uncertainty. Points: individual rats.

## Uncertainty guided exploration accounts for lapses

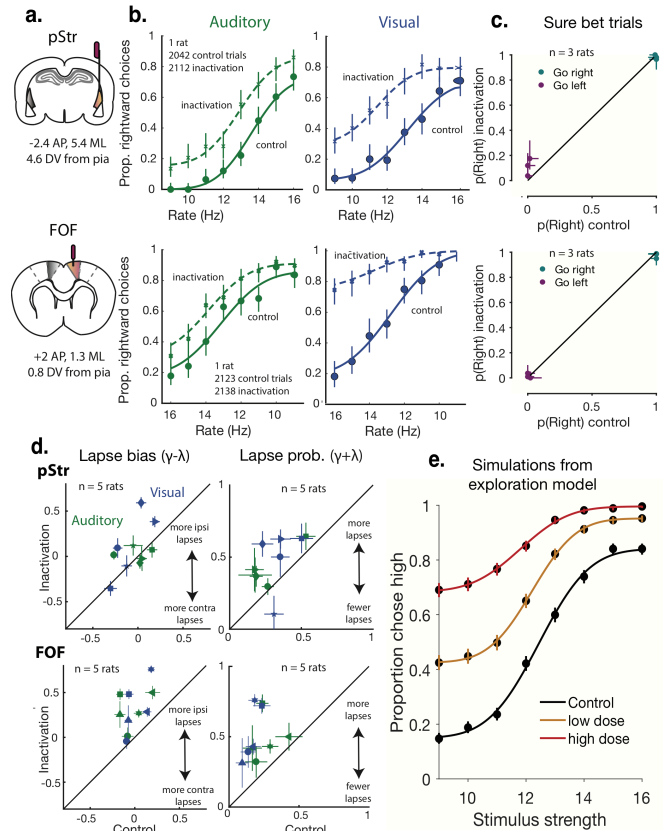
The effects were parsimoniously explained by an alternate model not normally used for perceptual decisions – uncertainty guided exploration. This is a well-known heuristic in value-based decisions that balances exploration and exploitation (Gershman, 2018). Surprisingly, the model favored by BIC (17 rats) was a Bayesian ideal observer followed by an exploratory "softmax" decision rule, with the exploratoriness modulated by uncertainty (Fig 2a,b). Since the explanation for lapses in this model is intimately tied to reward, we tested its predictions by increasing the reward magnitude for one decision outcome relative to the other. The uncertainty-guided exploration model correctly predicted that this would shift the probability of lapses in favor of this decision in uncertain conditions (Fig 2c,d), while all other models incorrectly predicted a criterion shift with minimal effects on lapse probability. We also tested the effects of the reward manipulation on "sure-bet" trials, which are a small fraction (6%) of trials on which the animal is given a salient LED unambiguously indicating the rewarded side. Since the uncertainty was so low on these trials, the model predicted that the animals would always exploit i.e. always pick the correct side, and remain unaffected by skewed rewards. Indeed, this is what we observed (Fig 2e).



**Fig 2:** Comparison of inattention and exploration models using BIC a) across rats and b) for individual animals c) Simulated model predictions for symmetric (solid) and skewed (dotted) rewards and d) rat performance on the same. e) Sure-bet trials are unaffected by skewed reward.

## Prefrontal and striatal inactivations affect lapses across modalities

To probe the neural substrates underlying lapses, we used muscimol to inactivate two regions previously shown to affect lapses in auditory decisions (Fig 3a): secondary motor cortex (Frontal orienting fields or FOF, Erlich et. al, 2015) and posterior striatum (Guo et. al, 2018). Reproducing previous findings, both areas significantly altered lapses in auditory decisions by increasing overall lapse probability and biasing the lapses towards the inactivated side (Fig. 3b,d).



**Fig 3:** a) Schematic showing injection sites. b) Performance of example rats with saline (solid) and muscimol (dotted) infusions in posterior striatum (top) and FOF (bottom). c) Performance on sure bet trials is unaffected d) Fit parameters showing inactivation effects on both lapse bias (left) and lapse probability (right). e) Simulations from the exploration model showing the effect of subtracting different amounts of value from left actions, qualitatively capturing the effects.

The exploration model allows for a novel interpretation of these effects as subtractive changes to the action value of the side contralateral to the inactivation (Fig. 2e). Consistent with this value-based explanation, the inactivations also affected lapses in visual decisions (Fig. 3b,d), and did not significantly impair sure bet trials (Fig. 3c) or movement times. Such an interpretation is consistent with the proposed role of prefrontal and striatal circuits in evaluating decisions and

balancing the exploration-exploitation tradeoff (Badre et. al, 2012; Frank et. al, 2009)

## Discussion

In summary, we propose a novel value-based explanation for lapses in perceptual decisions – that they are driven by uncertainty-guided exploration, and hence dependent on prefrontal and striatal action value representations. Our new model suggests that lapse rates are not a nuisance, but are instead informative of individual animals' exploration-exploitation tradeoff.

## Methods

### Behavior:

Rats initiated trials by poking into a center port and maintaining fixation for 1s while they received visual, auditory or multisensory events ranging in rate from 9-16Hz. Rats were rewarded for reporting rates >12.5Hz with rightward choices and <12.5Hz with leftward. All modalities were interleaved; auditory uncertainty was manipulated by changing the sound intensity from trial to trial. On multisensory “catch” trials, the visual rate was fixed at 12Hz making it uninformative.

### Modeling:

**Inattention/Motor error model:** This model fits choice probability to a cumulative normal function of the animal's criterion and posterior uncertainty, scaled by lapse rates. The model assumes lapses are random guesses made on some fraction of trials, either because the animal failed to attend to the stimulus or made an incorrect movement:

$$p(R) = p(\text{guess}) \cdot p(R|\text{guess}) + (1 - p(\text{guess})) \cdot p(R|\text{stim}) \\ = \gamma + (1 - \lambda - \gamma) \cdot p(R|\text{stim}) \Rightarrow p(\text{guess}) = \lambda + \gamma \\ p(R|\text{stim}) = \varphi(x; \mu, \sigma)$$

Independent fits for each condition were obtained using the PALAMEDES toolbox, constrained fitting and model comparison was done with custom maximum likelihood fitting code using MATLAB's `fmincon`.

**Exploration model:** This model transforms the animal's posterior belief of stimulus category into action values by multiplying them with left and right rewards, and applies an exploratory softmax decision rule:

$$Q(R) = p(R|\text{stim}) \cdot \text{reward}_R; Q(L) = (1 - p(R|\text{stim})) \cdot \text{reward}_L \\ p(R) = 1 / (1 + e^{-\beta(Q(R) - Q(L))}) \\ p(R|\text{stim}) = \varphi(x; \mu, \sigma)$$

The exploratoriness is controlled by the inverse of the slope  $\beta$  of the softmax, and can be constrained to be proportional to the posterior uncertainty.

**Bayesian inference:** For both models, an additional constraint of Bayes-optimal multisensory integration can be imposed, forcing the multisensory posterior to be proportional to a product of unisensory posteriors (Landy et. al, 2011)

$$p(R|\text{visual}, \text{auditory}) \propto p(R|\text{visual}) \cdot p(R|\text{auditory})$$

### Inactivations:

Rats were implanted with cannula bilaterally in secondary motor cortex (FOF, +2 AP, 1.3ML, 0.8DV) or posterior Striatum (pStr, -2.4AP, 5.4 ML, 4.6 DV) and infused unilaterally with saline or muscimol (0.1-0.4 ug for FOF, 0.075-0.125ug for pStr) once a week on consecutive days.

## Acknowledgments

We thank Simon Musall, Matt Kaufman, Kachi Odoemene, Ashley Juavinett, Farzaneh Najafi, Edward Lu, Steven Gluf, Anup Khanal and Barry Burbach for scientific advice, discussion and technical assistance; and financial support from NIH EY022979, Simons Collaboration on the Global Brain, Pew Charitable Trusts, Klingenstein-Simons Foundation, DOD Multi University Research Grant, the Watson School of Biological Sciences and Cold Spring Harbor Laboratory.

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