

My research investigates the ways in which behaviors thought of as irrational can instead be understood as individual. I think that this project can address two important puzzles. The first is why, when repeatedly faced with what appears to be the same set of options, humans (and animals) sometimes choose in ways unlike they have before, and against what might be expected from the experiences they've had. The second is how, and for what reason, decisions can vary so widely between individuals, even when those individuals have what previously appeared to be identical experiences and preferences. Normative theories lump this choice-to-choice and individual-to-individual variation in with "noise" — stochasticity in perception, evaluation, or action selection; deviations from the non-noisy predictions are sometimes considered irrational, even suboptimal. My overarching aim is to uncover the mechanisms that give rise to these individual, individuated decisions.

Episodic memory is arguably the most idiosyncratic feature of our cognition: No two individuals, not even identical twins raised together, will have the exact same set of experiences. Similarly, even one individual will not, at two different moments in time, have the exact same set of episodic memories available to them. New experiences will arrive, older memories will transform with time, and our recollections are buffeted by events: seemingly incidental aspects of the external environment and our internal state will make some memories more accessible than others. The fundamentally individual nature of our decisions may in part be attributed to the fundamentally individual nature of our memories.

Cognitive psychology and neuroscience have uncovered a wealth of understanding about the nature of episodic memory and its neural substrates. Simultaneously, the study of decision-making has yielded a litany of seemingly idiosyncratic features of choice behavior that are often difficult to reconcile with normative models that rely on external measures of optimality. My work brings these two rich literatures into contact, applying the products of memory research to the puzzles of decision-making.

Moving forward, I have begun to build on this work to understand how memories can influence multiple areas of action, perception, and cognition. My work uses model-based studies of behavior, psychophysiological, and neuroimaging data to ask two main questions: How can features of episodic memory explain puzzling behaviors? How do episodic memories affect the dynamics of decisions based on other information — e.g. working memory, sensory input?

Episodic sampling in decisions for reward. Across two earlier studies, I demonstrated a role for forward-looking hippocampal activity in goal-directed decision-making (Bornstein & Daw 2012 *Eur J Neurosci*; 2013 *PLoS CB*). This activity, and linked activations in ventral temporal cortex, matched the predictions of an evidence accumulation model. On the basis of these studies, I hypothesized that the role of hippocampus in goal-directed decisions was linked to its role in episodic memory formation and retrieval. Specifically, I tested the hypothesis that the accumulator-like activity involved reinstating, or sampling, episodic memories, and that this sampling process could influence decisions in the kinds of sequential reward tasks typically used to study Reinforcement Learning (RL). I formalized this prediction using a computational model that selected one or more memories for past choices, drawn stochastically according to their recency (Bornstein et al., 2017, *Nat Comms*). This model proved a superior fit to choices

and fMRI signals in a previously-collected dataset from a canonical RL task. Next, I directly tested the episodic sampling hypothesis by introducing into the sequential choice task trial-unique photographs, and using these photographs to later remind participants of individual past trials. According to episode sampling, but *not* traditional RL, these probes should affect the next choice by refreshing the memory of the trial on which they had received that ticket, making it more likely to be sampled. Indeed, choices after probes were in fact biased in favor of the machine rewarded on the reminded trial.

This finding and model provide a novel and potentially widely useful tool for connecting the rich literature on the cognitive neuroscience of episodic memory to the study of decisions. For instance, episodic memories consist of more than just stimulus-reward associations. They also encode the *context* of experiences. This context affects subsequent recalls — for instance, if reminded of a given restaurant, I am likely to next remember other restaurants on the same street. Do these subsequent recollections also impact choice?

I extended the choice task used in the previous experiment so that choices took place across several different visual contexts, with payoffs that changed within each context (Bornstein & Norman, 2017 Nat Neurosci). This feature made it possible to distinguish whether the reminder probes brought to mind just the individual trial, or other trials from the context. After probes, decisions showed distinct influences of *both* the individual trials brought to mind *and* other trials in the same context. A follow-up fMRI experiment replicated this behavioral finding, and used multivoxel pattern analysis (MVPA) to show that reinstatement of specific contexts predicted the effect of context on decisions for reward. This finding shows that episodic sampling can produce choices that are not a simple function of experience; the resulting behavior can be difficult, if not impossible, to predict without a reliable measure of *which* memories are being reinstated — at each individual decision.

Episodic memory reinstatements affect the dynamics of perceptual and working memory judgements. The previous studies show that episodic memories reinstated in advance of a decision can bias option values in a sequential choice task. In two recent studies, we extended this work to two different kinds of decisions — perceptual inference and a working memory matching task. Taken together, these studies show that the way that memory samples bias decisions is via altering the dynamics of evidence accumulation; they further show that the character of this influence can depend on the way the task is structured. Most importantly, the results provide a mechanistic explanation for variability in decision dynamics — across trials and between individuals — that had previously been ascribed to noise.

In the first study (Hoskin et al. under review at Nat Hum Behav), participants performed a delayed non-match to sample task without distraction during the maintenance delay. Stimulus words used in the task were paired with images in a training session; these created episodic ‘tags’ with which we could identify later reinstatements of the words. Performance on this task is at ceiling, and has long been inferred to depend exclusively on working, rather than episodic, memory. Our study revealed, for the first time, an influence of episodic memory even absent distraction — on response time, rather than the match decision itself. Using pattern analysis, we measured which episodic memories participants reinstated during the maintenance period, and showed the fidelity and content of the reinstatements affecting the magnitude and direction of the effect on response times. We hypothesized that the reinstated memories affected response

times by introducing either conflicting or consistent information into working memory. We modeled this hypothesis using a canonical evidence accumulation model, the Drift-Diffusion Model (DDM). Traditionally, fluctuations in the parameters of these models — e.g. starting point and drift rate — are modeled as gaussian-random noise. Here, we show that the model's fit was significantly improved by removing this noise, and instead setting the each trial's drift rate to be a function of reinstatement evidence on that trial.

These evidence accumulation models are predominantly used to model perceptual inference, in tasks which allow experimental control over the precise content and coherence of sensory evidence. I have previously shown that the quality of memory evidence can be similarly controlled, albeit indirectly, by varying the predictiveness of stimulus-stimulus associations (Bornstein & Daw 2012 EPN, 2013 PLoS CB). Building on this work, I show in a new study (Bornstein et al., submitted to Science) that memory and sensory evidence are combined according to their relative reliability, and that this weighting emerges from a single mechanism that samples from both sources. Participants in a novel, cue-guided perceptual decision task could use associative memories to establish expectations about the specific content of an upcoming, noisy perceptual stimulus. Memories sampled on each trial influenced *both* the starting point and the drift rate of sensory evidence accumulation on that trial. I modeled this effect using a multi-stage extension of the Drift-Diffusion Model (MS-DDM), in which perceptual decisions result from the continuous sampling of memory and sensory evidence, as each becomes available, and with drift rate a function of the quality of each kind of evidence. This finding raises the possibility that memory sampling can underlie the trial-by-trial variations in decision dynamics that have been observed, but explained away or inconsistently treated, in a wealth of perceptual inference studies.

Future directions. There are two primary benefits of the work I have performed on episodic sampling to date. First, it characterizes the influence of episodic memory on decisions in terms of evidence accumulation models, which have been quantitatively well-characterized. This allows us to make quantitative predictions about how the contents of memory samples should affect decisions, as in perceptual decision study above. Second, characterizing samples as episodic allows us to use known properties of episodic memory to constrain the evidence accumulation process. We have shown that initial samples in support of decisions for reward are likely to be recency-weighted and/or to be triggered by cues in the current environment, and that successive samples may be linked by their encoding context; these results encourage us to investigate whether other known features of episodic memory recall also meaningfully influence sampling in support of other behaviors. Moving forward, I plan to build on this framework by pursuing two mutually-reinforcing research directions.

One direction of my research program will be to leverage memory sampling to address outstanding puzzles in choice behaviors. An immediate application of these ideas is to drug addiction. I have proposed that memory sampling can explain addiction behaviors that frustrate previous models, in particular the phenomenon of cue- and context-induced cravings. Relapses are often triggered by mere exposure to stimuli incidentally related to drug experiences (“people, places, and things”). Factors that promote relapse, like environmental uncertainty and acute stress, also influence episodic memory recall. Studies in humans and animals identify parahippocampal cortex as a causal mediator of the effect of uncertainty and stress on relapse;

on this basis, I hypothesized that uncertainty and stress should preferentially impact the retrieval of context information during episode sampling, decreasing the effective generalization of sampling-based decisions, and resulting in behavior that is less goal-directed. This hypothesis yields specific experiments that extend the above tasks to new model-based fMRI and EEG experiments. I will manipulate uncertainty and acute stress during these tasks and see whether these manipulations yield changes in the parameters and dynamics of episode sampling, thus investigating a novel connection between these factors' influence on memory and their role in decisions to seek rewards. Most importantly, because behaviors which rely on memory sampling are in part constructed at the time of action, there is a possibility that they can be altered in the moment, for instance by guiding which memories are sampled. This mechanism may explain the efficacy of behavioral interventions — or suggest new ones.

The other direction of my research program will be to understand the normative and computational properties of memory sampling. This work will augment the above-described evidence accumulation model by incorporating what is known about the neural and psychological mechanisms of episodic memory — e.g. the timecourse of memory reinstatement, the role of inhibitory and gating neurotransmitters in encouraging encoding or retrieval, psychologically rich sample selection functions. The resulting model will not only inform new predictions about behaviors made on the basis of episodic memories, but it will permit new investigations of the relative properties of sampling from multiple memory systems. I hypothesize that samples from episodic memory are integrated with samples from semantic and procedural memories, paralleling the combination of memory and sensory evidence observed in the perceptual decision study above. Differentiating these systems on the basis of their dynamics yields testable predictions; early simulations show that simply allowing for different timecourses of memory retrieval yields an effective uncertainty-weighted, habit-biased, transfer of control between episodic, semantic, and procedural systems, without the need for an external arbitration mechanism. Further extensions of the model will be grounded in, and motivate the collection of, neuroscientific and psychological data on the nature of memory retrieval and transformation. These data, to be collected in my lab and those of collaborators, should further link the study of episodic memory to other aspects of cognition, perception, and behavior.