Aaron Bornstein Research Statement

My research investigates the ways in which behaviors thought of as irrational can instead be understood as individual. This program addresses two 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, or against what might be optimal given their experiences. The second is how, and for what reason, decisions can vary so widely between individuals, even when those individuals have what otherwise appear to be very similar, if not identical experiences and preferences. Normative theories sometimes treat this variability as "noise" — stochasticity in perception, evaluation, or action selection — or as individual traits, which when deviating from the prescribed norm are irrational or suboptimal. My overarching aim is to uncover mechanisms that give rise to these individual, individuated decisions.

The fundamentally individual nature of our decisions may be connected to the fundamentally individual nature of our memories. 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 equal access to the same episodic memories: New memories will form, older memories will transform with time, and our recollections of past experiences are buffeted by events in the present, as seemingly incidental aspects of the external environment and our internal state will bring some memories to the fore more than others. If decisions are influenced by memories, then each factor that affects memory retrieval may also affect decisions.

There is no shortage of potential connections between memory and behavior. Cognitive psychology and neuroscience have produced a rich understanding of the nature of episodic memory and its neural substrates. At the same time, the study of decision-making has uncovered a litany of seemingly idiosyncratic features of choice behavior; these are often difficult to reconcile with normative models which rely on external measures of optimality. My work to date has focused on applying the products of memory research to the puzzles of decision-making.

Episodic sampling guides decisions for reward. I began my research program by isolating a functional role for the hippocampal memory system in decisions. Across two studies, I found that anticipatory hippocampal reactivation of learned stimulus-stimulus associations contributed to both simple sequential responses and deliberative, goal-directed decisions (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 investigated whether hippocampal activity in these tasks is linked to this structure's known role in episodic memory. Specifically, I tested the hypothesis that the accumulator-like activity informed action selection by reinstating, or "sampling", episodic memories. 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 standard Reinforcement Learning (RL) task. Next, in a separate experiment, I directly

tested whether this process drew on episodic samples, by adding trial-unique photographs to the choice task. On later trials, these photographs were used to remind participants of individual past choices. According to episodic sampling, but *not* traditional RL, these probes should affect the next choice by refreshing the memory of the trial on which participants had received that ticket — thus making memories more likely to be sampled. Indeed, matching episodic sampling, and not RL, choices after probes were biased in favor of the option rewarded on the reminded trial.

This finding and model establish a mechanism that directly links episodic memory and decision-making, and suggest that other features of episodic memory should influence behavior. For instance, episodic memories consist of more than just stimulus-reward links: They also carry dense, incidental associations, called *context*. The context of a recalled memory predicts subsequent recalls — for instance, if reminded of an experience at a given restaurant, I am likely to next remember others on the same street. I next asked if these subsequent, context-inflected 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 abruptly within each (Bornstein & Norman, 2017 Nat Neurosci). This feature made it possible to distinguish whether choices after the reminder probes were influenced by the individual reminded trial, or by 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 action selection. The previous studies established that episodic memory reinstatements influence decisions for reward. My next task was to understand, at a quantitative level, how memory samples affect action selection. To investigate this, I performed two studies of decisions that made different use of memory samples. In both studies, I modeled action selection using a canonical evidence accumulation framework, the Drift-Diffusion Model (DDM); targeted modifications to this framework captured specific hypotheses about the way in which memory samples affect the dynamics of action selection. Taken together, these results establish that memory samples are treated as *anticipatory* evidence accumulation — before the decision options are presented — and that the content of these samples can, depending on task demands, affect either or both of the drift rate and the starting point of later sequential sampling. In so doing, the results provide a principled, mechanistic explanation for variability in decision dynamics — across trials and between individuals — that had previously been modeled as noise.

The first study (Hoskin et al. in revision) show that memory samples can serve as evidence for a decision even several seconds into the future. We modified a delayed-non-match-to-sample task to allow tracking of memory samples using neuroimaging. Stimulus words used in the task were learned as part of a list; each list was paired with a

different context photograph, which served as a neuroimaging marker for later reinstatement of words from those lists. On each trial, four words from the same list were presented as targets, and followed by a distraction-free delay. Accuracy in this sort of task is consistently at ceiling, which has lead researchers to infer that responses depend exclusively on working, rather than episodic, memory. However, the presentation of the target words should trigger reinstatements from episodic memory during the delay period; following the results of the context-augmented memory sampling study above, these reinstatements should be largely of other words from the same context. We asked whether these delay-period reinstatements are treated as memory samples towards the following decision. Indeed, while, consistent with previous findings, there was no signature of episodic memory in response outcome, the specific content of reinstated memories did affect reaction time. We hypothesized that the reinstated memories affected response times by introducing either conflicting or consistent information into working memory. Supporting this hypothesis, the effect was best explained by using neuroimaging measures of delay-period reinstatement to set the drift rate on each trial.

Evidence accumulation is predominantly used as a 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 EJN, 2013 PLoS CB). Building on this work, I show in a new study (Bornstein et al. submitted to Nat Neuro) 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 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. Broadly speaking, my research leverages insights from memory research and uses them to advance the study of decision-making. 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.

Applications to behavior and clinic. Understanding individual behaviors is critical to developing targeted treatments for individual dysfunction. 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"), suggestive of a role for episodic memories. Further, factors that promote relapse, like environmental uncertainty and acute stress, also impact episodic memory: Studies in humans and animals identify parahippocampal cortex as a causal mediator of the effect of uncertainty and stress on relapse; these same factors inhibit elaborative memory retrieval. 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, 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 — and so provide extensive opportunities for collaboration with clinical researchers.

Along the same line, much is known about the way in which endogenous and exogenously-induced variation in neurotransmitter levels can guide the episodic memory system to favor encoding or retrieval; these conditions should have pronounced impact on the content and dynamics of memory sampling, and thus on behaviors that are informed by them. The same neurotransmitter systems are also known to have influence on learning and decision-making. I will investigate whether these two roles are connected, by formally modeling these neurotransmitter systems' influence on the content and dynamics of episodic sampling. Using well-understood sequential choice tasks alongside MR spectroscopy, genomic, and blood level measures (to measure variation between-subjects) and pharmacological challenges (to introduce variation within-subjects), I aim to produce results that both further elucidate the mechanisms of memory in decisions and shed new light on how these mechanisms might give rise to behaviors classified as non-normative, or even psychiatrically symptomatic.

Theory development. The other direction of my research program will be to develop the normative and computational underpinnings of episodic sampling, in service of explaining a wider variety of behaviors. Specifically, I will build on the rich history of psychological and neural investigations of the episodic memory system to more fully characterize how episodic sampling

is distinguished from, and interacts with, evidence accumulation from other modalities. For instance, the time it takes to reinstate an episodic memory is roughly an order of magnitude greater than the time it takes to incorporate a sensory sample — a similar ordering likely separates the influence of episodic memory on value representations from that of motor sequences. This distinction between the timescale of sampling means that, when both kinds of information are sampled in parallel, the resulting behavior will show a greater influence of episodic memory when motor experiences have been less consistent, but, asymmetrically, greater influence of motor experience when both kinds of representations are equally consistent. This pattern matches the observed transfer of control between multiple forms of learning, but differs from extant theory by doing away with the need for an external arbitrator, a proposal that has found little empirical support. This prediction will be tested in a straightforward extension of my previous sequential learning task with stimulus-stimulus associations varying independently from motor sequences. These data will be fit by the two-part evidence accumulation model, with drift and samples rates calibrated by high temporal resolution neural measurements. Using a similar approach I will investigate transfer of control between episodic and semantic representations, the latter kind traditionally associated with “model-based” behavior. Besides the import for computational theory, a successful test of this hypothesis could dramatically impact the study of behaviors thought to depend on top-down control, upending existing theory while at the same time expanding potential targets for intervention in behavioral deficits of control.

Taken together, the research program outlined above builds directly on my existing findings, deepening the connections with other areas of cognitive and clinical neuroscience, while providing plentiful opportunities for collaboration with experts across the field. This work aims to unlock questions that the field has been building towards for decades, and promises to continue yielding opportunities for deeper understanding of the incredible variation in human cognition, at the level of both populations and individuals.