



The legacy of Adam Johnson

The first descriptions of Adam Johnson are always a combination of his brilliance, his infectious enthusiasm for science, his sense of humor, his willingness to listen, and his kindness and generosity. As many of Hippocampus' readers know, although Adam is still working and active, and although we all hope he remains so for a very long time, Adam nonetheless has a terminal illness¹. As a mentor and collaborator he has touched the lives of many working scientists, both senior and junior. The community of scientists he has touched wanted to celebrate the impact he has had on all of us while he is with us. We therefore asked Adam's colleagues, mentees, and friends (many of us are all three) to write their memories and impressions of Adam and got an outpouring of comments. These have been collected in the Supporting Information (SI) with this tribute to his contributions as a scientist, colleague, and a friend.

Adam received a BS in Physics & Psychology from Minnesota State Mankato in 2002. He received his PhD in 2008 from the University of Minnesota where one of us (ADR) served as his dissertation advisor. In 2006, Adam won a Fulbright fellowship to work in Trondheim, Norway with future Nobel Laureates Edvard and May-Britt Moser. At Trondheim, he was one of the first exchange students to arrive after the discovery of grid cells and "contributed importantly to the development of the lab in those early days" (SI, Moser & Moser). In 2008 he accepted a faculty appointment at Bethel University, a liberal arts college with an evangelical mission in suburban Minneapolis. At Bethel, Adam mentored numerous undergraduates who have gone on to contribute to science in both academia and the private sector. Throughout his faculty career, he has maintained an adjunct appointment at the University of Minnesota and, more recently, Boston University, visiting Boston University each of the last several summers.

Scientifically, Adam is best known for his 2007 paper with ADR (Johnson & Redish, 2007) in which we first reported that, during occasional pauses at T-shaped choice points, the hippocampal representations swept forward ahead of the rat, alternating between the potential options. This "landmark" (SI, Moser & Moser) paper was "groundbreaking" (SI, Kentros) and "foundational" (SI, Newman). As a consequence it "inspired a generation of hippocampal physiologists" (SI, van der Meer). To this day, it remains "one of the most influential articles on hippocampal mechanisms for memory-guided behavior" (SI, Hasselmo & Stern). This remarkable paper opened up three very important avenues of research.

First, it reinvigorated the study of *vicarious trial and error* (VTE), a behavior first observed by Evelyn Gentry and Karl Meunzinger in 1931

and then studied extensively by Tolman in the 1930s and 1940s. VTE is a behavior where the rat pauses at a decision point and orients first one way and then the other. Gentry, Meunzinger, and Tolman suggested that it entailed the rat "imagining" the future and "mentally" (i.e., vicariously) testing through trial and error. What Adam found was that they were absolutely correct and that during VTE, the rat really was "lost in thought." Second, the discovery that rats were imagining the future during VTE provided the clearest direct evidence that animals (both human and not) imagine future outcomes during deliberation (Redish, 2016). This result has influenced an entire field of cognitive neuroscience on episodic future thinking by demonstrating the possibility of a neurophysiological marker of cognitive processing. Third, and perhaps most importantly, the 2007 paper pioneered the decoding of neural ensembles to interpret cognitive perspectives. It was one of the first papers to look at how the cognitive map was "used to form a decision" (SI, van der Meer). This led to a new perspective of working "in decoded space," in which one decodes the information represented by a neural ensemble and identifies times that it represents things other than the original encoding (Johnson, Fenton, Kentros, & Redish, 2009). As noted by Andre Fenton (SI), this paper "gave many of us the confidence to interpret neural activity in decoding space rather than observable, occupied space." As such, it pioneered an extensive subsequent literature on non-spatial "conceptual maps" in both rodents and humans.

Over the last several summers, Adam has visited the Center for Memory and Brain at Boston University, a relationship that was formalized in a faculty appointment last year. Last summer, Adam's visit was supported by a Collaborative Research in Computational Neuroscience grant between one of us (MWH), Howard Eichenbaum and Adam. The focus of the Center for Memory and Brain has always been to develop an understanding of the cognitive computations underlying the function of the hippocampus and related brain regions. The ability to make a reasonable guess about a rat's thoughts from decoding brain activity was indeed "revolutionary" (SI, Barry) and provides a "foundational" (SI, Newman) bridge between cognitive models of memory and decision-making and recordings of neural representations. Adam's work has always fit beautifully into the intellectual life of the Center. His breadth of knowledge and interests has enabled him to talk to very different groups of scientists. It is therefore not surprising that Adam has worked with all of the core faculty in the Center (Eichenbaum, Hasselmo, Stern, and Howard). Beyond his intellectual contributions, Adam's impact on the people working in the Center is reflected in the comments of BU researchers at a range of career stages. He has

¹Adam's insight into his cancer remains as remarkable as his insight into science. See Johnson (2017).

“transfected us with enthusiasm” (SI, Newman) and the “fervor and energy” of his research has been “contagious” (SI, Chang).

Howard Eichenbaum would often say “People’s actions reveal their priorities.” Adam’s actions over the last several years, traveling back and forth between Boston and Minneapolis during very demanding medical treatments, reveal his priorities as a mentor and a scientist. Although his doctors told him not to travel this fall, he attended the Society for Neuroscience conference (SFN) because he wanted to see the science and the people. You can see the impact his priorities have had reflected in his students. Rachel Nordberg (SI) writes that it’s “humbling to know that someone could do anything with the last years of his life, and he’s chosen to pour into you.” Luke Horstman (SI) observes that Adam’s actions had a lasting impact on him as a student: “Because he treated me as a collaborator, I felt I needed to perform as more than just a student.” Adam’s actions challenging his students in order that they may acquire a “deeper worldview” (SI, Nordberg) reveal the degree to which he values intellectual honesty and the joy that comes from scientific discovery.

Adam always understated his impact. It’s a very Minnesotan thing to do. But I (ADR) remember one time that Adam came back from SFN telling me about a strange experience—he was at somebody’s poster asking questions and the person suddenly stopped and looked at him “differently” (as Adam told me) and said “Oh! You’re THAT Adam Johnson!” Our Adam Johnson is a truly unique individual who has contributed mightily to our scientific understanding. He has affected us in ways beyond measure and has a legacy in the field of hippocampal study and beyond. We will always remember him as THAT Adam Johnson.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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Remembrances of Adam Johnson

These remembrances have not been edited and have been included verbatim as submitted. If anyone wishes to add their remembrance to this document, please send an email to Marc Howard marc777@bu.edu or David Redish redish@umn.edu.

He was one of the first students to come for an exchange visit after we found the grid cells. He came with lots of enthusiasm and ideas, with an analytical mind, he was interactive, always willing to share, and he was much liked in the lab. He contributed importantly to the development of the lab in these early days. Also, on the more international stage, in particular his discovery and analysis of forward-looking place cells stands as a landmark in the history of the hippocampus.

- *Edvard and May-Britt Moser*

I had Adam in an advanced lecture course on learning and later in a seminar on advanced topics in learning. Adam was the top student not just in test performances but in the questions he asked, the comments he gave, and his presentations. They were marked by their depth of understanding and reference to materials well beyond the course materials. Sometime I was stumped by these—and motivated to explore further. It was a learning experience for us both. I had done some work on expectancies of rewards as possible cues for choice, and mentioned Tolman's theorizing and, as well, the concept of vicarious trial and error (VTE). We spent a lot of time on becoming clear on what Edward Tolman was arguing about "expectancies" and what a VTE might be; the writings were decades old, but Adam made them contemporary and this carried over into his novel researches. Sharing these times with Adam was such a positive experience personally and intellectually that he will always be with me.

- *Bruce Overmier*

We've had wonderful opportunities to work and discuss science with Adam Johnson over the past few years as he spent time at Boston University's Center for Memory and Brain as a visiting scientist. We have always been deeply impressed by Adam's outstanding contributions to research on the cortical mechanisms of memory guided behavior. Adam's impressive accomplishments include both highly significant neurophysiological experiments and computational models of goal-directed behavior.

Adam Johnson wrote one of the most influential articles on hippocampal mechanisms for memory-guided behavior (Johnson and Redish, 2007). The significance of this article was described in a news article in *Science* at the time of its publication. Extensive research had showed that lesions of the hippocampus impair the performance of rats in tasks such as delayed spatial alternation that could be solved if the rat generated retrieval of trajectories into previously visited arms and then avoided the previously visited arms. However, no-one had previously demonstrated neural activity associated with retrieval of previously-traversed trajectories in the hippocampus during choice behavior. In his article in the *Journal of Neuroscience* (Johnson and Redish, 2007), Adam explicitly demonstrated neural activity at choice points corresponding to the retrieval of previous trajectories experienced by the rat on a tone-cued alternation task. In these experiments, he determined the spatial locations coded by individual neurons, and then showed that when the rat performed vicarious trial-and-error at the choice point of a tone-cued task, the activity of neurons corresponded to the retrieval of segments of previously experienced trajectories starting from that point. Thus, Adam published the first neurophysiological

data showing memory retrieval during choice behavior. This was the first evidence for such prospective activation of trajectories, and the result has been confirmed by subsequent studies showing representations of future trajectories that correlate with the behavioral choices of the animal. With this breakthrough finding, Adam has assured his place in the history of neuroscience.

Over the course of his career, Adam has worked with both experimentalists and theoreticians. His work includes both sophisticated neurophysiological experiments and computational models of brain function. In his research, Adam generated an impressive range of publications that include detailed analysis of the role of hippocampal replay mechanisms in enhancing the learning of goal-directed behavior in a model using temporal difference learning (Johnson and Redish, 2005). In addition, he published articles about models of the interactions of hippocampus and striatum (Johnson et al., 2008) and about modeling of addiction. The neurophysiological projects performed by Adam required very sophisticated analysis techniques for establishing the spatial locations coded by individual neurons, and he also used sophisticated computational methods for reconstructing head direction from simultaneously recorded head direction cells (Johnson et al., 2005). This work all demonstrated Adam's exceptional intellect and skills built on his training in Mathematics and Physics.

Adam has also made important contributions to the theoretical analysis of neuronal activity and behavioral patterns, developing sophisticated Bayesian theoretical models to simulate the choice behavior of rodents and humans in a range of memory tasks. Over the past couple of years Adam has worked extensively with one of our (CES) labs on a project looking at rule learning in humans. Through these interactions, Adam developed very close ties with some of my students, Andrew Whiteman and Allen Chang, and has served as a wonderful mentor and role model for both of them. Together we recently submitted a paper examining the variations in individual rule learning behavior in humans.

Throughout all of his scientific achievements, Adam has always demonstrated the exceptionally friendly and self-effacing personality so often associated with his home state of Minnesota. Speaking with Adam always made one of us (MEH) feel a little bit homesick for his home state and being around people like him. We've always enjoyed our discussions with Adam and always look forward to his trips to Boston. We will always be thankful for our friendship in addition to the important contributions he has made to our field.

- Michael Hasselmo and Chantal Stern

Adam's insights spearheaded and gave many of us the confidence to interpret neural activity in decoding space rather than observable, occupied space. What an enormous accomplishment! Consider how very hard it was for the place cell cognitive map pioneers to convince neuroscientists that the neuron's discharge represented current location in space, an abstract quantity that is poorly controlled, but a thing that could at least be observed directly. Adam's papers stretched our comprehension by showing us the cells could also represent the remote locations rats and people might evaluate, remember and think about without being there; these are quantities that cannot be observed directly or controlled. Adam is simply and fundamentally brave; and by his example, he has helped many of us and the field to be brave too. Thank you Adam for leading and showing the way.

- Andre Fenton

I got to know Adam when we were both postdocs through meeting at SfN. Two things stood out about Adam from that first meeting that have stayed with me through the years. Firstly, he is one of kindest and most generous people that I have met in science. His sense of humour and positive outlook combined with his humility and infectious interest in science makes him one of the people that you seek

out in a conference of 30000 people. Secondly, he is very intelligent without being arrogant or aggressive which makes him one of the best people to discuss science with that I know. He has made a great contribution to the field and his Journal of Neuroscience paper with Dave in 2007 is still one of my favourites that I teach to my undergraduate classes each year.

- Jaimie Ainge

Adam Johnson has impacted my life and career at many levels -- through his scholarly works, his trainees, his friendship, and his professional mentorship.

With regard to the impact of his scholarly efforts on my own work - Adam's use of reconstruction driven approaches to 'see' the structure in the noise of neural spiking activity was foundational in paving the way for my transition from using similar approaches in human neuroimaging data to answering questions about cognitive processes in rodents. It provided for me the exemplar work of how structure in the noise of spiking can sometimes give the clearest picture of what types of mechanisms are really at play. Moreover, the lucid and convincing description of this approach portrayed by Johnson et al. (2009) was all that I needed to convince my trainees that we were onto something great. It was required reading for all who started working with me for years. Beyond any single line of work, however, Adam transfected me with his enthusiasm for understanding the principles that shape cognitive processes. Speaking with Adam about some new line of thinking he was pursuing was about all I ever needed to be utterly convinced that he was onto something great.

I am clearly not the only one affected by Adams infectious enthusiasm. An undergraduate that heard Adam speak about the brain at an outreach event was clearly similarly moved. She immediately sought out a research assistant position with Adam. Upon graduating she moved to Indiana to help me build my lab from scratch. Exemplifying Adam's influence - she was excited about understanding structured processing by the brain, comfortable with sophisticated analytical approaches to handling spiking data, and convinced that the intersection of physiology and computation is ripe for discovery. She has now gone onto Princeton for a PhD program, but my lab benefitted appreciably from the 'Johnsonian' values she carried with her. She helped to instill these principles into many of the remaining lab members via the influence she had as an inaugural member. Thus, his infectious enthusiasm continues to spread as his trainees continue on to successful careers as scientists.

Throughout the decade, or so, that I have known Adam, he has been a warm, supportive, and cherished colleague of mine. I would regularly see him during his visits to Boston University. He was always genuinely interested to hear whatever update I had to offer on my own efforts and to provide constructive inputs when I sought his input. His guidance in mentorship was crucial in helping me to build my lab from scratch.

As I've told countless people over the years - Adam Johnson is my science crush. His scholarly endeavors never fail to excite my interest. His professional interpersonal style sets a standard I endeavor to meet. I'm grateful for his contributions to my own thinking, my lab, and to the field at large.

-Ehren Newman

I could tell from the beginning of our collegiate relationship that Adam not only has a passion for uncovering mysteries of neuronal function, but also a passion for sharing the excitement of the hunt and the discoveries made along the way. The undergraduate students he collaborated with developed similar passions and began to make significant contributions to the field. Adam initiated a tradition at Bethel of summer research lunches, in which students from any department on campus could present

the projects in which they were engaged to an interdisciplinary audience, thus developing students' skill at explaining their work to well-educated people who were not experts in the topic area. With those who possessed some expertise in related fields of study, Adam loved to sit down and delve into speculations on how the neural systems were functioning and on ways to do research and analysis that would better illuminate those functions. I feel privileged to have shared many such think-sessions with him over the years, and they have proven to be extremely valuable to me personally.

- Carole Young



Woods Hole 2014

Front to back, left to right:

Carrie Peffley, Adam Johnson, Jeremy Barry, Jennifer Bilbo, Juan Marcos Alarcon, Ain Chung, Olivia Monteiro Baptista, Rosamund Langston, Matt Van Der Meer.

I first met Adam Johnson in the early 2000s at my first SFN. The year and the city are somewhat hazy in my memory, but what stands out is the impression he made on me. There were several of us that were new graduate students at the time. As is the usual way, constantly running into each other at posters and becoming fast friends, sharing mutual interests and common challenges. It was clear to me at the time that Adam was on somewhat of a different plane, not only because of the breadth of his knowledge, but how he was pushing neuroscience into realms I hadn't even dreamt of. Adam seamlessly blended math, statistics and physiology in the service of psychological concepts underlying spatial decision-making. Just being a passive observer in debates between Adam and Mark Fuhs was an education in and of itself. I learned a lot from Adam, even though it might have taken a few years for those lessons to be completely understood.

Adam's most important contribution is evident in the 2007 Johnson and Redish paper where his talents were on full display. Their use of Bayesian decoding of cell ensembles in the right behavioral task was revolutionary in that it demonstrated that the hippocampus was planning routes ahead of the animal, representing future possibilities rather than travelled paths. That these paths were mirrored in spatial decisions and recovery from errors is what truly made my jaw drop. Adam's animations to demonstrate this finding were enough to win over the most cynical neuroscientists. After presenting the paper in journal club and showing one of these cartoons to my PhD mentor Bob Muller, who often bristled against his own conservative tendencies, said "I don't quite understand it yet, but if it's right it's going to change everything". That the paper has been cited more than 500 times in 10 years is testament to the fact that Muller's prediction was correct.

Apart from his scientific accomplishments, Adam has stood out as exemplar teacher. His commitment to his scholarship, students and family, particularly after his diagnosis, is inspirational. Adam carried on doing what he loved and continued to share his knowledge with others. He taught me that being a scientist and a teacher is a privilege and a gift, and that the joy of our lives comes from sharing these

gifts for as long and as often as these mortal coils will allow. Adam, I'm so thankful for what you've given us and it's been an honor to share with you and to have you as a colleague and friend.

- Jeremy Barry

When I moved to Minnesota, I had never driven in snow. It was Adam who cheerfully taught me, encouraging me to skid the car in a huge empty parking lot before going out on the road. It was a lot of fun, and I've driven many safe snow miles since. I came to think of that episode as illustrating two things about Adam: first, he is an outstanding teacher and mentor. Second, he knows how to get traction on some very slippery problems, as demonstrated by his contributions to the hippocampal field.

Adam's 2007 J Neurosci paper inspired a generation of hippocampal physiologists, myself included. In this study, Adam pioneered the application of ensemble decoding methods to hippocampal activity to access a covert cognitive process during behavior. His iconic movies of decoded hippocampal activity during vicarious trial-and-error provided a compelling visualization of what it might look like to not just have a cognitive map in the form of place cells telling you where you are, but to use this map dynamically to inform a decision -- a watershed moment for the field that has spawned dozens of studies since.

Observing cognitive processes unfold at fast timescales, as Adam had done, is a cognitivist's dream. Adam realized that many of the questions and lines of work that had been opened up by his work had deep historical roots. In his 2008 Cognitive Critique piece, Adam wove together different branches of these roots in a modern computational re-interpretation, culminating in the synthesis of a wide-ranging formal theory of hippocampal function (2012, *Frontiers in Human Neuroscience*). The originality and scope of this work is remarkable, bringing together behavioral and neural phenomena from several different subfields at a time where integrative theories seem increasingly rare in a sea of data. Not only does this paper offer one of the most coherent and productive answer to the perennial question of "what does the hippocampus do?" but goes further to actually implement an explicit computational implementation of the proposed cognitive processes underlying several different tasks.

This combination of a deep knowledge of the literature and computational modeling enabled Adam to unpack nebulous concepts into precise formulations that would then be amenable to be tested on experimental data. Here, Adam did not just limit himself to the brilliant application and modification of existing tools to new questions as in his 2007 paper; he also worked to develop new methods. Figure 6 in his 2007 book chapter is a hidden gem, showing how generative models of hippocampal activity allow the identification of multiple timescales of processing in the hippocampus -- an approach that I expect will become increasingly important in the field. Recalling that these contributions used ensemble recording data that Adam himself collected makes I regard Adam as a truly original thinker, one of the most brilliant scientists of his generation, and feel fortunate to have been touched by his ideas. The full impact of his contributions, both in the form of published contributions as well as in the form of seeds sown in the minds of his collaborators and students, will continue to grow.

- Matthijs van der Meer

When Eric Kandel and I discovered that the degree of stability of place fields depended upon what the mouse was doing at the time (Kentros et al, 2004), we knew we were onto something big. We interpreted this result as a role for attention in the stabilization of hippocampal representations of space, much as has been shown innumerable times for behavioral memory in humans. Isabel Muzzio and colleagues (Muzzio et al, 2009) provided a valuable follow-up experiment by showing that the animals had to do a spatial task to stabilize their spatial representations (a nearly identical nonspatial

odor-matching task did not stabilize them), suggesting that selective attention to space, rather than simply generalized arousal, was necessary to stabilize a hippocampal representation of space. However, there was a crucial piece of the puzzle missing, which we were at a loss to fill in. While it was perhaps reasonable to assume that the task-related difference in place field stability was due to the animal paying attention to the available spatial cues, attention is something that happens on the millisecond timescale, and all of our analyses were averaged over the entire 30' session.

The landmark paper by Johnson and Redish (2007) provided the evidence we needed to know that attention did indeed play a role in the moment-to-moment firing of hippocampal neurons. By using an innovative decoding approach combined with high-density recordings during the execution of a task, they showed that when the animal approaches a choice point, the reconstructed hippocampal representation sweeps forward down one path and the other, as if the animal was thinking about where to go next. This extremely underappreciated paper demonstrated that rather than always firing where the animal actually is, the spatial firing of hippocampal neurons appears to fit William James' 1890 definition of attention as "the taking possession by the mind of one out of what may seem several simultaneously possible objects or trains of thought." This was both groundbreaking and intellectually courageous, and counts as one of my top 5 most important papers in the place cell literature, regardless of where they were published.

Adam's intellectual curiosity, insight, courage, humility and laconic wit in the face of adversity are an example to us all. I know that like his published work, his lasting impact on his colleagues will go far beyond what most of us can ever hope for.

- *Cliff Kentros*

I saw Adam at SfN soon after he first discovered the "forward sweep" effect. He snuck off to a wall at the convention center (which city I don't recall) to show an animation of it to Jeremy Barry. Adam and I were relative strangers, and he was being discreet. He could well have slammed his laptop closed as I approached, but instead invited me to join. The finding was impressive, but he was still very cautious about it. He wasn't showing it off, he seemed to just want to see if others found it as exciting as he did.

I never really understood Bayesian reconstruction/decoding until Adam explained it to me over a lunch (again, at SfN--again, don't remember which city or even which year). I was very excited to start using the method to understand how the cingulate cortex was and was not tracking trial phase. Adam was very happy to offer any kind of guidance or help that I might need. I can't believe I didn't follow-up on that. Based on how I now think about the region, I believe the collaboration could have yielded some major revelations that would not only have improved my dissertation thesis, but also made an impact in the field. Maybe I will email Adam right now with my idea...

On social media Adam always seemed open to expressing both his faith and his science. I quite enjoyed this, but was also impressed that he seemed to do this without upsetting either his Christian or his neuroscientist acquaintances.

Generally, across every experience I have had with Adam, he has been incredibly generous intellectually and personally. I have always been very impressed with him, but he never spoke down to me nor engaged with me competitively. I really should have followed-up on that Bayesian decoding of trial phase plan.

- Nate Insel

I started at Adam's lab as a freshman, excited about neuroscience but still just learning what the term even meant. I didn't intend to continue at Bethel beyond my first year, but Adam convinced me otherwise, and somehow I became part of a neuroscience lab studying concepts entirely new and rather challenging for me. The guidance Adam provided then and still provides now leads me to state without overstatement that whatever future career I have in neuroscience is due to Adam. He took the time and patience—and still takes the time and patience—to teach me not only neuroscience but also what it takes to succeed within a research career. I've heard Adam say countless times that he got to where he is because he's always been okay being the "village idiot"—it doesn't matter if a question sounds stupid, he'll ask it anyway because to avoid doing so would eliminate the possibility of true understanding. Adam has set an example of this in our lab, which has made working with him incredibly enjoyable and invaluable to me.

Adam's example and mentorship, both in academics and in life, has been the most important thing I've personally received from him. What I quickly learned about Adam as I got to know him was that he has no trouble whatsoever challenging beliefs, no trouble stepping on toes as long as a student gains a deeper worldview as a result. His challenges have pushed and stretched me, not only regarding the content of my beliefs but also on why I believe what I believe. In his classes he often enters into mini-rants about something particularly wrong with society or the protective bubble in which our school community resides. Because of Adam's ideas, I know that I've gained in wisdom and have a richer view of the world.

I'd never personally known someone battling cancer, and to see Adam look death in the eye and tell it he's going to fully live his life anyway has caused an impact I don't truly know the extent of. Chemo appointments and sick days happen, but Adam is back at school as soon as he can each time. It's humbling, really, to know that someone could do anything with the last years of his life, and he's chosen to pour into you. So much of what Adam has done over the last year has been to set his lab up for when he is no longer here.

What Adam can't set up for me, however, and what I will miss the most is the mentor in AC344 who will sit and listen when I'm trying to decide between future paths. I'll miss him putting into words my future aspirations that I can't entirely synthesize and him showing me exactly how I can reach that goal. I'll miss the fresh honesty and straightforwardness that is not always easy to come by. I'll miss emails ending in "cheers" and the consistent, never-ending encouragement.

You've played a huge part in who I am, Adam, and in other students that have passed through your lab. Thank you for the time and care you've spent on us. I've never, nor will I ever, take it for granted.

- Rachel Nordberg

Adam was my research advisor, mentor, and friend during my years as an undergrad at Bethel University from 2012-2016. He took me under his wing my first year at Bethel and has been a great contributor to my success as a science student (I am currently pursuing a Ph.D. in optics). My first project was to analyze how rats explore novel objects and how this could be explained by the hippocampus. This extended into one trial learning simulations and ultimately into the analysis of hippocampal spiking data from awake, behaving rats using spatial and non-spatial Bayesian decoding methods. We were able to reconstruct the position of a rat in its environment solely from hippocampal data. This led into more exciting questions of how the brain makes navigational choices.

Adam is an electric scientist to be around; his drive to invent and discover is contagious. The way his eyes light up and the excitement in his voice when explaining a new topic is captivating. Even as a freshman, Adam would speak to me as if I were a post doc who had been in his lab forever. Because he treated me as a collaborator, I felt I needed to perform as more than just a student. It made me a better academic and showed me how the scientific world operates. Almost daily, Adam would pull me into his office to show me the latest project he had been working on all night. He warned me early on that as we worked, I would have to remind him of our lunch breaks and the end of the day. This occurred frequently during our sessions because he would become lost in a topic. When taking his class I was always in awe at how he would eloquently merge whatever benign thing we were chatting about before class into the exact topic he had intended to teach us that day. One second I would be telling a few peers some weird encounter I had had that day, and the next Adam would be explaining how that same encounter could be explained by the way our brains process information. We hung on his every word; even on the short pauses as he took a sip of his warm coke (extreme sensitivity to cold drinks was a side effect of his cancer treatment).

Adam was more than an advisor to me, he was a friend. He was quick to ask me how I was doing, how classes were going, and if my stress was at an adequate level. The empathy he held for others was at such a degree that he told me he couldn't watch the show 'Friends' because he felt too terribly when the characters got into embarrassing situations. His dark humor and quick wit was always on. I lived near the hospital that administered his chemotherapy so I would frequently meet him to work while he was receiving his 'poison', as he called it. One evening, I arrived at the hospital and asked him how he was doing. He responded immediately that the chemo gave him the opportunity to get back at mosquitos. "How's that?" I asked. With a satisfactory grin on his face he explained that if they bit him, they would surely die from all the chemicals in his blood. Even if his glass was completely empty, I think Adam would still try to convince us that it was, in fact, half full.

Adam is truly one of the smartest people I have ever met, while also being one of the most enjoyable people to be around. Those things rarely go together. I miss our time together, and selfishly hope to have just a little bit more. Stick around as long as you can, Adam, as the world needs more humans like you.

- Luke Horstman

I hope that every person has the opportunity to meet someone like Adam Johnson. Adam is one of the most remarkable humans that I've ever known and to say that he has had anything less than a monumental impact on our understanding of memory would be insufficient. Adam approaches his research with a fervor and energy that is contagious. His mind works so quickly that he is always three steps ahead of every conversation. Thankfully, whenever I talk to him, Adam is fond of using the phrase "Functionally, what this means ...", to summarize what I am more slow to grasp. Simply getting to sit down and talk to Adam is a pleasure. He generously gives his time to students and colleagues alike, and he makes you feel that your research is important and essential. He is also a wonderful storyteller. He has a story about any situation that you could encounter in life and research, and he tells you about his experiences as much to teach as he does to entertain. As a mentor, Adam works tirelessly to provide opportunities for his students. He has often told me about his humble beginnings in Minnesota, and how this has driven him to try to provide his students with as much exposure to the research of others as he can. I remember him asking me this summer if I would sit down with some of this students over lunch to talk about what pursuing a PhD was like and him telling me that he would arrange everything if I was willing. He is truly the type of person that goes beyond what is necessary for others. I feel lucky to

count Adam as a colleague, mentor, and friend, and I think that I am just one of many in saying that our lives are all the better for it.

- Allen Chang

Adam was probably my most influential mentor; I wouldn't be in neuroscience if it wasn't for him. It was his work on hippocampal representations of space and memory that drew me to the field, and his passion, enthusiasm, and dedication towards his work and towards mentoring his students that kept me there. From multiple poster presentations to a publication, Adam was there helping me build a foundation in neuroscience at a college with limited opportunity in the field. If not for him, I wouldn't have found myself as a research assistant for Ehren Newman or started graduate school in neuroscience at Princeton University. To this day I use methods he taught me as an undergraduate, and I know that the things he taught me will continue to influence my own research. I feel very fortunate to have been a part of his lab, and I aspire to put as much passion and enthusiasm into my work as he did and continues to do.

To pave the way for future students, Adam strove to make neuroscience a real force at Bethel University. He set up a collaboration with Boston University to allow Bethel students to do research there over the summer, and I was fortunate enough to see the product of that research at the undergraduate poster session at SfN this year. Also after years of hard work, a research-focused Neuroscience major now exists at the university. I have no doubt that the momentum started by his own passion and enthusiasm for research in neuroscience will continue through this program for many exciting years to come.

Adam has truly been a lasting influence on my own life, at my undergraduate institution, and on the field at large. He has been such a positive influence on me and so many others, and I know that there are many students that have been drawn to neuroscience because of him. His impact can be seen in his research, and also in all the students he's trained to be a part of the next generation of neuroscientists. Needless to say, Adam is awesome.

- Sarah Venditto

It's daunting—writing when you know you can never hope to do your subject justice. I can tell you about my experience working with Adam in the field. I can reconstruct memories about what he's like as a person, about his incredible ability to mentor and support; his wit and habit of turning phrase on life, tenure, and living with disease; his dauntless energy for his work. Those of you fortunate enough to call Adam your friend and colleague know all of this already. A few poor words on my part cannot replace the experience of meeting the man.

If you haven't met Adam or his wife, Peffley ("never pair up with a philosopher if you want to win an argument"), I highly recommend it. I first encountered Adam over a summer spent doing research in Boston before my Senior year. He was a visiting Professor and introduced himself one sunny afternoon when I took lunch beneath a tree. I imagine he was making an effort to talk to every student in the lab, but I felt relatively unimportant as an undergrad and, having already spent a few years in Boston by then, had grown a little unaccustomed to that brand of kindness. Nor was I prepared for his openness—he told me about his illness within 5 minutes' conversation. It was an immediate flag for how different Adam is from most people, and made me remain under that tree for a while to reconsider life and how humans interact (or not) with each other.

Adam pushes the envelope in so many different directions to the edges of uncertainty, but that's part of what makes him such an outstanding educator. I can't speak for everyone, but I think all of his mentees could talk endlessly about his ability to teach. If you come to Adam with a compelling idea, he somehow will make time to explore it with you. His own research interests have often centered around how an agent uses exploration to learn about the world, and this idea becomes so perfectly complete in his interaction with students. I think he loves to observe that process of discovery firsthand and does everything he can to encourage it. Adam will set aside his own bias in order to appreciate his students' approach to problems; he will value others' opinions, no matter how ill-posed; he can find a test statistic in even the most tongue-tied explanation of data. It's clear to me he's so good at what he does because he possesses a deep humility about his own abilities, and an even deeper respect for other people.

When recounting a particularly frustratingly political interaction with Unnamed Dean from Unnamed College, he recalled (the first of several successive punchlines) that he had had a mid-sentence epiphany: "wow... I'm really much smarter than this person!" He described the sentiment as a lifetime first, and, knowing him, I have absolutely no trouble imagining that was one of very few times in his life he's thought himself above another. In a world full of too many people with too much ego, it's restorative to commune with someone so unassuming. He is of course a genius (on that most definitive of all sources, ratemyprofessors.com, one of his former students confirms: "absolutely BRILLIANT") and one of the most admirable human beings around besides, as I've no doubt other contributions in this issue will attest.

Unconventional, open, and honest, with a penchant for making you rethink human norms, Adam is actually remarkably easy to talk to. And the stories of interest never end. Over the course of becoming friends and collaborating on research projects I've been privileged to his opinion on everything from Bayesian thought, to Detroit's artist revival; from the history of Christianity, Western philosophy, and politics, to personal stories of wine-lubricated Philip Larkin holiday poetry smashes. Do you know what happens when you're programming and you try to initialize a matrix with more atoms than particles in the universe? Adam does. Your code takes a while to run. When a man looks you in the eye and tells you about how, after an especially repercussive bout of chemo, he has to relearn how to walk, your own world is suddenly a very different place. When you feel for him and his family so strongly but can't really, truly imagine, words fail. You're stuck for a moment painfully, selfishly considering how his story affects you because you're helpless to internalize it otherwise. When shortly thereafter the tale turns and the same man takes up running to throw a middle finger in cancer's face, you set all that down and you're again humbled, inspired, changed.

If you're reading this Adam, I hope you realize how much impact you have on the many people around you, and how much we support you, Peff, and your daughters from wherever we are. My friend, for meeting you we are all better scholars and more importantly far, far better people.

- Andrew Whiteman

I got to know Adam well during his summer visits to Boston University. These visits came at what I think of as a pivotal moment in my lab's thoughts about the function of the brain and models of cognition. In recent years, we've started wrestling with fundamental questions about how the brain computes—basically how thinking is implemented in the brain. Although we're still very much in the process of figuring this out, there were a handful of papers that inspired me to make this leap and the Johnson & Redish 2007 paper is near the top of that list and early discussions with Adam during his summer visits were also instrumental in leading us to take this leap.

This past summer, Adam brought several outstanding undergraduates with him as part of CRCNS grant we have together. The summer students (I referred to the group collectively as Adam's Family!) were engaged and prepared. I was consistently impressed by the way they weighed in at lab meeting with thoughtful responses and the level of emotional and intellectual maturity they displayed in all of their interactions with PhD students, post-docs and even senior faculty members. I have no doubt that Adam would attribute this to their outstanding qualities as students, and that is no doubt true. But it's also true that his mentorship and guidance played a strong role in their development and confidence.

In addition to the science, it has been a real joy interacting with Adam as a person and a friend. Boston can be a pretty gruff town; visiting with Adam in Boston is like a breath of fresh air. He displays humanity and humility in all his interactions, no matter who he's interacting with. He is really amazing at taking the perspective of others. This is like a superpower that improves the environment for everyone he comes into contact with. I really admire these personal attributes Adam shows and aspire to do a better job of emulating them.

Finally, I want to say a little something about Howard Eichenbaum, who passed away unexpectedly this past summer. If Howard had not passed away, I have no doubt whatsoever that he would have contributed to this project. It's not my place to put words in Howard's mouth but I think his actions--- hosting Adam as a summer visitor, working together on our grant as a co-Investigator, meeting with the summer students---reveal a great deal about how much he valued working with Adam.

It's a privilege to work as a professional scientist. Like all people, our time is finite. Like all people, the actions we take shape the development and future actions of our family and friends for decades. Our actions as scientists not only affect our students and colleagues, but can also add to our cumulative knowledge and insight into the natural world and the human condition. Adam Johnson should be proud of the lasting impact his work has had (and will continue to have) on so many.

- Marc Howard

Adam was the third graduate student to join my lab. His work literally changed the entire direction of my research. When Adam joined my lab in 2002, we were studying spatial learning; by the time Adam graduated, we were studying cognition and decision-making. Our trajectory into both of those fields is due in very large part to Adam's work, both at the theoretical and experimental levels. Adam has a remarkable ability to integrate literatures, ideas, theories, experimental data, and computational models and bring that synthesis to the table.

Within a month of his arrival, Adam was in the lab recording neural ensembles of head direction cells. These recordings (pioneered by a then-undergraduate in the lab, Kelsey Seeland) were the first large ensemble recordings of head direction cells, and thus, the first ones from which one could do moment-by-moment decoding of behavioral variables. Adam showed that it was possible to reconstruct the orientation of the animal from the neural ensemble firing patterns and that internal measures of representational self-consistency could be used to predict the accuracy of that decoding (thus potentially providing the animal with a means to decide whether to believe the representation or not) [Johnson, Seeland, Redish 2005 *Hippocampus*]. I now see how this early work set Adam up for the 2007 breakthrough paper.

The journey to the 2007 paper [Johnson, Redish 2007 *Journal of Neuroscience*] remains one of my favorite scientific "hunts". My memory is that my first graduate student (Neil Schmitzer-Torbert) had done recordings in the dorsal striatum and as I was giving one of the early talks from my lab (probably

2004 or so), and I realized that I didn't know what hippocampus would do on a decision task, so I convinced Adam to do some hippocampal recordings. I figured we would just find the basic place field results and I could then use that as the control against the striatal data. Adam claims that we were still debating whether to do ventral striatum or hippocampus (as a first comparison to the dorsal striatal data) and that he flipped a coin while the rat was on the stereotax. That is certainly not how I remember it, but it is a sign of Adam's quirky humor that to this day I don't know if he is kidding or not.

Nevertheless, Adam implanted the hyperdrive over hippocampus and started recording neural ensembles on a simple behavioral decision task. Along the way, we were working on decoding techniques and new ways to look at the data. And that set us up for the day Adam came into my office and said "Dave, my rats are doing mental time travel". To say my reaction was skeptical would be an understatement – what I think I said was "we don't use words like that in public" – but Adam knew (because he had researched the literature) that mental time travel was an important construct in the cognitive psychology literature and he knew he had it.

While this story has become a foundational myth in my laboratory, it is the subsequent part of the story that really speaks to me as a scientist. These first videos were from sometime around 2005. Importantly, however, it took more than a year to subsequently determine that these "sweeps" were not happening during sharp waves, were aligned to the theta rhythm, went down each option individually, and were correlated with, but not identical to the orientation of the rat towards each individual option. Those years of nailing down those controls remain some of my favorites because it really was about "the passion of the hunt" (as Carole Young describes in her remembrance). Adam was taking a class with Bruce Overmier at the time and Bruce suggested Adam go back to the old Tolman literature on Vicarious Trial and Error (VTE). Although extensively studied in the early 1930s and 1940s, VTE had mostly vanished from the memory and navigational literature. (The term is not in O'Keefe and Nadel's 1978 *Hippocampus as a Cognitive Map*, nor is it in Cohen and Eichenbaum's 1993 *Memory, Amnesia, and the Hippocampal System*, nor in my 1999 *Beyond the Cognitive Map*.) Walking around SFN this year (2017), it was remarkable how many different laboratories are now studying VTE in all kinds of species (from mice to rats to monkeys to humans).

Along the way, Adam did an early DYNA model of the effect of replay on learning [Johnson, Redish 2005 *Neural Networks*] and was an important part of our journey into computational psychiatry. (He is a co-author on our early modeling and review papers such as our paper on craving (Redish and Johnson 2007 *Annals of the New York Academy of Sciences*) and our manifesto on addiction (Redish, Jensen, Johnson 2008 *Behavioural and Brain Sciences*). As noted by others in the quotes, the 2009 TICS paper (Johnson, Fenton, Kentros, Redish 2009 *Trends in Cognitive Sciences*) remains a defining technique for analysis. The key figure from it remains a staple of nearly every talk I've given in the last decade.

Adam has always been the complete scientist. His students coming out of Bethel have been nothing short of amazing. In 2011, Adam co-taught a class at the University of Minnesota with me. I had seen Adam mentor students before, but co-teaching with him, I learned just how wonderful a teacher he was. His teaching constructs that he made for the class (grading rubrics and the like) became models that I still work off of today.

And through it all, Adam has kept us going with his humor and grace. I sometimes wish I could handle anything in my life with the grace he has dealt with his current illness. As we note in the main document, Adam's insight into his illness is as keen as his insight into science (see his commentary in the

2017 Minneapolis City Pages). He has been a friend and colleague and has left us a legacy of science and students to carry on.

Adam is an amazing person. He has contributed mightily to our understanding of the world. I often tell my students that the goal is to “put a brick in the wall” of this scientific endeavor we are all working on. There is no question in my mind that Adam has done that.

-A. David Redish
