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IN MEMORIAM

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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 illness[1]. 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

[1]Adam'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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