

Krishna V. Shenoy (1968–2023)

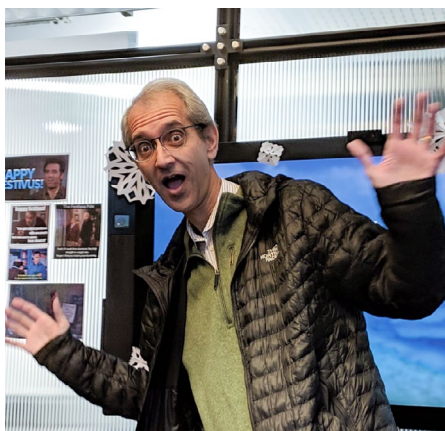
By Mark M. Churchland & Paul Nuyujukian

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Krishna Vaughn Shenoy died on 21 January 2023 at the age of 54. He had lived for over a decade after a diagnosis of pancreatic cancer. Krishna's scientific and moral leadership was such that his absence was felt – suddenly, acutely and deeply – by all those that knew him. Kindness, decency and devotion to truth were central to both Krishna the person and Krishna the dreamer. Krishna's ambition was massive yet patient and never centered on himself. His work transcends him and lives on in others not simply because of its quantity and quality, but because Krishna meant for it to be that way from the very beginning.

Krishna had the mind of a scientist but the organizational skills of a religious leader or chief engineer. He looked ahead not years, but decades and lifetimes. His dream was to lay a scientific and engineering foundation that would aid people with paralysis by enabling them to control prosthetic devices directly with their brains. There was no hubris in this goal. Krishna saw what was possible at the time and what would soon become possible. He knew how to build on what others were doing, how to avoid short-term flashiness, and how to create long-term collaborations that could leverage that great temporal nonlinearity: progress is slower than you expect in any given year, yet stuns you with its swiftness over decades. Krishna had an unusual ability to subjugate his own ego in the service of this enterprise. It wasn't his success that was important, it was the overall success of everyone he inspired to follow him in pursuit of shared goals. It was hope of making a large difference in the lives of patients. It was the belief that knowledge has lasting value, against which our petty daily vanities are uninteresting. You sensed that immediately, and it generated exactly the kind of trust and loyalty needed to sustain a project of the scope he envisioned.

Krishna was born in Sabetha, Kansas, USA, and always retained an unassuming Midwestern sensibility. Following in the footsteps of his engineer father, Pandu, Krishna studied electrical engineering as an undergraduate at the University of California, San Diego and University of California, Irvine. He obtained a PhD in electrical engineering and computer science at the Massachusetts Institute of



Technology (MIT), where his dissertation won the Hertz Foundation Prize. Throwing himself into the culture of 1990s MIT, Krishna honed his skills as a prankster and agitator – skills he would unleash on the unsuspecting to remarkable effect even decades later. (To protect the innocent, stories can be provided discreetly upon reasonable request.) While at MIT, Krishna became acquainted with and inspired by world-class neuroscientists, including Ann Graybiel and Emilio Bizzi. Krishna was assured a plum job in industry, yet against the sensible advice of friends and family he chose to pursue a postdoctoral fellowship in neuroscience. In the laboratory of Richard Andersen at the California Institute of Technology, Krishna was surrounded by some of the best visual neuroscientists of the time and quickly found an intellectual home. Visual neuroscience was highly amenable to engineering-inspired approaches. Krishna made good use of this synergy and published important work on the neural basis of motion-based heading perception (think hyperdrive in Star Wars and you get the general idea).

This grounding in visual neuroscience was important to Krishna's later work in motor control. In many visual areas, population-level computations can be understood as extensions of single-neuron response properties. Krishna thus knew what this type of population coding looked like in its canonical form. Knowing when a paradigm works well is often critical to knowing when not to use it, and this would prove to be the case when Krishna later began recording in motor and premotor cortex. While in the Andersen laboratory,

Krishna gained deeper familiarity with computational neuroscience. He met Maneesh Sahani, a computational neuroscientist who became a long-term collaborator and close friend. Krishna also gained familiarity with early examples of how neural network modeling could aid the understanding of empirical data. He took to heart a subtle message: individual neurons can have 'non-canonical' and seemingly strange response properties, yet participate in an overall computation that is readily understood using the right level of abstraction. Although he did not know it at the time, this would become a central theme of his research in motor cortex.

Krishna started his laboratory at Stanford University in the fall of 2001, with the goal of developing brain–computer interfaces (BCIs) that leveraged neural activity recorded from motor and premotor cortex. Almost immediately this goal forked into two: to better understand the mechanistic purpose of neural activity and to figure out how best to use it for BCI engineering. These scientific and engineering goals were intentionally synergistic. Yet very consciously, each was allowed its own life and not expected to serve the other until the time was right. As Krishna's work expanded to encompass a greater range of topics, his laboratory always maintained these two separate but cross-fertilizing streams.

Scientifically, Krishna is known for championing a specific conceptual approach to systems neuroscience. This approach has been referred to by a handful of names: dynamical systems, network dynamics, computation through dynamics, factor dynamics. All mean the same thing: trying to understand empirical neural responses using the same language that theorists use to understand artificial networks. For many computational problems, there exist network dynamics that provide a mechanistic solution. These solutions make sense at the population level, yet can yield time-evolving activity patterns that are difficult to interpret neuron by neuron. Here Krishna's engineering perspective was important: nature would be happy with such solutions, even if they were initially confusing to neuroscientists.

This network dynamics approach was driven not by ideology but by desperation. The laboratory's initial recordings from

motor and premotor cortex were shocking if one's prior experience was with visual areas V1, MT and MST. If you have seen one MT neuron, you have more or less seen them all. Yet anterior cortical areas trend towards what Krishna's longtime collaborator Bill Newsome referred to as 'the neural zoo'. Nowhere is this more evident than in motor cortex, where neural responses are floridly complex and heterogeneous. In visual areas, it had typically been possible to anticipate population properties from single-neuron properties. In the early days of Krishna's laboratory, it became apparent that the opposite strategy was required: understand computation first at the population level, then explain single-neuron responses. Fortunately, computational neuroscientists had long used population-level descriptions as a primary way of understanding network computations. A natural goal was thus to use artificial-network solutions to generate empirically testable predictions.

Given the temporal complexity of motor cortex responses, the candidate model networks were recurrent (that is, activity flows not only forward, but also in circles). There were not yet reliable methods for training recurrent networks, making it necessary to employ educated guesses regarding the solutions they might use. These educated guesses were later confirmed when network-training techniques advanced. Yet, even before that confirmation, these guesses made testable predictions that were borne out by neural and behavioral data. Thus, the network dynamics hypothesis was a valid 'way that things might work' that was compatible with the zoo of single-neuron responses.

This work paralleled similar conceptual shifts in other laboratories studying a variety of brain areas across a range of tasks. The network dynamics perspective yielded tools for expressing hypotheses that would have been difficult to express any other way. This approach is now standard. It is not appropriate for all brain areas or all situations, but it is often the simplest way to understand network computations. In this way, an approach that might have appeared radical from the outside

was actually conservative – at the time, it was just the simplest way of embracing inescapable facts.

Krishna's approach to BCI design can also be seen as conservative: large improvements result from doing many small things well, then allowing advances to accumulate over time. Krishna was adamant that progress must be quantifiable to allow accumulation of progress not only within the group but across laboratories. Krishna was a consummate engineer. When it came to issues of human health and engineering integrity, Krishna-the-slightly-scampy-prankster disappeared. He felt the weight of what it meant to do something that could matter to the well-being of others and of what it meant to take public funds to improve public health. Krishna the engineer was unusually thoughtful, careful, and earnest; you can't think on such timescales without developing a deep sense of responsibility.

Krishna developed BCI systems that set performance records, initially focusing on discrete target selection and continuous cursor control. Combined with his scientific vision, this work earned Krishna awards and funding from the Howard Hughes Medical Institute, allowing him to broaden and expand the scientific and engineering efforts of the laboratory. He worked closely with a neurosurgeon, Jamie Henderson, to move BCI technology into humans. The most recent demonstrations of handwriting and speech BCIs from this collaboration are simply stunning in their performance. Continuing advances are almost certain to improve performance further.


Krishna envisaged well-engineered BCI systems that could be broadly deployed. This ability is not yet here, but it is clearly reachable. His work demonstrates that potential beyond any doubt. His dream unfolded as he foresaw, delightfully unpredictable in its details but assured at the level of broad goals. There is solace in this, but not enough. Those who know him know that Krishna handled his diagnosis with unusual dignity and grace. We also know he should not have had to. He still had many more pranks to play and much more science to give.

Krishna was a Howard Hughes Medical Institute Investigator, a member of the National Academy of Medicine, and a fellow of both the American Institute for Medical and Biological Engineering and the Institute of Electrical and Electronics Engineers. His research awards included a Burroughs Wellcome Fund Career Award, a Sloan Fellowship, a McKnight award, US National Institutes of Health EUREKA and Pioneer awards, and the Andrew Carnegie Prize. He was a member of the BrainGate team that translated BCI devices for use in human participants, was a co-founder of Neuralink, and served on the advisory boards of several health- and technology-related companies. Krishna is survived by his family, including his daughters Thanh-Nga Shenoy and Kim-Nga Shenoy, his mother Rosa Louise Shenoy, and his wife Bach-Nga Shenoy. He spoke of his family often and fondly, and Bach-Nga remembers well the early days of Friday nights at Fry's as she and Krishna made many trips to that iconic Silicon Valley institution while building the laboratory. Krishna never left any doubt about the fact that family matters most, while at the same time treating so many of us like family.

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Published online: 20 March 2023