Eric Lenneberg and Motor Control

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1. Preamble

I began my graduate career in 1970. I was somewhat familiar with Eric Lenneberg, having met him during an event for faculty in Psychology and Neuroscience—the fields in which I was interested at the time. He had just arrived at Cornell, as had I, and he didn't have many other graduate students at that time. I chose him as my graduate faculty advisor. He directed me toward the study of the development of motor control, one of his fields of interest (cf. Lenneberg's classic, *Biological Foundations of Language*, 1967). His other students were urged to study the development of language, in which he was most well known. These students went with Eric to New York to study patients with aphasia, while I stayed behind at Cornell in Ithaca, with my young children. That ended up suiting me well!

When I began graduate school, I was unsure of the direction or level I wished to attain. This was the 1960s and women were not particularly accustomed to graduate school or aiming high, especially if already married with children, which I was. My husband was a faculty member in the Cornell Mathematics Department, and our children were quite young: one was six and one was four. Eric Lenneberg, who had just begun his time as a faculty member at Cornell University, had participated in a forum I organized for theoreticians of science, and was the only faculty member of neuroscience I knew at all well, since he had participated in the forum.

My thesis, when finally completed also included results of a project done after Eric's death with Professors Carl Gans, University of Michigan, and Farish Jenkins, Harvard University, on rat muscle activity during running. Both sets of results were integrated into my dissertation on rat locomotion, unfortunately, with Professor Gans as my advisor and without Eric on my committee.

As a post-doctoral fellow, I remained at Cornell for a few years with funding from a National Institutes of Helath (NIH) grant, which fortunately, I was able to obtain independently. At that point I also became interested in mathematical modeling of the phenomena on which I was working, another area that Eric had urged me toward and about which he was enthusiastic. This resulted in my most cited publication: Cohen, Holmes & Rand (1982). It has been perhaps my most important publication and the fact that it was and still is being widely cited is a testament to its importance in establishing theoretical neuroscience.

After this work, which was completed early with two mathematical colleagues, Philip Holmes and Richard Rand, both professors at Cornell at that time, I continued doing research in my own laboratory, also at Cornell. I chose the detailed study

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of the production of spinal waves of neural activity as seen in fish swimming as my topic, employing electrophysiological techniques I had learned from Sten Grillner in Sweden while doing post-doctoral work there immediately after completing my thesis. The experimental model I kept relying on I had chosen as a post-doctoral student in Grillner's laboratory prior to returning to Cornell, namely the lamprey spinal cord (Cohen & Wallén 1980). I continued modeling with Philip Holmes and another former Cornell former graduate student, Tim Kiemel. It is this field in which I worked happily and productively until my retirement in August 2013.

You might wonder what the link was between the development of language and motor control—and fish swimming? In fact, the link is very complex, but clear. Speech production is a motor process, albeit difficult to study in precise detail, but interesting nonetheless. For example, apraxia of speech and some forms of aphasia are conditions which rob you of the ability to communicate, to speak, or even use language. They can affect your ability to speak, write, and understand language, both verbally and/or in its written form. This can occur either following a stroke or head injury, as well as following other injuries that impact the parts of the brain that are involved in speech production and language processing. Aphasia is field of study that has a long history, almost as long as the field of speech production if not longer. Not being an expert, myself, I leave that to others to elaborate. My task here is to elaborate a bit on the field of motor control, how Eric led me to it, to what purpose and to what effect.

2. How did Eric lead me to motor control?

Eric suggested that the area of motor control was often neglected, but was extremely important, as it was foundational of all activities, such as speech production and any other type of movement. He would be unable to assist me very much, but would do all he could. I also found that others in the department could be helpful. So I was off and running on motor control! Unfortunately, it was shortly after this decision, that Eric died, so he did not accompany me on this part of the journey.

Shortly after starting graduate school, and after Eric's death, I went with my husband to University of Michigan for the semester, where I found Dr. Carl Gans. He helped me move ahead on my dissertation work with some experiments on rats (Cohen & Gans 1975), plus he really enabled me to dig deeply into motor control, since that was his area of specialization. Around that time, I also took a short trip to Harvard to allow me to incorporate into my thesis work, X-ray cinematography with Professor Farish Jenkins. For this I put white rats into a specially redesigned running wheel with a plastic side wall to allow the X-ray beams to reach the running rats. The contraption worked well, and we made some great images of running rat skeletons (Cohen 1979).

As a post-doctoral fellow at Cornell I had one other diversion. This one took me toward mathematical description of my work, or theoretical neuroscience, another area that had been important to Eric and to which he would have been happy I embarked upon. Fortunately, I had close ties to the Department of Mathematics, as my husband is a mathematician (Marshall Cohen, a topologist at Cornell in those years). A couple of his colleagues, Philip Holmes and Richard Rand worked with me to perform a theoretical dynamical systems analysis of rhythmic movements such as locomotion or swimming. This resulted in perhaps my most important, and certainly my most cited paper, already mentioned above, co-authored with Philip Holmes and Richard Rand who were in Theoretical and Applied Mechanics at Cornell at that time (Cohen, Holmes, & Rand 1982). The paper also helped one to understand the movement that I was beginning to study: swimming of a very primitive fish-like vertebrate, the lamprey, which is the animal at the base of the vertebrate tree. It lacks bones and cartilage, the latter only appears later in sharks.

3. What is motor control and why is it important?

Motor control has been defined in many ways. My definition: motor control is the means by which organisms coordinate and activate their muscles to perform any movement . This requires the integration of sensory information from the body of the organism as well as with its environment. The organism must determine the appropriate set of muscle forces to generate the desired movement or action. To do this, there must be cooperative interaction between the central nervous system and the musculoskeletal system. Thus, sensory input must be available to provide the current status of the organism in its environment; it must also be able to provide the impact of any action that is performed. The motor system must be able to utilize this information, and respond appropriately.

4. Where it all led me and how it linked back to the theory of motor control

My thesis from Cornell was a variation on a project begun by Roger Sperry in 1942 (Sperry 1945a, b). He cross innervated muscles to determine if they maintain their functional identity if connected to a new functional destination. That is, if the nerve to a flexor is connected to an extensor, will it continue to activate the muscle at the same time as it did originally. Sperry did it after removing all the other neighboring muscles and their nerves, thereby removing the possibility of their being feedback regarding how their activity is stretching and contracting as compared to the normal activity. I did the same thing, but left all other innervation intact, including the sensory nerves to muscle. This had the disadvantage that if I wanted to know when the muscle was activated, I was required to record its activity. This I did with electromyography of the relevant muscles, and I found that, indeed, the nerve continued to be activated as it usually did, even though it now was attached to a new muscle. However, it was impossible to determine what the nerve was functionally achieving. This I was able to do in normal animals by using X-ray cinematography of the rats moving in running wheels with a plastic side replacing the wire partitions normally present (Cohen & Gans 1975). However, in animals with crossed innervation, it was not possible. So, the result described in my thesis remained largely indeterminate. I ended up calling this resulting paper, colloquially as: 'My life as short communication . . . " (Cohen 1978).

Eric had sent me on the road to neuroscience, since he had a joint appointment in the Departments of Biology and Psychology, and I was in Biology (which, at that time, was actually still called Zoology). He gave very little guidance, which suited me fine. Helen Neville, another student of Eric's, and I became good friends, and she helped me navigate the field.

As a consequence, I moved on in related but less complicated directions. In particular, I was determined to keep things simple and determinant. My next preparation was the spinal cord of a primitive vertebrate, the lamprey, an animal at the base of the vertebrate tree. The spinal cord is clear, fully formed and easily removed from skin and muscle for monitoring and manipulating in vitro. What more could I ask? This work was begun with Dr. Sten Grillner at the Karolinska Institute on an NIH post-doctoral fellowship, and continued with Dr. Carl Rovainen and his student Jim Buchanan (Buchanan & Cohen 1982) in St. Louis at Washington University.

After this short stint as a post-doctoral fellow with Dr. Rovainen I returned to Cornell, where my husband was teaching. The university provided me with a lab after I obtained an NIH grant to further study the lamprey spinal cord. After some time on my own at Cornell, I obtained a faculty position at the University of Maryland, College Park. Once there, it was relatively smooth sailing!

Using the simple lamprey spinal cord, activated either chemically (the work begun with Carl Rovainen) or neurally from attached brain activation (much later, done on my own), I was able to specify the impact of the various forms of activation on the lamprey spinal cord (Cohen et al. 1996). Thus, I was able to demonstrate the output of the "central pattern generator" for locomotion in basal vertebrates. Importantly, it was very straightforward. The spinal cord when activated chemically produces a beautiful traveling wave of motor bursts that by themselves can produce the pattern of traveling waves of the fish as it moves through the water. Impressively, the traveling wave under even this condition has the proper delays between adjacent segments, and the strict alternation between the two sides (Buchanan & Cohen 1982). This simple pattern, we showed much later with activation of a theoretical model or robotic animals (Leftwich et al. 2012), produced the proper movement seen in lampreys as they swim naturally. Yes, the brain stimulation could alter the pattern in very complex ways (Cohen et al. 1996), as presumably needed, but when swimming steadily, the lamprey could swim perfectly with simple spinal cord activation, and the simple lamprey spinal cord alone produced the basics all by itself.

In 2005, the Japanese invited me to help them develop motor control, what they called "mobiligence" or smart movement by intelligent design. Their goal was the development of smart robots. So, I spent a month in Japan traveling between researchers giving lectures on motor control. After my departure, they did, indeed, do some beautiful work on mobile robots, some inspired by my visit (Kimura, Fukuoka & Cohen 2006) and a great deal from their own invention.

5. Conclusion

In a nutshell, that is my output during my experimental years in the lab. I also contributed to the literature with *Neural Control of Rhythmic Movements in Vertebrates*, a collection of articles by distinguished scholars in the field (Cohen, Rossignol & Grillner 1988). Lastly, I would like to say that Eric's sensitivity and insights helped to guide me through my intellectual journey, and I remain eternally grateful to him.

6. References

Buchanan, James T. & Avis H. Cohen. 1982. Activity of identified interneurons, motoneurons, and muscle fibers during fictive swimming in the lamprey and the effects of reticulospinal and dorsal cell stimulation. *Journal of Neurophysiology* 47, 948–960.

Cohen, Avis H. 1978. Functional recovery following cross-innervation of antagonistic forelimb muscles in rats. *Acta Physiologica Scandinavica* 103(3), 331–333.

Cohen, Avis H. 1979. Relationship between forelimb coordination and movement asymmetries during fast gaits, canter and gallop. *Brain Research* 164, 325–356.

Cohen, Avis H. & Carl Gans. 1975. Muscle activity in rat locomotion: Movement analysis and electromyography of the flexors and extensors of the elbow. *Journal of Morphology* 146, 177–196.

Cohen, Avis H . & Peter Wallén. 1980. The neuronal correlate to locomotion in fish: "Fictive swimming" induced in an in vitro preparation of the lamprey spinal cord. *Experimental Brain Research* 41, 11–18.

Cohen, Avis H., Philip J. Holmes & Richard H. Rand. 1982. The nature of the coupling between segmental oscillators of the lamprey spinal generator for locomotion: A mathematical model. *Journal of Mathematical Biology* 13, 345–369.

Cohen, Avis H., Serge Rossignol & Sten Grillner (Eds.). 1988. *Neural control of rhythmic movements in vertebrates*. New York, NY: Wiley.

Cohen, Avis H. , Lan Guan, J. Harris, Ranu Jung. & Tim Kiemel. 1996. Interaction between the caudal brainstem and the lamprey central pattern generator for locomotion. *Neuroscience* 74(4), 1161–1173.

Kimura, Hiroshi, Yasuhiro Fukuoka & Avis H. Cohen. 2006. Adaptive dynamic walking of a quadruped robot on natural ground based on biological concepts. *The International Journal of Robotics Research* 26, 475–490.

Leftwich, Megan C., Eric D. Tytell, Avis H. Cohen & Alexander J. Smits. 2012. Wake structure behind a swimming robotic lamprey with a passively flexible tail. *Journal of Experimental Biology* 215, 416–425.

Lenneberg, Eric H. 1967. *Biological Foundation of Language*. New York, NY: Wiley.

Mobiligence: Symposium on learning through motor action. Sapporo, Japan, December, 2005

Sperry, Roger W. 1945a. The problem of central nervous reorganization after nerve regeneration and muscle transposition. *The Quarterly Review of Biology* 20, 311–369.

Sperry Roger W. 1945b. Restoration of vision after crossing of optic nerves and after contralateral transplantation of eye. *Journal of Neurophysiology* 8, 15–28.

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