

DEDICATION TO CARLO A. TERZUOLO

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This edition of the Archives is dedicated to the life and career of Carlo Terzuolo, who was Professor of Neurophysiology at the University of Minnesota from 1959 to his retirement in 1994. His untimely death in October, 1999 left a large scientific legacy for Neuroscience in the scientists he trained and collaborated with.

The issue contains a set of papers written by the attendees to a conference held at Brainerd, Minnesota on September 26-30, 2001, and organized by his students and colleagues at the University of Minnesota to celebrate his life and career. It seemed fitting to model this tribute after a most successful conference Carlo organized 33 years ago. He invited some of the leading investigators in the frontier area we now call computational neuroscience to hold a workshop to which he invited promising

graduate students and post-doctoral fellows. In keeping with the theme of that conference, which helped to establish many research directions and collaborations, we also set as our goals to bring together colleagues having a common interest in the workings of the nervous system and to provide a forum for the young and promising investigators in the field. To this end we invited the participants of the 1969 Brainerd conference as a legacy of Carlo's dream for that conference, and we also invit-



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ed some of the most promising young investigators in the field today. In that sense, this Brainerd Conference of 2001 was dedicated to Carlo Terzuolo as a reunion and rededication of the Brainerd Conference of 1969.

Carlo Terzuolo was an intense person who was fiercely dedicated to his science. He was ambitious for science and particularly for young people (the future of science). He had a strong faith in the power of the independent investigator and he promoted that faith to both colleagues and students. For example, a review of his bibliography does not reveal the names of many of his trainees because they published their work under their own names. He was interested in big questions yet he pursued each experiment with a focussed intensity. His research contributions ranged over topics as diverse as nerve membrane biophysics and the organization of movement in handwriting and typing.

The scientific career of Carlo Terzuolo began just after World War 2 when he received the MD degree from the University of Turin. Shortly afterward he went to Pisa to study electrophysiology under Prof. G. Moruzzi. It was there he developed his interest in the functions of the cerebellum and brain stem structures along with his friend and colleague H. Terzian (29, 30). In 1951 he moved to Brussels to study for 2 years with Prof. F. Bremer where he was introduced to the intracellular micro-electrode and studied the neurophysiology of sleep and arousal (6, 7, 8).

About this same time Carlo received an invitation from Sheibel and Sheibel, with whom he had started an informal collaboration, and from H. Magoun to go to UCLA. Thus in 1954 Carlo Terzuolo and his wife Silvia arrived in California to begin his scientific career in the US.

Altogether he spent 4 years at UCLA in the Department of Anatomy where he developed many friendships among the leaders of neuroscience at that time and became a US citizen. His developing interest in the process of inhibition led along a number of paths (the cardiac ganglion of lobster (22), the cerebellum (20) and the spinal motoneuron (21)). This latter interest in the motoneuron may have developed while he was at the NIH to satisfy a year of military service in 1956-57, working with R. Galambos. It led to a notable neurophysiological first in the successful voltage clamp of the motoneuron, which he first published with Araki in 1959 (4, 5).

In 1958, Maurice Visscher, who was then the Head of Physiology at the University Minnesota visited UCLA and invited Carlo to come to Minnesota to head a Laboratory of Neurophysiology. Thus in 1959, he moved to a newly renovated laboratory at the University of Minnesota Medical School as the Hill Family Professor of Physiology.

One prominent aspect of his scientific career was his ability to recognize and develop scientific talents in young people. His laboratory in Minnesota soon became a training ground for many who went on to become prominent researchers. The initial focus of the laboratory was on the neuron as it was being explored by intracellular recording. But he was never satisfied with just an experimental approach or with a particular question at hand. He strongly believed, and imparted this to students and colleagues, that:

“the more risks taken in pursuing a research effort, the more likely it is that new insights of general significance may eventually be gained” (23).

In fact, his scientific career at Minnesota, which spanned three and half decades went through at least three major phases:

The first was concerned with the neuron and the properties that could be revealed and quantified with the then new microelectrode technology. Here he made a number of important contributions to our understanding of nerve cell function. In particular, his studies with R. Llinas that showed the role of dendritic compartmentalization in the processing of information in motoneurons (11, 12, 24), and his work with Washizu demonstrated the special excitability properties of the axon initial segment that gave rise to the production of the action potential (31, 32, 13).

The second phase of his research interests developed from a desire to understand neuronal circuits and to employ quantitative methodologies borrowed from physics and engineering (systems analysis). This interest was launched to some extent by the Brainerd conference of 1969. He realized at this point that a purely reductionist approach would not answer the larger questions about brain function. He began by applying these new tools to the basic reflex circuitry of the spinal cord and demonstrated a surprisingly linear processing of sensory and motor parameters at this level (14, 15, 16). He also explored quantitative control relationships in a series of simple motor tasks (27, 28, 25, 18, 26, 1, 2, 3).

Finally, a more generalized application of the systems analysis approach formed a third phase in which he sought to understand the computational functions of the nervous system, functions that were to be best understood from a top-down or even psychophysical approach. His real curiosity – no doubt a partial legacy from Moruzzi and Bremer – was to understand the function of major neuronal systems (how the brain works). During this period he explored more general questions about the organization of motor functions in the context of natural 3-dimensional movements. He and his colleagues showed that the nervous system deals with the complexities of such movements by means of suitable approximations and imposed constraints. For example, they found that arm movements could be decomposed into segments of planar ellipses in space that were specified by the phase relationship between joint angles (10, 17, 19), and the kinematics of arm movement are constrained by a specific relationship to the figural aspects of the movement (the 2/3 power law; 9).

While this work was proceeding at Minneapolis, Carlo also made important contributions to science in his home of Italy. In 1965, he was asked by his mentor Prof. Moruzzi to establish the Institute of Neurophysiology of the CNR in Pisa. With his usual energy, Carlo not only set up the institute, but personally designed the building and led the operation for several years. Later in 1982, he established a similar Institute for Neurophysiology in Milan. Both institutes have had a productive history of scientific accomplishment.

REFERENCES

1. ANDERSON, J.H., SOECHTING, J.F. AND TERZUOLO, C.A. Dynamic relations between natural vestibular inputs and activity of forelimb extensor muscles in the decerebrate cat. I. Motor output during sinusoidal linear accelerations. *Brain Res.*, **120**: 1-15, 1977.
2. ANDERSON, J.H., SOECHTING, J.F. AND TERZUOLO, C.A. Dynamic relations between natural vestibular inputs and activity of forelimb extensor muscles in the decerebrate cat. II. Motor output during rotations in the horizontal plane. *Brain Res.*, **120**: 17-33, 1977.
3. ANDERSON, J.H., BERTHOZ, A., SOECHTING, J.F. AND TERZUOLO, C.A. Motor output to deafferented forelimb extensors in the decerebrate cat during natural vestibular stimulation. *Brain Res.*, **122**: 150-153, 1977.
4. ARAKI, T. AND TERZUOLO, C.A. Voltage-clamp of the inhibitory post-synaptic potential. Pp. 115-117. ROBERTS, E. (Ed.) *Inhibition in the Nervous System and γ -Amino-butirgic Acid*. New York, Pergamon Press, 1960.
5. ARAKI, T. AND TERZUOLO, C.A. Membrane current in spinal motoneurons associated with the action potential and synaptic activity. *J. Neurophysiol.*, **25**: 772-789, 1962.
6. BREMER, F. AND TERZUOLO, C. Role de l'ecorce cerebrale dans le processus du reveil. *Arch. Int. Physiol.*, **69**: 228-231, 1952.
7. BREMER, F. AND TERZUOLO, C. Nouvelles recherches sur le processus physiologique du reveil. *Arch. Int. Physiol.*, **61**: 86-90, 1953.
8. BREMER, F. AND TERZUOLO, C. Contribution a l'eétude des mécanismes physiologiques du maintien de l'activite vigile du cerveau. Interaction de la formation reticulée et de l'ecorce cerebrale dans le processus du reviel. *Arch. Int. Physiol.*, **62**: 157-178, 1954.
9. LACQUANITI, F., TERZUOLO, C.A. AND VIVIANI, P. The law relating the kinematic and figural aspects of drawing movements. *Acta Psychologica*, **54**: 115-130, 1983.
10. LACQUANITI, F., SOECHTING, J. AND TERZUOLO, C.A. Constraints on point-to-point arm movements in three-dimensional space. *Neurosci.*, **17**: 313-324, 1986.
11. LLINAS, R. AND TERZUOLO, C.A. Mechanisms of supraspinal actions upon spinal cord activities. Reticular inhibitory mechanisms on alpha extensor motoneurons. *J. Neurophysiol.*, **27**: 579-591, 1964.
12. LLINAS, R. AND TERZUOLO, C.A. Mechanisms of supraspinal actions upon spinal cord activities. Reticular inhibitory mechanisms upon flexor motoneurons. *J. Neurophysiol.*, **28**: 413-422, 1965.
13. LOWENSTEIN, W.R., TERZUOLO, C.A. AND WASHIZU, Y. Separation of transducer and impulse generation processes in sensory receptors. *Science*, **142**: 1180-1181, 1963.
14. POPPELE, R.E. AND TERZUOLO, C.A. The myotatic reflex: input-output relationship. *Science*, **159**: 743-745, 1968.
15. ROBERTS, W.J., ROSENTHAL, N.P. AND TERZUOLO, C.A. A control model of the stretch reflex. *J. Neurophysiol.*, **34**: 620-630, 1971.
16. ROSENTHAL, N.P., MCKEAN, T.A., ROBERTS, W. AND TERZUOLO, C.A. Frequency analysis of the stretch reflex and its main subsystems in triceps surae muscles of the cat. *J. Neurophysiol.*, **33**: 713-749, 1970.
17. SOECHTING, J., LACQUANITI F. AND TERZUOLO, C.A. Coordination of arm movements in three-dimensional space-sensory motor mapping during drawing movements. *Neurosci.*, **11**: 295-311, 1986.
18. SOECHTING, J.F., PALMINTERI, R. AND TERZUOLO, C.A. Studies on the control of some simple motor tasks. IV. Relation between parameter of motion and motor output in squirrel monkey. *Brain Res.*, **62**: 247-252, 1973.
19. SOECHTING, J.F. AND TERZUOLO, C.A. An algorithm for the generation of circular wrist motion in an arbitrary plane in three-dimensional space. *Neurosci.* **19**: 1395-1405, 1986.

20. TERZUOLO, C.A. Cerebellar inhibitory and excitatory actions upon spinal extensor motoneurons. *Arch. Ital. Biol.*, **97**: 316-399, 1959.
21. TERZUOLO, C.A. AND GERNANDT, B.E. Spinal unit activity during synchronization of a convulsive type (strychnine tetanus). *Am. J. Physiol.*, **186**: 263-270, 1956.
22. TERZUOLO, C.A. AND BULLOCK, T.H. Acceleration and inhibition in crustacean ganglion cells. *Arch. Ital. Biol.*, **96**: 117-134, 1958.
23. TERZUOLO, C.A., FOHLMEISTER, J.F., MAFFEI, L., POPPELE, R.E., SOECHTING, J.F. AND YOUNG, L. On the application of systems analysis to neurophysiological problems, *Arch Ital. Biol.* (Volume in honor of Professor G. Moruzzi) **120**:18-71, 1982.
24. TERZUOLO, C.A., LLINAS, R. AND GREEN, K.T. Mechanisms of supraspinal actions upon spinal cord activities. Distribution of reticular and segmental inputs in cat's alpha motoneurons. *Arch. Ital. Biol.*, **103**: 635-651, 1965.
25. TERZUOLO, C.A., SOECHTING, J.F. AND PALMINTERI, R. Studies on the control of some simple motor tasks. III. Comparison of the EMG pattern during ballistically initiated movements in man and squirrel monkey. *Brain Res.*, **62**: 242-246, 1973.
26. TERZUOLO, C.A., SOECHTING, J.F. AND RANISH, N. Studies on the control of some simple motor tasks. V. Changes in motor output following dorsal root section in squirrel monkey, *Brain Res.*, **70**: 521-526, 1974.
27. TERZUOLO, C.A., SOECHTING, J.F. AND VIVIANI, P. Studies on the control of some simple motor tasks. I. Relations between parameters of movements and EMG activities. *Brain Res.*, **58**: 212-216, 1973.
28. TERZUOLO, C.A., SOECHTING, J.F. AND VIVIANI, P. Studies on the control of some simple motor tasks. II. On the cerebellar control of movements in relation to the formulation of intentional commands. *Brain Res.*, **58**: 217-222, 1973.
29. TERZUOLO, C. AND TERZIAN, H. Sul meccanismo della rigidità da decerebrazione in arti anteriori cronicamente deafferentati. *Boll. Soc. Biol. Sper.*, **27**: 1317-1318, 1951.
30. TERZUOLO, C. AND TERZIAN, H. Riflessi di Magnus e tono posturale in arti sottoposti a deafferentazione acuta o cronica. *Boll. Soc. Biol. Sper.*, **27**: 1319-1320, 1951.
31. TERZUOLO, C.A. AND WASHIZU, Y. Relation between stimulus strength generator potential and impulse frequency in stretch receptor of Crustacea. *J. Neurophysiol.*, **25**: 56-66, 1962.
32. WASHIZU, Y. AND TERZUOLO, C.A. Impulse activity in the crayfish stretch receptor neuron. *Arch. Ital. Biol.*, **104**: 181-194, 1966.