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FOREWORD

Biological Cybernetics

Structural aspects of biological cybernetics: Valentino Braitenberg, neuroanatomy, and brain function

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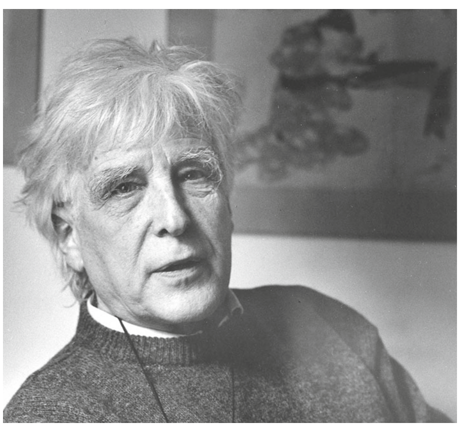
1 Introduction

The best way of introducing Valentino Braitenberg is by quoting one of his distinctive arguments [99, p. 31]:[1]



[1] The referencing in this Foreword is twofold. For the Foreword itself, the Harvard style referring to authors by year is used whereas for the publications of Braitenberg himself recourse has been taken to the Vancouver style, which uses angular brackets such as [1]. Both lists appear at the end in the order as just described.

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"When a new science emerges every couple of centuries, those who are privileged enough to witness it from its very beginnings to its full development during the span of their own lifetime can indeed count themselves lucky. My colleagues and I, who became fully fledged after World War II, had precisely this privilege. The science to which I refer still has no proper name, but its existence can be testified to by the matter-of-course way in which physicists, biologists, and logicians discuss issues that do not fall into any of the categories of physics, biology or logic. Their consensus is not so much interdisciplinary (which does not bring us much more than admiration from people who don't know much about it) as decidedly neodisciplinary, i.e., based on a new language and terminology that convinces all sides and that is already so well established that it hardly needs to be discussed any further. Some call this new discipline informatics, others information science; it may sometimes be narrowed down to neuroinformatics or 'technical informatics.' The term cybernetics, which does not meet with universal approval, has, nonetheless, a good chance of asserting itself in the long run. This is not least due to the fact that the term was coined by its most brilliant founder, the mathematician Norbert Wiener. His solid philosophical and philological background is reflected in the fitting name that he gave to this science. The designation cognitive science, which is currently popular, might well one day apply to everything that we still refer to as informatics and cybernetics. But then again, the plain (and rather sloppy) term computer science might come up trumps at the end of the day, as a tribute, if you like, to the fact that the whole thing did not get off the ground until large electronic data processors were invented.

Yet one thing is for sure; this new area that has arisen between the humanities and natural sciences, while not professing to belong to either discipline, actually succeeds in querying the boundaries of both. Although no one can be universally knowledgeable, there is no longer a wall to prevent us from taking a peek to see what is on the other side […]".

So far this is Valentino Braitenberg in 1999 and how he described the science to which this journal is dedicated and to which he was committed in his own research. The books by Wiener (1948) and Shannon and Weaver (1949) hit him, the prospective brain scientist, "like a thunderbolt," as he mentions in the article quoted above. Educated as a psychiatrist and neurologist in Rome up to 1954, Valentino Braitenberg was driven by the wish to understand the neurobiological mechanisms' *underlying* behavior. He was convinced that the study of brain structure and, hence, neuroanatomy in conjunction with brain theory is a tool to reach this goal. Research stays took him to the neuroanatomists Oskar Vogt and Karl Kleist in Germany and later to Yale Medical School in New Haven, Connecticut, where he made the acquaintance of the protagonists of cybernetics (Wiener, McCulloch, von Foerster). Back in Italy, he obtained his habilitation in 1963 in the discipline *Cybernetics and Information Theory* and became Director of the Department of Biocybernetics at the Consiglio Nazionale delle Ricerche in Naples. In 1968, at the suggestion of Werner Reichardt and, together with Karl Götz and Kuno Kirschfeld, he was appointed to be one of the co-founding directors of the Max Planck Institute for Biological Cybernetics in Tübingen, Germany. Other appointments were that of honorary professor at the Faculty of Physics at the University of Tübingen and at the Faculty of Biology at the nearby University of Freiburg.

The present special issue of *Biological Cybernetics* is dedicated to the memory and, hence, to the impressive scientific heritage of Valentino Braitenberg (*1926 in Bolzano, † 2011 in Tübingen). In actual fact, he stemmed from South-Tyrolean nobility and his full name was Valentino von Braitenberg. His work had and continues to have a strong influence on modern brain science. Starting from his clinical experience as a psychiatrist, he committed himself to the investigation of connectivity schemes in the brain and of their respective roles for brain function. The focus of his attention was on the visual system of the fly, the cerebral and the cerebellar cortex of vertebrates, and their role in perception, memory, movement, and language. It led to seminal contributions in all these various fields. Moreover, he was a master in bridging the gap "between humanities and natural sciences," which is evident from most of his books [1–9]. This mastery also characterized his lectures and seminars, spanning a wide range of themes related to the brain, from neuroanatomy and neurophysiology via automata theory, information theory, and logic through to clinical topics, to language and music, never remaining superficial, but providing the participant with practical tools to contribute constructive ideas to open questions, a fascinating and remaining source of inspiration for many.

The link between humanities and natural sciences is also reflected by the collection of contributions to the present special issue. All of them have a relation to Valentino Braitenberg's multifaceted work. In this foreword, we give Valentino Braitenberg not only the first but also the last word, by reprinting at the end his fascinating *Manifesto of Brain Science*—first published in 1992, but having lost nothing of its sparkling actuality till the present day.

2 Overview of Valentino Braitenberg's scientific work

Valentino Braitenberg's contribution to a new phase in neuroscience beginning in the 1950s was the resuscitation of neuroanatomy, a branch of science that had been dormant since the monumental works of Ramón y Cajal (1909–1911) and Lorente de Nó (e.g. 1922, 1949). He almost single-handedly made neuroanatomy into a pillar of brain theory by providing examples of a direct translation of neural structure into functional schemes that had not yet emerged from the then prevalent method of neurophysiology. His impact on modern brain science is comparable to that of the founders of neurocybernetics, who introduced around the same time the logical analysis of nerve nets (McCulloch and Pitts 1943), the concept of feedback in homeostatic mechanisms (Wiener 1948), the concepts of information and redundancy in perception (Shannon 1948), and the neural theory of associative learning and cell assemblies (Hebb 1949).

Three of his discoveries were epoch-making.

(1) *The cerebellum as a millisecond clock*. Braitenberg's early work on the cerebellum [10–23] presented the first example of a neuroanatomical morphology, interpreted in terms of its function down to the level of individual neurons and synapses. His conclusion that the cerebellum is specialized for the measurement of time intervals with a precision better than one millisecond has become common knowledge, even if not undisputed. The later versions of his model, together with his own and his group's experimental work, continue to provide inspiring explanations of the role of the cerebellum in motor control.

(2) *Exact neural wiring in insects*. His work on the *visual ganglia* of insects [24–41], originally inspired by the behavioural analysis of Werner Reichardt and his group in Tübingen (which Braitenberg later joined), led to the first complete and undisputed explanation of the intricate structure of a neuronal network, that of the fibers connecting the fly's eye to the visual ganglia. His neuroanatomical analysis provided the proof [26]—in par-

allel to Trujillo-Cenóz and Melamed (1966)—for the 'neuronal superposition eye' predicted by Kirschfeld (1967). The principle involved assigns a precise origin and destination to every fiber of the network and was shown to hold with unerring precision. Apart from its importance for visual physiology, this finding was of great importance for developmental neurobiology, as it showed the precision with which genetically preprogrammed networks can be expressed and, ultimately, implemented.

(3) *The cerebral cortex as an associative memory*. The structure and function of the *cerebral cortex* was one of Valentino Braitenberg's dominant themes since the beginning of his career [2, 6, 42–71]. The book *Anatomy of the cortex* [6] summarizes the results of many years of painstaking experimental work. It proposes a view of the cortex quite different from the traditional one, in that the essence of its wiring seems to support the principle of a great, "mixing machine," where all data are maximally dispersed, so that convergence of as large as possible a sample of cortical activity is guaranteed to impinge onto any one small region of cortex. The high degree of divergence and convergence, together with the finding that most synapses in the cortex are weak, excitatory, and modifiable, strongly endorse the idea that the cortex specializes in embodying memories in the form of "cell assemblies" (Hebb 1949). Meanwhile, there is a remarkable convergence, and hence reciprocal confirmation, between the anatomical findings of Braitenberg and his associates in Tübingen and the physiological results of various groups around the world, first and foremost the group of Moshe Abeles in Israel.

(4) *Work in related fields.* From his main interest in brain structure, Braitenberg derived collateral interests in various subjects connected with brain science. Besides his contributions to histological and electrophysiological methods [1, 46, 72-79], he ventured competently and convincingly into such various fields as *motor control* [12, 13, 17, 80, 81], *visual physiology* [56, 61, 62, 63, 68, 82], *perception* [83, 84, 62, 82], *information* [9, 85–89], *language* [5, 90–93], *logic and philosophy* [4, 7, 8, 85, 94–100], and *behaviour and artificial intelligence* [3, 51, 101–104, 87]. His book *Vehicles* [3, in five languages] was internationally very well received as an unconventional, yet highly effective introduction to the problems of artificial intelligence.

3 Structure of the present special issue

After the Preface to this special issue, the reader finds the paper by *Mario Negrello*, who reviews a substantial part of Braitenberg's work, including some of his early, less well-known studies, and elaborates on his particular, neuroanatomical, approach to brain research. The paper by *Liewald* et al. continues this approach in a quantitative neuroanatomical study of axon diameter in the human cortical white matter and the role of conduction times.

The next two articles are based on the topic of Hebbian cell assemblies. *Günther Palm* et al. take up the title of Braitenberg's fundamental paper "Cell assemblies in the cerebral cortex" from 1978 [54]. The authors summarize developments in this field since then and discuss computational aspects of the Hebbian theory from a modern perspective. *Friedemann Pulvermüller* et al. also revisit Braitenberg's ideas on cell assemblies and apply this concept to explaining the mechanisms behind a broad range of cognitive functions, such as the relation between action and perception, decision making, attention, language, concepts, and meaning.

In the next three articles, we move from the topic of Hebbian learning, via Braitenberg's *Vehicles* [3] to robotics. Hebbian learning also plays a role in the article by *Niels Birbaumer* and *Friedhelm Hummel*, which deals with the communication of locked-in patients with their surroundings in the context of brain–machine interfaces. The authors show the limitations of this method in severe cases in which the relation between a voluntary response and its (non-existing) effect is lost, relating it to the loss of Braitenberg's "thought-pump." The authors also give an exciting new perspective on how these limitations may be overcome by means of a classical semantic conditioning paradigm. The paper by *Katharina Muelling* et al. deals with learning strategies in table tennis, tackling through this intricate game the interplay between learning and decision making in a highly complex motor task. It leads us once again to Braitenberg's *Vehicles,* which are also the link to the article by *Verena Nitsch* and *Michael Popp*, on emotions in Robot Psychology. This article deals with the interesting question as to what degree emotions can/should or should not be implemented into robots or—vice versa—if it can be avoided at all.

With the next two articles, we move on to sensory systems. *Sadra Sadeh* and *Stefan Rotter* propose a new theory of orientation selectivity in the visual cortex. It is related to Braitenberg's theory on this topic [56, 62, 68] in that it is based on *statistical* connectivity instead of a specific wiring pattern, but it deviates from it in the assumption that orientation selectivity may already be explained by a statistical connectivity between thalamus and cortex. The paper by *Israel Nelken* leads us into the auditory system. It describes and reviews the interesting phenomenon of stimulus-specific adaptation and goes into depth about the possible mechanisms behind it.

The essays by *Moshe Abeles* and by *Fahad Sultan* bring us back to two of the main structures investigated by Valentino Braitenberg, the cerebral and the cerebellar cortex. *Moshe Abeles* developed a new approach for the analysis of magneto-encephalographic data that enables him to detect coordination of activity between cortical areas. He shows how this coordination differs under different conditions, such as conditions of rest and of task performance. *Fahad Sultan* provides an excellent review of the cerebellum, including Braitenberg's theories of the clock in the millisecond range and—later—as a detector of velocities by way of a tidal wave mechanism. Building up on the tidal wave idea, Sultan proposes a theory of cerebellar function in which this mechanism is used for movement optimization.

The final two articles have in common that they enter the realm of natural history and philosophy and focus on the interaction between theory and experiment, though in two very different fields. *Robert Miller* deals with the topic of psychiatry. He supports the ambition to define psychiatry as a scientific discipline, but believes that this goal has not yet been achieved. Starting from a summary of the history of science, he shows what one can learn from it for the validation of concepts in psychiatry, leading the reader up to the idea of psychosis as an exaggeration of the reinforcement function of dopamine and to a theory on the non-psychotic traits of schizophrenia.

The combination of experiment and theory was one of the strengths of Valentino Braitenberg and it also plays a major role in the article by *J. Leo van Hemmen*. He raises the question, whether universally valid principles exist in neuroscience and whether they can be formulated in mathematical terms. He elaborates on the importance of finding the appropriate key concepts and the appropriate scale. As Robert Miller, he is motivated by the history of science, illustrates the universality and the importance of scales by examples from neuroscience, and concludes that the outlook of theoretical neuroscience is at least as good as that of theoretical physics.

The final word of this Foreword has Valentino Braitenberg in his *Manifesto of Brain Science* [97]. We are convinced that it will make for fascinating reading:

Manifesto of Brain Science*

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1. We believe that there are questions of such philosophical import that they deserve being pursued without any consideration of utility. One of them refers to the nature of thought processes, or more generally, of complex behaviour.

2. We are convinced that ultimately a satisfactory explanation of thought and behaviour will be given in a language akin to that of physics, i.e. in mathematical terms.

3. The physics of living organisms, with its specialized branches of physiology and biochemistry will undoubtedly underlie such an explanation, but it will not be sufficient by itself as a theory of behaviour. In fact, when boiled down to physical fundamentals, a mouse or even a worm is not very different from man. But we are ultimately interested in thought and behaviour of people, not of worms.

4. The difference in behaviour in different species reflect different ways of coping with the environment, or with distinct niches of the environment. These different behaviours have their material counterpart in different brains. Therefore the peculiar nature of any animal brain cannot be explained from the physical components alone, the explanation necessarily involving causes residing outside the animal, i.e. information derived from the environment.

5. Concepts such as (Shannonian) information, coding, computation, are outside of physics (even if the formulas look like physics) but are central to brain science. They are also fundamental concepts in electronics and computer science. This is the basis for a lively discourse between certain branches of engineering and brain science. Another common aspect is that both deal with functions directed to a goal, which physics does not.

6. Our object being the discovery of computer-like operations in brains, the hypotheses we test in our experiments are really inventions of computing schemes, and are therefore necessarily more complex than hypotheses in other branches of science. Thus we are inventors of computing devices much as our colleagues in Artificial Intelligence are and we can learn from them as much as they learn from us. Some ideas in brain science (e.g. neural networks) have already turned into eminently practical applications.

7. Computation in brains is a fine-grain operation, requiring a spatial resolution of about one to ten micrometers. The functional elements are fibers and neurons, and in most cases many neurons are involved in a significant functional pattern. This requires special techniques of observation which are being developed: multiple electrode recording, optical recording by means of voltage sensitive dyes. In most cases the vast amount of information produced by these recording techniques can only be stored and digested by means of large computers. Their theoretical analysis also requires sophisticated computing techniques, and often computer simulation.

8. We believe that the distribution of electrical signals observed at a spatial resolution of 1 μm and a temporal resolution of about 1 ms is all we need to know as the material counterpart of behaviour. Behaviour may be modified

* This was prepared for a meeting in Brussels where the European Commission considered the future of Neurobiology in Europe.

by hormones, or by pharmaca, or by pathological unbalance of some transmitter substance, but the actual effect of these is always expressed in terms of the occurrence or not occurrence of action potentials in neurons.

A more fine-grain analysis, say at the molecular level, is relevant for the understanding of the individual cell, but probably unnecessary for the understanding of behaviour, or may even obscure the picture there.

9. Developmental neurobiology is a branch of general biology, not of brain science as defined here. "How do the fibers from the eye find their way into the optic tectum?" The answer to this question will tell us much about how the arteries find their way into the kidney, or the roots of a tree into the earth, but very little about the problem of the analysis of visual information in the optic tectum.

10. Efficient research groups in brain science are small. Everybody is groping for experimental techniques and for conceptual models. If someone draws up a gigantic project in order to solve the problem by brute force, he is likely to have missed the complexity of the situation and is sure to produce much waste.

To illustrate my points, I want to mention some successes of modern brain science in its interaction with information engineering.

(a) The paper by McCulloch and Pitts (1943) proposed an equivalence between nets of neurons connected by synapses and propositions of Boolean logics. The terminology and the diagrams of this paper were immediately taken over by the designers of calculating machines (e.g. J. v. Neumann) and the basic ideas became the starting point for more than one theoretical development, e.g. Automata Theory and Chomskian linguistics (via the formalization proposed by Kleene, 1956).

(b) Some ideas were exchanged repeatedly to and fro between brain science and engineering. The idea of the Perceptron (Rosenblatt 1962), a randomly connected image processor, was inspired by neuroanatomy and neurophysiology. It has admirable technological consequences even today (Sejnowski 1987). It received criticism on theoretical grounds by Minsky and Selfridge, who thought that a machine equipped with preset form detectors ("Pandemonium") would be much more efficient. The Pandemonium inspired neurophysiological work by Lettvin and others which turned into the seminal paper "What the frog's eye tells the frog's brain" (1959). Parallel to it, in the same intellectual environment, work on the cat (and monkey) visual cortex in the hands of Hubel and Wiesel produced splendid, Nobel prize winning results. The Hubel and Wiesel "feature detectors" in turn gave the engineers ideas, who produced several efficient image processing devices along the same theoretical lines.

(c) Filter theory, auto- and crosscorrelation, generalized Fourier analysis are theoretical concepts developed in electronics. Reichardt (1970) described the results of his (and Hassenstein's) experiments on opto-motor reactions in insects in those terms. This was the first model of animal behaviour which made detailed predictions on the neurological wiring underlying the behaviour, and the predictions were in part confirmed anatomically (Braitenberg 1977). The technological fallout was a patent for a device designed to measure the direction and velocity of a moving panorama.

(d) Associative memory was postulated by psychologists (Hebb) as a principle underlying cognition and behaviour. This idea turned into a variety of mathematical models, one of which, the neural net of the Hopfield kind, is hailed now as the cornerstone of a new age of computing technology. It was shown that the statistics of connections within the cerebral cortex (Braitenberg and Schüz 1991) can best be explained as being specialized for associative memory. The global states of activity which the Hopfield theory postulates, a sort of resonant modes or "eigen-states" of the cortex, have been shown with computer analysis of multiple electrode recordings (e.g. Aertsen and Gerstein 1991; Vaadia and Aertsen, this volume).

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