Chapter 1
Introduction: Keylevels of Biocommunication of Ciliates

Guenther Witzany

Abstract Similarly to other organisms of all domains of life from bacteria to complex animals ciliates are sensitive organisms that assess their surroundings, estimate how much energy they need for particular goals and then realize the optimum variant. They take measures to control certain environmental resources. They perceive themselves and can distinguish between self and non-self. They process and evaluate information and then modify their behavior accordingly. These competences are made possible by sign-mediated communication processes within the ciliate body (intraorganismic), between the same, related and different ciliate species (interorganismic) and between ciliates and non-ciliate organisms (transorganismic). In order to generate an appropriate response behavior ciliates must be able not only to sense but also to interpret and memorize important indices from the abiotic environment and adapt to them accordingly. This is decisive in coordinating growth and development, mating, shape and dynamics. However, these communication, interpretation and memory processes can also fail. In such cases the overall consequences can mean disease or even death for the ciliate. In this respect biocommunication method applied to ciliates could integrate the various levels of ciliate signaling processes.

1.1 Introduction

If we look at recent advances in biocommunication research we find that the investigations of sign-mediated interactions between cell tissues, organs and organisms in all kingdoms have increased in the last decade. It is common knowledge that if such biological entities want to coordinate their behavior or in more specialized cases the cells of organs which share a genetically conserved identity it needs not only the generation of biomolecules that serve as signaling

G. Witzany (✉)
Telos-Philosophische Praxis, Vogelsangstr. 18c, 5111 Buermoos, Austria
e-mail: witzany@sbg.at

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tools to transport important messages and their use in different contextual circumstances but the signals to act within interactional motifs to reach certain individual or common goals. Communication is essential to reach such goals and the investigations on biocommunication tell us whether communication functions as the ultimate pre-condition to reach such goals or it does not function for one or several reasons and the message is deformed or damaged so common goals cannot be reached. In the case of cell coordination or organization of organs or group behavior in organisms this might lead to disease or similar problems.

Ciliates are well investigated unicellular eukaryotes and together with other phyla of alveolates have a broad variety of lifeforms and lifecycles (Lynn 2008). Of additional interest in this context of identifying sign-mediated interactions of ciliates is that these single-celled eukaryotes seem to represent the most evolved and complex protozoans. As they are very old in evolutionary terms and date back to the origins of unicellular eukaryotes they can be found on the whole planet except in dry land ecospheres. This tells us that they are excellently adapted and have successfully colonized most ecospheres on this planet and in several cases are interaction partners of symbiotic lifestyles.

Ciliates in most cases are free-living, few of them are parasitic, and some may cause diseases in fish aquacultures. Others are stabilizing bacteria in the gut of hoofed mammals, which is a kind of symbiotic lifestyle. Most ciliates feed on bacteria, other ciliates (cannibalism), fungi or algae.

Of special interest is the parallel representation of two nuclei in most ciliates: a micronucleus which serves as a competence center for reproduction and a macronucleus which serves as a competence center for metabolism and development (Schoeberl and Mochizuki 2011). Ciliates reproduce asexually by division. The micronucleus undergoes mitosis whereas the macronucleus splits into two. Yet ciliates can also reproduce sexually in that two partners of opposite mating types conjugate via a cytoplasmatic bridge. Then the micronuclei divide by meiosis, the macronuclei disintegrate and the conjugating cells exchange haploid micronuclei. Then they segregate, reform the macronuclei from their micronuclei and divide.

1.2 The Concept of Biocommunication

When we consider the biocommunication of ciliates, we must first become familiar with the current terms of communication (and with the signaling system, which we would term language or code, the essential tool for communication).

When we speak about language and communication we usually think of humans that talk to each other and communicate to organize common goals and to coordinate common behavior. However, since Karl von Frisch received the Nobel Prize for detection and investigation of bee languages and dialects it is evident that even non-human social animals may communicate to construct complex behavioral patterns. The Nobel Laureate Manfred Eigen insisted nearly at the same time that when we speak about the genetic code we are speaking about a real language, not just a metaphor (Witzany 1995). Concerning these fundamental insights I developed the biocommunicative approach which investigates both communication (1) and language (2) as universal requirements for life. The first such investigation was published in 1993 (Witzany 1993) followed by an updated version in 2000 (Witzany 2000) as a draft on the theory of communicative nature. The results in virology and the role of viruses in evolution and developmental processes in particular exemplified a variety of the proposed pre-assumptions therein (Witzany 2009; Villarreal and Witzany 2010, 2013a, b, 2015). The theory of biocommunication was outlined first as a program in 2007 updated in 2010 (Witzany 2010) concerning bees, corals, plants, fungi, bacteria, viruses and subviral RNAs. Several more detailed exemplifications followed in a series of books I edited between 2011 and 2014 with leading researchers in their field (Witzany 2011, 2012a, b, 2014; Witzany and Baluska 2012a, b).

1.2.1 The Mechanistic Narrative Used to Explain Communication Is Outdated

The method for analyzing any part of a machine in detail to get a picture of the whole functional blueprint, which can then be used to reproduce or manipulate it, or to produce an even more perfect example, to take artificial genetic engineering as an example, is still useful if we are dealing with machines.

In contrast, communication between cells, cellular components, tissues, organs and organisms is far from being a procedure that can be reduced to mechanistic input/output or cause/reaction descriptions. It is evident that communication processes between living organisms include a variety of non-mechanistic circumstances and competences that must be satisfied in parallel if communicative acts are to have successful consequences; for example, innovating common coordination to adapt to new environmental conditions. Machines cannot create new programs out of a functional blueprint, which is in contrast to the abilities of living organisms that are able to communicate with each other. The universal Turing machine and the self-reproducing machines of von Neumann still remain at the conceptual stage. However, no single self-reproducing machine has ever been produced within the last 80 years. There are good reasons for this, because it is, in principle, impossible that an artificial machine could reproduce itself (Witzany and Baluska 2012b). In contrast to the artificial machines which cannot reproduce themselves, living cells and organisms can reproduce themselves and additionally generate an abundance of behavioral motifs for which no algorithm can be constructed, such as de novo generation of coherent nucleotide sequences.

1.2.2 Communication Is Interaction Between Living Agents Mediated by Sign(al)s

Coherently with current knowledge about natural communication processes communication is defined as the sign-mediated interaction between at least two living agents which share a repertoire of signs (which represent a kind of natural language) that are combined (according to syntactic rules) in varying contexts (according to pragmatic rules) to transport content (according to semantic rules). This means monological concepts such as the sender-receiver narrative, in which the sender codes information and the receiver decodes it according to inherited programs, cannot explain the emergence of commonly shared meanings.

Contrary to former concepts the importance of this result is that these three levels of semiotic rules (*semeion* = sign) are complementary parts of any natural language or code. If one level is missing, according to Charles Morris, we cannot seriously speak of language- or signal- mediated communication. Therefore, the most recent definition of communication is: sign-mediated and rule-governed interactions, i.e. interactions that depend on a shared repertoire of signs and rules (Witzany 2010). However, these features are lacking in abiotic interactions; no semiotic rules are necessary if water freezes to ice.

Additionally, we know that mathematical and mechanistic theories of language are less helpful in investigating natural language and real-life communication processes, because such theories cannot explain typical features of communication between living entities, which are not formal (i.e. for which no algorithm is available), such as (1) the de novo generation of coherent, sentences or sequences or (2) different and even contradictory meanings of identical syntactic sequences/sentences. This means that no natural language or code speaks, or codes, itself but requires living agents that are competent in such languages or codes (Witzany 2010).

In the biology of the twentieth century, the physiology of all manner of cells, tissues, organs and organisms was the mainstream direction of biological research and experiments. In the 1970s, an increasing use of “communication” as a metaphor also arose in biology. During the last decade of the twentieth century, interest in communication (no longer used as a metaphor) within, and between, organisms overtook that of the purely physiological understanding of organisms. This was owed to concrete communication processes designating varying contexts in real-life circumstances. Cell-to-cell communication now dominates contemporary cell biology, including knowledge of a great variety of signaling pathways, serving for both organization and coordination of production, release, uptake, interpretation and processing of context-dependent “information” (content) within and between cells. Context dependency determines the crucial fact that it is not the syntax (grammar) of a sequence of signs (information) which determines the meaning (semantics), but the context (pragmatics) in which the concrete use of the sequence occurs.

In parallel, the use of “language” as a metaphor has increased since the middle of the twentieth century with the improved knowledge of the genetic code. Most of the processes that evolve, constitute, conserve and rearrange the genetic storage medium (DNA) are terms that were originally used in linguistics. For example: nucleic acid language, genetic code, "code without commas" (F. Crick), coding, copying, translation, transcription, "genetic text" (F. Jacob), sequence homology, etc. Meanwhile, the linguistic approach has also lost its metaphorical character, and the similarity between natural languages and codes and the genetic storage medium of DNA have not only been accepted but adopted in epigenetics, comparative genomics, bioinformatics, biolinguistics, biocommunication theory and biosemiotics.

1.2.3 Communicative and Linguistic Competencies and the Primacy of Pragmatics

First, no single organism is able to communicate as an emerging property; it must be part of a community, society or swarm of organisms that share an identity and have the ability to sense whether others are part of this identity or not (self/non-self differentiation competence), even if this competence is solely shared genetically. For communication it is necessary for organisms to have assets that serve as signs, signals or symbols, such as chemical molecules, either produced directly by the organism or as secondary metabolites, or even molecules in the surroundings, which can be manipulated according to the organism's needs. In the case of animals, especially complex ones, visible and audible sign repertoires have evolved.

Second, organisms must also share the ability to use these signs in a coherent manner, which means using them in a strictly temporal and spatial context. In most cases it is not just one sign but several that are combined in a specific manner to transport messages or information. This represents a common feature of sign use in communication processes, and is termed the correct combination or syntax.

Third, organisms are part of the natural habitat in which they live, together with similar organisms of the same or related species, but usually also with an abundance of unrelated organisms. This historically developed context fully represents the natural history of swarms or communities and the way in which they have evolved certain abilities and are able to mount appropriate response behaviors to enable their survival. These competencies, which include sensing, monitoring, learning and memory, are preconditions for faster adaptation.

Finally, signaling molecules, which serve as signs, transport messages with meanings (semantics). The informational (semantic) content which is transported triggers certain response behaviors in the same, related, or even unrelated, organisms. Interestingly, the signal sequence or content does not necessarily depict a strict meaning, i.e. a function, but can vary according to different situational contexts. This means that identical signs can transport a variety of different messages according to different contextual needs. The different uses of identical signs, or sequences, enable the generation of dialects within the same species that can transport messages which are microecosphere-specific. This includes very sensitive self/non-self recognition between slightly differently adapted populations of the same species in the same ecological habitat (Witzany 2000).

Although sign-mediated interactions (i.e. communication processes) are very reliable in most cases, they do not function mechanistically in a strict sense. Syntax (combination), pragmatics (context) and semantics (content) must function in parallel to ensure and optimize the coordination and thus survival of group members.

These three levels of semiotic rules (syntax, pragmatics and semantics) do not function mechanistically but can be varied, deleted, or, in certain circumstances, and in contrast to the capabilities of machines, generated de novo. Additionally, semiotic rules do not function by themselves but need semiotic subjects, i.e. living organisms that utilize such rules. If no living organism is present, semiotic rules, signs and communication are absent. Although highly conserved semiotic rules are modifiable, environmental circumstances, such as stress, can trigger adaptive responses. In such cases, signals may transport new messages which previously did not exist, broadening the communicative competences of organisms, i.e. broadening their evolutionary capabilities.

Natural communication assembles the full range of signal-mediated interactions that are necessary in order to organize all evolutionary and developmental coordination within, and between, cells, tissues, organs and organisms. To identify biocommunication of organisms we therefore have to look at the interaction motifs in the real lifeworld context of the organisms (Witzany 2010).

1.3 In Vitro Analyses Lack Context-Dependent Behaviors of Real-Life Habitats

In vitro investigations focus on ecological setups, which do not represent the entire interactional context in which an organism is involved in vivo. The evolution and development of each organism depends on the in vivo habitat with its inter-, intra-, and transorganismic triggers of genetic reading patterns, which are absent from in vitro setups. Therefore, it is likely that isolated organisms in laboratory setups lack a variety of features which would be triggered in in vivo habitats by natural phenomena such as symbiotic and parasitic microorganisms. This may lead to limited conclusions regarding their intra- and interorganismic biocommunicative capabilities.

1.4 The Biocommunication Method Applied to Ciliates

The advantage of a methodical adaptation of communication and linguistic terminology is that it provides appropriate tools for differentiation at specific levels, which are otherwise difficult to describe in non-reductive terms with pure

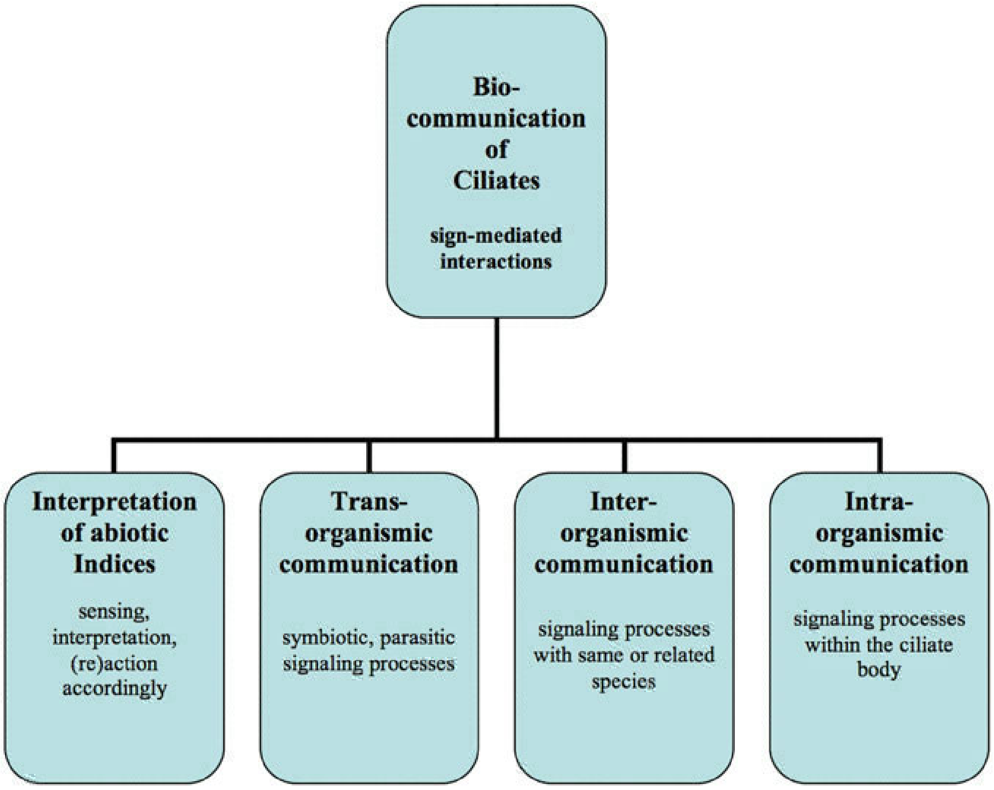

Fig. 1.1 The several levels of biocommunication of ciliates

physiology. The result of this is that language-like structures and communication processes occur at the simplest levels of nature. Language and communication are not the evolutionary inventions of humans, nor are they anthropomorphic adaptations for describing non-human entities. It is an empirical fact that all coordination and organization within and between cells, tissues, organs and organisms needs signs, i.e. molecules that serve as signals or symbols in messages, or serve as vital indicators of environmental conditions. Because no natural code can encode itself, in the way that no natural language can speak itself, these signs must be sensed and interpreted in the correct way by biological agents, i.e. there must be subjects of sign production and sign interpretation. The consequence of this is that sensing, as well as interpretation and memory storage, may fail. This can result in inappropriate behavior of, or even have fatal consequences for, cells, tissues, organs, and organisms.

The biocommunication approach can integrate empirical data into a holistic perspective of an organism and its interactional patterns at various levels (Fig. 1.1).

1.4.1 Designation of the Semiochemical Vocabulary

Investigations may start with the identification of the used semiochemicals, i.e. chemicals such as hormones, secretions, secondary metabolites that serve as signs within interactions of various motifs, such as reproduction, mating, feeding, attack or defense, etc. In this respect it is important to interconnect the semiochemicals with the concrete interactional motif (Luporini et al. 1995, 2006). Identical signals may be used in several interaction motifs with quite different meanings and this indicates the context dependence of signals.

1.4.2 Sensing, Interpretation, Memory and Coordination of Response to Abiotic Indices

The next level to be identified in this perspective is the empirical data on how ciliates sense their abiotic environment, i.e. pH level, temperature, light, moisture, gravity, etc. Such sensing is crucial for the survival of these organisms because it may decide their behavior (Weisse 2014). Sensing may lead to correct interpretation, which means the comparison with lasting experiences in this field memorized. Epigenetic markings are essential tools in this respect (Nowacki and Landweber 2009). The benefit of correct interpretation is that it may lead to faster and more appropriate reactions.

1.4.3 Intraorganismic Communication in Ciliates

The various behavioral motifs as appropriate response behavior to environmental sensing, interpretation and memory leads us to various signaling pathways within ciliate organisms (Prescott 1994, 1999; Zufall et al. 2006). This will focus on signalling within the cell nuclei and between cell nuclei and surrounding cell bodies to generate available resources for the generation of signaling of the ciliates to other organisms (Swart et al. 2014). In ciliates we see the first evolutionary separation of the germline and the soma (Chalker 2008). The special kind of signaling which is needed for that is of exceptional interest and leads us to the interactions between ciliates and persistent viruses.

1.4.3.1 The Role of Persistent Viruses

Viruses have long been accepted only as disease-causing, epidemic phenomena with lytic and therefore dangerous consequences for infected organisms. However, new research has corrected this picture. Viruses are part of the living world, in most

witzany@sbg.at

cases integrated in the cytoplasm or the nucleoplasma of cells without harming the host. Viruses are on their way to representing the best examples of symbiotic relationships, because there is no living being since the start of life that has not been colonized by them, most often in the form of multiple colonizations (Villarreal 2005).

As mentioned in recent years, the lytic consequences of viral infection are a special case if viruses are not able to develop a sessile lifestyle without harming the host. In most cases, viruses living within organisms help to ward off competing parasites from the host and become part of its evolutionary history. Persistent viruses are decisive for species diversity and host genome editing (Villarreal 2009). The persistent status is most often reached by a competing genetic parasite that counterregulates their competences, now co-opted by the host organism for regulating all replication-relevant pathways and intron excision (Villarreal 2005, 2015).

In ciliates the dual nuclei merit special attention in this respect. The genome-wide DNA rearrangements in the macronucleus are different from most other organisms. In the macronucleus the sequences are precisely excised and degraded. The excision is controlled epigenetically and during development thousands of these sequences are excised. Some thousand of deletion events occur during the formation of the somatic macronucleus which include sequences containing long terminal repeats (LTRs), which resemble transposon-like elements. Such LTRs are indicators of genetic parasites and represent repeat sequences that reached a persistent status in the ciliate genome by counteregulation of other genetic parasites. The remaining LTR sequences clearly resemble regulative functions co-adapted to the ciliate genome (Villarreal 2005).

The benefit for host organisms colonized successfully by persistent viruses that remain as co-adapted regulatory tools is the immune function against similar genetic colonizers (Villarreal 2011; Sharma et al. 2016; Seligman and Raoult 2016). This may explain why there are so few DNA viruses in ciliates. As mentioned, the presence of LTR transposons protects the replicons of the ciliates from DNA degradation and prevents the ciliate organisms from lytic infection by any DNA viruses.

Interestingly there are some indicators that both nuclei derived from large doublestranded DNA virus infections that reached a persistent lifestyle within the ciliates. In particular the silent status of the micronucleus is quite similar to latent genomes of DNA viruses. Also, the silent nucleus involved in germine transmission possesses the general ability of latent viruses to be associated with sexual reproduction. In parallel the transcriptional activation and overreplication of the macronucleus during sexual reproduction represent a virus-like behavior such as the lytic activation of a latent DNA virus characterized by DNA amplification outside cell cycle control and consequent degradation of non-amplified DNA sequences (Villarreal 2005). The ciliate's dual-nucleus identity represents a very interesting example of how infective agents reached a persistent status in host genomes and serve as competent regulatory tools for the host organism (Swart and Nowacki 2015).

1.4.4 Interorganismic Communication in Ciliates

Sign-mediated interactions between ciliates can be investigated by comparing signaling and the behavioral motifs (Schtickzelle et al. 2009; Jacob et al. 2015). In mating ciliates produce and exchange a variety of signals that are sensed and interpreted. Additionally the coordinated behavior between two ciliates depends on correct uptake of the signals by the receptors and transport to the intracellular domain of the ciliate for further information processing (Wood and Rosenbaum 2015).

1.4.5 Transorganismic Communication in Ciliates

If ciliates interact with non-ciliate organisms we can identify several signaling pathways which coordinate this interaction either in a variety of symbiotic or parasitic lifestyles (Nakajima et al. 2013; Lobban and Schefter 2014). As parasitic ciliates can cause serious damage to the aquaculture of fish it is important to identify such parasitic lifestyles to prevent further damage.

1.5 Summary

An overview of all significant levels of ciliate communication shows that identification of signal-mediated processes in signaling pathways are context-dependent both within and among ciliates as well as between ciliates and other organisms. Depending on the context, semiochemicals (molecular components) are integrated into unique signaling pathways where they are used to transport certain meanings. Such meanings are subject to change, i.e. they rely on various behavioral contexts, which differ under altered conditions. The interactional context determines the semantic relationship, i.e. its meaning and the function of the chemical components, and forms a signal-mediated communication pattern in ciliates.

After recognizing how versatile ciliate communication competences really are we can see that one main principle is followed throughout all these signaling processes: ciliates coordinate all their behavioral patterns with a core set of chemical molecules. The interactional context and the different modes of coordinating appropriate response behavior in e.g. development, growth, mating, attack, defense, feeding, etc. determine the combinations of signals that generate the appropriate meaning function, i.e. the informational content of messages. These generating processes normally function in a very conservative way but under certain circumstances may fail, or selective pressure may lead to changes that can be a driving force in ciliate evolution. Additionally it must be recognized that the persistent lifestyle of viruses is a driving force in ciliate evolution in that they are the main resource for immunity and genetic identity.

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witzany@sbg.at