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## The Contribution of Electrophysiology to Entomology

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By definition, electrophysiology "is the study of the electrical properties of biological cells and tissues". Thereby the flow of ions in biological tissues (living organisms, excised tissues / organs and cells) is assessed. This tool has been initially developed for human health (e.g., electrocardiography, electroencephalography...). In the mid 20<sup>th</sup> century, electrophysiology started to be used in entomology.

In 1960 an electronic method was designed to monitor electrically the biting and feeding behaviour of piercing-sucking phytophagous and hematophagous insects [1,2]. This technique was first used to record the probing, penetration, salivation, engorgement and withdrawal of mosquitoes in relation to their hosts [3]. It was thereafter extensively used to discern hemipteran stylet activity within plant tissues [4,5]. This technique, now universally termed electrical penetration graph (EPG), is used to monitor routinely insects feeding in order to understand the mouthpart pathway and activity into host tissues. More than 200 papers have been published, mostly on aphid and leafhopper feeding [5,6]. EPG has also been largely used to understand the mode of virus transmission by hemipteran in plant tissues [6]. It can also be used to monitor chewing insects (e.g. caterpillar [7]), and more generally to monitor the organ insertion of insects into hosts such as ovipositor insertion of parasitic wasps into the host body (Backus E., personal communication).

The peripheral nervous system in insects has been extensively examined by electrophysiology. In 1957, the German biologist Schneider invented the electroantennogram (EAG) [8], which ables to "measure the average voltage output of the insect antennae to the brain by an odour". Since then, this technique has been largely used for a comprehensive identification of the presence of receptors in insect antennae to given odours. Since [9], a blend of odours can now be screened by coupling EAG with GC (gas chromatography) and to identify the compound(s) from the blend that is/are detected by the insect. Although these techniques have been developed initially for pheromone detection, they are now largely used for semiochemicals (kairomones and allomones) detection in general. At the end of the last century, single cell recording (SCR) was developed to record the action potential in single olfactory receptor neurons [10]. By SCR, the specificity in each neuron can be revealed. Simultaneously, another tool has been also developed to record the action potential in single taste receptor neurons [11,12], allowing screening the detection of hydrosoluble compounds of single taste receptors in insects. More recently, Hiroi et al. [13] adapted this technique to enable the screening of hydrophobic substances. The patch clamp technique, which allows studying single or multiple ions channels in cells, was also applied in entomology [14]. The patch clamp technique was initially used to study the effect of insecticides on insect cell membranes and it is now used to study the neuronal function of the insect brain [15] and, in general, the mode of action of molecules in the cell physiology of insects.

The patch clamp technique allowed examining the physiology of the central nervous system in insects. Associated to that, the development of a new class of voltage-sensitive dyes [16] has offered "the possibility to optically image the functionality of neuronal circuits at both the single neuron and whole brain level". The development of calciumsensitive dyes [17] has provided another universal and sensitive method

to "study distinct information processing pathways in whole neural networks in particular when used in combination with two-photon laser scanning microscopy [18]". In the last years, these developments have been increasingly used in entomology and tremendous insights into the insect's olfactory system have been gained.

The current trend of entomology is to use routinely electrophysiology. This trend is likely to continue and combined with other studies like genomics/transcriptomics can give deeper physiological insights into the insect's chemosensory system, which is the crucial system interacting with the environment.

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