

Horst Wobig

The Propagation of Nerve Impulses

IPP 13/16
November, 2009

The Propagation of Nerve Impulses

Horst Wobig

Max-Planck-Institut für Plasmaphysik, Garching bei München, EURATOM-Ass.

Abstract

The paper presents a theory of ion acoustic waves in the axoplasm of nerve fibres. A set of non-linear wave equations can be established from first principles starting from the Vlasov equation - a collisionless Boltzmann equation - and its moment equations. There exists a density regime where collisions are negligible and the entropy is conserved. In this regime nerve pulses experience little or no attenuation. The linear theory shows a rich spectrum of ion acoustic modes depending on the composition of the axoplasm. These waves travel in the interior of the nerve fibre and not along the membrane as in the theories of Hodgkin-Huxley and Heimburg-Jackson. The non-linear theory of ion acoustic modes exhibits nonlinear waves and solitons. The relation to the Korteweg-de-Vries equation is discussed. The theory identifies the importance of organic molecules in nerve pulse propagation, however, a unique identification is not possible. The paper investigates the excitation of nerve pulses via plasma-beam interaction, which may be one explanation how mechanical signals can be converted into electric signals.

1 Introduction

The excitation and propagation of nerve pulses is one of the fundamental problems of biophysics and biochemistry. Nerve pulses are electric pulses and they propagate along nerve fibres or axons with velocities of about 100 m/s or less. A typical diameter of a nerve fibre is 1-10 μm enclosed by lipid membrane. This membrane is permeable for light ions like sodium and potassium and since the concentration of ions differs inside and outside the axon there exists an electric potential across the membrane, the resting potential. Influx and outflux of ions through voltage-controlled channels in the membrane are the basis of the Hodgkin-Huxley model (H-H-model) [1] where non-linear differential equation of the electric potential has been derived. Modern computers allow to solve this equation and by proper adjustment of the numerical parameters it is possible to reproduce many features of the experimental findings. The propagation velocity, however, is not derived from first principles, it is also adjusted to the experimental findings. In this model only sodium and potassium ions play the dominant role in creating the action potential and its propagation along the axons. Protein molecules - neither as neutrals nor as ions - do not occur in this theory.

The theory of Heimburg and Jackson [2][3] introduces thermodynamic aspects and starts from a non-linear wave equation of fourth order for sound propagation in the membrane which allows solitary wave solutions. In contrast to the H-H-model reversible processes and conservation of entropy play a significant role in this theory. Phase transitions in the membrane from a sol state to a gel state are the key for understanding the function of anesthetics. As a consequence of the density wave there exists a piezo-electric wave which makes the propagation visible to the diagnostics. It should be emphasised that in this theory as well in the H-H-theory nerve pulse propagation is localised to the region of the membrane, which is a few nm in diameter, while the interior of the nerve fibre being 1000 times larger has no effect on this mechanism.

Nerve signals are electric signals. They are electrostatic transient phenomena and not electromagnetic waves. Electrostatic fields are governed by Poisson’s equation which does not occur in the theories mentioned above. Time-dependent electric fields imply moving electric charges which play a important role in the H-H-theory, the motion of charged particles, however, is governed by the force balance either of single particles or in the frame of a fluid theory. The axon or nerve fibre is filled with water and various molecules and atoms in neutral or charged states. It is an electrolytic medium and besides ordinary sound waves ion acoustic waves carried by charged particles can be excited. In context of nerve pulse propagation there are several important issues:

- What is the mechanism of converting acoustic, optical, mechanical and thermal stimuli into electric signals?
- What is the mechanism of nerve pulse propagation in the axon?
- What are the conditions for zero or small damping of nerve pulses?
- Which ions play the dominant role in nerve pulse propagation?
- How is the electric signal transmitted across the synaptic cleft?

The present paper does not give answers to all questions, a better understanding of the pulse propagation, however, may help to clarify the other issues.

In the present model we focus the attention on the cytoplasm inside the axon. The cytoplasm consists mainly of water (about 80%), amino acids, polypeptides, lipids, about 1% sodium, chloride and potassium[13]. Also magnesium and calcium may play a role in nerve pulse physics. However the exact composition is not known in all details and may also differ among the living species. A large fraction of the cytoplasm is in dissociated state with positive and negative ions. Let be $1 \leq k \leq K$ the number of charged molecules or atoms and m_k, n_k, q_k, p_k the mass, the density, the charge and the partial pressure of the constituents. Due to the long-range Coulomb forces the charged particles are in thermodynamic equilibrium with a common temperature of $T \approx 310$ K. This is a dense and weakly ionised plasma and as in gaseous plasmas electrostatic waves can be excited. Any magnetic field effect may be neglected and the basic equation the for electric potential is Poisson’s equation and the main problem is to compute the density of the charged molecules as function of space and time. In contrast to gaseous plasmas with electrons and hydrogen ions such “axoplasma” consists of positive Na-atoms or K-atoms and charged protein molecules with large mass. For example, amino acids or polypeptides exhibit a dipole character and in aqueous solution they become positively and negatively charged and the fraction depends on the pH of the axoplasma. At the isoelectric point pI the fraction of positively and negatively charged ions is equal. Due to hydration the Na-ions or K-ions are surrounded by water molecules which raises the effective mass of these ions. The thermal velocity of charged ions depends on the temperature and the effective mass and is given in the following equation $V_k = 9.77 \times 10^3 \sqrt{T/A_k}$ [m/s] ; T in eV. A_k is the atomic weight or molecular weight. At body temperatures of $T = 310K = 0.028\text{eV}$ typical ion velocities are given in the following table:

Atomic weight	H	Na	K	Ca	Mg	Cl	300	1000	10000
Velocity [m/s]	1597	340	262	258	333	276	94	50	16

Table 1: Ion thermal velocities

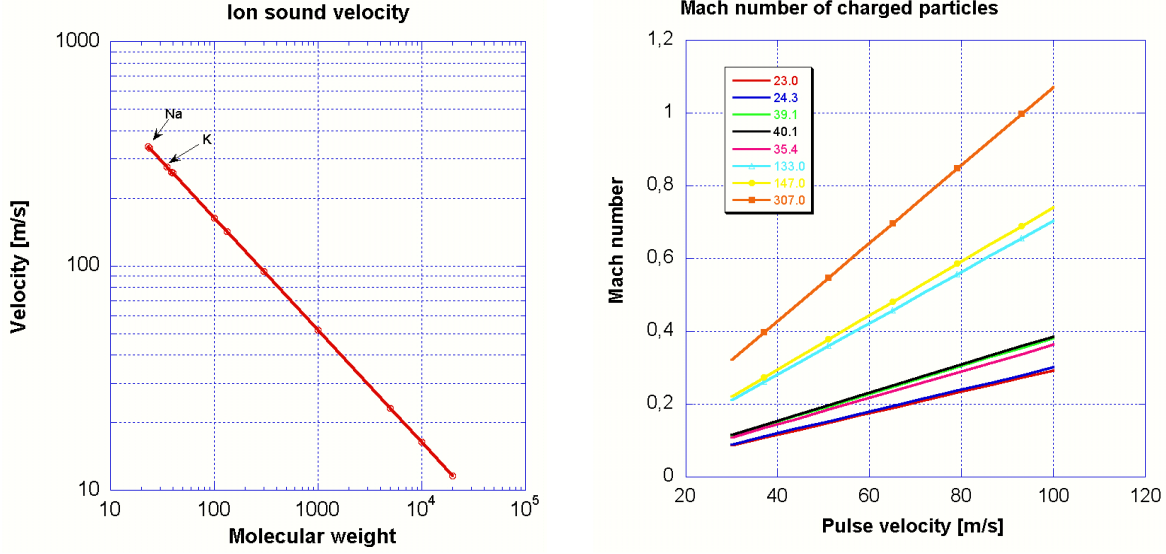


Figure 1: Left: Thermal velocity of various molecules or atoms at $T=310$ K. Right: Mach number of various molecules vs propagation velocity

Glutamic acid and aspartic acid are prominent members of the axoplasm, the thermal velocity in case of glutamic acid ($A=147$) is $V_k=134.8$ m/s and in case of aspartic acid ($A=133$) $V_k=141.1$ m/s. Below a molecular weight of $A \approx 260$ the thermal velocity according the equation above is above 100 m/s. For these particles a nerve pulse below 100 m/s runs with subsonic speed. If heavy polypeptides participate in nerve pulse propagation the speed of propagation is supersonic. Glutathione - a tripeptide with molecular weight 307 - has a thermal velocity of 93 m/s. Thus, at propagation velocities below 90 m/s also tripeptides are subsonic. However, it should be noted that this definition is made with the thermal velocity of the ions. If the sound velocity differs from the thermal velocity this will also affect the definition of subsonic and supersonic propagation. Due to hydration the effective mass of the Na and K ions can be larger than the mass of the bare ions. 6 water molecules add a weight of $A = 108$ to the weight of the ions. This implies that the thermal velocity of such a complex is of the order 130-140 m/s. As will be shown later these velocities V_k are also the phase velocities of ion acoustic modes in the cytoplasm. The sound velocity C_k depends on the equation of state $p_k = p_k(n_k, T)$. It is defined by

$$C_k^2 = \frac{dp_k}{m_k dn_k} \quad (1)$$

and for $p_k = T_k n_k$ it coincides with the thermal velocity. In fast processes like ion sound propagation, however, an adiabatic law conserving entropy is more appropriate and with $p_k \propto n_k^\gamma$ the sound velocity is

$$C_k^2 = \frac{dp_k}{m_k dn_k} = \frac{\gamma p_{k,0}}{m_k n_{k,0}} \left(\frac{n_k}{n_{k,0}} \right)^{\gamma-1} \quad (2)$$

where $p_{k,0}, n_{k,0}$ are some reference data. γ is the coefficient of adiabaticity. With $p_{k,0} = T n_{k,0}$ we get

$$C_k^2 = \gamma V_k^2 \left(\frac{n_k}{n_{k,0}} \right)^{\gamma-1} \quad (3)$$

This approximation becomes invalid in the vicinity of phase transitions which may be relevant for amino acids. Amino acids and polypeptides exhibit a dipole character which certainly has an

effect on the equation of state. Due to the electric dipoles the molecules couple and the result is a modification of the equation of state and a change of the effective mass. The effect depends on temperature similar to magnetic dipoles in ferromagnetism below and above the Curie point. If the equation of state follows the van-der-Waals law the sound velocity decreases with decreasing temperature. Approaching the region of phase transition the sound velocity $C_k^2 \propto p'(n_k) \rightarrow 0$ tends to zero. The idea of phase transition in the membrane from sol to gel as proposed by Heimburg and Jackson can be transferred to the polypeptides in the interior of the axon.

2 The axoplasma

Nerve pulses are electric pulses and unlike electromagnetic waves they need a material carrier with charged particles. The basic equations to describe the propagation of electric pulses in charged media are the momentum balance, the equation of continuity and Poisson's equation correlating the charge density to the electric potential. This raises the question whether the laws of continuum mechanics are applicable to the fluid inside the axon. The width of an axon is more than 1 μm while the size of a molecule stays below 1 nm. The difference is more than 3 orders of magnitude which justifies the model of a continuum. An alternative would be a kinetic theory. The excitation of a nerve pulse, however, will be discussed in the frame of kinetic theory.

The starting point of our analysis is a multi-species plasma with N charged ion species. In a hydrogen plasma N is 2 (electrons and protons), in a fusion plasma containing D,T and alpha-particles N is 4. In space physics dusty plasmas consists of heavy macro-particles which are negatively charged and light positive ions. In such a mixture of positively and negatively charged ions electrostatic waves can exist and propagate. We assume zero momentum source to the plasma thus avoiding a situation where plasma rotation is excited by external sources. Ion sources are described by a source term in the equation of continuity. A sudden influx of ions can be the reason for electrostatic waves similar to a falling stone which creates waves in water. Charged particles are deflected by magnetic fields. The radius of gyration of single-charged ions is

$$\rho = 1.45 \times 10^{-4} \sqrt{\frac{A_k T}{B^2}} \text{ [m]} \quad \text{B in T} \quad (4)$$

$A_k = 100$ and $T = 0.028$ eV yields $\rho = 2.4 \times 10^{-4}/B$ m. In the earth magnetic field the radius is several meters and therefor no effect on nerve pulses is expected. Even at magnetic fields of $B = 1$ Tesla the radius is much larger than the diameter of the nerve fibre and therefor no effect on the movement of charged particles inside the axon may be expected. In the following analysis any magnetic field effects will be neglected. The situation may be different in a moving coordinate system where the Lorentz force $\mathbf{v} \times \mathbf{B}$ enters the force balance of the axoplasma. If the nerve system is sensitive to this force this would be a method to detect the orientation of the earth magnetic field. This effect could be the key to understand the annual north-south migration of birds.

Charged particles interact among each other by Coulomb forces. The characteristic length is the Landau length defined by 90° deflection. The equation $\lambda_L = 4.8 \times 10^{-10} T^{-1}$ [m] (T in eV) yields $\lambda_L = 1.7 \times 10^{-8}$ [m]. The Landau length is much smaller than a typical radius of the axon but by a factor of 10-100 larger than the radius of the molecules below $r < 10^{-9}$ m. Since the cross section of Coulomb interaction is larger than the cross section of neutral molecules charged particles interact more strongly among each other than with the neutral background.

In the Debye-Hückel theory the Debye-length is defined as the screening distance of a charged particle by a cloud of particles with opposite charge. The theory yields $\lambda_D = 7.42 \times 10^3 \sqrt{T}/\sqrt{n}$ [m], which yields $\lambda_D = 1.24 \times 10^3 1/\sqrt{n}$ [m]. Taking into account the dielectric constant of water yields $\lambda_D = 1.1 \times 10^4 1/\sqrt{n}$ [m] Only if the Debye length is smaller than the

diameter of an axon we may consider the ensemble of charged particles as a plasma and apply the standard techniques of plasma physics. However, in a dense axoplasma, where the fraction of charged particles is about 1% of the number density of water the Debye length is smaller than the Landau length, which implies that the idea of binary collisions among charged particles collapses. The number of particles in the Debye volume is less than unity and the axoplasma is a strongly coupled plasma, in contrast to gaseous plasmas with larger Debye length. The density of charged particles in the axoplasma is much larger than in a gaseous plasma, with a fraction of 1% the density is $3.3 \times 10^{26} [\text{m}^{-3}]$. The following table lists the data of an axoplasma with mass ratio $\mu = m_i/m_p = 36$.

Table 2: Main parameters of the axoplasma, $\mu=36$

Temperature	0.028	[eV]
Ion density	3.0×10^{26}	$[\text{m}^{-3}]$
Plasma frequency	3.55×10^{12}	$[\text{s}^{-1}]$
Debye length	0.63×10^{-9}	[m]
Wigner-Seitz radius	1.36×10^{-9}	[m]
Landau length	1.7×10^{-8}	[m]
Coupling parameter Γ	12.5	

In contrast to dusty plasmas and colloidal suspensions the molecular weight of the heavy ions is about several hundred and they carry one positive or negative charge. A survey on the issues of strongly coupled charged colloids, polyelectrolytes and biomolecules has been given in [4].

A basic property of an ensemble of charged particles is the existence of plasma oscillations. The force balance leads to

$$\frac{d^2 \delta x}{dt^2} + \omega_p^2 \delta x = 0 \quad ; \quad \omega_p^2 = \frac{q_k^2 n_k}{\epsilon \epsilon_0 m_k} \quad (5)$$

which is the equation of an harmonic oscillator. ϵ is the relative permittivity, which is 80 in water, ω_p is the plasma frequency. The maximum displacement is limited by the energy of the oscillator. Setting the energy equal to the thermal energy defines a maximum displacement of the oscillator

$$\omega_p^2 (\delta x)^2 = V_k^2 \implies \delta x = \frac{V_k}{\omega_p} = \lambda_D \propto \sqrt{\frac{T}{n_k}} \quad (6)$$

Here the Debye length is defined without referring to the concept of shielding. Let us consider the ions of one kind consider as an array of coupled oscillators, where the interacting electric field is screened at distances larger than a Debye length. Such a case can be simulated by the Yukawa system [5], which in the literature is being widely discussed as a model of strongly coupled plasmas. A simple model of nerve pulse propagation is the one-dimensional Toda lattice[6][7] with charged particles surrounded by a Yukawa potential. Energy and momentum injected at one end of the chain travel as a soliton to the other end. However, this implies that the screening cloud with opposite charge moves together with the ions, a model which certainly does not apply when the masses of the charged particles are about equal.

The electric field in the plasma is the averaged field plus the fluctuating field of individual particles. The fluctuating field is the origin of particle collisions, the exchange of energy and momentum. Each particle species can be described by the kinetic equation

$$\frac{\partial f_k}{\partial t} + \vec{v} \cdot \nabla f_k + \frac{q_k}{m_k} \delta \vec{E} \cdot \nabla_v f_k = \text{Coll} \quad (7)$$

$f_k(\mathbf{v}, \mathbf{x}, t)$ is the distribution function of the particle species k . The electric field is computed with the aid of Poisson's equation. The collision term Coll describes the energy and momentum exchange of particles. In weakly coupled plasmas binary collisions are dominant and these can be modelled by a Boltzmann term, a Fokker-Planck term or a Landau term. If the number of particles in the Debye sphere is much larger than unity the collisions among charged particles are binary collisions, however in opposite case of a strongly coupled plasmas collective effects are dominant. The Lenard-Balescu equation [8][9] accounts for collective effects and Debye screening. As shown by Balescu [10] the collisions can be neglected in the limit of small Debye length (Debye length much smaller than Landau length). The kinetic equation without collisional term is known as the Vlasov equation. A remarkable result of the Vlasov equation is the existence of the H-theorem which is interpreted as the law of entropy conservation. If collisions can be neglected the processes are reversible and occur without energy dissipation. This agrees with remarkable fact that nerve pulses propagate without significant attenuation. If such an attenuation or blocking is detected it is a sign of a disease.

2.1 Fluid description

In order to investigate the basic features of plasma oscillations and ion acoustic waves in the axon plasma we start from the macroscopic equations which are the moment equations of the Vlasov equation. The formulation will be kept as general as possible without focussing on a specific kind of atoms or molecules. The equation of continuity of every particle species with charge q_k is

$$\frac{\partial n_k}{\partial t} + \nabla \cdot n_k \mathbf{v}_k = \frac{dn_k}{dt} + n_k \nabla \cdot \mathbf{v}_k = S_k \quad (8)$$

where n_k is the particle density and S_k the source term. The source term describes chemical processes like ionisation, dissociation and recombination. In steady state or in slow changes these processes are in equilibrium and subject to the law of mass action. However, in fast processes like ion acoustic waves and solitary waves these atomic processes are negligible. The momentum balance equations of every particle species

$$\frac{\partial}{\partial t} m_k n_k \mathbf{v}_k + \nabla \cdot (p_k \mathbf{I} + m_k n_k \mathbf{v}_k : \mathbf{v}_k) = q_k n_k \mathbf{E} \quad ; \quad k = 1, \dots, N \quad (9)$$

can also be written as follows

$$\frac{\partial \mathbf{v}_k}{\partial t} + \frac{1}{2} \nabla \mathbf{v}_k^2 - \mathbf{v}_k \times \vec{\omega}_k + S_k \mathbf{v}_k = -\frac{1}{m_k} \left(\frac{\nabla p_k}{n_k} + q_k \nabla \Phi \right) \quad (10)$$

where the vorticity $\vec{\omega}_k$ of each particle species is defined by $\vec{\omega}_k = \nabla \times \mathbf{v}_k$; $\mathbf{E} = -\nabla \Phi$ is the electric field. Here k is the index of the particle species with charge $q_k = eZ_k$. Z_k is positive for positive ions and negative for negative ions. Scalar pressure and density are linked by an equation of state $p_k = p_k(n_k, T)$. The electric potential is determined by Poisson's equation

$$-\epsilon_0 \epsilon \Delta \Phi = \sum_k q_k n_k \quad (11)$$

which after normalising to $\Phi \longrightarrow \Psi = e\Phi/kT$ becomes

$$\sum_k Z_k \frac{n_k}{N_0} = -\lambda_D^2 \Delta \Psi \quad ; \quad \lambda_D^2 = \frac{\epsilon_0 \epsilon kT}{e^2 N_0} \quad (12)$$

N_0 is a reference density. ϵ_0 is the dielectric constant of the vacuum and ϵ is the relative permittivity ($\epsilon = 80$ in water). The Debye-length λ_D is rather small. For this reason macroscopic plasmas may be treated in quasi-neutral approximation. If the dimensions of the plasma are

comparable with the Debye-length, the quasi-neutral approximation is no longer applicable. The terms $\nabla \cdot \pi_k$ are the viscous forces which will also be neglected. As will be shown later this is justified for long wave perturbations.

The pressure is described by the energy conservation law which is

$$\frac{3}{2} \frac{\partial p_k}{\partial t} + \nabla \cdot \left(\mathbf{q}_k + \frac{3}{2} p_k \mathbf{v}_k \right) + p_k \nabla \cdot \mathbf{v}_k = 0 \quad (13)$$

A complete description of the plasma would add another equation for the heat fluxes \mathbf{q}_k , however in the following we consider the two extreme cases: An isothermal plasma where the heat fluxes are large and the temperature is constant which is appropriate to describe the quiescent state. The other extreme case neglects the heat fluxes and conserves the entropy density $s_k = 0$ which in an ideal gas is defined by $s_k = \ln p_k - 5/3 \ln n_k = \ln T_k - 2/3 \ln n_k$. Eq.(13) is now

$$\frac{d}{dt} \ln \left(\frac{p_k}{n_k^{5/3}} \right) = 0 \quad (14)$$

This models applies to wave propagation.

3 Collision-less approximation

In the following we neglect all collisional effects and investigate an irrotational flow. Given an equation of state $p_k = p_k(n_k, T)$ we define the sound velocity and the functions F_k by

$$C_k^2 = \frac{dp_k}{m_k dn_k} \quad F_k(n_k) = \int \frac{dp_k}{m_k n_k} = \int C_k^2 \frac{dn_k}{n_k} + C \quad (15)$$

C is a constant of integration. This result shows that the pressure term in Euler's equation can be written as the gradient of a scalar F_k . The adiabatic equation of state yields

$$F_k = \frac{\gamma}{\gamma - 1} V_k^2 \left[\left(\frac{n_k}{n_{k,0}} \right)^{\gamma-1} - 1 \right] \quad (16)$$

In the case of an ideal gas law we get

$$F_k(n_k) = \int \frac{dp_k}{m_k n_k} = \frac{T}{m_k} \ln \frac{n_k}{n_{k,0}} \quad (17)$$

where $n_{k,0}$ is a constant reference density. This form suggests to introduce a new variable $P_k = \ln n_k/n_{k,0}$ instead of n_k .

$$F_k(n_k) = V_k^2 P_k \quad , \quad F_k = \frac{\gamma}{\gamma - 1} V_k^2 \left[(\exp(P_k))^{\gamma-1} - 1 \right] \quad (18)$$

In the limit $\gamma \rightarrow 1$ the two versions coincide. The curl of eq.(10) leads to

$$\frac{\partial \vec{\omega}_k}{\partial t} - \nabla \times (\mathbf{v}_k \times \vec{\omega}_k) = 0 \quad (19)$$

which yields the conservation of ‘‘potential vorticity’’

$$\frac{d}{dt} \left(\frac{\vec{\omega}_k \cdot \nabla G}{n_k} \right) = 0 \quad (20)$$

where G is a conserved quantity. In two-dimensional flow in the x, y -plane the vorticity has a z -component, only, and with $G = z$ the equation can be reduced to

$$\frac{d}{dt} \left(\frac{\omega_{k,z}}{n_k} \right) = 0 \quad (21)$$

Since the potential vorticity is a conserved quantity it remains zero if it is zero initially. This suggests to investigate non-linear wave propagation with zero vorticity and longitudinal oscillations only. In this case the velocity is the gradient of a scalar $\mathbf{v}_k = \nabla U_k$ and the Euler equation can be written as

$$\frac{\partial \nabla U_k}{\partial t} + \frac{1}{2} \nabla (\nabla U_k)^2 + \frac{1}{m_k} \left(\frac{\nabla p_k}{n_k} + q_k \nabla \Phi \right) = 0 \quad (22)$$

or

$$\nabla \left\{ \frac{\partial U_k}{\partial t} + \frac{1}{2} (\nabla U_k)^2 + \left(F_k(n_k) + V_k^2 Z_k \Psi \right) \right\} = 0 \quad (23)$$

and after integration the general Bernoulli equation is

$$\frac{\partial U_k}{\partial t} + \frac{1}{2} (\nabla U_k)^2 + F_k(P_k) + V_k^2 Z_k \Psi = g_k(t) \quad (24)$$

where g_k is an arbitrary function of time which is fixed by the initial conditions at the terminal of the axon $x = 0$. In order to compute a steady state solution the ideal gas law may be appropriate while in case of ion sound propagation the adiabatic compression should be taken into account. Using the variable $P_k = \ln n_k/n_{k,0}$ we write the equation of continuity as follows

$$\frac{\partial P_k}{\partial t} + \nabla U_k \cdot \nabla P_k + \Delta U_k = 0 \quad (25)$$

After another time derivative we get a non-linear wave equation

$$\frac{\partial^2 P_k}{\partial t^2} - \nabla \cdot C_k^2 \nabla P_k = \Delta V_k^2 Z_k \Psi + \Delta \frac{1}{2} (\nabla U_k)^2 - \frac{\partial}{\partial t} (\nabla U_k \cdot \nabla P_k) \quad (26)$$

The sound velocity is a non-linear function of P_k and if one neglects the right hand side every particle species has its own sound wave. Such a non-linear wave equation is the basis of the Heimburg-Jackson theory [2], however, this theory does not describe charged particles. The electric field on the right hand side couples the waves of charged particles and may lead to a solitary wave where all partners propagate with the same group velocity. Together with Poisson's equation

$$\sum_k Z_k c_k \exp(P_k) = -\lambda_D^2 \Delta \Psi \quad ; \quad c_k = \frac{n_{k,0}}{N_0} \quad (27)$$

eqs.(24) and (25) provide well-posed initial value problem. The coefficients c_k characterise the fraction of charged particles.

In order to solve Poisson's equation one needs boundary conditions. Since there are no conducting walls it is difficult to specify boundary condition for the electric potential. In a quiescent state Dirichlet conditions $\Psi = 0$ is an appropriate condition - at least in cylindrical geometry. This condition allows one to compute the resting potential. However, nerve fibres are curved and cylindrical geometry is only a local approximation. Let be $G(\mathbf{x}, \mathbf{X})$ which satisfies the boundary conditions. The solution of Poisson's equation can be written as

$$\lambda_D^2 \Psi(\mathbf{X}) = \int G(\mathbf{x}, \mathbf{X}) \sum_k Z_k c_k \exp(P_k) d^3 \mathbf{x} \quad (28)$$

A simple condition is to require zero potential in the limit $\mathbf{X} \rightarrow \infty$ which leads to

$$\lambda_D^2 \Psi(\mathbf{X}) = \sum_k \int \frac{Z_k c_k \exp(P_k)}{4\pi |\mathbf{X} - \mathbf{x}|} d^3 \mathbf{x} \quad (29)$$

Any transient variation of the charge density is visible also in the external region and not only inside the axon. Let us start from a time-independent solution where all parameters depend on the radial coordinate y and the velocity is zero. This case will be discussed in the next section. A sudden influx of positive ions - Na^+ or K^+ or a positive organic molecule - at the end of the axon disturbs the force balance in x -direction and leads to an excess of positive charge and to an x -dependent potential $\Psi(x, y)$. The resulting electric field accelerates all negative ions towards the positive charge and drives the positive charges in the opposite direction. This creates a positive excess charge in the vicinity of the initial position and by repeating this step the positive charge migrates in x -direction. It should be noted that this is a migration of a wave rather than of individual ions.

Based on this collision-less approximation we will investigate the steady-state solution, the linear and nonlinear ion acoustic waves and the solitary waves in the next sections.

4 The resting potential

A time-independent solution is governed by Poisson's equation and the balance between pressure and electric potential. Since pressure and density are correlated by an equation of state the choice of this equation is important. A simple approximation is the ideal gas law and in the following this will be the main candidate. However, it should be kept in mind that this approximation may be a good description for Na^+ , K^+ , Cl^- -ions, however, in case of charged molecules - in particular for zwitterions with dipole character - an equation of state taking into account the van-der-Waals forces may be more appropriate. In particular, if phase transitions occur as a consequence of temperature changes or by changes in the chemical composition due to drugs and anesthetics this will have consequences on the resting potential and nerve pulse propagation.

Since the velocity is zero Bernoulli's equation (24) and the ideal gas law lead to

$$P_k + Z_k \Psi = 0 \quad (30)$$

and the dimensionless Poisson's equation becomes

$$\sigma(\Psi) = \sum_k Z_k c_k \exp(-Z_k \Psi) = -\kappa \frac{d^2 \Psi}{dy^2} \quad ; \quad c_k = \frac{n_{k,0}}{N_0} \quad ; \quad \kappa = \frac{\lambda_D^2}{a^2} \quad (31)$$

where a is the radius of the axon. The constant g_k has been set to zero. Instead of the Debye length we take the radius a of the axon as the reference length. At the boundary $y = 1$ we impose the boundary condition $\Psi = 0$.

The issue of uniqueness has a simple answer: Because of $\sigma'(\Psi) = \sum_k Z_k^2 c_k \exp(-Z_k \Psi) > 0$ any solution of Poisson's equation is unique. The situation changes if some of the constituents - in particular the charged protein molecules - are subject to phase transitions, which may be initiated by changes in temperature or chemical composition. Instead of the ideal gas law we must start from $F_k(P_k, T) + Z_k \Psi = 0$ and

$$F'_k(P_k) \frac{dP_k}{d\Psi} + Z_k = 0 \quad ; \quad F'_k(P_k) = p'_k(n_k) \quad (32)$$

If $F'_k(P_k)$ is positive the resting potential is unique while in case of negative $F'_k(P_k)$ or $p'_k(n_k)$ the uniqueness is not guaranteed and multiple solutions and bifurcations can arise.

As a simple example we consider singly charged ions $Z_k = \pm 1$ and write the Poisson equation as

$$c^- \exp(\Psi) - c^+ \exp(-\Psi) = \kappa \frac{d^2 \Psi}{dy^2} \quad (33)$$

c^+ is the number of positive charges and c^- the number of negative charges. If these are equal $c^+ = c^-$ the solution is $\Psi = 0$. This equation can be solved iteratively if the Debye length is large enough. The iteration breaks down if the Debye length is small. If the Debye length is much smaller than the radius a , the right hand side may be neglected and the potential is constant over the radius except a small region at the boundary.

$$\sum_k Z_k c_k \exp(-Z_k \Psi) = 0 \implies \Psi = \Psi_0 \quad (34)$$

In case of single-charged ions we get

$$c^+ \exp(-\Psi_0) - c^- \exp(\Psi_0) = 0 \implies 2\Psi_0 = -\ln \frac{c^-}{c^+} \quad (35)$$

Because of $\sigma' > 0$ the solution is unique. If ions are small enough they can freely move through the semipermeable membrane while heavy molecules are confined inside the axon, for large and heavy molecules the membrane is impermeable. This model requires only a fixed size of the pores but no active mechanism which opens or closes the gates. Such an equilibrium across a semipermeable membrane with fixed pores is known as the Donnan equilibrium[14]. On the basis of Poisson's equation MacGillivray [15] has investigated the Donnan equilibrium which follows the same line as the present analysis. In this respect our model differs from the Hodgkin-Huxley model, where the ion channels are closed or open depending on the radial electric field.

Following this rationale we write the charge density as $c^+ \rightarrow C^+ + c^+$, $c^- \rightarrow C^- + c^-$ where now c^+, c^- are the light ions Na, K, CL etc and C^+, C^- denotes positive and negative amino acids and polypeptides. The potential is negative except in a small boundary region of the order Debye length where the transition to $\Psi = 0$ occurs. If there are more positive charges than negative ones the potential has the opposite sign.

Since the membrane is permeable to the light ions we compute the potential in the external region by inserting the external charges into Poisson's equation. Overall charge neutrality requires a positive excess charge in the external region. The same arguments as above can be applied to this region and the external voltage drop is

$$2\Psi_1 = \ln \frac{c^+}{c^-} \quad (36)$$

The total voltage drop - or resting potential - is

$$2(\Psi_0 - \Psi_1) = -\ln \frac{(C^- + c^-)c^+}{(C^+ + c^+)c^-} \quad (37)$$

It should be noted that the sign of the potential is a matter convention. If we define the electric field by $\mathbf{E} = \nabla\Phi$ the potential changes sign in all results.

The coefficients in eq.(37) are not independent. Inside the boundary region of the order Debye length the Poisson equation provides a smooth transition between the external and the internal potential. In this small boundary layer the charge density is approximated by a constant

$$C = \kappa^2 \frac{d^2\Psi}{dy^2} \quad (38)$$

which provides a parabolic solution. The free parameter in this solution are determined by the condition of continuity of potential and electric field at $y = 1$ and at $y = 1 \pm \kappa$. The results of this procedure is

$$\Psi = \Psi_0 - \frac{\Psi_0}{\kappa^2} (y - 1 + \kappa)^2 \quad (39)$$

in the internal region and

$$\Psi = \Psi_1 - \frac{\Psi_1}{\kappa^2} (y - 1 - \kappa)^2 \quad (40)$$

in the external region. The continuity at the membrane $y = 1$ demands

$$\frac{(C^- + c^-) c^-}{(C^+ + c^+) c^+} = 1 \quad (41)$$

which demonstrates that the coefficients are not independent. It can easily be shown that in case of $C^- = C^+$ the result is $c^- = c^+$. positive and negative charges are equal and the resting potential is zero. In the limit $c^- \ll C^-$ and $c^+ \ll C^+$ we get the result

$$\frac{C^- c^-}{C^+ c^+} = 1 \Rightarrow (\Psi_0 - \Psi_1) = -\ln \frac{C^-}{C^+} = -\ln \frac{c^-}{c^+} \quad (42)$$

This results show that only those ions which cannot tunnel through the membrane are responsible for the resting potential. The magnitude of the resting potential depends on the excess of negative or positive charges. Polypeptides in aqueous solution exist in both charged states and at a specific pH - the isoelectric point - the charge concentrations are equal and the resting potential is zero. Since the ratio between C^- and C^+ depends on the pH of the axoplasm the resting potential depends on the pH, too. However, this conclusion can be drawn if the cytoplasm only consists of one species of heavy molecules. The analysis so far neglected

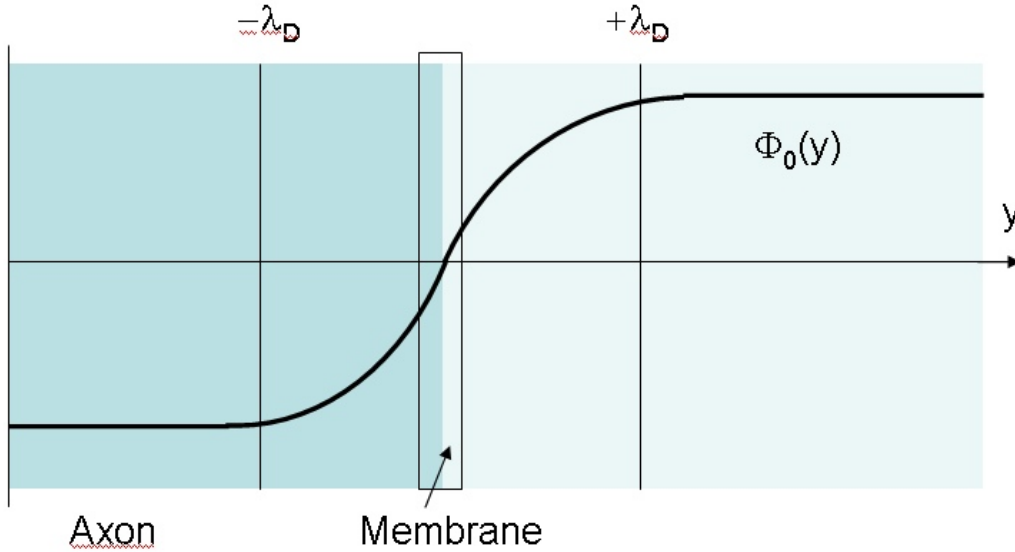


Figure 2: Resting potential

ions with multiple charges. The general form of the condition (34) leads to polynomial in $X = \exp(-\Psi)$ which in case of additional double-charged ions is

$$c_1 X^{-1} - c_2 X + 2c_3 X^{-2} - 2c_4 X^2 = 0 \Rightarrow c_1 X^1 - c_2 X^3 + 2c_3 - 2c_4 X^4 = 0 \quad (43)$$

where c_3, c_4 are the fraction of double-charged ions. This equation has only one positive solution, there is uniqueness of the resting potential.

These results are found by separating the boundary layer of the order Debye length from the bulk of the quasi-neutral plasma. In the following we shall discuss the exact procedure without

referring to the smallness of the Debye length. Poisson's equation is three-dimensional and in cylindrical geometry it reduces to the one dimensional equation.

$$\sigma(\Psi) = \sum_k Z_k c_k \exp(-Z_k \Psi) = -\kappa \frac{1}{r} \frac{d}{dr} r \frac{d\Psi}{dr} \quad ; \quad \kappa = \frac{\lambda_D^2}{a^2} \quad (44)$$

As discussed above the coefficients c_k inside the axon ($r < 1$) are different from those in the external region $r > 1$ which is caused by the semipermeability of the membrane. Let us simplify this equation to

$$\sigma(\Psi) = \sum_k Z_k c_k \exp(-Z_k \Psi) = -\kappa \frac{d^2 \Psi}{dy^2} \quad ; \quad \kappa = \frac{\lambda_D^2}{a^2} \quad (45)$$

which can be integrated once leading to the "conservation law"

$$\frac{\kappa}{2} \left(\frac{d\Psi}{dy} \right)^2 - \sum_k c_k \exp(-Z_k \Psi) = E \quad (46)$$

E is a constant which is related to the boundary conditions. These are $\Psi = 0$, $y = \pm 1$ and $\Psi' = 0$ $y = 0$. The differential equation is invariant against the transformation $y \rightarrow -y$, which implies that any solution is symmetric $\Psi(y) = \Psi(-y)$. The first order differential equation for $\Psi(y)$ is

$$\frac{d\Psi}{dy} = \pm \sqrt{\frac{2}{\kappa} \sqrt{E - W(\Psi)}} \quad ; \quad W(\Psi) = - \sum_k c_k \exp(-Z_k \Psi) \quad (47)$$

The potential $W(\Psi)$ is negative and has a maximum at $\Psi = \Psi_0$. Depending on the sign of Ψ_0 the solution Ψ is either positive or negative. Let us consider a negative solution with a minimum at $0 > \Psi_m > \Psi_0$. The differential equation yields

$$\sqrt{\frac{\kappa}{2}} \int_{\Psi_m}^0 \frac{d\Psi}{\sqrt{W(\Psi_m) - W(\Psi)}} = 1 \quad (48)$$

which determines the lowest potential Ψ_m . In the opposite case of positive Ψ_0 the solution is bounded by Ψ_0 . In summary we find that in the case of small Debye length the excess charge is localised to the boundary and constant potential in the main part of the axon. If the Debye length is comparable with the radius of the axon ($\kappa \approx 1$) the resting potential varies over the radius rather smoothly. These results are independent of the nature of the ions, only the charge and the relative abundancies c_k are important.

5 Ion acoustic waves

Wave-like phenomena usually are studied by linearisation around a steady state solution. The steady state solution depends on the radial coordinate y while the waves travel in z -direction. In the following we focus on a case with small Debye length where the electric potential Φ_0 is nearly constant and the steady state solution is homogeneous over the radius. In a quiescent and homogeneous state the solutions are: $n_k = n_{k,0}$, $\mathbf{v}_k = 0$, $\Phi = C$. Since the electric field is zero, the quiescent state is quasi-neutral $\sum_k q_k n_{k,0} = 0$. Any finite electric potential requires deviation from quasi-neutrality and the density is $n_k = n_{k,0} + \delta n_k$ or $P_k = P_{k,0} + \delta P_k$. The linearised version of eq.(26) without source term and Poisson's equation are

$$\frac{\partial^2 \delta P_k}{\partial t^2} - C_k^2 \Delta \delta P_k = \nabla \cdot V_k^2 Z_k \nabla \delta \Psi \quad ; \quad -\lambda_D^2 \Delta \delta \Psi = \sum_k Z_k c_k \exp(P_{k,0}) \delta P_k \quad (49)$$

Without the electric field we would get a set of uncoupled ion sound waves, but the electric potential couples the various ion acoustic waves. Because of the smallness of the Debye length the coupling is strong. In contrast to the Hodgkin-Huxley model the ion sound waves are longitudinal waves and not transverse waves. The equilibrium condition $P_{k,0} + Z_k \Psi_0(y) = 0$ shows that the coefficients in this equations are not constant. This refers mainly to the Debye sheath at the boundary while the inhomogeneity can be neglected in the main body of the axon.

5.1 Plane wave geometry

Based on the approximation of a homogeneous equilibrium Fourier ansatz in all spatial variables and time leads to an algebraic system

$$\omega^2 \delta P_k - K^2 C_k^2 \delta P_k = K^2 V_k^2 Z_k \delta \Psi \quad ; \quad \lambda_D^2 K^2 \delta \Psi = \sum_k Z_k c_k \exp(P_{k,0}) \delta P_k \quad (50)$$

$\mathbf{K} = k_x, k_y, k_z$ is the wave vector. In a model of a plane wave the wave vector is arbitrary. However, imposing the boundary condition $\delta \Psi = 0$ on the boundary of the axon makes k_x and k_y multiples of π/a , where a is the radius of the axon. This result fits to an axon with rectangular cross section, in cylindrical geometry we would get Bessel functions instead of sin and cos-function. The boundary condition $\delta \Psi = 0$ confines the transmission of ion acoustic waves to the interior of the axon, the external region is not involved. Eliminating the functions δP_k yields

$$K^2 \lambda_D^2 \delta \Psi = \sum_k \frac{1}{(\omega^2 - K^2 C_k^2)} V_k^2 Z_k^2 K^2 \delta \Psi \quad (51)$$

and the dispersion relation

$$1 = \sum_k \frac{\omega_{p,k}^2}{\omega^2 - K^2 C_k^2} \quad ; \quad \omega_{p,k}^2 = \frac{V_k^2 Z_k^2 c_k \exp(P_{k,0})}{\lambda_D^2} = \frac{q_k^2 n_{k,0} \exp(P_{k,0})}{\epsilon \epsilon_0 m_k} \quad (52)$$

This system describes acoustic modes coupled to plasma oscillations. The dispersion relation is a polynomial in ω^2 which has only positive roots with $\omega^2 > 0$. As an example we consider a two-component plasma where the dispersion relation is a quadratic polynomial in ω^2 .

$$1 = \frac{\omega_{p,1}^2}{\omega^2 - K^2 C_1^2} + \frac{\omega_{p,2}^2}{\omega^2 - K^2 C_2^2} \quad (53)$$

or

$$(\omega^2 - K^2 C_1^2)(\omega^2 - K^2 C_2^2) = \omega_{p,1}^2 (\omega^2 - K^2 C_2^2) + \omega_{p,2}^2 (\omega^2 - K^2 C_1^2) \quad (54)$$

There are two solutions

$$\omega^2 = \frac{a}{2} \pm \sqrt{\frac{a^2}{4} - c} \quad (55)$$

$$a = K^2 (C_1^2 + C_2^2) + (\omega_{p,1}^2 + \omega_{p,2}^2), \quad c = K^4 C_1^2 C_2^2 + K^2 (\omega_{p,1}^2 C_2^2 + \omega_{p,2}^2 C_1^2) \quad (56)$$

In the general case with N particle species the dispersion relation is a polynomial of the order N in ω^2 . There are N branches $\omega^2 = \omega^2(K^2)$. We assume equal temperature of all particles and consider a plasma with an ion species being much heavier than the other particles ($m_i \gg m_k, \forall k \rightarrow C_i \ll C_k$). This corresponds to the case of negatively charged protein molecules. In the neighbourhood of $\omega^2 \approx K^2 C_i^2$ we may start from a dispersion relation

$$1 = \frac{\omega_{p,i}^2}{\omega^2 - K^2 C_i^2} - \sum_k \frac{\omega_{p,k}^2}{K^2 C_k^2} \quad (57)$$

We define an effective Debye length by

$$\frac{1}{\lambda_D^2} = \sum_k \frac{\omega_{p,k}^2}{C_k^2} \quad (58)$$

and write the solution of the dispersion relation as follows

$$\omega^2 = K^2 C_i^2 + \frac{K^2 \lambda_D^2 \omega_{p,i}^2}{1 + K^2 \lambda_D^2} \quad (59)$$

In case of long wave lengths ($K^2 \lambda_D^2 \ll 1$) we get acoustic modes with phase velocity V_i . For molecules with molecular weight above 300 the phase velocity of long-wave acoustic modes is below 100 [m/s]. Another interesting case is that of two heavy ion species, while all other ions have small masses. The dispersion relation is

$$1 = \frac{\omega_{p,1}^2}{\omega^2 - K^2 C_1^2} + \frac{\omega_{p,2}^2}{\omega^2 - K^2 C_2^2} - \sum_k \frac{\omega_{p,k}^2}{K^2 C_k^2} \quad (60)$$

The sum runs over all particle species except $k = 1, 2$. The dispersion relation has two solutions, a slow wave and a fast wave. The solutions of the dispersion relation

$$\left(\omega^2 - K^2 C_1^2\right) \left(\omega^2 - K^2 C_2^2\right) = \frac{K^2 \lambda_D^2 \omega_{p,1}^2}{1 + K^2 \lambda_D^2} \left(\omega^2 - K^2 C_2^2\right) + \frac{K^2 \lambda_D^2 \omega_{p,2}^2}{1 + K^2 \lambda_D^2} \left(\omega^2 - K^2 C_1^2\right) \quad (61)$$

is

$$\omega^2 = \frac{a}{2} \pm \sqrt{\frac{a^2}{4} - c} \quad (62)$$

$$a = K^2(C_1^2 + C_2^2) + \frac{K^2 \lambda_D^2 (\omega_{p,1}^2 + \omega_{p,2}^2)}{1 + K^2 \lambda_D^2}, \quad c = K^4 C_1^2 C_2^2 + \frac{K^2 \lambda_D^2 (\omega_{p,1}^2 K^2 C_2^2 + \omega_{p,2}^2 K^2 C_1^2)}{1 + K^2 \lambda_D^2} \quad (63)$$

This dispersion relation is applicable to zwitter ions with positive and negative charges. Neglecting the mass difference between the two states leads to $C_1 = C_2$ and the dispersion relation is reduced to

$$1 = \frac{\omega_{p,1}^2 + \omega_{p,2}^2}{\omega^2 - K^2 C_1^2} - \sum_k \frac{\omega_{p,k}^2}{K^2 C_k^2} \quad (64)$$

which has the same solution as displayed in eq.(59) except that the plasma frequency is modified

$$\omega^2 = K^2 C_1^2 + \frac{K^2 \lambda_D^2 (\omega_{p,1}^2 + \omega_{p,2}^2)}{1 + K^2 \lambda_D^2} \quad (65)$$

In this equation only the sum of zwitter ions occurs, the result is independent of the ratio between positive and negative charges. For this reason the pH has little or no effect on the dispersion relation.

In plane wave geometry the wave vector is arbitrary, in a finite wave guide geometry, however, there is a lower limit of k_x and k_y as discussed above. This implies that the phase velocity in z -direction may become large for small k_z .

$$\left(\frac{\omega}{k_z}\right)^2 = \frac{k_z^2 + k_x^2 + k_y^2}{k_z^2} C_1^2 + \frac{k_z^2 + k_x^2 + k_y^2}{k_z^2} \frac{\lambda_D^2 (\omega_{p,1}^2 + \omega_{p,2}^2)}{1 + K^2 \lambda_D^2} \quad (66)$$

Information is transmitted by the group velocity which in the long-wave-length limit $K \lambda_D \ll 1$ is

$$v_g = \frac{d\omega}{dk_z} = \frac{k_z}{\sqrt{k_x^2 + k_y^2 + k_z^2}} C_1 \quad (67)$$

The group velocity is smaller than the sound velocity C_1 . This implies that information by nerve pulses cannot be transferred faster than with ion sound velocity.

5.2 Circular approximation

In the rectangular model described previously the solution consists of trigonometric functions. In a cylindrical model Bessel functions occur. The Laplace operator in cylinder geometry

$$\Delta = \frac{1}{r} \frac{d}{dr} r \frac{d}{dr} + \frac{d^2}{dz^2} \quad (68)$$

satisfies the equation

$$\Delta J_0(\alpha r) \exp(ik_z z) = -(k_z^2 + \alpha^2) J_0(\alpha r) \exp(ik_z z) \quad (69)$$

where $J_0(\alpha r)$ is the lowest order Bessel function. In this ansatz the angular dependence is zero. The corresponding mode in wave guide theory of radar technique is the E_{00} -mode. Imposing the condition of zero potential on the boundary leads to $J_0(\alpha a) = 0$. The further procedure follows the same line as above, the wave vector K^2 is replaced by $k_z^2 + \alpha^2$.

5.3 Excitation of plasma oscillations

The dispersion relation derived above has no unstable roots and the question remains how these waves are excited. The H-H-model assumes that a sudden influx of sodium ions starts the action potential, however the mechanism of propagation remains unexplained. Following this line we assume that due to a pressure rise in the dendrites at the axon terminal a jet of charged particles is injected. The nature of this jet need not to be specified, the following computations are valid for any kind of ions. In order to model the resting potential we assumed that the membrane of the axon is permeable for low mass ions like sodium, potassium etc. This assumption may be also valid for the boundary between dendrites and the cell body, the soma. A difference in pressure between dendrites and soma leads to an influx of ions into the soma. Such a pressure difference may occur as a result of a mechanical impact or a sudden rise of temperature in the dendrites. The injected jet of charged particles triggers an oscillation of the cytoplasm and these oscillations couple to ion acoustic modes travelling along the axon. The mechanical signal is converted into an electric signal, which travels in the axon like microwaves in a wave guide or light in glass fibres. However, we do not exclude that at high external pressure also ion channels of amino acids will be open. The H-H-model does not explain the nature of ion channels and the control by the radial voltage, in the present model a pressure difference is sufficient to open a channel.

In plasma physics beam-driven instabilities are a well-known phenomenon and the question arises whether this mechanism may be responsible for nerve pulse generation. A sudden influx of ions into the cell body disturbs the distribution function of ions and leads to a deviation from a Maxwellian. Such a unidirectional ion beam creates a ‘‘bump-in-tail’’ instability which usually is described in the frame of kinetic theory with the aid of the Vlasov equation. The macroscopic picture simulates this case with a lowest order velocity $v_{0,k} = \nabla U_{k,0}$. In the terminal region the influx of fast ions creates a finite averaged velocity of the ions in this region. The instability arising in such case has been widely investigated in the theory of weakly coupled plasmas.

The macroscopic picture does not describe all details of instabilities created by a unidirectional beam. A microscopic model starting from the Vlasov equation - or collisionless Fokker-Planck equation - may be more appropriate. The linearised Vlasov equation of a particle species is

$$\frac{\partial f_k}{\partial t} + \vec{v} \cdot \nabla f_k + \frac{q_k}{m_k} \delta \vec{E} \cdot \nabla_v F_k = 0 \quad (70)$$

where $F_k(\vec{v})$ is the lowest order distribution function and f_k the perturbation caused by the electric field $\delta \vec{E} = -\nabla \delta \Phi$. In a quiescent plasma the lowest order distribution function is a

Maxwellian. The injected beam distorts the Maxwellian and creates a second maximum in the distribution function if the beam is strong enough. A model of such a distribution is

$$F_k(u) \propto \left[\exp\left(-\frac{u^2}{V_k^2}\right) + b \exp\left(-\frac{(u-u_0)^2}{u_k^2}\right) \right] \quad (71)$$

$F_k(u)$ is the reduced distribution function, integration over two velocity space variables has reduced the three-dimensional distribution function to an one-dimensional one. u is the velocity variable in direction of the beam. V_k is the thermal velocity of particles k and u_0 is the mean velocity of the beam. The factor u_k characterises the width or “temperature” of the beam ($u_k < V_k$). If the factor b is large enough the distribution function has a second maximum and the conditions for a beam-driven instability can be met. If the beam is absent a homogeneous Maxwellian plasma is stable, any perturbation will be damped by the mechanism of Landau damping[16]. The following procedure is standard and need not to be described in detail[17]. Fourier and Laplace transform convert the differential equation into an algebraic equation and by inverse Laplace transform we obtain the density perturbation as a linear function of the perturbed electric potential. Inserting this into Poisson’s equation yields the desired dispersion relation. The result is

$$1 = \sum_k \frac{\omega_{p,k}^2}{K^2} \int_c \frac{F'_k(u) du}{u + s/iK} \quad (72)$$

s is a complex variable and the integration in the complex u -plane is computed on the Landau-contour c . The shape of $F'_k(u)$ is the decisive factor. It can be shown that a “single-humped” distribution function has no solution with $Re(s) > 0$, however, if two maxima of F_k exist, such a positive root exists if the second maximum is strong enough. It suffices if one particle species has such a non-Maxwellian distribution as described in eq.(71). The energy of the beam particles is coupled to the electrostatic wave and via Landau damping this energy is transferred to the Maxwellian background plasma. If the energy source in the beam is strong enough the wave can be maintained. In macroscopic theory a threshold of the instability does not occur since Landau damping is a mechanism of kinetic theory. The Landau damping is strong for short wave lengths of the order Debye length and less effective for long wave lengths.

A strongly coupled dusty plasmas has been investigated by Kalman and Rosenberg [11] where it has been shown that a uni-directional beam leads to plasma oscillations as in the case of weakly coupled plasmas.

6 Solitary waves

As shown in the previous section there exists a large spectrum of ion acoustic modes in the axoplasma. If several modes are excited the non-linear interaction leads to energy exchange, some modes may grow on the expence of other modes. The extreme case is when all energy is accumulated in one mode, in a soliton. A soliton is a voltage pulse which does no change its shape when moving along the axon in z -direction. The linear approximation as discussed in the previous sections is only valid if the amplitude of the waves is small. With an increase of the amplitude mode coupling may lead to the formation of solitary waves and non-linear waves. In such a wave all quantities are functions of $u = z - Vt$, where V is the propagation velocity of the solitary wave in z -direction. V is a free parameter which will be determined later in this section. The Mach number is the normalised V is of the soliton. In the co-moving frame Bernoulli’s equation (24) is

$$-V \frac{\partial U_k}{\partial z} + \frac{1}{2} (\nabla U_k)^2 + F_k + V_k^2 Z_k \Psi = g_k \quad (73)$$

and the modified equation of continuity

$$-V \frac{\partial P_k}{\partial z} + \nabla U_k \cdot \nabla P_k + \Delta U_k = 0 \quad (74)$$

which can also be written as

$$-V \exp P_k \frac{\partial P_k}{\partial z} + \nabla \cdot \exp P_k \nabla U_k = 0 \quad (75)$$

For any given P_k the last equation is a linear elliptic differential equation for U_k . In order to solve the equation boundary conditions are needed. These are either Dirichlet conditions $U_k = 0$ or Neumann conditions $dU_k/dy = 0$. The first condition implies that the tangential flow on the boundary (the membrane) is zero but the particles can freely move across the membrane. This applies to Na-ions or K-ions. However, a flow across the membrane through small pores will certainly be subjected to frictional losses which attenuate the wave propagation. Furthermore, a flow across the membrane incorporates the external region into the propagation mechanism, and, since the external region is interrupted by cell membranes any motion of charged atoms or molecules in this region will be strongly damped. The Neumann condition describes zero flow across the membrane which confines the propagation mechanism to the interior of the axon. This condition certainly applies to heavy polypeptides. In this case nerve pulse propagation has a strong similarity to propagation of light in a glass fibre, however, unlike glass fibres the electric signal of nerve pulses is measurable also outside the axon. There are no boundary conditions for the electric potential on the boundary of the axon. Together with Poisson's equation

$$-\lambda_D^2 \Delta \Psi = \sum_k Z_k c_k \exp P_k \quad (76)$$

we get a closed system of non-linear equations for Ψ, P_k, U_k .

6.1 One-dimensional soliton

In one-dimensional approximation all terms depend only on the $u = z - Vt$ -coordinate. This implies that the velocity in y -direction is zero and no flow across the membrane occurs. It should be noted, however, that this implies a finite tangential flow on the membrane. A more natural boundary condition would be to set all components of the velocity equal to zero which requires a twodimensional treatment.

In this one-dimensional approximation the momentum balance can be integrated once leading to

$$\frac{1}{2} \left(\frac{dU_k}{du} - V \right)^2 - \frac{1}{2} V^2 + F_k(P_k) + V_k^2 Z_k \Psi = g_k \quad (77)$$

The continuity equation is

$$\frac{d}{du} \left[\left(\frac{dU_k}{du} - V \right) \exp P_k \right] = 0 \quad (78)$$

which yields

$$\frac{dU_k}{du} - V = -V \exp(P_{k,0} - P_k) \quad ; \quad P_{k,0} + V_k^2 Z_k \Psi_0 \quad (79)$$

and together with eq.(77)

$$\frac{1}{2} V^2 [\exp(2P_{k,0} - 2P_k) - 1] + F_k(P_k) + V_k^2 Z_k \Psi = g_k \quad (80)$$

In isothermal approximation this

$$\frac{M_k^2}{2} (\exp(2P_{k,0} - 2P_k) - 1) + P_k + Z_k \Psi = g_k \quad ; \quad M_k^2 = \frac{V^2}{V_k^2} \quad (81)$$

and adiabatic approximation

$$\frac{M_k^2}{2}(\exp(2P_{k,0} - 2P_k) - 1) + \frac{\gamma}{\gamma - 1} \exp((\gamma - 1)P_k) + Z_k \Psi = g_k \quad ; \quad M_k^2 = \frac{V^2}{V_k^2} \quad (82)$$

M_k is the Mach number of the particle species k . As shown above the function $F_k(P_k)$ depends on the equation of state $p_k(n_k, T)$, which in case of heavy polypeptide molecules may differ from the ideal gas law. A van-der-Waals type of equation of state has a region of small sound velocity if one approaches the regime of phase transition. Approximating the sound velocity in eq.(??) by a constant yields

$$F_k(P_k) \approx \frac{C_k^2}{V_k^2} P_k \quad (83)$$

Inserting the solution $P_k = P_k(\Psi)$ into Poisson's equation provides us with a non-linear equation for Ψ .

$$\sigma(\delta P_i) = \sum_k Z_k c_k \exp(-Z_k \Psi_0) [\exp(\delta P_k) - 1] = -\lambda_D^2 \frac{d^2 \delta \Psi}{du^2} \quad (84)$$

and

$$\frac{M_k^2}{2}(\exp(-2\delta P_k) - 1) + \delta P_k = g_k - Z_k \delta \Psi \quad (85)$$

with $\delta \Psi = \Psi - \Psi_0$ and $\delta P_k = P_k - P_{k,0}$. In adiabatic approximation this equation is

$$\frac{M_k^2}{2}(\exp(-2\delta P_k) - 1) + \frac{1}{V_k^2} F_k(P_{k,0} + \delta P_k) + Z_k \Psi_0 = g_k - Z_k \delta \Psi \quad (86)$$

The function on the left side of eq.(85) has two zeros and one extremum. The zeros are $\delta P_k = Y_k = 0$ and $\delta P_k = Y_k \neq 0$. The position of the extremum is $\delta P_k = Y_m = \ln M_k$ and the value of the $\delta \Psi$ -function is

$$g_k - \ln M_k + \frac{1}{2}(1 - M_k^2) = Z_k \delta \Psi(Y_m) \geq g_k \quad (87)$$

$M_k = 1$ is the extremum of the left hand side. The inverse function $\delta P_k(\delta \Psi)$ has two branches, a lower branch $\delta P_k^l(\delta \Psi) : \delta P_k < Y_m$ and an upper branch $\delta P_k^u(\delta \Psi) : \delta P_k > Y_m$. By inserting the functions $\delta P_k(\delta \Psi)$ the charge density becomes a function of $\delta \Psi$. Integrating Poisson's equation once yields

$$\frac{\lambda_D^2}{2} \left(\frac{d\delta \Psi}{du} \right)^2 + W(\delta \Psi) = E \quad ; \quad \frac{dW}{d\delta \Psi} = \sigma(\delta \Psi) \quad (88)$$

The function $W(\Psi)$ is known as the Sagdeev potential. The mechanical analogue of this equation is a particle with the potential energy $W(\delta \Psi)$. If the potential has a local minimum which is negative, the expansion around this minimum yields a parabola and the solutions are periodic functions of $u = z - Vt$. All charged particles are coupled and form a single non-linear wave. The soliton is the aperiodic limit of these waves.

In the extreme case of low Mach number the approximation to δP_k is $\delta P_k = g_k - Z_k \delta \Psi$, while the other extreme of a large Mach number yields

$$\exp(\delta P_k) = \left(1 - \frac{2}{M_k^2} (g_k - Z_k \delta \Psi) \right)^{-0.5} \quad (89)$$

This approximation fits to heavy particle with a thermal velocity much below the propagation velocity V while the first approximation fits to light particles with large thermal velocity. This approximation often is applied to dusty plasmas in space physics.

6.2 Small amplitude expansion

As another approximation we consider the small amplitude expansion and set all $g_k = 0$ for the sake of simplicity. In the neighbourhood of $\delta\Psi = 0$ the expansion with respect of $\delta\Psi$ is

$$\sigma(\delta\Psi) = B(\delta\Psi) + C(\delta\Psi)^2 + \dots \quad (90)$$

The constant term is zero. The Sagdeev potential is

$$W(\delta\Psi) = \frac{1}{2}B(\delta\Psi)^2 + \frac{1}{3}C(\delta\Psi)^3 \quad (91)$$

The conditions for soliton solutions are $E = 0, B < 0, C > 0$ and the solution is

$$\delta\Psi = \frac{-3B}{2C} \frac{1}{\cosh^2(uB/2)} \quad (92)$$

$2/B$ defines the width of the soliton. In order to find the coefficients B, C we expand δP_k around the zero point Y_k

$$\delta P_k = Y_k + A_k Z_k \delta\Psi + B_k Z_k^2 (\delta\Psi)^2 + \dots \quad (93)$$

and

$$\exp(\delta P_k) = \exp(Y_k) + \exp(Y_k) A_k Z_k \delta\Psi + \exp(Y_k) \frac{1}{2} (A_k^2 + 2B_k) Z_k^2 (\delta\Psi)^2 + \dots \quad (94)$$

where the coefficients A_k, B_k differ between the lower and upper branch. These are

$$A_k = \frac{1}{M_k^2 \exp(-2Y_k) - 1} \quad ; \quad B_k = \frac{M_k^2 \exp(-2Y_k)}{(M_k^2 \exp(-2Y_k) - 1)^3} \quad (95)$$

Case 1: The expansion at $Y_k = 0$ leads to

$$A_k = \frac{1}{M_k^2 - 1} \quad ; \quad B_k = \frac{M_k^2}{(M_k^2 - 1)^3} \quad (96)$$

and

$$\exp(\delta P_k) - 1 = \frac{Z_k}{M_k^2 - 1} \delta\Psi + \frac{1}{2} \frac{3M_k^2 - 1}{(M_k^2 - 1)^3} Z_k^2 (\delta\Psi)^2 + \dots \quad (97)$$

For the sake of abbreviation we define

$$D_k = Z_k c_k \exp(-Z_k \Psi_0) \quad ; \quad \sum_k D_k = 0 \quad (98)$$

and write charge density as

$$\sigma = \sum_k D_k \frac{Z_k}{M_k^2 - 1} \delta\Psi + \sum_k D_k \frac{1}{2} \frac{3M_k^2 - 1}{(M_k^2 - 1)^3} Z_k^2 (\delta\Psi)^2 \quad (99)$$

and the coefficients in the Sagdeev potential

$$B = \sum_k D_k \frac{Z_k}{M_k^2 - 1} \quad C = \sum_k D_k \frac{1}{2} \frac{3M_k^2 - 1}{(M_k^2 - 1)^3} Z_k^2 \quad (100)$$

As an example we consider two ion species with opposite charge $D_+ + D_- = 0$ and M_+, M_- and write the coefficients

$$B = D_+ \left(\frac{1}{M_+^2 - 1} + \frac{1}{M_-^2 - 1} \right) \quad ; \quad C = D_+ \frac{1}{2} \left(\frac{3M_+^2 - 1}{(M_+^2 - 1)^3} - \frac{3M_-^2 - 1}{(M_-^2 - 1)^3} \right) \quad (101)$$

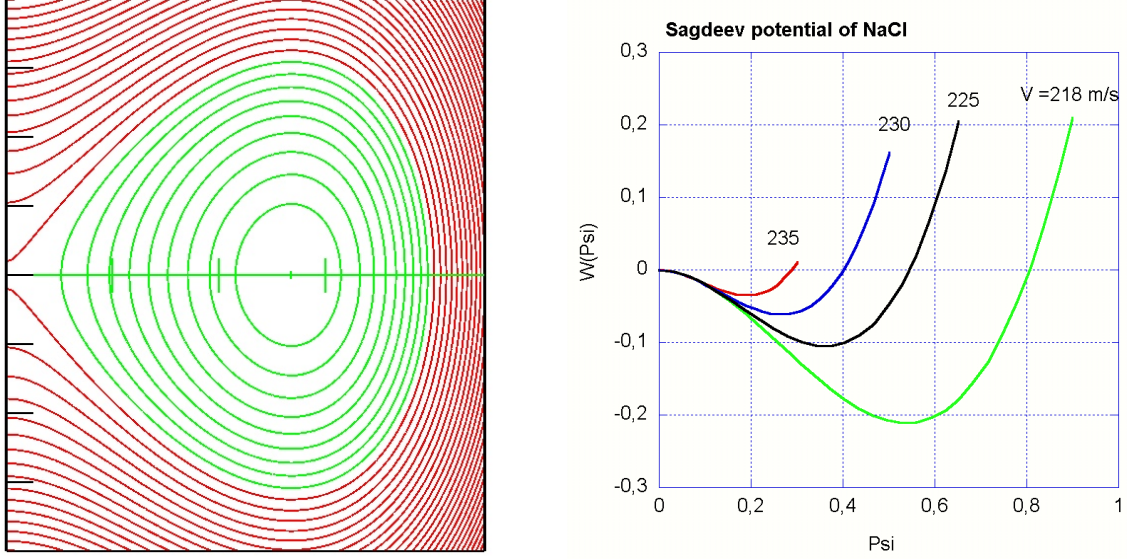


Figure 3: Left: Contours of constant energy E according to eq.(88). The vertical axis is the derivative of $W(\Psi)$ and Ψ is the horizontal axis. The green region describes periodic solutions while the separatrix between the green and the red region describes the soliton. Right: Sagdeev potential of Na^+, Cl^-

The coefficient C is zero for $M_+ = M_-$ and positive if $M_- > M_+$. If $M_- < 1$ and $M_+ < 1$ the coefficient $B < 0$ is negative and the condition for small positive solitons can be met. An example is Na_+, Cl_- . The Mach number scales with the square root of the mass and therefore $M_+ < M_-$ - the Mach number of chloride is smaller than the Mach number of sodium. This case is illustrated in fig.(3). If we consider potassium instead of sodium the relation is $M_+ > M_-$ (potassium is heavier than chloride) and the coefficient $C < 0$ is negative. In this case the soliton has a negative potential. The results of the sodium-chloride computations show that the propagation velocity is by a factor of two larger than the measured data of $V = 100$ m/s or less. This excludes this simple model as the candidates for nerve pulse propagation. The same argument applies to K -ions.

Next, we assume hydrated Na-atoms and Cl-atoms with 6 water molecules. The effective molecular weight is $A_{\text{Na}} = 131$ and $A_{\text{Cl}} = 143$. This combination allows soliton solutions with propagation velocity of $V = 119$ m/s, but this is also larger than the observed data. On the other hand, one must not exclude other ions with larger mass in the cytoplasm since an electric field accelerates all charged particles.

As discussed in the introduction all amino acids or tripeptides below a molecular weight of $A=300$ are subsonic if the propagation velocity is below 90 m/s. If no other heavier ions are participating the coefficient B is always negative. The sign of the coefficient C depends on the sign of $D_k(3M_k^2 - 1)$. A sufficient condition for positive solitons is $D_k(3M_k^2 - 1) < 0 \forall k$. The following figures exhibit the result of Na-ions and negatively charged peptides with molecular weight $A = 307$ (Glutathione). The propagation velocity of solitons is 70 – 80 [m/s]. The results are nearly unchanged if the Na-ion is replaced by a hydrated Na-ion with $A = 131$.

As shown in the previous section the resting potential can be understood if heavy negative and positive ions exist in the axoplasm. Depending on pH-value zwitterions in aqueous solutions will be in positive and negative state. To account for this fact we assumed 10% of the peptides as positive ions. The result in figure (4) shows that the propagation velocity is only slightly changed. At the isoelectric point the density of positive and negative ions is equal and the net charge of zwitterions vanishes, which implies that the coefficient C is zero and the soliton does

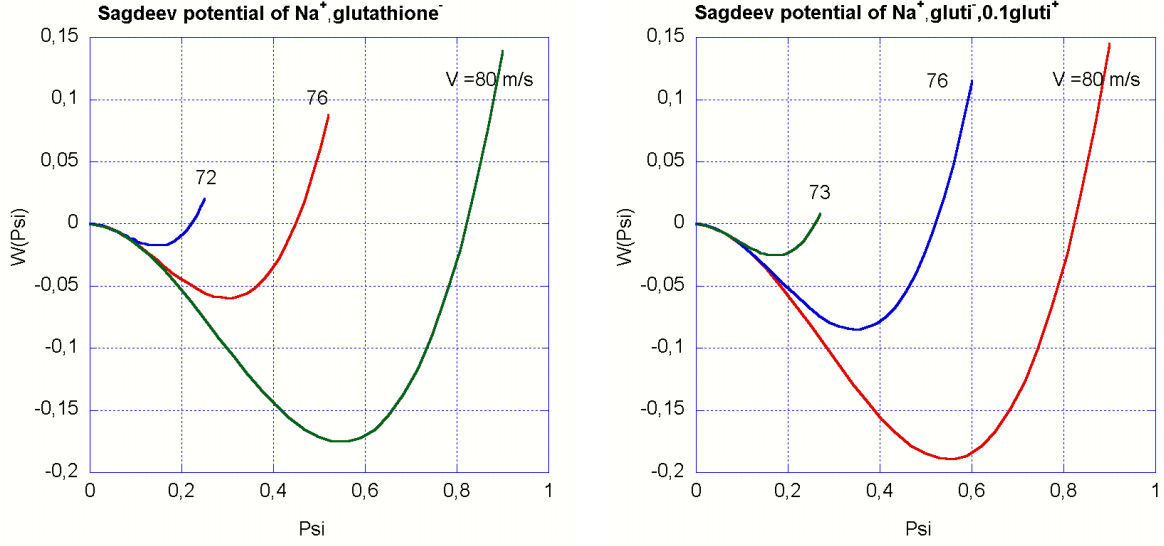


Figure 4: Left: Sagdeev potential of a Na-Glutathione plasma. Right: 10% of the glutathione are positively charged

not exist.

If heavier ions of polypeptides participate in the formation of an action potential the Mach number of these is certainly larger than unity. Compared with a thermal velocity of 10-50 m/s the nerve pulse velocity of 50-100 m/s is supersonic. This causes some problems in satisfying the condition $B < 0$ since $M_k^2 > 1$ provides positive terms in eq.(99). However, if M_k is large enough the positive terms scale with $1/M_k^2$ and the negative terms dominate. The question is: Given a cytoplasm with positive and negative ions. Can we always find a propagation velocity V such that $B(V) < 0$? The answer is yes. A trivial solution is $M_k < 1$ for all ions as previously shown. Depending on the sign of C we get either positive or negative solitons. In order to get positive solitons the condition is $D_k(3M_k^2 - 1) < 0$ or $Z_k(3M_k^2 - 1) < 0$ which can always be satisfied if the number of different ions is large enough.

For heavy charged peptides, however, the Mach number exceeds unity and the situation becomes more complex. The index k denotes the subsonic ions and K the supersonic ions. The coefficient B is

$$B = \sum_k D_k \frac{Z_k}{M_k^2 - 1} + \sum_K D_K \frac{Z_K}{M_K^2 - 1} \quad (102)$$

This coefficient is negative if one of the subsonic constituents has a Mach number close to unity. If $M_k^2 \ll 1$ and $M_K^2 \gg 1$ the condition is

$$B = - \sum_k D_k Z_k + \sum_K D_K \frac{Z_K}{M_K^2} < 0 \quad (103)$$

The second coefficient is

$$C = \sum_k D_k \frac{1}{2} \frac{3M_k^2 - 1}{(M_k^2 - 1)^3} Z_k^2 + \sum_K D_K \frac{1}{2} \frac{3M_K^2 - 1}{(M_K^2 - 1)^3} Z_K^2 \quad (104)$$

or in the limit

$$C = \frac{1}{2} \sum_k D_k Z_k^2 + \frac{3}{2} \sum_K D_K \frac{Z_K^2}{M_K^4} \quad (105)$$

The coefficients D_k, D_K are positive and negative and the total sum is zero. Due to the large number of parameters there is always the chance for positive C .

So far only soliton solution have been investigated. These are characterised by setting $E = 0$. For all E between $E = E_{min}$ and $E = 0$ non-linear periodic solutions exist. This is the green region in fig.(3). The solutions can be expressed in terms of Jacobi elliptic functions. The wave length of these solutions grows when approaching the soliton solution defined by $E = 0$.

6.3 Relation to Kortevveg-deVries equation

Solitary waves in hydrodynamics and plasma physics often are described by the Kortevveg-deVries equation which in its one-dimensional form is

$$\frac{\partial \Psi}{\partial t} + \frac{\partial^3 \Psi}{\partial z^3} + 6\Psi \frac{\partial \Psi}{\partial z} = 0 \quad (106)$$

The soliton ansatz $\Psi(z - Vt)$ yields

$$-V \frac{\partial \Psi}{\partial u} + \frac{\partial^3 \Psi}{\partial u^3} + a\Psi \frac{\partial \Psi}{\partial u} = 0 \quad (107)$$

which after integration leads to

$$\frac{\partial^2 \Psi}{\partial u^2} - V\Psi + \frac{a}{2}\Psi^2 = A \quad (108)$$

A is a constant. This is a Poisson-type equation with a ‘‘charge density’’ as given in eq.(90). The solution has the same structure as shown in eq.(92). Our small amplitude expansion is equivalent to the solution of a KdV-equation.

6.4 Large amplitude waves

The previous analysis is restricted to waves and solitons with small amplitude and the approximation breaks down if the Mach number is close to unity. The non-linear theory, however, is valid for any Mach number. When the amplitude grows the non-linear terms in Bernoulli's equation become important. As already mentioned above the function $P_k(\Psi)$ is not unique and there are two branches of P_k . This function cannot given in analytic form and therefor approximative solutions at finite amplitude of the soliton will be discussed. We restrict the analysis to an isothermal equation of state. The function

$$y(P_k) = \frac{M_k^2}{2}(\exp(-2\delta P_k) - 1) + \delta P_k \quad ; \quad y = g_k - Z_k\Psi \quad (109)$$

has an extremum at $\delta P_k := P_m = \ln M_k$ and the value at this point is (see eq.(87))

$$y_m = \ln M_k + \frac{1}{2}(1 - M_k^2) \quad ; \quad y_m \leq 0 \Rightarrow y \geq y_m \quad (110)$$

Any solution of the coupled system - Bernoulli equation and Poisson equation - is subject to $g_k - Z_k\Psi \geq y_m$. The coefficient g_k accounts for the initial value in Bernoulli's equation (24). A plausible choice of this constant is

$$g_k = F_k(P_k) + Z_k\Psi_0 \quad ; \quad z = 0 \quad (111)$$

At the initial position $z = 0$ of the soliton a possible initial condition is $U_k = 0$ and $\Psi = \Psi_0$. Only P_k is different from $P_{k,0}$. If we approximate $F_k(P_k)$ by $C_k^2/V_k^2 P_k$ the minimum is at

$$\delta P_k := P_m = \ln \left(\frac{V_k}{C_k} M_k \right) \quad \Rightarrow \quad y_m = C_k^2/V_k^2 P_m + \frac{1}{2}(C_k^2/V_k^2 - M_k^2) \quad (112)$$

The smallest value is reached at $C_k = 0$, $y_m = -M_k^2/2$.

Very often in literature the approximation of small or large Mach number is made, however in the neighbourhood of $M_k = 1$ an analytic inversion is not possible. In order to elucidate the situation we consider a two-component plasma with positive and negative ions. In order to obtain finite amplitude waves or solitons we need a minimum of the Sagdeev potential at finite Ψ . The neighbourhood of this minimum is the region of finite amplitude waves as discussed in the previous sections. A sufficient condition is the existence of a finite Ψ with $\delta P_k = \delta P_i$. At this point the charge density is zero since $D_+ + D_- = 0$ and the Sagdeev potential has a second extremum. In order to find a second point with zero charge density the condition $\delta P_+ = \delta P_- = \delta P$ and $\Psi_+ = \Psi_- = \Psi$ must be satisfied. This yields the two conditions

$$-\Psi = \frac{M_+^2}{2}(\exp(-2\delta P) - 1) + C_+^2/V_+^2\delta P \quad ; \quad +\Psi = \frac{M_-^2}{2}(\exp(-2\delta P) - 1) + C_-^2/V_-^2\delta P \quad (113)$$

where with set $g_+ = g_- = 0$. The condition for δP is

$$0 = \left(\frac{C_+^2}{V_+^2} + \frac{C_-^2}{V_-^2} \right) \delta P + \frac{M_+^2 + M_-^2}{2} [\exp(-2\delta P) - 1] \quad (114)$$

This equation has two solutions, one solution is $\delta P = 0$ which is independent of the Mach number. The second solution, however, depends on the Mach number. The minimum of the function is at

$$2\delta P = \ln(M_+^2 + M_-^2) \left(\frac{C_+^2}{V_+^2} + \frac{C_-^2}{V_-^2} \right)^{-1}$$

which can be either positive or negative. This implies that the second solution is also positive or negative. The potential at the roots of eq.(114) is

$$2\Psi = g_- - g_+ + \frac{M_-^2 - M_+^2}{2} [\exp(-2\delta P) - 1] \quad (115)$$

If the charge density has two roots of $\sigma(\Psi) = 0$ the derivative $\sigma'(\Psi)$ changes sign, the Sagdeev potential has a minimum and a maximum. The analysis shows that both, positive and negative solitons can exist. Let us consider a state with $M_-^2 - M_+^2 > 0$ and $g_+, g_- = 0$, the heavy molecules are negatively charged and the light ions are positive. If $M_+^2 + M_-^2 < 2$ the position of minimum in the Sagdeev potential is negative and according to eq.(115) a positive soliton is possible. If $M_+^2 + M_-^2 > 2$ the soliton is negative. These investigations show that the behaviour of non-linear ion acoustic waves is rather complicated and that further analysis including numerical computations is needed.

7 Summary

In contrast to the theory of Hodgkin-Huxley and Heimburg-Jackson the theory of this paper discusses the propagation of electric signals in the axoplasm. The axoplasm contains charged particles, which via Coulomb interaction are able to form ion acoustic waves and solitons. It can be shown that in a density regime $n = 10^{20} - 10^{22}$ [m⁻³] of charged particles these waves experience negligible attenuation and the theory can be formulated in the frame of a Vlasov equation leading to the conservation of entropy. This density regime is the regime of weakly coupled plasmas. In a more realistic density regime with $n = 10^{26} - 10^{27}$ [m⁻³] the theory of strongly coupled plasmas or complex plasmas is the appropriate description. Since the coupling parameter stays below 100 we start from a fluid picture and describe the plasma with the help of the equation of motion and the equation of continuity of each particle species. All

particles are linked by Poisson's equation for the electric potential. In contrast to the theory of Hodgkin-Huxley charged amino acids in form of polypeptides also participate in the nerve pulse propagation. This suggests that any perturbation of the composition and chemical reaction of polypeptides in the axoplasm may lead to a perturbation of the nerve pulse propagation.

The theory above approximates the equation of state by an ideal gas law in case of the quiescent plasma or in case of ion acoustic wave by an adiabatic law. However, polypeptides exhibit an electric dipole, which affects the inter-molecular interaction and can be possibly described by a van-der-Waals type equation. This effect opens the chance of phase transition which is an essential element in the Heimburg-Jackson theory.

The resting potential arises due to the imbalance of charged particles inside and outside the axon. In the present paper we start from a minimum of assumptions where the membrane is permeable to light ions - sodium, potassium etc.- and impermeable to charged organic molecules. No voltage-controlled gates are required. As in the theory of MacGillivray [15] Poisson's equation is utilized to compute the resting potential. As a result the resting potential depends on the fraction of positive and negative organic ions and on the pH-value of the axoplasm.

The linear theory of wave propagation discussed in chapter 5 exhibits a rich spectrum of ion acoustic waves, which are longitudinal waves. It can be shown that vorticity and shear waves do not arise during nerve pulse propagation. This is a remarkable fact since viscous damping of shear waves is stronger than viscous damping of longitudinal waves. Apparently the evolution has found a parameter regime where attenuation of nerve pulses is a minimum or zero. The linear theory of acoustic modes also shows that light ions like Na^+ , K^+ and Cl^- are not the only carrier of nerve pulses since the thermal velocity is much larger than the observed velocities which are below 100 m/s. It needs the cooperation of light positive ions and heavy negative ions to achieve a phase velocity and group velocity below 100 m/s.

The non-linear theory demonstrates that all linear waves can couple and form a non-linear wave or a soliton. Several approximations can be applied in order to clarify the behaviour of non-linear acoustic waves. In a small amplitude expansion the solution can be found in terms of Jacobi elliptic functions, soliton solutions are described in terms of a hyperbolic cosine. As in the case of linear ion acoustic modes it is found that the propagation velocity of a plasma consisting of Na and Cl is in the order of 200 m/s. Only if heavy organic molecules with a weight above 300 participate in the formation of non-linear waves and solitons, the propagation velocity is below 100 m/s. It can be easily shown that the small amplitude expansion is equivalent to a solution of the Korteweg-de-Vries equation which describes solitary surface waves in hydrodynamics. The theory large amplitude non-linear waves is still in an unsatisfactory state since a reduction of the system of equations to a non-linear Poisson equation is not possible as in the case of small amplitude expansion.

An important issue is the excitation of ion acoustic modes. One candidate is beam-plasma interaction which has been discussed above. Injection of charged particles into the soma or main body of the nerve fibre causes a deviation from a Maxwellian which is a source of instability - the axoplasm begins to oscillate. Duration and intensity of the oscillation in the soma depend on the duration and the intensity of the jet. These oscillations couple to plasma waves which carry the information along the axon. Such a jet may be caused by an enhanced pressure in the dendrites originating from a mechanical or thermal impact.

The theory of ion acoustic waves outlined above presents a carrier for information along the axon. Solitons are one possible form, however, in order to transmit a permanent signal one needs a dense sequence of solitons. Another possibility is the non-linear waves, where the amplitude and the duration is variable and thus can transmit a large spectrum of information. This scenario bears some resemblance to radio transmission, where a high-frequency carrier wave is modulated in amplitude and duration. The theory presents a general framework for propagation of nerve signals. Although there is a clear indication that organic molecules play

a significant role in nerve pulse propagation, an identification of a specific polypeptide is not possible. Glutamic acid in form of glutathione has been used as an example in the numerical analysis, however it cannot be stated that this is the only candidate. Here a cooperation between physics and biochemistry is required.

Acknowledgements: I should like to acknowledge valuable comments and criticism by T. Heimburg, Copenhagen and by V. Erckmann and P. Helander, Greifswald.

References

- [1] A.L. Hodgkin and A.F. Huxley, *J. Physiol.* (1952) 117, 500 - 544
- [2] T. Heimburg and A.D. Jackson, *Biophys. J* **92**,3159 (2007)
- [3] T. Heimburg and A.D. Jackson, *Biophysical Review and Letters* **2**,No.1,57-78 (2007)
- [4] H. Löwen et al. *J. Phys. A: Math. Gen.* **36**(2003) 5827-5834
- [5] S. Hamaguchi, *Plasmas and Ions* **2**(1999) 57
- [6] M. Toda, *J. Phys. Soc. Japan* **22**(1967) 431
- [7] M. Toda, *Nonlinear Waves and Solitons* Mathematics and its Application, 5, Kluwer (1989)
- [8] A. Lenard, *Ann. Phys.* **3**(1960) 390
- [9] R. Balescu, *Phys. Fluids* **3**(1960), 52
- [10] R. Balescu, *Transport Processes in Plasmas* Vol. I, North Holland 1988, p. 130
- [11] G.B. Kalman and M. Rosenberg, *J. Phys. A: Math. Gen.* **36** (2003), 5963-5969
- [12] M. Rosenberg, G.B. Kalman, S. Kyrkos, Z. Donko *J. Phys. A: Math. Gen.* **39** (2006), 4613-4618
- [13] B.A. Koechlin, *J. Biophys. and Biochem. Cytol.* (1955) Vol.1, No. 6
- [14] F.G. Donnan *Z. Elektrochem.*(1911),xvii,572
- [15] A.D. MacGillivray *J. Chem. Phys.* **48**,2903 (1968)
- [16] L.J. Landau, *J. Phys. USSR* **10**, 25 (1946)
- [17] A. Simon, *Plasma Physics*, IAEA, Vienna 1965, p. 163-195