Protoplasma (2006) 229: 235–242
DOI 10.1007/s00709-006-0211-1

PROTOPLASMA
Printed in Austria

Microgravity dependence of excitable biological and physicochemical media

W. Hanke[1,*], **V. M. Fernandes de Lima**[2,3], **M. Wiedemann**[1], and **K. Meissner**[1]

[1] Institute of Physiology, University of Hohenheim, Stuttgart
[2] Laboratório de Sistemas Integráveis, Escola Politécnia, Universidade de São Paulo, São Paulo, São Paulo
[3] Centro de Biotechnologia, Instituto de Pesquisas Energéticas e Nucleares, Comissão Nacional de Energia Nuclear, São Paulo, São Paulo

Received July 4, 2005; accepted November 3, 2005; published online December 16, 2006

Summary. Neuronal tissue and especially the central nervous system (CNS) is an excitable medium. Self-organisation, pattern formation, and propagating excitation waves as typical characteristics in excitable media consequently have been found in neuronal tissue. The properties of such phenomena in excitable media do critically depend on the parameters (i.e., electromagnetic fields, temperature, chemical drugs) of the system and on small external forces to which gravity belongs. The spreading depression, a propagating excitation depression wave of neuronal activity, is one of the best described of the those wave phenomena in the CNS. Especially in the retina as a true part of the CNS it can be easily observed with optical techniques due to the high intrinsic optical signal of this tissue. Another of such waves in neuronal tissue is the propagating action potential in nerve fibres. In this paper, data from our laboratories concerning the influence of gravity on the velocity of propagating waves in excitable media are summarized mainly in terms of the retinal spreading depression and propagating action potentials. Additionally, we have used waves in gels of the Belousov–Zhabotinsky reaction as the physicochemical model system of biological activity as the properties of these waves follow the same theories as the spreading depression and action potentials and they have some striking similarities in wave behavior. Thus propagating Belousov–Zhabotinsky waves are described by their gravity dependence.

Keywords: Gravity; Neuronal tissue; Excitable medium; Wave propagation.

Introduction

Spreading depression (SD) waves as an example of self-organisation and pattern formation in neuronal tissue have been observed in all parts of the vertebrate central nervous system (CNS), including the retina (Leao 1944, Fernandes de Lima et al. 1999). Such SD waves, after a proper stimulus, are typically propagating through the tissue with a velocity of 3–5 mm/min and are accompanied by a variety of parameter changes in the tissue, e.g., potential changes, changes in ion homeostasis, variation of intra- and extracellular space, changes in ion channel parameters of the cells involved, and finally also changes in the optical properties of the tissue. All changes concomitant with the SD are transient, thus the tissue completely recovers after a certain period. The wave itself is followed by an absolute refractory period of about 1 min and a relative refractory period of up to 20 min (Fernandes de Lima et al. 1999).

Although known for more than 50 years, some basic mechanisms of SD waves are still not fully understood. Additionally, in the last decade the medical relevance of SD became more obvious as SD waves are involved in a variety of pathophysiological events including global amnesia, certain forms of epilepsy, early poststroke events, and especially classical migraine (Milner 1958).

The properties of SD waves according to the theory of excitable media depend critically on the chemical and physical parameters of the system and on changes in these parameters. Thus, small changes in system parameters can result in dramatic changes in the measured properties of the SD waves due to intrinsic amplification and feedback of excitable media (Fernandes de Lima et al. 2002, Fujieda et al. 2001, Hanke et al. 1998).

Also, waves in excitable media and thus SD waves are critically depending on small external forces to which gravity belongs, and indeed SD wave parameters are reacting to gravity changes (Hanke et al. 2001). Gravity is a small but permanently present stimulus on Earth, the presence of which might have severe consequences for the behavior of

* Correspondence and reprints: Institut für Physiologie (230), Universität Hohenheim, Garbenstrasse 30, 70599 Stuttgart, Federal Republic of Germany.
E-mail: hanke@uni-hohenheim.de

the system anyhow, as well as changes of gravity in possible environments with a gravity different from the Earth value will affect SD waves and consequently the CNS.

Until now only very little is known about the influence of gravitation on the properties of neuronal tissue due to its behavior as an excitable medium. However, another basic process in neuronal tissue, propagating action potentials (AP), can also be seen as waves in excitable media, which thus should consequently react to gravity changes. This has been proven recently (Meissner et al. 2003) as an important finding itself, but additionally the AP results may serve to explain the behavior of SD waves under conditions of changing gravity. The data about propagating APs in nerve fibers have been confirmed by measurements utilizing spontaneously spiking neurons from leech in the drop tower in Bremen. It was found that the number of APs per time unit changes when gravity changes (Meissner and Hanke 2005).

SD waves finally are known to behave quite similar to the well-described waves in the Belousov–Zhabotinsky (BZ) reaction in oscillating chemical media (Zaitkin and Zhabotinsky 1970). It has been found that BZ waves indeed depend on gravity, too (Fujieda et al. 1999, 2001; Piqueira et al. 2003). According to some striking similarities of the systems, it can be expected that effects found in BZ experiments at least partially can also be assigned to SD and AP experiments, thus waves in the BZ reaction can ideally serve as a model for excitable systems.

Independent of the similarities between AP, SD, and BZ, and the fact that very similar theories (Tuckwell and Miura 1978) have been applied for all systems, their basic mechanisms are significantly different. Whereas BZ waves are basically dependent on diffusion mechanisms and chemical reactions in a chemical soup, SD waves are dependent on the properties of single cells of the neuronal tissue with all their metabolic and membrane events, the connectivity, and other properties of the neuronal tissue. APs in their classical mechanistic interpretation are dependent on membrane processes and here mainly on ion channels (voltage-activated fast-inactivation sodium channels). As already mentioned, the occurrence and propagation of SD waves also depends mainly on the membrane processes like the action of ion channels and ion pumps. Therefore, the gravity dependence of the ion channels may also explain mechanistically the gravity dependence of the SD waves.

Finally, some types of ion channels themselves are dependent in their parameters on gravity, as has been shown by recent experiments (Wiedemann et al. 2003) and might also contribute to explaining the gravity dependence of APs and SD, and membrane potential of cells as measured by fluorescent dye changes under microgravity (Meissner 2005).

In this paper we summarize some data about the gravity dependence of APs, SD waves, and waves in BZ systems. First, in order to provide a novel approach to the question of how living systems, especially the CNS, might perceive gravity independently of specialized organs; and second, to demonstrate that basic properties of the brain are gravity dependent and thus possibly also the mental capabilities of humans in space, with a variety of consequences for future manned spaceflight.

In all SD experiments cited we used the well-established system of the retinal SD due to experimental advantages in its observation by its high intrinsic optical signal (IOS) (Fernandes de Lima and Hanke 1997, Fernandes de Lima et al. 1999). According to its ontogenesis, the retina is a true part of the brain and has some striking advantages compared with in vivo SD experiments or brain slice preparations. The outstanding advantage is the very high IOS of the waves, which is caused by changes in light scattering, due to cell volume changes and is up to three decades higher than in other parts of the brain. This high IOS allows the observation of SD waves in the retina even with the naked eye and experimentally with all standard video techniques. By video imaging techniques, the behavior of retinal SD waves can be measured resolved in time and space, which is usually not as easy with electrophysiological techniques. BZ wave experiments, especially in gel systems, can be performed by almost the same techniques. APs experiments cited have been investigated in a variety of electrophysiological approaches (Meissner et al. 2003).

Material and methods

Spreading depression waves

Retinal eyecups were prepared from 7- to 21-day-old chicken as described in detail previously (Fernandes de Lima et al. 1999). The eyecups were then mounted in chambers adequate for the experimental platform used. Typically a Ringer solution (100 mM NaCl, 6 mM KCl, 1 mM $MgSO_4$, 1 mM $CaCl_2$, 1 mM NaH_2PO_4, 30 mM $NaHCO_3$, 10 mM Tris, 30 mM glucose, pH 7.4) was used for the experiments. The chambers were mounted in a setup either in the aircraft, for 25 s microgravity experiments (10^{-2} **g**), or on the platform of a sounding rocket. Figure 1 shows the setups used. The retinas were always observed with digital video cameras to record the IOS of the waves and data were stored on videotape for later computer-based video imaging and evaluation. Temperature was controlled and kept at about 30 °C. SD waves were elicited mechanically with fine needles that were integrated into the cover (4 needles per chamber) and were moved by remote control of a stroke magnet for the sounding-rocket experiments. During parabolic flights, one stimulation needle was integrated flexibly in the experiment chamber and was hand-operated. The primarily investigated parameter of the waves was their propagation velocity. Velocity was always measured relative to control values measured at 1 **g**. Furthermore, the latency of the waves was also measured from the videos as the time interval between the stimulus and the onset of the wave. This latency has been shown to be a reliable measure for the excitability of the tissue (Weimer and Hanke 2005). Finally, changes of the IOS induced by variations in

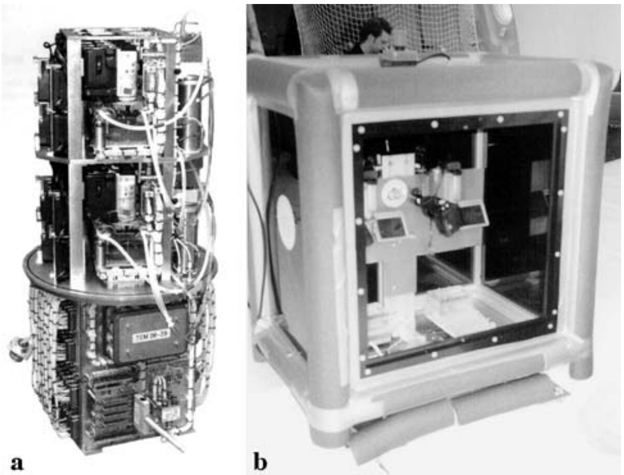

Fig. 1 a, b. Setups for SD experiments. **a** The experiment module for the sounding-rocket experiments consists of two identical platforms, each with 4 chambers containing the retinas and 4 camcorders for data acquisition. **b** The setup used for the SD experiments on parabolic flights consists of a dark box containing two experiment chambers and two camcorders above

gravity were recorded. As a complete IOS recording of an SD wave accordingly lasts about 15 min (Fig. 2), only partial recordings were possible in the sounding rockets and only the first peak was recorded in the parabolic-flight experiments. To the different phases of the IOS, molecular processes can be assigned as given in Fig. 2 and thus changes in these processes as induced by microgravity can be estimated from the analysis of the IOS data.

Belousov–Zhabotinsky reaction waves

Silica gels for the BZ reaction were made according to a procedure modified from Yamaguchi et al. (1991). In brief, a solution (5 ml of 5% $Na_2Si_2O_3$, 1 ml of 25 mM ferroin solution, 0.5 ml of H_2O bidest, 1 ml of 1 M H_2SO_4) was given right at the bottom of proper chambers to a height of about 20 mm. After polymerization, gels were covered with 0.33 M H_2SO_4

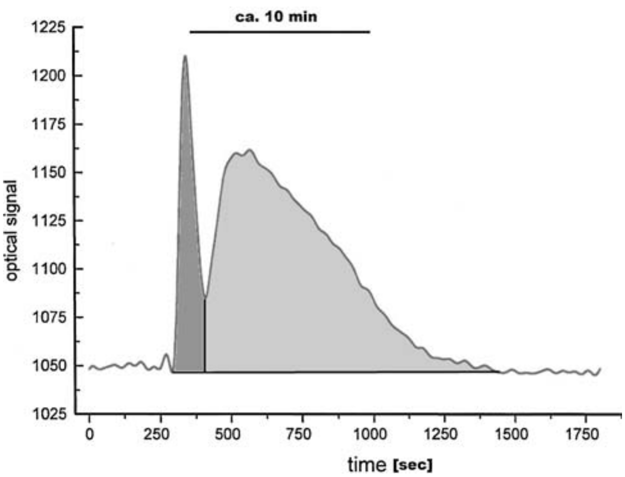

Fig. 2. Complete IOS recording of a retinal SD wave with its different phases. The mechanistic processes which are the basis of the different phases are: activity of ion channels in the rising part of the first phase, increase in pump activity in the falling part of the first phase, and metabolic processes and ATP build-up in the second phase. The first phase is indicated in dark grey, the second phase in pale grey

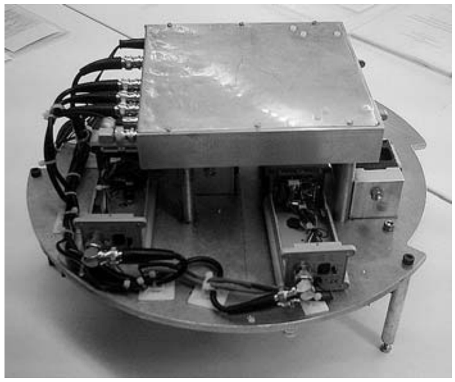

Fig. 3. The new setup from our laboratory to be used for gel type experiments with the BZ reaction on sounding rockets; most probably it will be used on a Brazilian VS30 sounding rocket

and then stored. Before use, the H_2SO_4 was removed and the chamber was filled with a reaction solution (0.33 M malonic acid and 0.33 M $NaBrO_3$ dissolved in 0.3 M H_2SO_4). The chambers with the gels were then placed in the centrifuge for hypergravity controls, and waves were monitored with a digital video camera and stored on tape for later data evaluation. Alternatively, chambers were mounted in the platform of a Brazilian VS30 sounding rocket for microgravity experiments. Figure 3 shows the new setup used for BZ experiments in sounding rockets. From the video recordings of the BZ reaction, the propagation velocity of the waves was calculated and values are displayed relative to 1 **g** control experiments. Spontaneously active gels were used in all experiments, thus latencies could not be determined.

Propagating action potentials

Living earthworms were mounted in specifically constructed plastic chambers for parabolic-flight experiments and stimulated electrically by

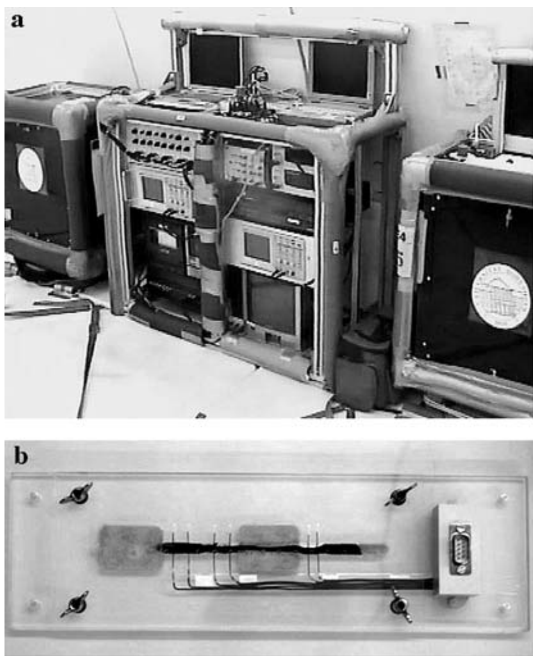

Fig. 4. a Complete setup for AP recording from earthworm (intact animal and isolated nerve) during parabolic flights. **b** Details of the chambers used for keeping the animals in proper shape during the flights

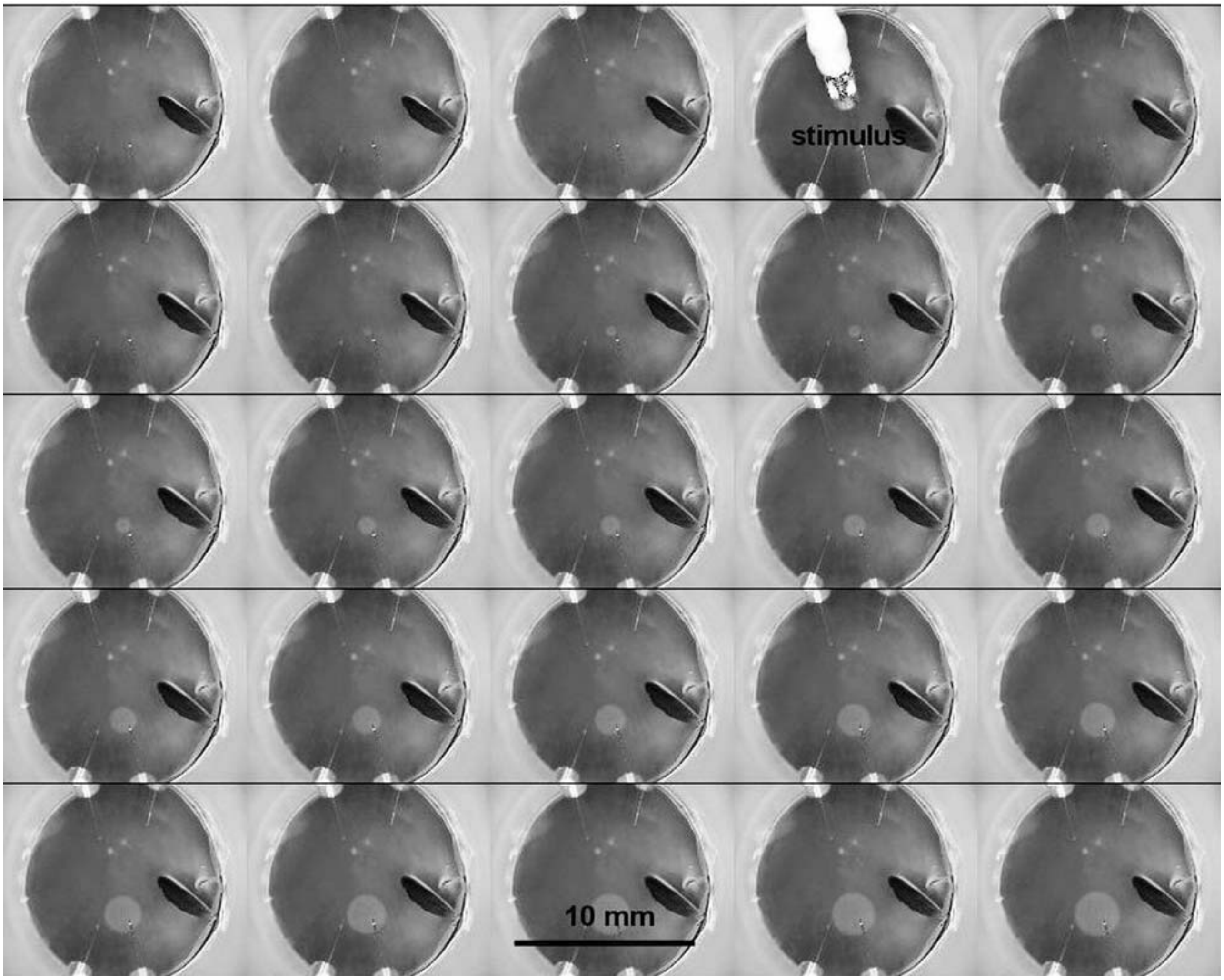

Fig. 5. Montage of a series of consecutive photos of an SD wave propagating in retinal tissue. The temporal spacing between 2 photographs is 1 s. The stimulus is marked in the fourth frame, and the elicited wave can be seen as an increasing milky area in the tissue

current pulses of defined length and amplitude to exhibit propagating APs in the dorsal nerve (Meissner et al. 2003). During parabolic-flight experiments, the chambers were mounted in dark boxes. APs were recorded at two distances from the stimulation spot, and the propagation velocity and the latency of the APs were calculated. Data were always stored additionally on a tape recorder and a computer for later detailed evaluation, to find differences between AP velocities at the different gravity phases of the flights, i.e., 1 **g**, microgravity, and 1.8 **g**. Giant nerve fibers from earthworm were prepared as described in the literature (Meissner and Hanke 2005). They were mounted in chambers with low-melt agarose and hydrophobic gaps and APs were elicited electrically as in intact earthworms. The recording technology for the APs was identical to that for the intact earthworms. In Fig. 4 some details of the setup for AP recording in a parabolic-flight mission are shown. Finally, the behavior of spontaneously spiking neurons from leech was investigated in electrophysiological experiments in a drop tower.

Results

SD waves propagate in neuronal tissue with a velocity of about 3–5 mm/min. In the retina as a true part of the CNS,

Table 1. Gravity dependence of retinal SD wave propagation velocity[a]

Gravity condition	Change relative to 1 **g** controls	
	Velocity	Latency
Microgravity, parabola	3% slower (n = 66)	30–60% longer (n = 12)
Microgravity, Texus	3–8% faster (n = 6)	14–30% longer (n = 6)
1.8 **g**, parabola	2% faster (n = 66)	ND[b]
2 **g**, centrifuge	3–10% faster (n = 66)	ND
3 **g**, centrifuge	6–8% faster (n = 6)	ND

[a] Possibly in Texus experiments the retina first adapts to the high acceleration at launch and then recovers only on a 5–15 min timescale. This, as well as the latency for hypergravity, has to be checked in future experiments
[b] ND, not determined

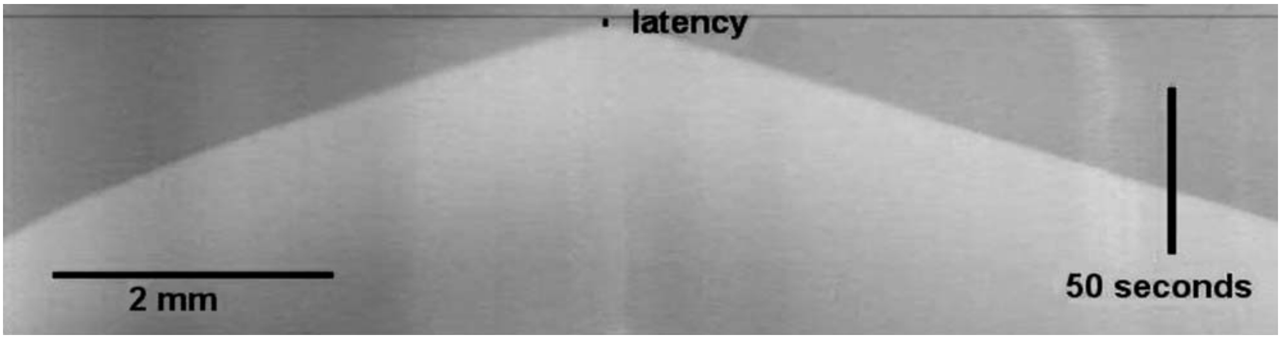

Fig. 6. Temporal development of a retinal SD wave given by stacking one line through a photo in time, the wave is given by the bright triangle in the figure, the slope of the border of this triangle depicts the wave propagation velocity. The mechanical stimulus to elicit the wave is the line at the top of the figure. The latency is the interval between stimulus and true wave onset

these waves are accompanied by a striking IOS. A montage of photographs of an SD in a retina is given in Fig. 5 to demonstrate this. From such recordings, the propagation velocity of SD waves can be recorded under conditions of different gravity conditions. In parabolic-flight campaigns, 1 **g**, 1.8 **g** for periods of about 20 s, and microgravity for periods of about 25 s are given. In sounding-rocket experiments, during takeoff a longer period (in the minute range) of high gravity, up to about 10 **g**, is given followed by a period of about 6 min of microgravity (Texus). From such experiments, the gravity dependence of the propagation velocity of SD waves has been extracted and the results summarised qualitatively in Table 1. Obviously, SD wave propagation velocity and latency (see below) are gravity dependent, however, in a nontrivial manner.

From the video recordings, stacks can be constructed as given by an example in Fig. 6, showing the behavior of wave propagation in time. From such stacks, the period between the stimulus eliciting the wave and the true wave onset (latency) can be taken, being a measure for the excitability of the tissue. As can be also seen from Table 1, latency depends on gravity, too, getting longer at decreasing gravity. Consequently, waves will be elicited more difficultly under microgravity.

Finally, the IOS as a time-dependent recording of tissue brightness can be recorded as pointed out in the Material and methods section. In Fig. 7, two recordings are shown, one under 1 **g** control conditions, the other after a period of high acceleration after a Texus launch at the beginning of the microgravity period. There are some clear changes to be seen in the IOS, especially the falling part of the first phase of the IOS seems to be shortened; however, for a serious interpretation more data will be necessary at longer lasting hyper- and microgravity phases, especially to get information about adaptation and long-lasting processes. It has to be taken into account here that the SD-related IOS lasts for about 15 min and that the relative refractory period of a wave is of the same duration.

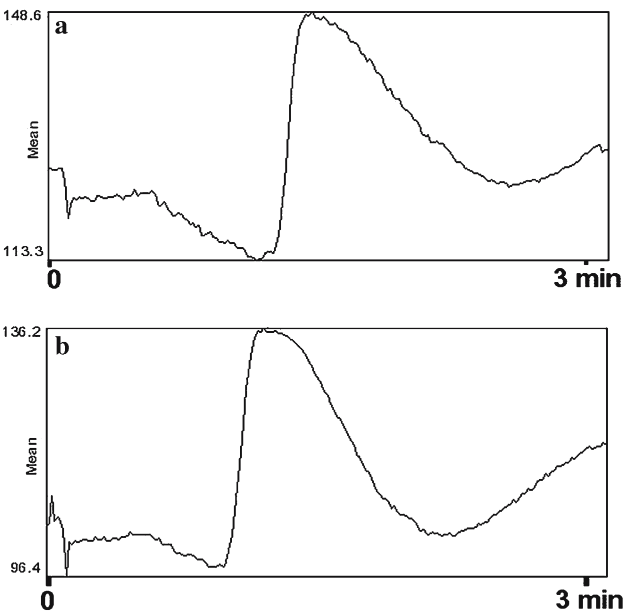

Fig. 7 a, b. Partial recordings of the IOS of a retinal SD wave from a Texus flight. **a** 1 **g** control; **b** microgravity, directly after the beginning of the microgravity phase. As can be seen, the recordings, depicting relative changes in tissue brightness, are different in a variety of their parameters in a complex manner. The recording length is about 3 min. The y-axis is scaled in arbitrary units of brightness

BZ waves, especially in gels, behave similarly to SD waves and amazingly have about the same propagation velocity (Fernandes de Lima et al. 1999). In Fig. 8, again a montage of a series of photographs is given to depict this. The propagation velocity of BZ waves in gels is only slightly gravity dependent, as shown in Fig. 9. The effects in fluid systems, however, are much more dramatic (Fujieda et al. 1999). One reason for this might be different diffusion rates in the fluid and the gel systems. Future sounding-rocket experiments will help to find out more details about the mechanisms involved. As the BZ waves are always mea-

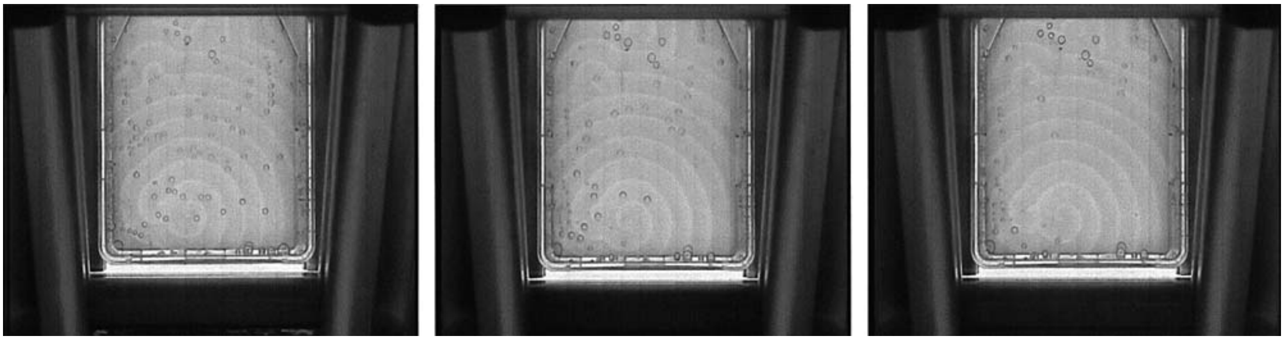

Fig. 8. Series of three photographs of propagating BZ waves in a gel as can be compared to Fig. 5 for the retinal SD. The size of the chamber is about 10 by 10 cm, the time difference between the 3 photographs is 1 min each

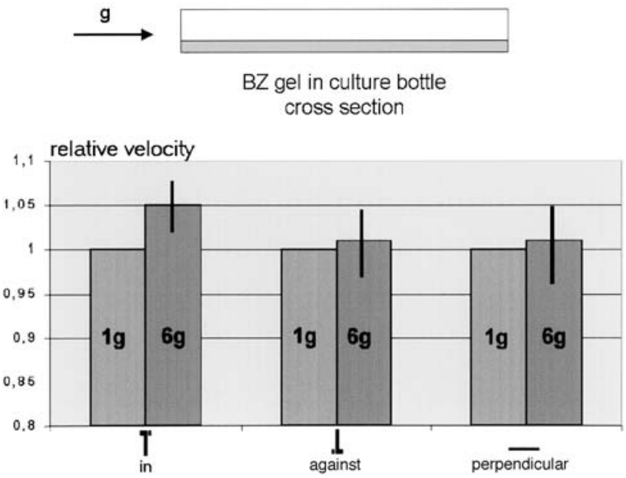

Fig. 9. Gravity dependence of BZ wave propagation velocity at 1 **g** and 6 **g**. These results are from centrifuge experiments in the laboratory, under conditions otherwise identical to the sounding-rocket experiments. The symbols on the x-axis indicate the direction of the propagating BZ waves according to the gravity vector

Table 2. Gravity dependence of properties of APs[a]

Gravity condition and sample	Change relative to 1 **g** controls	
	Velocity	Latency
Microgravity in parabola, earthworm	3% slower (n = 72)	about 1% longer, sometimes also shorter (n = 25)
Microgravity in drop tower, leech neuron	ND[b]	up to 30% shorter[c] (n = 3)
Microgravity in parabola, axon	<1% slower (n = 49)	no clear change
1.8 **g** in parabola, axon	<1% faster (n = 49)	no clear change
1.8 **g** in parabola, earthworm	2–31% faster (n = 72)	up to 12% longer

[a] The original data had a very high scatter, especially concerning latency, thus the presented results are indicating principles and direction of changes better than accurate values
[b] ND, not determined
[c] Given by a higher number of spikes in a spontaneously active cell

sured in spontaneously active systems, latencies cannot be determined; however, in future experiments, the number of waves in a given time interval possibly can be taken as a comparable measure.

Additionally, for both types of waves, SD and BZ, it could also be that not only the gravity amplitude itself but also the orientation of the wave propagation relative to the gravity vector affects the wave parameters. For both the SD and the BZ waves, the biggest effects of hypergravity were found when the wave propagates in the direction of the gravity vector (Wiedemann et al. 2002).

APs are affected by gravity in a complex manner, and the results so far are summarised in Table 2. Both latency and velocity are affected. Additionally, the number of APs in a given time interval increases in single-cell experiments with spontaneously active neurons.

Discussion

The CNS is a thermodynamical open system, far from equilibrium with feedback, amplification, and nonlinear properties (Hanke et al. 1998). Thus, it is an excitable medium by definition, allowing self-organisation, oscillations, and propagating waves to exist. This is generally accepted, and an increasing number of experiments have been presented to verify the concurring theories. However, excitable media not only allow certain structures to show up but also are critically dependent on system parameters and small external forces. For system parameters of the CNS, especially those of chemical nature, this is widely accepted and the SD has been thoroughly investigated in its pharmacology dependence (Fernandes de Lima et al. 1999).

Other questions, especially concerning the action of small external forces of physical nature on the CNS, are still more controversially discussed. To these belongs the interaction of the CNS with small electromagnetic fields, which presently is a highly popular question.

Another small external force is gravity, which usually is constant at 1 **g** on earth. However, during possible future manned spaceflights constant 1 **g** will no longer hold, and it must be asked whether changes in gravity (longer and short-lasting) might cause direct changes in the behavior of the CNS.

Our experiments (Wiedemann and Hanke 2002, Wiedemann et al. 2002, Meissner et al. 2003) and those of other groups (Fujieda et al., 2001, Pojman et al. 1997) have clearly proven that gravity interacts with excitable media, especially the CNS, changing their behavior, as it has been shown that some processes of CNS tissue are affected by gravity, for example, the retinal SD. Concluding from these experiments that classical migraine might be reduced under microgravity is surely a popular and true statement; however, the consequences are much more dramatic.

Basic processes in the CNS such as the parameters of ion channels in cell membranes and the resting potential of cells interact with gravity (Wiedemann et al. 2003). The open-state probability of some ion channels decreases at microgravity and membrane potential gets depolarised (Meissner 2005). The interaction of gravity with ion channel parameters could be a direct action of the gravitational force on the molecule being the ion channel. Alternatively, gravity could change the thermodynamics of the entire membrane and by this affect membrane fluidity and thus induce changes in ion channel parameters (open-state probability).

Propagating APs (which behave like waves in excitable media themselves) have been demonstrated to depend on gravity in their parameters (Meissner et al. 2003, Meissner and Hanke 2005), slowing down at microgravity and having a smaller latency, which would be consistent if the above statement about ion channels can be generalized. According to the fact that SD waves strictly depend on the parameters of cells of the neuronal tissue and on the electrical connectivity of this tissue, changes in SD wave propagation under microgravity could be expected. Our results are thus consistent and might help to understand the direct action of gravity on neuronal tissue.

The different results about SD wave propagation from parabolic flights and from the sounding-rocket mission can be explained by long-term adaptation (the IOS of an SD wave lasts about 15 min, indicating recovery from adaptation on the same time scale) of the tissue to the conditions of hypergravity given during the launch of the rocket.

Nevertheless, future experiments should be performed to investigate in more detail the gravity dependence of vertebrate nerves and ion channels to clearly address the uprising questions.

Obviously, not only the behavior of the cardiovascular system, the sensory system, and muscles and bones have to be taken into account in the physiology of manned spaceflight (Keller and Sahm 2000), but also the human brain itself, which as a consequence of the results presented in this paper must surely directly interact with gravity. The question can thus no longer be whether this interaction is given, but what are the consequences, as this is basically an open question presently. Experiments directly involving human physiological and neurophysiological experiments under conditions of changing gravity are thus a challenge for the future.

Acknowledgments

This work was supported by the DLR (German Space Agency) by grant nr. 50 WB0221.

References

Fernandes de Lima VM, Hanke W (1997) Excitation waves in central grey matter: the retinal spreading depression. Prog Retinal Eye Res 16: 657–690

Fernandes de Lima VM, Goldermann M, Hanke W (1999) The retinal spreading depression. Shaker, Aachen

Fernandes de Lima VM, Piqueira JRC, Hanke W (2002) Development of an experimental module to study the modulation of the propagation velocity of chemical excitation waves in gels by weak external forces (gravity). J Gravit Physiol 9: 347–348

Fujieda S, Mogami Y, Zhang W, Shinohara H, Handa S (1999) Automated experimental assembly for studying the reaction-diffusion behaviour of Belousov–Zhabotinsky reactions under microgravity. Anal Sci 15: 159–164

Fujieda S, Mori Y, Nakazawa A, Mogami Y (2001) Effect of gravity field on the nonequilibrium/nonlinear chemical oscillation reactions. Adv Space Res 28: 537–543

Hanke W, Goldermann M, Brand S, Fernandes de Lima VM (1998) The retinal spreading depression: a model for non-linear behaviour of the brain. In: Parisi J, Müller SC, Zimmermann W (eds) A perspective look at non-linear media: from physics to biology and social sciences. Springer, Berlin Hedelberg New York, pp 227–243

Hanke W, Wiedemann M, Rupp J, Fernandes de Lima VM (2001) Control of the retinal spreading depression by weak external forces. Faraday Discuss 120: 237–248

Keller H, Sahm R (eds) (2000) Bilanzsymposium Forschung unter Weltraumbedingungen. WPF, Aachen, pp 677–773

Leao AAP (1944) Spreading depression activity in the cerebral cortex. J Neurophysiol 7: 359–390

Meissner K (2005) Elektrophysiologische Charakterisierung neuronaler Prozesse unter veränderten Schwerkraftbedingungen. Dissertation, Universität Hohenheim, Stuttgart, Federal Republic of Germany

Meissner K, Hanke W (2005) Action potential properties are gravity dependent. Microgravity Sci Technol 17(2): 38–43

Meissner K, Schwertner J, Hanke W (2003) Hoch hinaus. Biologie in unserer Zeit 6: 390–395

Milner PM (1958) Note on a possible correspondence between the scotomas of migraine and spreading depression of Leao. Electroencephalogr Clin Neurophysiol 10: 705

Piqueira JRC, Fernandes de Lima VM, Hanke W (2003) Microgravity effects in Belousov–Zhabotinsky (BZ) reaction. J Gravit Physiol 10: 115–116

Pojman J, Kahn AM, Mathias LJ (1997) Frontal polymerization in microgravity: results from the Conquest I sounding rocket flight. Microgravity Sci Technol 10: 36–40

Tuckwell HC, Miura RM (1978) A mathematical model for cortical spreading depression. Biophys J 23: 257–276

Weimer M, Hanke W (2005) Propagation velocity and triggering threshold of retinal spreading depression are not correlated. Exp Brain Res 164: 185–193

Wiedemann M, Hanke W (2002) Gravity sensing in the central nervous system. J Gravit Physiol 9: 43–44

Wiedemann M, Fernandes de Lima VM, Hanke W (2002) Gravity dependence of waves in the retinal spreading depression and in gel type Belousov–Zhabotinsky systems. Phys Chem Chem Phys 4: 1370–1373

Wiedemann M, Rahmann H, Hanke W (2003) Gravitational impact on ion channels incorporated into planar lipid bilayers. In: Tien HT, Ottava-Leitmannova A (eds) Planar lipid bilayers and their applications. Membrane science and technology, vol 7. Elsevier, Amsterdam, pp 669–698

Yamaguchi T, Kuhnert L, Nagy-Ungvarai Z, Müller SC, Hess B (1991) Gel systems for the Belousov–Zhabotinsky reaction. J Phys Chem 95: 5831–5837

Zaitkin AN, Zhabotinsky AM (1970) Concentration wave propagation in two-dimensional liquid-phase self-oscillating system. Nature 225: 535–537