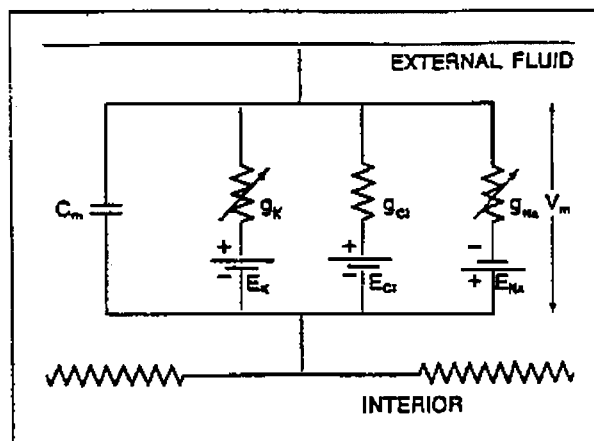


(Subject area: Neural signaling, communications and processing.)

1. Equivalent Circuit diagram:



2. A nerve cell membrane can be modelled in terms of electrical capacitance  $C$  and several conductances (or resistances  $R$ ) specific to particular ions which carry charge across the membrane. These currents  $I$  into and out of the nerve cell affect its voltage  $V$  in accordance with Ohm's Law for resistance ( $I = V/R$ ) and the law for current flow across a capacitor ( $I = C \frac{dV}{dt}$ ). The charge-carrying ionic species are sodium ( $Na^+$ ), potassium ( $K^+$ ), and chloride ( $Cl^-$ ) ions.
3. The crucial element underlying nerve impulse generation is the fact that the conductances (resistances) for  $Na^+$  and  $K^+$  are not constant, but voltage-dependent. Moreover, these two voltage-dependent conductances have different time courses (time constants). The more the voltage across a nerve cell rises due to  $Na^+$  ions flowing into it, the lower the resistance for  $Na^+$  becomes. ( $Na^+$  current continues to flow until its osmotic concentration gradient is in equilibrium with the voltage gradient.) This positive feedback process causes a voltage spike, which is a nerve impulse.
4. Since the positive feedback process is unstable, causing the voltage to climb higher and higher, faster and faster, it can be described as a catastrophe, rather like an explosion. Once combustion starts in a small corner of a keg of dynamite, matters just get worse and worse. The positive climb of voltage only stops when, on a slower time-scale,  $K^+$  begins to flow in the opposite direction. Once the trans-membrane voltage falls below its threshold, the resting state of ionic concentrations can be restored by ion pumps and the catastrophe (the nerve impulse) is over.
5. The process described above is complete within about 2 milliseconds. There is a refractory period for restoration of ionic equilibrium that lasts for about 1 millisecond, so the fastest frequency of nerve impulses is about 300 Hz. The speed of nerve impulse propagation down an excitable myelinated axon, by saltatory spike propagation, can reach 100 meters per second in warm-blooded vertebrates.
6. A nerve impulse reaching an axonal branch would normally go down both paths, unless vetoed at either one by other shunting synapses. Some axonal branches are "steerable" by remote signalling.

(continued...)

7. The two approaching nerve impulses would annihilate each other when they collided. The minimum refractory period of excitable nerve membrane prevents the impulses from being able to pass through each other, as they would if they were pulses propagating in a linear medium such as air or water or the aether.
8. The linear components of nerve cells (i.e. their capacitance and any non-voltage-dependent resistances) behave as linear integrators, providing linear (but leaky) summation of currents over space and time. However, the fundamentally non-linear interactions at synapses can implement logical operations such as AND, OR, NOT, and veto. The basic factor which underlies this "logico-linear" combination of signal processing is the mixture of excitable ("logical") and non-excitable ("linear") nerve cell membranes.
9. It is very difficult to distinguish between processing and communications in living nervous tissue. The generation and propagation of nerve impulses is the basis for both. A steerable axonal branch particularly illustrates the impossibility of making such a distinction.
10. Stochasticity in nerve impulse time-series may provide a means to search very large spaces for solutions (e.g. to pattern recognition problems) in a way resembling "simulated annealing." Evolutionary computing (blind variation and selective retention of states) can be the basis of learning in neural networks, and stochasticity may provide the blind variation.

[2 marks each, for 20 marks total]