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Autor: Henn, Volker
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Where Physics Meets Biology

By Volker Henn

Neurology Dept, University Hospital, CH-8091 Zurich, Switzerland
vhenn@neurol.unizh.ch

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Abstract. Taking examples from oculomotor research it is shown how physics was instrumental in stating the logical problems of how to generate eye movements in response to various sensory stimuli, while biological research shows how different solutions evolved. In an ideal way, the two approaches combine. While the physicist wants to work out general rules, the biologist has to observe every detail including all deviations from the rule when describing the endless inventions and variations of evolution.

Let us make the assumption both reasonable and, today probably undisputed, that biological processes do not evade, but obey all physical laws. That means that we do not have to invoke additional factors, like a 'vital force' that would be needed to explain biological processes. Then, who would be better prepared to do biological research than a physicist? Indeed, physicists have made decisive contributions, as Helmholtz (physicists like to consider him one of their own breed, although by training he was an army surgeon) or Mach, to mention just two, give testimony. Both of them changed the field of biological research at their times, and established the foundations for visual, oculomotor, and vestibular research, on which this paper will focus.

The two approaches to research in biology

In biology, two very different approaches, which are sometimes difficult to bring together, play a complementary role. In simplified terms, the one approach investigates the logical operations that are necessary to perform a certain task, while the other approach investigates mechanisms. For example, to stabilize vision during head movements, motion has to be detected, and in response the eyes have to move to stabilize the retinal image in space. This example, at first sight, might seem simple, or even trivial: one needs a system to measure angular and linear acceleration, one needs to integrate this information twice to yield a position signal which is used to activate muscles. Indeed, animals low on the evolutionary scale have solved the problem with a very limited number of neurons. To formulate the problem, however, is by no means always as easy, and often enough unsolved, as will be shown below. The other approach is to find out how the problem was solved biologically, i.e. how the receptor system is built; how muscles are geometrically arranged to move the eyes; by which neuronal pathways the two systems are connected; and what neuronal codes are used to convey the necessary information. Here we are faced with the endless variations that evolution created, never for a specific purpose, but nevertheless well adapted over many generations to help the species survive.

If biologists and physicians increasingly turn to physicists and engineers seeking cooperation, and some very fruitful collaboration develops, it is still astonishing how approaches are vastly different. The biologist might start with careful observation of behavior, the physician extrapolates mechanisms from deficits which he observes in patients, the physicists might first want to define the logical problem, and the engineer will think of an optimal solution, as he is accustomed to build machines which are optimized for a certain task. A machine which is not, is considered to be of bad workmanship, and a machine without a task is a contradiction, unless it is declared to be a work of art. It seems that most interesting results were obtained when all types of approaches were successfully combined, as shown below with the description of some developments in oculomotor and vestibular physiology.

Logical problem stated, biological realization partially known

How to obtain a visual image with high resolution?

The receptor density varies considerably within the retina with the highest packaging density in the fovea. This is the reason for the high resolution which is matched by relatively wider representation of the foveal region at cortical levels. If all parts of the retina had similarly high receptor densities, and even if all cortex was dedicated to analyze just visual input, the surface area of the cortex would still be insufficient. Eye movements to targets of interest that need detailed visual analysis seem to have solved this problem. One can differentiate between saccadic movements that are optimized for speed to bring the eye to a new position of fixation, or pursuit movements that are optimized for continuously following a moving

target.

The logical requirements to solve this task are: (i) to measure the position or velocity of the target relative to the fovea, (ii) to translate this into a command to move the eyes, (iii) and to interpret the visual world as stable, although perceived with moving eyes. Decisive progress in investigating biological mechanisms was made with the introduction of techniques to record the activity of single cells in animals that were alert and could move their eyes in response to physiological stimuli [9, 20], and a training method to induce monkeys to fixate light spots [31].

The eye can rotate about any axis in space. This fact can be observed as compensatory movement during active or passive head movements, obviously to stabilize vision in space. When we do not move our head, but make spontaneous eye movements, or voluntarily in response to a target, it becomes apparent that we can move the eyes in a horizontal or vertical direction, but not about a torsional axis, i.e. the axis about the line of sight. Donders [8] was the first to make actual measurements with the help of after-images whose orientation he measured while the subject looked at different targets. Johann Benedict Listing, professor for physics in Göttingen, went a decisive step further and formulated the exact geometrical relations. He came to the conclusion that all eye positions can be reached from a reference position by a single axis rotation, and that all such axes lie in one plane. Either it was too evident for him or nobody showed real interest in such an elusive problem that he never bothered to publish his results. Helmholtz, however, realized the problem, saw the significance of Listing's work, and gave a full description of the geometry of eye movements in his book 'Physiologische Optik' [13]. Helmholtz stated 'This requirement leads . . . directly to the above already mentioned principle of Listing which this sharp-witted optician had communicated to Ruete, but without giving any proof and without explanation, how he arrived at this law' [12]. The importance of Listing's law goes wide beyond oculomotor physiology [16, 17, 18]. Similar laws can be found for head or arm movements. One sees the immediate significance, as eye, head, and arm movements have to be closely correlated when grasping something.

Reduction of degrees of freedom for motor control

It is only a few decades back that engineers started to build moving robots, which in their early stages would tumble and get into problems of instability. Engineers realized that first the general problem has to be solved of what control signals are needed to move multi-joint robot arms or legs in 3-dimensional space, in real time, and under the influence of gravity. Is this really a problem for physics? In a way, it is not, because it involves plain and well-known mechanical engineering. In a practical way, however, it imposes a huge problem, if one requires that the control job has to be done in real time, to varying demands, with unreliable hardware, and a limited set of computing power.

Nature had to invent a reduction of degrees of freedom for movement, shortcuts to

computing. In general terms, Bernstein [2] recognized the principle that for motor control the degrees of freedom of movement are reduced. On the sensory input side, neuronal mechanisms for feature extraction and object recognition have been the subject of both neurophysiological and computational work, recognizing the vast reduction of parameters as one moves from retinal pixels to limited classes of objects. Take as an example that you walk and something attracts your attention. You naturally turn your eyes and head to target the object which not only starts barking, but jumps at you. Visual input leads to a two-dimensional retinal image which projects to different cortical areas, and combines with directional acoustic input which continuously changes because you move your ears with the head. Besides parameter reduction, it requires a representation of different sensory inputs in a common spatial reference frame. As the result of the analysis a command is sent to the motor areas of the head and the eyes to turn towards the target. However, a simple displacement signal to be fed to motoneurons of the eye muscles is not sufficient, as angular rotations are not commutative, and the starting position of the eye has to be known to compute the orientation of the velocity axis for movement in three dimensions. The same applies for the signal to be fed to motoneurons of the neck muscles. As we walk, we not only move our head, but because the eyes are stabilized in space by the vestibulo-ocular reflex, eye position is continuously adjusted in three dimensions. One strategy could be to treat sensory input signals as two-dimensional with a third dimension for depth, and to compute motor commands within the same reference system as two-dimensional displacements [28]. In this way dimensions would be reduced as much as possible, when only at the very last output stage instantaneous positions are considered to compute actual rotation axes for the eyes, the head, and the rest of the body.

Take as another example handwriting: whether you write by just moving your fingers and your hand, or holding them stiff and write on a blackboard by moving your shoulder, the handwriting is so much the same that it can instantly be recognized. This can be taken as further support of the notion that central commands generate an abstract movement pattern, which only downstream, near to motor output systems, is translated into motor signals for motoneurons which have to take into account not only instantaneous limb position but also actual mechanical loads and the position of the limb relative to gravity. If that example still seems trivial to you, consider the hardware you have with synaptic transmission times of a few milliseconds. If you want to have a reaction time of less than 200 ms, and realize that most of this time is taken up by conduction velocities of about 50 m/s, then an optimization of multi-dimensional sensori-to-motor transformation by reduction of degrees of freedom not only makes sense, but is an absolute requirement.

Listing's law reduces the degrees of freedom of movement

Only recently had the full impact of Listing's law been realized, after tools had been developed to measure eye positions in 3 dimensions with high spatial and temporal resolution using the magnetic search coil method as introduced by Robinson [24]. General aspects

and biological implications had been described by Hepp [15] and he could not refrain from stating that this communication had first been rejected by a neuroscience journal. It seems that history repeats itself, if we read in Mach [22]: ‘Aristotle has said that ‘The sweetest of all things is knowledge’. And he is right. But if you were to suppose that the *publication* of a new view were productive of unbounded sweetness, you would be mightily mistaken. No one disturbs his fellow-men with a new view unpunished.’

There had been an on-going debate whether Listing’s law for the eye is the result of neuronal control, or mechanical properties of the eye-muscle plant, and there were good arguments for both opinions [29]. It seems that both views are right, but only to a certain extent. The eye together with its muscles is suspended in the orbit such that there is a position of rest, and that mechanical constraints of movements of the eye about different axes are very different. On the other hand, there are clear indications that neuronal control puts decisive precision to the movement. If optimization of motor control is stated as the reason for Listing’s law, this is an overinterpretation, because other functions evolved with it, which would be impossible, if eye movements did not adhere to Listing’s law. Horizontal disparity of retinal images is a decisive clue for stereoscopic vision. We do not have analyzers at the cortical level which could interpret torsional disparity, and stereovision would be severely impaired without Listing’s law. This is another example to illustrate that biological laws are never optimized towards a singular function. Mutations are random, and competition eliminates solutions which are worse than others within a given environment, but the evolutionary process does not optimize functions.

The challenge is that nature did not chose between alternatives like an engineer would do, but took advantage of most or all of these construction principles. Considered this way, the closest analogy might be a huge computer program developed over many years by many different programmers, which nobody wants to give up because it does its job. Compare this to nature which in the first place had no logical plan, developed its programs over millions of years, and void of a single line of documentation.

The generation of eye movements

To move the eyes from one fixation position to the next, Robinson [25] stated the logical problem: the motoneurons have to provide activation to a given muscle proportional to the change of eye position along the on-direction of the muscle and, to make the movement rapid, activation proportional to eye velocity. If one considers horizontal movements only, and relates motoneuron activity in abducens or medial rectus motoneurons to horizontal eye position, then the above statement can easily be quantified giving very reasonable results. The question arises, how can this equation be generalized to 3 dimensions, as the eye is attached to six muscles whose synergistic action has to be considered. The simple answer is, we do not know. After the anatomy of eye muscles had been known in detail since 250 years [32], and intricate mechanical models had been built in the last century, known as ophthalmotropes, it was early realized by surgeons who did strabismus surgery that eye

muscles might not take the shortest path between origin and insertion. Only recently had this problem been quantified [26]. There are mechanical constraints in the form of pulleys which hold the muscles in certain position, and the pulleys are themselves controlled by smooth muscles. That refers to the mechanical part. The neural control part is that we can measure activity of individual motoneurons, but in the alert animal only measure the change in eye position. Is motoneuron activity better related to force or length change? Can all motor units be characterized in a uniform way? A motor unit is defined as one neuron which usually innervates several muscle fibers. Some of the fibers run through the whole length of the muscle, and thereby relax fibers which run in parallel, other fibers run only over short distances of the muscle, stretching fibers which are put in series. Further differences relate to energy metabolism with specializations for speed or maintained contraction.

Biological variations of eye movement control

Let us make the speculative assumption that we would have finally understood how motoneurons control extraocular muscles and move the eye, and that this knowledge is firmly based on ophthalmological experience in patients and backed by experimental work in rhesus monkeys. If we want to generalize and turn to other animal species, take a look at their eyes and attached muscles, then we realize how little can be generalized. According to Block [3] the swordfish has developed a huge superior oblique eye muscle, which is primarily being used to keep the swordfish's brain at a constant temperature while cruising through waters of changing temperatures. Of course, every muscle produces heat during activation, but in this species heating seems to have become the main purpose, although the swordfish somehow still manages to move its eyes. Actually, the biological solution seems to be even more clever. Our own preliminary investigations¹ show that the marlin displays a full range of eye movements during the vestibulo-ocular reflex in three dimensions. Near the globe, all eye muscles are of normal appearance, while only towards the back of the orbit, in the immediate vicinity of the brain, eye muscles are gradually transformed to become heater organs. Again, a clever solution, adding a specialized function without giving up the task of moving the eyes.

Another example: the stargazer, a bottom dwelling fish of tropical and subtropical oceans, has a large part of the eye muscles transformed to an electric organ. The discharges are strong enough to immobilize prey, but they might also be used to localize it in the first place. To deliver highly synchronized electrical discharges, motoneurons in the oculomotor nucleus use electrical transmission [1], instead of chemical transmitters which seem to be prevalent in all other species.

Take the jumping spider: two of its 6 eyes can direct the line of sight into different directions, but the anterior part of the eye is fixed. The spider simply moves the back part

¹J.D. Pettigrew, K. Fritsches, V. Henn (Vision, Touch and Hearing Research Centre, University of Queensland, Brisbane, Australia): unpublished observations.

of the eye with the retina [21]. The tiny sea-born creature *Copilia quadrata* has even gone one step further: it has got just one photoreceptor which scans the image behind a fixed lens [10]. It slowly moves from one side to the other with a rapid reset. Or, take certain species of cephalopods like the squid which have up to 14 eye muscles, some of them running from one eye to the other, obviously a clever invention if one wants to symmetrically converge [5].

We take it for granted that both eyes move together. Indeed, it was one of the fundamental insights about eye movement control forwarded by Ewald Hering [19] that eye muscles receive equal innervation, so that the brain can consider eye movement control to be a task to move just one cyclopedian eye. In primates, i.e. men and monkeys, anatomical pathways and their physiological functions had been worked out in great detail (review: [14]). In particular, it was shown how activation of symmetrical structures in the brainstem are one of the preconditions to generate eye movements in three dimensions, i.e. to deliver appropriate, in first approximation symmetrical, activation and inhibition to all 12 eye muscles.

However, there are several species of animals which move their eyes independently, e.g. chameleons, some fish like the sandlance [23], while many birds show unequal amplitudes while moving their eyes. This is striking, because so far no clear anatomical differences have been found in the relevant brainstem structures.

Chameleons, e.g. belong to a very old species. They can move their eyes over a range of more than ± 90 deg, and do so for each eye independently. Direct inspection of their eye movements suggest that their eyes certainly do not move at random, but obey some rules akin to Listing's law. It is astonishing how similar environmental conditions might lead to similar adaptations. Chameleons and sandlances, a coral fish, follow similar strategies for food hunting. It seems that their eye as well as prey catching mechanisms show very close functional similarities [23].

It came as a surprise, when Dell'Osso [7] described a genetic defect in a dog, where the affected individuals moved their eyes independently, while unaffected siblings showed conjugate eye movements. This finding runs counterintuitive to all our understanding of oculomotor organization, if a defect produces an independent pattern of movement control for the two eyes, which the unaffected animal is not able to do. For somebody, who is accustomed to a theoretical approach, this is nightmare, while the biologist is simply delighted.

Many movements are done *not* to target. Whether observing a monkey colony at a zoo or being at a cocktail party: evidently, eye movements displayed have an important social function, a quick glance, staring at somebody, or averting gaze. One might argue that the logical analysis is trivial. This must be contrasted with the problems people encounter which cannot move their eyes normally. E.g., with the disease of progressive supranuclear palsy, the eyes are wide open and the patient has a staring look with conveys quite an uncomfortable feeling even to the neurologist who interviews the patient and who knows about the problem. Or take somebody with a strong squint, where you might not know with which eye he fixates; or somebody in whom the synergistic action of eye and facial muscles are at fault, where unexpected combinations of eye, lid and facial motions occur. These patients might have a

greater social disadvantage than somebody who is obviously blind. We are so accustomed to 'normal' eye movements that any deviation makes us feel uncomfortable.

Returning to the problem of averting gaze. During social contact, when gaze is averted, one has to know from whom to avert. Obviously we can direct attention in a direction that is different from the line of sight. The coupling or uncoupling of attention with eye movements, or the lack to direct attention can become a major problem in patients with neglect, usually as hemineglect to the left side, who, although they have vision to the left side, and can move their eyes in all directions, have their attention in a pathological sense directed only to the right side.

Comparative approach to find general rules

The above discussion might lead to the wrong impression that biological problems are so much intertwined and mechanisms so diverse that it will be hopeless to find general rules. Even if eye movements have certainly not evolved for the sole reason to optimize foveal vision, it obviously is a very useful asset so that genetic modifications going into other directions might be at a disadvantage. Let us take a look at the eye of an octopus. Although its macroscopic appearance is very similar to a vertebrate eye to such an extent that the experience of looking an octopus into its eye – hopefully also vice versa – invariably leaves the feeling of contact with an intelligent and inquisitive beast. Still, its eye went through evolutionary stages from a very different starting point. That can easily be shown as the receptor layer face opposite sites in the vertebrate and the octopus retina. The number and arrangement of eye muscles is completely different as mentioned above. Still, the vestibulo-ocular reflex in these animals seems to be functionally equivalent to the vertebrate reflex [6]. Eye movement functions in non-vertebrates like crayfish seem to have again evolved incorporating very similar functional principles [27]. It will be a challenge to investigate other animals, as distant as possible on an evolutionary scale.

This biological excursion was intended to illustrate how *one* biological requirement like vision can be solved by pursuing very different strategies; on the other hand, that *one* functional principle might emerge from very different anatomical constructs; most important, evolution does not lead to optimization of single functions, it rather makes it difficult for bad solutions to survive.

Logical problem not formalized, biological realization unknown

Face recognition is an innate biological ability. We take it for granted that we can with certainty recognize within 500 ms the faces of family members or friends among the 6 billion inhabitants of the earth. We do so independent of mood expression, sun-burnt or pale, with or without spectacles, hairstyle, or even the process of aging. 500 ms means that probably

not much more than 100 steps are involved, although in a highly parallel fashion. Contrast this to the enormous effort and results which had gone into automatic pattern recognition. Patients with a small lesion at the base of the occipital-parietal cortex on the right side can lose the ability to recognize faces [11]. Although their vision is otherwise normal, although they might be perfectly able to acoustically recognize people on the phone, they are lost when confronted with the face only. Usually they have learned tricks for recognition like a particular hairstyle, or spectacle frame, but they are lost when one changes such attributes. That we do not know what is being formally analyzed can best be seen by the fact that it is impossible to select a person just by verbally describing his or her face.

Language is another striking example where the logical problem has not been formalized. Of course, one might argue that one necessarily runs into the problem of recursiveness, but we still face the problem in a negative sense, that we are seldom able to formally describe deficits of language after focal lesions in the nervous system. Aphasia had been a central topic of many research efforts since their first scientific descriptions by Broca [4] and Wernicke [30], but only rather global classifications have been given. Conceding that every patient must remain an individual and singular case, because all his experiences, abilities and personality in some way reflect the phenomenology of disease and how it is experienced, the striking fact remains that with the same anatomical lesion in two different patients, the symptoms can be so far dissimilar that we cannot reduce them to the same formal functional deficit.

Logical problem formalized, biological realization unknown

Chess might be the one game where logical strategy means all, and luck nothing. How does it then come that still in 1996 the world chess champion Gary K. Kasparov was able to beat Deep Blue, a pair of 16-node parallel-processing computers? In the three minutes allowed for pondering each move, the computer was able to evaluate 2×10^{10} moves. This is certainly not what Kasparov did. Similar as the above calculation for face recognition, one can estimate that over three minutes, the human performed about 2×10^4 steps of serial computing (not knowing how many steps are necessary to evaluate just one move), but over an unknown number of parallel processors. Understanding the rules of parallel computing and formalizing them in a way that they are useful to describe the activity of large-scale neural networks, might be the most challenging task for the next decades.

Conclusion

As physical laws have taught us, without exemption, our world is on the road to maximal entropy, living creatures included. But biology has found a clever way to create order temporarily and within a well-defined space. To do so, many tasks have to be solved which in many cases can be stated in well-defined terms, although biological realization might be very complex and completely different from an engineering solution, and the solutions might not

be the same for different species. Biological research cannot 'give' anything to physics, but it can challenge physicists to understand complex rules like evolution or parallel information processing.

Physics has provided the theoretical framework to define many of the tasks and the analytical tools to analyze biological problems; physics as foundation for all engineering provided the technical possibilities to perform sophisticated experiments; but one should never forget that what makes engineering interesting is the optimization of a machine for a certain purpose, and what makes biology interesting are the strategies to survival which abound in 'inventions' and tricks which are never restricted to a single solution, because the conditions of the game continuously change. While the naturalist accumulates detail and is fascinated by the exception, the physicist strives to arrive at a general level of description. The physicist has to abstract from the rich phenomenology of biological solutions and can thereby give biologists the tools to understand the endless variations of biological solutions.

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