

Intricacies of movement control. An essay

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The synthetic approach of robotics and the analytic approach of motor physiology have not yet reached much common ground. To be sure, some ideas first formulated in engineering have entered the vocabulary of the physiologist (e.g. position feedback, bang-bang control, stability, frames of reference) thereby making the writings of each camp more palatable to the other. However, the engineers still regard the biological system as just one possible solution among many, almost certainly not the most efficient one. Conversely, to the physiologist, the robot looks much too clumsy to be ever taken seriously as an approximation of the real thing.

I believe that we could come closer to each other if each would actively invade the other's territory, the physiologist inventing machines unhampered by restraints of technical feasibility, and the engineer explaining the brain in ignorance of the (indeed scanty) physiological evidence. I will do a little bit of both, putting myself in the role of both kinds of trespassers, combining so to say two kinds of ignorance in the hope of achieving some fruitful synthesis.

1. PHENOMENOLOGY OF ANIMAL MOVEMENT

Movement is a change of the position of parts of the animal relative to each other. We shall distinguish this from locomotion (often also termed movement in ordinary language) which is a change in the position of the animal relative to external coordinates. In most cases locomotion implies movement, but it may occasionally be almost independent from changes of the animal's configuration, as in the case of a medusa drifting in the ocean.

Neglecting forces generated within the animal tissue, we may distinguish *movement against an opposing (external) force* from simple *deformation*. Both categories admit of further classification.

Deformation may or may not change the position of the center of mass within the body. In the first case it is *asymmetrical deformation*, as in the case of an amoeba protruding a single pseudopodium from the bulk of its body. Extending or flexing one arm is of this kind too. In the other case, when the deformation is *symmetrical* with respect to the center of mass, the latter keeps its position within the body. We may think of a human (in space) thrusting his arms upward and extending his legs just in the right proportion. Note that movement symmetrical with respect to the median plane, the plane of bilateral symmetry, is not a sufficient condition: lifting both arms symmetrically will raise the position of the center of mass.

Extending a pseudopodium (or an arm) may not only change the position of the center of mass within the body, as it would if the force producing the extension were radial with respect to the center of mass, but may also produce a *rotation* of the bulk of the body if it is not. There is also the case of a rotation of the body without movement of the center of mass, as in the antisymmetric extension of two pseudopodia along separate lines lying on either side of the center of mass.

The principal form of movement in animals with either exo- or endoskeleton is rotation of one part with respect to the other around a hinge or joint. It is remarkable how jointed appendages (limbs) are more similar to pseudopodia than would appear at first, since *extension* and its opposite *flexion* are the dominant mode of action in limbs consisting of two main (i.e. more bulky) segments such as upper arm and forearm, thigh and lower leg. When in extension or in flexion the two segments rotate in opposite directions, as they mostly do, the principal effect is that of extending or shortening the limb, i.e. of shifting the center of mass of the limb away or towards the body like in a pseudopodium protruding or contracting. The angular momenta of the two segments tend to cancel each other, thereby minimizing the torque transmitted to the rest of the body.

Swinging an appendage on its hinge (e.g. an arm around the shoulder) will produce an opposite rotation of the bulk of the body around a correspondingly smaller angle. The change in the orientation of the animal would seem to depend on a change in its conformation, since the body returns to its original orientation when the arm is swung back to its previous position. Can an animal perform any movement such that it ends up in a new orientation with the original relative position of the moving part and the bulk of the body? A machine with an internal fly-wheel can of course do this if the fly-wheel turns an integral number of times around its axle.

A body appendix may act as a *fly-wheel* if the hinge connecting it to the body has two degrees of freedom. This is the way a cat thrown into the air lands on its feet after it regained its upright position by swinging its tail around appropriately, roughly describing the surface of a cone. It is an interesting question whether the same effect can be achieved by movement of a limb in one plane. We have already seen that a rigid limb will not do, but a pseudopodium could swing its center of mass in a circle by an appropriate combination of contraction/expansion and swinging. A jointed limb such as our arms and legs can do the same. It is noteworthy that this depends on the body being heavier than the two segments of the limb. A "*worm*" made of three equal segments connected by joints with motors cannot change its position in space by any combination of movements in the two joints: starting from a stretched conformation it will always end up stretched in the same orientation as before. However, if one of the segments (except the middle one) is longer, or heavier (= has a greater moment of inertia) than the others, there are patterns of movement that will result in a change in orientation, as can be readily shown by computation of elementary mechanics. Of course, a worm consisting of four equal segments can also do the trick, since it can double over two of its segments to make one heavier one as it were.

Note that a flexible body as a whole can perform a similar motor strategy. Think of a skater threatening to fall over forward or backward. Since he cannot exert any (horizontal) force against his support, he is in a situation similar to a man in space. He will shorten his body by bending his knees, then stretch out again and at the same time bend his

body, the whole performance designed to regain the vertical position (of course in this case we cannot exclude the role of forces exerted vertically against the support).

A kind of movement where the opposing forces are mostly internal is *oscillation*. Periodic to and fro movement occurs in many biological contexts (a dog scratching itself, a woodpecker pecking etc.). Of particular importance is harmonic, pendular oscillation. In it the kinetic energy of the movement is stored in the restoring forces instead of being dissipated, as it is in other kinds of movement.

Deformations of the body *against external forces* are of a different kind. We may distinguish the following cases: An important category is movement against or in the direction of gravity. This is important especially in keeping the upright *posture*. Gravity is much less important, however, in limb movement where, at the speed of ordinary motor performance (such as bringing a glass of wine to one's mouth) the inertial forces generated by the movement always exceed gravity. An impressive demonstration is swinging a pendulum around. The angular velocity at which the pendulum hangs at 45° , i.e. the centrifugal force equals gravity, is much below the speed of so-called "fast voluntary movements". With the elbow bent at 90° , and $r = 0.2\text{m}$ (the length of the upper arm), the centrifugal force on the forearm $mr\omega^2$ exceeds gravity mg for all speeds beyond 1.1 rotations per second, a fairly moderate speed, comparable to that of an orchestra conductor beating *adagio*.

Pushing and *pulling* are movements in which the active animal becomes involved in a mechanical system comprising other bodies. Pushing away or pulling towards are clearly defined by changes in the relative position between the two partners. But these terms apply also to situations in which the relative position does not change. Pushing a cart is exerting a force against a force that tends to shorten the distance, without actually changing it, pulling against one that tends to lengthen it. Pushing or pulling downhill, however, demonstrates that the position in front or behind the object being pulled also plays a role.

Pushing and pulling become highly involved when both partners, being animate, participate actively in the interaction. In such a situation there is room for complex planning of motor actions with the reactions of the partner homogeneously involved in the computation of one's own movement. Pushing (or pulling) against frictional forces is at the basis of locomotion.

Jumping and *throwing* are special cases of pushing where the contact between the agent and the object is interrupted at some point. The obvious difference between the two is the relative bulk of the object, much bigger than the agent (= the earth) in the case of jumping, smaller in the case of throwing. They have in common the dynamics of the limb acting on the object. In order to achieve sufficient velocity the force has to be applied for some time while the contact is kept between the agent and the accelerating object. For this either the motor must accelerate while it applies the force, or there must be a variable coupling. The rolling joint of the human knee may have something to do with this.

Touching and *holding* are the gentlest forms of movement, if indeed they can be called that. In touching the position is controlled by the elastic forces arising in the deformation of the tissue at the point of contact. Holding is a more complicated performance and involves the readiness to react to unforeseen disturbances. Holding a chopstick between

the index finger of both hands while moving both arms remains one of the most astonishing motor performances.

There are other situations in which the concept of movement as it is mostly held becomes elusive. Think of a *piano player*. Most of the time his arms do not move, only his fingers execute tiny movements in precisely predetermined sequences and combinations. Energy is hardly of concern here, nor are the masses of the fingers such that inertia would play a significant role. As in handwriting or in typing, in the execution of music the individual movements are completely at the service of a channel of communication, the entire performance being of the nature of information rather than of the mechanical interaction between an animal and its environment.

Locomotion, the other main category of movement beside deformation, occurs in a great variety of types, ranging from the crawling of a snake to the gaits of a horse, not to mention various techniques of swimming and flying. These have all been well analysed and offer fewer conceptual challenges than the types of deformations mentioned before.

2. MOTOR CONTROL

The preceding excursion into the taxonomy of movement was aimed at conveying a feeling for the complexity of the task facing the nervous system at its output end. Studies on motor control have often concentrated on isolated simple situations such as movement of a human arm in one or two joints, or have given up on an exhaustive analysis in more complex cases, such as that of a human maintaining his upright posture while being shaken on a movable platform. I believe that situations considered in isolation may lead the interpretation astray. For instance, the tendency of the hand to follow a straight trajectory when reaching a target away from the body (Wadman et al. 1980, Morasso 1981) and less so, when the movement involves swinging the whole arm sideways is only puzzling if the fundamental mode expansion - contraction is not taken into account. As we have seen, this involves rotation of two segments in opposite directions, annulling angular momentum and having the straight trajectory as a trivial geometrical consequence.

Another case in point is the movement of the man keeping himself upright on skates, or being shaken on a platform. Once we have realized that for any fast movement the inertial forces are much more important than gravity, we will not be surprised to observe correcting forces directed against the support which seem actually to destabilize the situation (Dichgans and Diener 1987). They are part of a motor strategy which the man would use if he wanted to change his orientation in free space, devoid of any support. He uses some part of his body as a fly-wheel to generate the angular momentum which brings the body into the desired position. The complex motor reactions of the man on the platform have not been analyzed with this idea in mind, but a simpler situation may illustrate the point. A beginner on skates leaning backward beyond the point of stability regains control by rotating his extended arms around a transversal axis through his shoulder, in the direction up in front and down in the back. In the up-in-front phase, considering only linear acceleration, he helps the action of gravity and would seem to contribute to his fall. But gravity is unimportant in the correction although it is in the threat of falling. The correction is a question of playing angular momenta against moments of inertia.

A third example. Soechting et al. (1986) wondered about the differences in the results

of drawing a circle (or rather a succession of superimposed circles) on a board transversally in front of the subject as opposed to drawing on a board oriented in the sagittal plane. In the first case the outcome is a good circle, while on the sagittal plane a very distorted figure is obtained. Here we must remember the tendency of limbs to adopt energy saving pendular motion. With the arm stretched toward the blackboard, the center of mass of the arm is roughly in the elbow. A combination of two pendular motions at right angles to each other and at the right phase angle will make the center of mass describe a circle, and the hand too. In the other situation the arm has to bend during the motion, with the center of mass of the arm moving to different positions on the bisectrix of the elbow angle depending on the angle. If the center of mass is again allowed to follow the energy (and control) saving circular trajectory, this time in a sagittal plane, the trajectory of the hand will be something very similar to the shape Soechting et al. have observed (Braitenberg 1988).

My plea is for the simplest possible principles of mechanics to be invoked in the explanation of movement since the motor system, in order to be efficient and economical, cannot but conform to such principles.

3. INVENTING THE CEREBELLUM

Most of the motor performances mentioned are quite complex and would involve a great deal of computing power for their control. On the other hand, if only the goals of the movements are considered, such as reaching a certain object with an arm or turning the body around a certain angle, the description is much simpler and the interplay of the movement with the sensory input turns into a more homogeneous affair.

If I were to invent a control system for movement, I would therefore distinguish two main tasks and assign each to a separate mechanism. The first task is movement as the deliberate influence on the state of the world whenever the sensory input does not conform to the desired picture. This we may call *action*. It is best described as the transition from one internal representation of the world, including the agent's position in it, to another more desirable one, with the motor output arising as a consequence of the transition.

The other task is keeping the body as a whole stable. *Stability* is threatened not only by perturbations coming from the outside, but even more so by the mechanical disturbances which every intended movement, when it is executed, necessarily communicates to the rest of the body. These disturbances are of various kinds. One is simply *actio = reactio*: every active movement of one part of the body provokes an opposite movement in the support. Another is connected with inertia: movements tend to overshoot. Another again is due to elastic elements which are involved in the machinery and which release their energy after the force ceases to act.

The mechanism which takes care of the first task, *action*, if we consider it in isolation, is of the simplest kind. We provide a cognitive machine, whose complex internal structure shall not detain us at this point, and see to it that all relevant states of the world are represented in states of activity within the mechanism. These internal states include representations of the animal's position in the world, and of the relative positions of its body appendages. Now we only have to arrange connections between the internal elements representing parts of the body and the parts themselves. The connections are

of two kinds, efferent and afferent. The efferent connections translate the states of the internal elements into signals to the motors which activate them exactly to the degree that corresponds to their state of contraction in the internal representation. The afferent connections, on the contrary, signal deviations from the internal representations and can then be used to assess external forces that are in the way of the motor realization. In this view, the position of the body is an automatic consequence of "thinking" that position. Movement is an equally automatic consequence of rethinking one's position, of changing one internal representation into another one (for whatever reason this may happen).

This scheme corresponds to an idea which was proposed as "equilibrium point control" in motor physiology by Feldman (1986) and by Bizzi et al. (1982). It is excellent for slow movements and quite plausible in terms of neural mechanisms. With fast movements, however, all the inertial, elastic and other complications come into play. Here we must add a more down-to-earth mechanical computer to the cognitive machine which proposes the action.

The *computer of stability* could in principle be informed about every transition planned by the cognitive machine. Incorporating knowledge of the laws of mechanics and of the quantities (mass, shape, elasticity, viscosity) involved, it could in principle compute all the deviations from the planned action and produce the corrections in real time. In praxis this does not seem to be feasible, judging from the reluctance of mechanical engineers to tackle simple multi-jointed and multi-motor-systems even with the aid of powerful computers. Hence for the problem of stability I would resort to a more empirical approach based on learning. The conditions for my machine are the following.

Since many different situations have to be dealt with for which there is no common solution, I would compartmentalize my machine. Each compartment I would make responsible for the corrections associated with one particular movement.

The trigger for each of the corrections is the planning of a particular movement. Since we decided to represent movement in the cognitive machine not as such but as a sequence of static representations, the trigger signal coming from there and reaching the stability machine will be a particular sequence of signals in time. The stability machine thus has sequences as input and must associate to each a particular output sequence. My machine would work in a sequence-in, sequence-out mode.

The best way to display a sequence in a machine (if it is not supposed to incorporate any moving carriers such as disks or tapes) is to display them in linear arrays in which different locations stand for different phases in the sequence. The compartments of my computer would have an elongated shape, with the long axis representing time. Many such elongated compartments arranged in parallel would give my stability machine a very characteristic architecture.

Signals from the cognitive machine would reach different compartments in different combinations and at different locations (signifying different phases). Thus each compartment would display a particular sequence of signals. I should like each compartment to react to the corresponding sequence. This can be achieved very simply by connecting the input points within the compartments through delay lines which produce exactly the delays between the elementary signals as they occur in the sequence. This way, when the elementary signals reach the compartment at different times in different places, through the delay lines they add up to a synchronous powerful signal. In other compartments, the

spatial distribution of the elementary signals and therefore the delays being different, the same signal would hardly produce any effect.

Having thus mapped sequences on compartments, all we need to do is to let the compartments produce the desired output sequences. With all the delay lines in the compartments already there, we have a device which can easily produce sequences by letting signals sweep through the delay lines in order to trigger appropriate output elements. The best way to do this is to use the signals set up by the input in the delay lines to activate the output elements.

The output elements would have to be connected to the delay lines at appropriate locations, dictated by the phase at which the correction must come in during the movement. I would let the choice of the phase happen in the course of a learning process. This would transform the clumsy, angular, overshooting movements of the beginner into the elegant performance of the accomplished violinist or gymnast. The learning process would be under the guidance of afferent input monitoring all the slinging, all the stresses and strains which are generated locally by less than perfect movement.

Finally, I would try to minimize expenditure of mechanical energy. What comes to mind is to make the corrections as much as possible by diminishing motor action rather than by counteracting the error actively. With all the passive inertial forces arising during movement, it would be wise to diminish the action of the motors that act in the direction of an inertial (e.g. centrifugal) force, rather than to counteract it by further expenditure of motor energy.

The reader will have observed that the machine I have been inventing has many features in common with the cerebellum. The cerebellar cortex is a large array of elongated compartments, the *folia* or *beams of parallel fibers*. They acquire their individuality by virtue of the system of inhibitory fibers (*basket* and *stellate cell* axons) which are arranged at right angles to the beams and therefore functionally isolate one beam from another. A large proportion of the input to the cerebellum is derived from the cerebral cortex (the "*cognitive machine*") via the pontine nuclei. The bulk of the internal connections in the cerebellar cortex is provided by the *parallel fibres* which, being long and slow may well act as delay lines. The output cells of the cerebellar cortex, the *Purkinje cells* are connected to the parallel fibers via dendritic spines, a trait which we take as an indication of *plasticity*, i.e. learning. The action of the Purkinje cells on the cerebellar nuclei and further in the motor output is *inhibitory*, in agreement with the energy saving principle we had postulated.

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