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"The Cerebellum and the Physics of Movement: Some Speculations"

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THE CEREBELLUM AND THE PHYSICS OF MOVEMENT: SOME SPECULATIONS

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Cerebellar Anatomy: physiological inferences

In order to catch the characteristic features of the wiring in the cerebellum, comparison with the cerebral cortex is useful.

Surface area and number of cells are of the same order of magnitude in the cerebral and cerebellar cortex. But in contrast to the cerebral cortex, the organization of which is best described by reference to the so-called cortical "plane", the cerebellum is not really a 2-dimensional network. It is more correct to say that it has a one-dimensional layout, given by the direction of the parallel fibres, repeated many times in parallel. The connections at right angles to that are of a completely different nature: axons of inhibitory interneurons and branches of afferent fibres. The first separate out "beams" of parallel fibres by neighbourhood inhibition. The afferents establish some sort of common interest in longitudinal strips of cerebellar cortex. (Of course, there are some who like to see it the other way: one-dimensional longitudinal strips as the working units of the cerebellum, most evident in projection-studies, interacting in some mysterious way via parallel fibres).

Then, the loops of excitatory connections which make the cerebral cortex into a network characterized mainly by positive feedback are missing in the cerebellum. The excitatory connections are all feed-forward (afferents and parallel fibres). This is why we don't get epileptic fits there.

Finally: the cerebellar cortex is continuous across the midline. This is quite unique: the plane of mirror symmetry of the body is not represented as a discontinuity in its projection on the cerebellar cortex.

Rereading the arguments which led, many years ago, to the idea of the cerebellar cortex as a device apt to transform space-intervals into time-intervals and vice versa (Braitenberg & Atwood, 1958), we find that they still stand up against the massive electro-physiological evidence that has since accumulated. And they do indeed explain much of the peculiar morphology of the cerebellar cortex and of its constituent elements. What is not so convincing is that part of the theory which has received the widest publicity: the idea of parallel fibres working like kitchen timers which produce signals after predetermined intervals, proportionate to the relative distance of input and output along a folium in the cerebellar cortex. Whatever the status of this "timing" scheme in contemporary motor physiology, it is hard to see how the intervals between the innervations of different muscles which are needed, say, for so-called bang-bang control of limb movements, could be produced by parallel fibres.

A single parallel fibre, with its length limited to a few millimeters, can produce time intervals of at most 10 ms, much too short to be relevant. Chaining of parallel fibres, to make longer "delay" lines, would require synaptic connections which are found neither anatomically nor electrophysiologically.

However, a system which establishes equivalences between space and time, so convincingly present in the cerebellar anatomy, may have other uses besides the generation of time intervals between agonist and antagonist innervations (Braitenberg, 1983). I propose the following (Fig. 1.A)

Let some sensory space be represented on the surface of the cerebellar cortex in such a way as to make movement in one direction through that sensory space produce a continuous movement of the image along the direction of the parallel fibres. It can be seen that, when the image moves through the cerebellum at the same speed v_0 as that of conduction in parallel fibres, a sort of tidal wave is set up in the system which will produce strong excitation in the neurons (Purkinje and stellate) which are contacted by the parallel fibres. In fact as the signal moves through the cerebellum a distance corresponding to the length of one parallel fibre, the travelling waves produced at the different locations will summate. If the signal moves further in the same direction, the "tidal wave" will stay at the same, maximal, amplitude. For signals moving at different speeds, either higher or lower than v_0, the tidal wave is lower. The expression for the amplitude of the wave is

$$E = \frac{v}{v-v_0}$$

It is plotted in Fig. 1.B. The expression and the graph disregard the fact that there is saturation of the tidal wave due to the limited length of the parallel fibres (only in the small cerebellum of the frog and perhaps of other small vertebrates do the parallel fibres reach from one end of the cerebellar cortex to the other).

Fig. 2 shows the development in space (horizontal) and time (vertical) of excitation set up in the cerebellar cortex by a stationary stimulus and by a stimulus moving toward the right at velocities equal to, larger than or smaller than the intrinsic velocity of the parallel fibres, v_0. The wave produced by the stationary stimulus peters out at a certain distance due to the limited length of the parallel fibres. The waves produced by a moving stimulus reach their maximum and then stay constant as long as the movement lasts. The peak excitation is highest for $v=v_0$.

Thus we interpret the cerebellar cortex as a velocity detector. It is tuned to the intrinsic velocity v_0 of conduction in parallel fibres. This may correspond to different velocities in the sensory spaces, depending on the magnification factor or scale at which the sensory space is represented on the cerebellum (Fig. 1C).

We must remeber that the connectivity of the molecular layer of the cerebellar cortex is essentially one-dimensional, at least as far as the system parallel fibres-Purkinje cells is concerned. Therefore, if the velocity of anything moving through the animal or its sensory spaces is

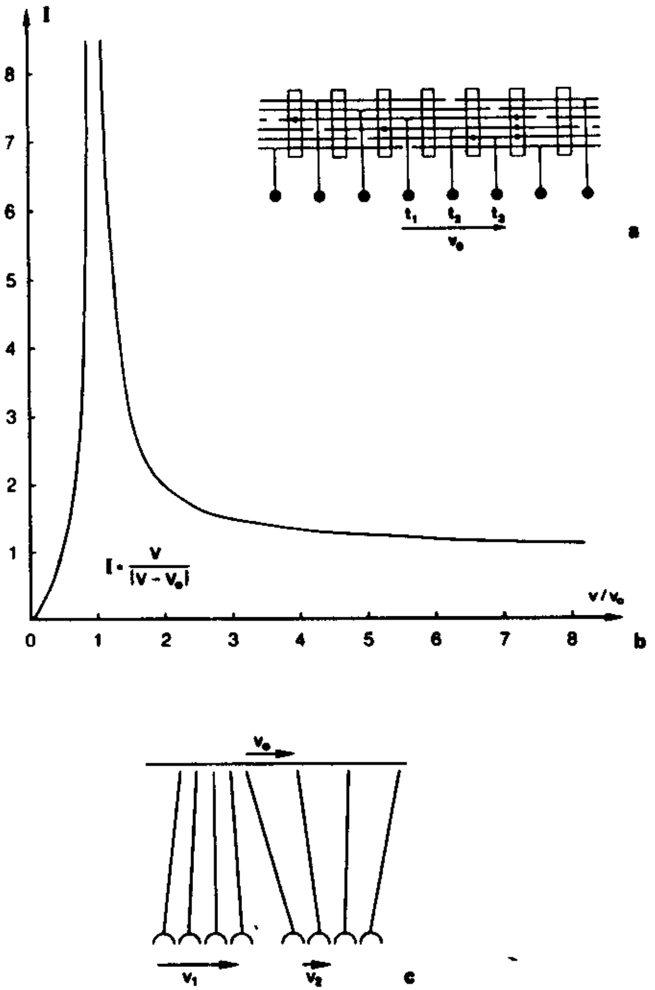

Fig. 1.A: Parallel fibres are shorter than the folia of the cerebellum in which they are located, and they are staggered. A stimulus reaching a row of granular cells at times t_1, t_2, t_3 corresponding to movement with the velocity v_0 of conduction in parallel fibres will produce coincident excitation (asterisks) or Purkinje cells (rectangles) (from Braitenberg, 1983, Fahle & Braitenburg, 1984).

B: Plot of the function I (v,v_0) which relates intensity of local excitation I to the velocity of the stimulus v and the velocity of conduction in parallel fibres v_0. In reality the magnitudes involved are of course finite and the function reaches a finite maximum at $v=v_0$.

C: Different velocities v_1 and v_2 in a sensory space may correspond to the intrinsic velocity v_0 of the cerebellum when different magnification factors are involved in the projection.

measured by the cerebellum, it is important to know how the sensory space, or the muscular system of the animal, is oriented in its projection on the cerebellar surface. The cerebellum can only measure velocities in one direction at a time, in the direction projected onto parallel fibres.

Detailed studies of somatotopy in the anterior lobe of the cat's cerebellum have been carried out by Oscarsson and his coworkers (Oscarsson, 1969, 1980; Ekerot & Larson, 1980; Andersson & Eriksson, 1981). If I read their results correctly, it seems to me that we can deduce three fundamental facts from them: (fig.3)

1) There are multiple representations of the cat's body on the anterior lobe.

2) The orientations vary. The direction of the parallel fibres in one of the projections corresponds to the antero-posterior axis of the cat, in another projection to the latero-lateral direction and in a third one to the proximal-distal direction of the extremities.

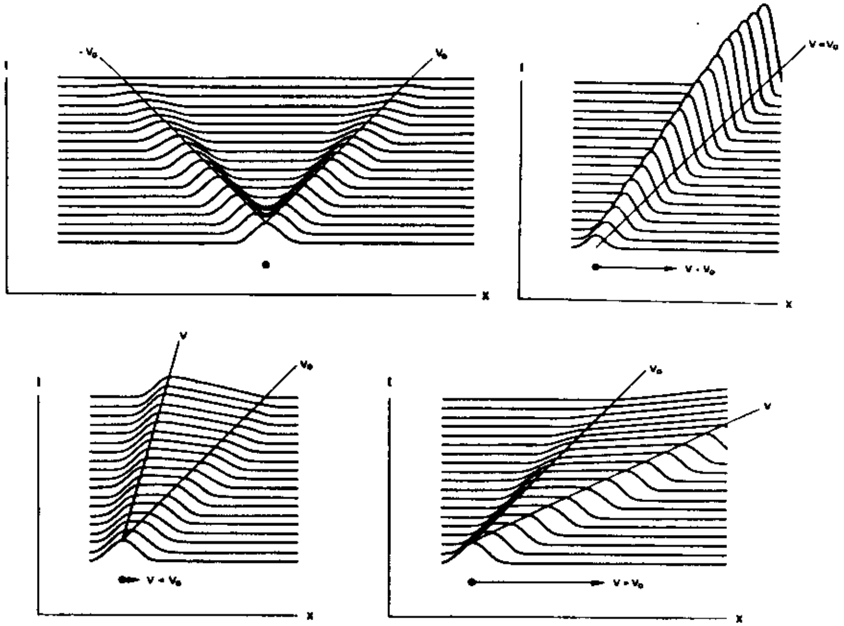

Fig. 2. Waves of excitation propagating in the molecular layer of the cerebellum (hypothetical). The direction of the parallel fibres is represented in the horizontal (x), time runs upward (t). Upper left: a pulse of excitation (black dot) sets up two waves running in opposite directions and extinguishing when the end of the parallel fibres is reached. Upper right: A stimulus moving at the intrinsic velocity v_0 sets up a "tidal wave" of maximal amplitude, whereas different velocities (lower left and right) produce lesser waves.

3) The magnification in the various projections varies considerably. In one map the entire length of the cat is represented on 1mm cortex, in other places the same length corresponds to more than ten times as much.

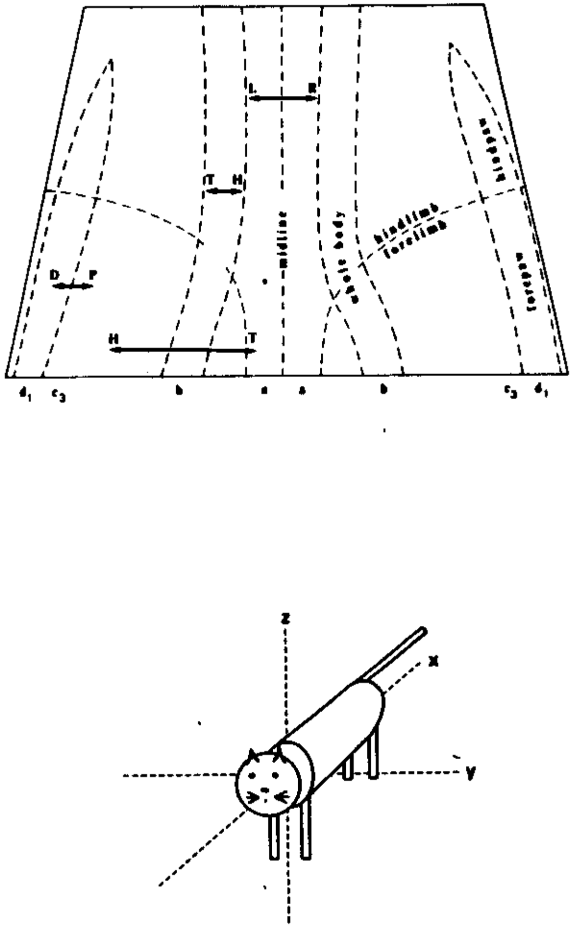

Fig. 3. (from Braitenberg, 1983, Fahle and Braitenberg, 1984) Simplified version of the somatotopy in the anterior lobe of the cat cerebellum as established by Oscarsson and his coworkers. The direction of the parallel fibres is horizontal on this map. It corresponds, in different somatotopic maps to the longitudinal (x), transversal (y) or vertical (z) coordinate of the cat's body, marked on the map as H-T (head to tail), L-R (left right) and D-P (distal-proximal). Data from Andersson and Eriksson, 1981; Ekerot and Larson, 1980; Oscarsson, 1969, 1980.

It would seem, therefore, that the cerebellar cortex measures separately certain kinds of movement that go through the body of the cat in various directions, and the varying magnification factor indicates that the characteristic velocity v_0 corresponds to different velocities in the body of the cat. What kind of movement can this be? A clue is provided by the region (the b-zone of Oscarsson) where the length of the cat corresponds to 1mm cortex. With that magnification, the intrinsic velocity of the cerebellum of 0.5 m/s corresponds to about 200 m/s in the body of the cat. This is in the range of the velocities at which mechanical waves propagate passively through compressible bodies. In other parts of the anterior lobe, where the maps of the cat's body are more extended, the intrinsic velocity of the cerebellum corresponds to lower velocities in the cat's body, perhaps those of transversal waves such as are generated by a bend which propagates through the body.

In the most general terms the idea that may be drawn from these observations is this: The cerebellum checks on global aspects of motor behaviour, especially on mechanical disturbances propagated passively through the animal's body. It is reasonable that the sequences of activation of various muscles should respect the phase of the mechanical waves which are set up

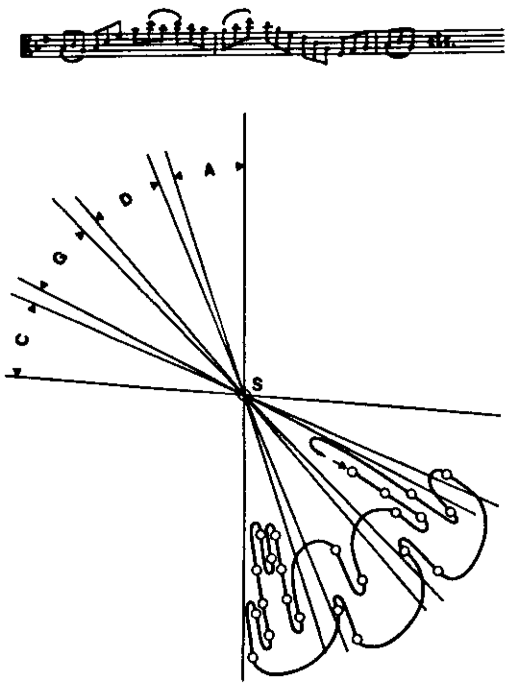

Fig. 4. In the execution of the passage above, the right arm of the violist performs movements toward and away from the point (S) where the bow touches the string, and rotational movements around S which determine which of the 4 strings of the instrument, A,D,G,C is touched by the bow. The two movements combined produce the trajectory to the right below. The white circles correspond to the quavers of the musical notation (about 160 ms). S can be thought of as the projection of the long axis of the instrument.

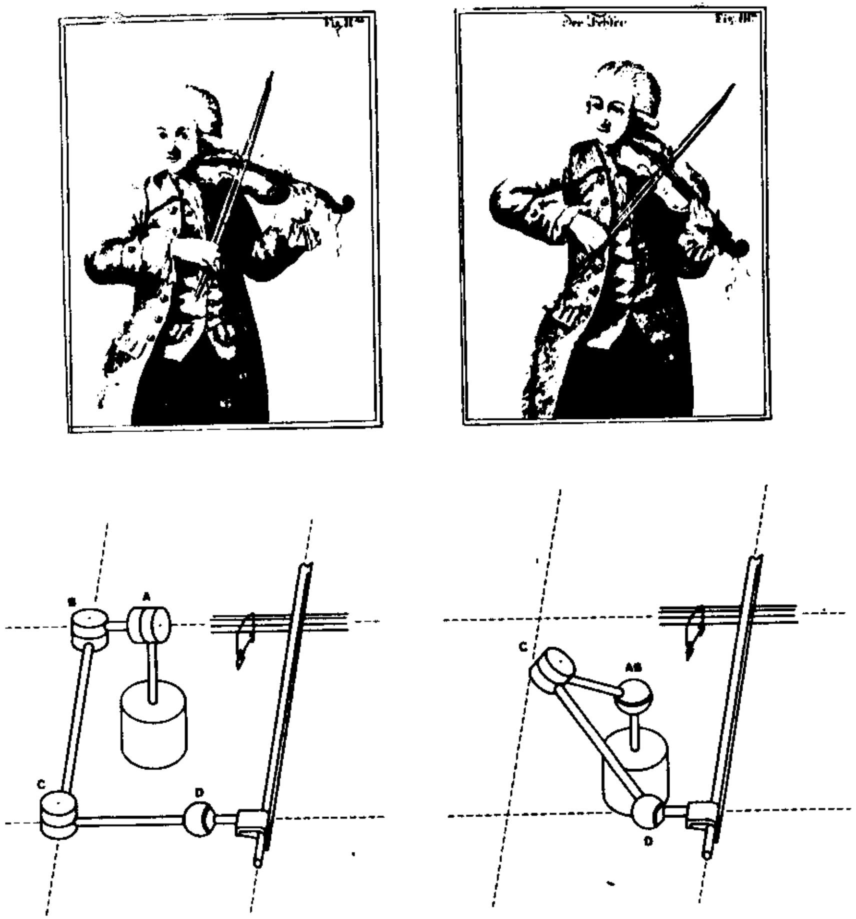

Fig. 5. Separation of tasks: the up and down movement of the bow and the inclination determining the choice of the string (see Fig. 4) in the correct position (left, from Leopold Mozart's school of violin playing) are subserved by different muscle groups. In the diagram below, rotation in the joint A produces string selection, while the up and down movement of the bow is accomplished mainly through rotation in the joints B and C. Upper arm, forearm and bow are coplanar. With the incorrect position (right, "Der Fehler") the three segments are not coplanar. The two rotations A and B are combined both in string selection and in the up-down movement of the bow. A,B correspond to the shoulder, C to the elbow and D to the wrist.

by external disturbances (e.g. by the shock produced in the landing after a jump) or by localized movement (e.g. by the contraction of a muscle at the proximal joint of a limb). This information must be considered in the timing of further movements, e.g. in the stabilizing adjustment after the jump, or in the movement of more distant joints after initiation of the movement in the proximal joint of a limb. Hence the role of the cerebellum in "timing". On the other hand, the mechanical wave propagation through the body is in itself dependent on the state of contraction of the muscles. When the temporal program of a movement is predetermined, it could be the speed of passive mechanical wave propagation which is adjusted to the timing by a control of the elastic constants (= by the control of stiffness). Hence the role of the cerebellum in "tonic" innervation of muscles.

The unifying concept of an organ taking care of global dynamic aspects of movement explains the two-faced symptomatology which follows cerebellar lesions: disturbances in the motor program (ataxia, decomposition of movement and the like) on the one hand and changes in the tonus on the other. But it would be premature to elaborate the mechanism in too much detail, since not enough is known about the connections between the cerebellum and the rest of the brain both on the input and the output side.

Problems of motor coordination in a concrete example

I will now show in one example how passive mechanical movement is combined with rather complex patterns of innervation to produce the movements of the bowing arm in string-instrument playing.

Fig. 4 represents the movement of the right hand of a violist playing the short passage above. The task is twofold: (a) moving the bow, in the direction of its long axis, away and toward the viola to set the string in vibratory motion, the changes in the direction of bowing being dictated by the rhythm of the music, and (b) rotating the arm with the bow around the long axis of the instrument in order to select the appropriate string (A,D,G, and C string on the viola).

Depending on the way the bow is held, the two tasks a and b are accomplished by more or less the same muscles of the right arm, or by different sets of muscles. The latter seems to be the more desirable solution, for beginning with Leopold Mozart's school of violin playing (1756) all 8 major schools emphatically favoured a position in which the upper arm, lower arm and the bow are coplanar: the motor mechanism of string activation is entirely confined to this plane, while the selection of the appropriate string is entrusted to another muscle, the deltoid which makes the plane of bowing rotate around an axis piercing the shoulder parallel to the axis of the violin (Fig. 5). Thus we learn that separation of tasks is an important principle in motor control. Whether it has anything to do with the cerebellum is not clear, although Pellionisz (1986) suggests that it is the business of the cerebellum (among other things) to calculate the transformations of the coordinates which are needed when the dimensions of the execution do not correspond to the dimensions of the task. If this is true, the first principle of violin bowing illustrated in Fig. 5 is one which frees the cerebellum as much as possible from the work which Pellionisz would assign to it.

Fig. 6 illustrates a difficulty which unavoidably arises when movement along a straight line, such as the movement of the bow across the string, is executed by a jointed arm. In the course of the extension of the arm, the movement which is at first in the upper segment, is slowly taken over by the lower segment. Eventually, in the last part of the extension, the upper segment moves in the opposite direction. All of this is simply geometry, but imposes important constraints on motor control. Among other things, the contraction of some of the muscles (involved in the extension/flexion of the upper arm) is not related in a monotonic fashion to position: the translation of position into muscular contraction may involve a change in the sign at a certain critical stage.

But even more interesting problems of motor control arise with the faster movements. Fig. 7 illustrates three standard strokes: smooth bowing (detaché) martellé and staccato. The diagrams very schematically indicate position, velocity and acceleration for the three cases. The last two lines show the muscular innervation that presumably takes place in the agonist and antagonist muscles involved. It can be seen that the pauses between the up and downstroke in the martellato case require each stroke

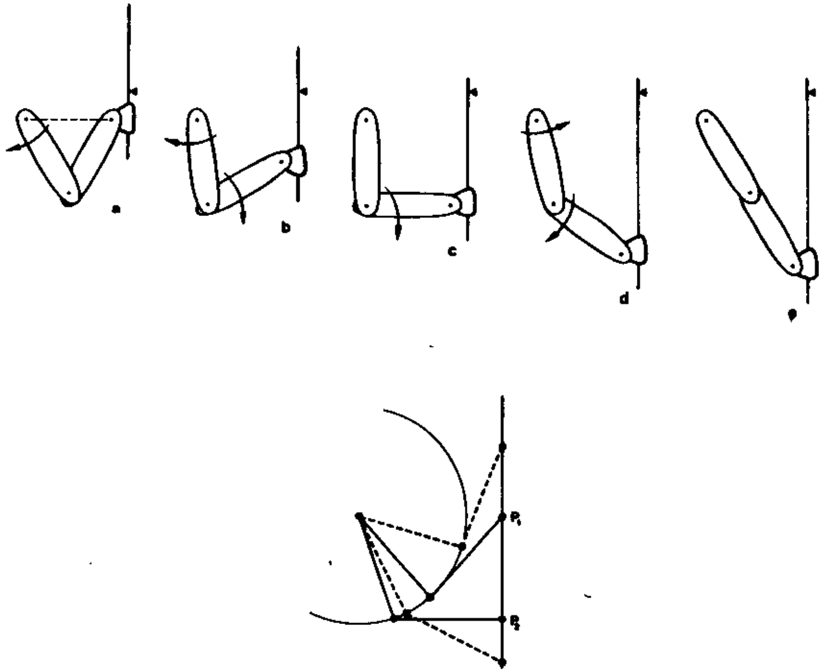

Fig. 6. Monotonic and non-montonic dependence of rotations in various joints from the position of the endpoint of the limb. The diagrams represent the right arm of a violinist drawing the bow down. The movement is accomplished by various degrees of clockwise rotation of both the upper arm and the forearm. In the last part of the movement the upper arm changes the sense of rotation to counterclockwise (d). The diagram below shows the region between P_1 and P_2 for which the dependence of both joints from bow position is monotonic. Above P_1 the forearm and below P_2 the upper arm change the sense of their rotation. P_1 is the projection of the shoulder on the line of the bow, P_2 is the position of the hand when the forearm is perpendicular to the bow. The region above P_1 is not used in violin playing.

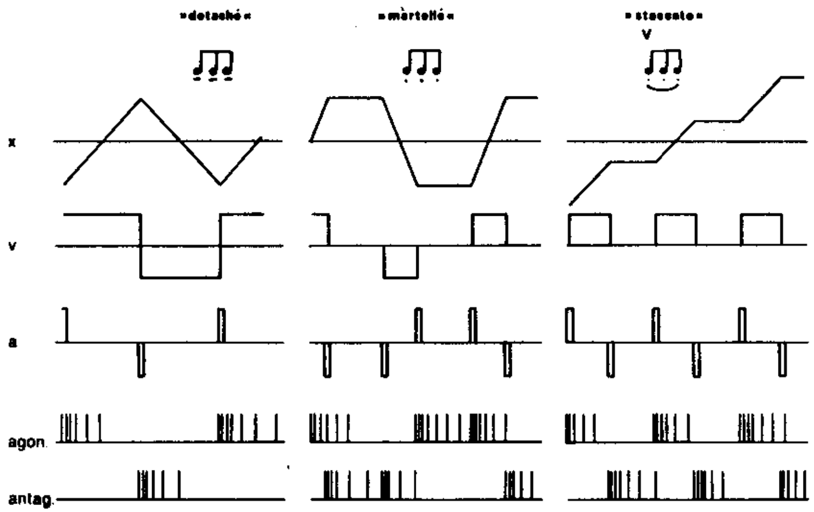

Fig. 7. Various "strokes" used in the bowing of stringed instruments, schematic. Time runs horizontal; x plots position, v velocity and a acceleration. If we suppose that the accelerations are produced by brief bursts of activity in agonist and antagonist muscles, we obtain the imaginary spike patterns below. Note that in the so-called martelle (middle) successive bursts in both muscles tend to fuse: martelle is of particularly difficult execution when the tempo is fast.

to be stopped by the muscle acting in the opposite direction. But very soon afterwards the same muscle has to be ready to initiate the opposite movement. Thus each of the muscles is activated twice in rapid succession. This becomes impossible when the movement is executed rapidly. Still, strokes of this sort, with pauses between the opposite phases of the movement, can be readily executed by a good violinist, even in a fast tempo. How is this done?

I suggest that this is where passive mechanical movement comes in. To a first approximation, the violinist's arm is a spring fixed at one end. Such a spring, having by necessity a node at one end and a belly at the other, vibrates at a fundamental frequency corresponding to the wavelength four times the length of the spring, and at higher frequencies 3 times, 5 times etc. the fundamental frequency (Fig. 8). Now, it is well known that the sum of the odd harmonics of the fundamental, with opportune coefficients (1, 1/3, 1/5 ..) add up to a square wave. We can ask ourselves whether this is the way a violinist can produce a periodic movement approximating a square wave. Obviously there are difficulties with the harmonics farther down the series, since a human arm, being constrained by

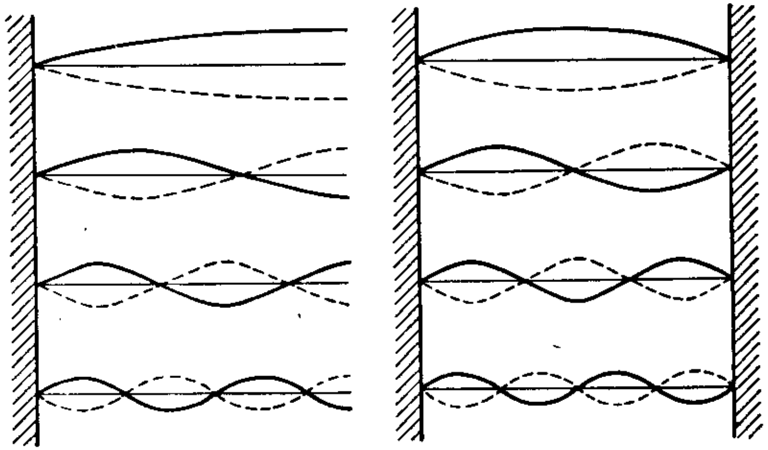

Fig. 8. Left: Vibrations of a string fixed at both ends have frequencies once, twice, three times etc. the fundamental frequency (the wave lengths of the standing waves being in the inverse proportion). Right: spring fixed at one end. The spring vibrates at frequencies which are odd multiples of the fundamental, for the various modes of oscillation must have a node at the fixed end and a belly at the free end of the spring. To a very rough approximation the arm may be considered a spring attached to the body at one end and free at the other.

the bones, cannot flex at all points. It is hard to see how anything beyond the third harmonic can actually be produced. The question is then: how good an approximation of a square wave can be achieved by a series of odd harmonics having only two terms?

The answer is given in Fig. 9. A trapezoid movement with a good enough plateau results when sin x and 1/9 sin 3x are added together. The coefficient 1/9 can be calculated by imposing that the second derivative is 0 at the position $\pi/2$. Such a movement would make good enough pauses between the strokes to produce the staccato effect. It could be produced purely mechanically by setting the tension of the arm at the right value for the fundamental frequency at which the arm is made to move. So it becomes an experimental question whether there is any evidence of the third harmonic in the movements that are produced by violinists.

The answer to this question is given in Fig. 10, a recording of the position of the bow in a slow and fast martellé stroke. In the fast stroke (lower trace) there is good evidence of a third harmonic, at an amplitude slightly higher than that which would produce the perfect plateau, but apparently compatible with the desired acoustic effect. Fig. 10 (lower trace) also presents evidence of a spring-like, almost perfectly sinusoidal motion of the arm which takes over when the detaché stroke becomes fast. Even more interesting, in Fig. 11 there is evidence for the proper oscillatory motion of the arm continuing with decreasing amplitude

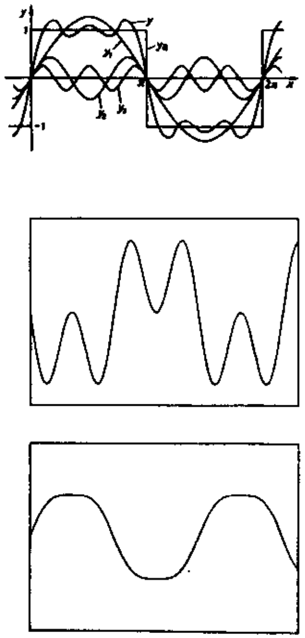

Fig. 9. The odd sinuses with opportune coefficients (sin x + 1/3 sin 3x + 1/5 sin 5x ...) add up to a square wave (upper diagram). But the first two terms of the series produce only a very rough approximation (middle trace). However, sin x + 1/9 sin 3x produce a curve with acceptable plateaus around the maxima and minima. This may be one of the ways by which the staccato effect is achieved in bowing.

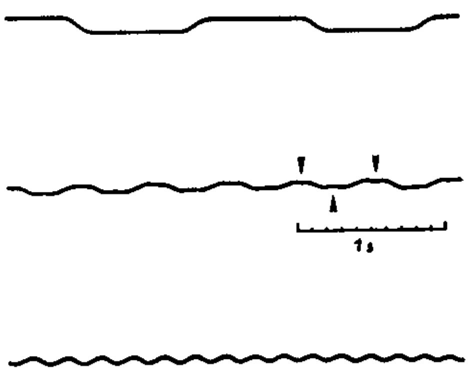

Fig. 10. Records of position of the bow versus time (left to right) in various kinds of bowing. Upper trace: slow martelle (see Fig. 7). Middle trace: faster martelle: the dents on the tracing where the bow should be at rest (arrows) clearly show the presence of the third harmonic; lower trace: fast detache which comes to the resonance frequency of the arm and therefore becomes very nearly sinusoidal.

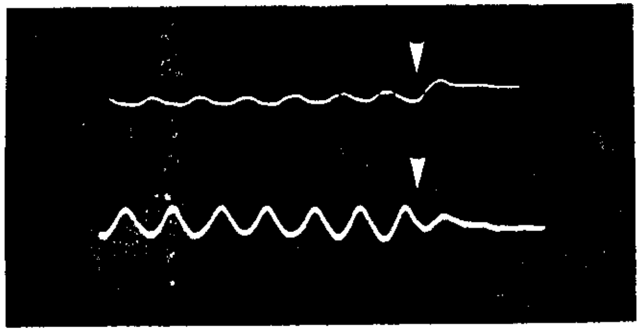

Fig. 11. Records obtained from two potentiometers attached to the shoulder and wrist respectively during the execution of a fairly fast detache stroke. The bowing was interrupted by mistake before the oscillographic trace was completed (arrow). There is evidence of a continuation of the oscillation, with diminishing amplitude, perhaps as a purely mechanical effect, indicating the contribution of passive spring-like motion to voluntary motor activity.

at the frequency of the previous "voluntary" oscillatory motion when the movement was suddenly discontinued. This strongly suggests that the frequency of the passive mechanical oscillation is adapted by neural control of tension, to the frequency imposed by the movement.

APPENDIX

There are various ways of deriving the function which is plotted in Fig. 1b. A simple way is a geometric construction (Fig. 12).

The diagram plots space along the direction of parallel fibres (x) against time (t). The horizontal lines represent a row of input position x_1, x_2, ... x_n. The black dots stand for pulses of input activation; an oblique row of such dots indicates input moving at the velocity v. Now, from each dot excitation is transmitted across space and time at the velocity v_0 of conduction in parallel fibres (oblique lines). The density of excitation reaching an element of the cerebellar cortex e.g. a Purkinje cell picking up excitation on its dendrtic tree, is proportionate to the density of these oblique lines in an element of the space-time surface. This density, as can be seen on the diagram, is the number of input lines activated in a unit of time (proportionate to v) divided by the length $v-v_0$ or v_0-v, whichever is positive. The case $v<v_0$ is plotted in the upper diagram, the other case in the lower diagram. Clearly the density of the oblique lines becomes infinite for $v=v_0$.

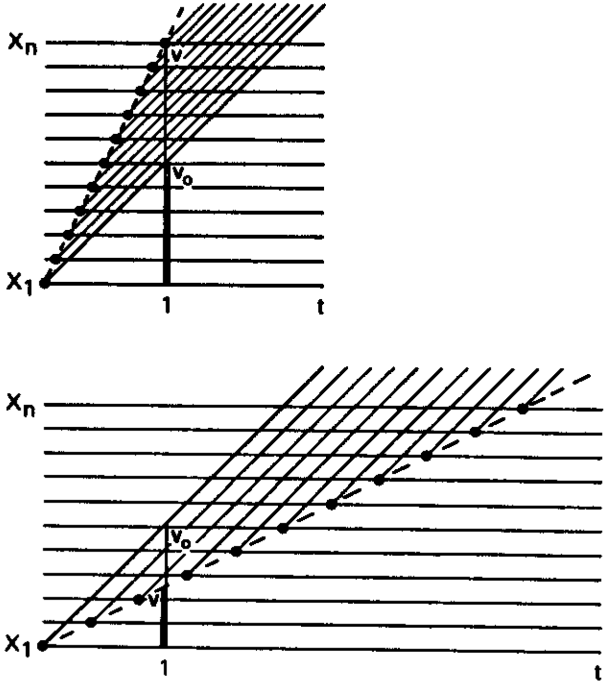

Fig. 12.

ACKNOWLEDGEMENTS

The impeccable precision of the bowing in Fig. 10 is that of Ernst John, the Tübingen virtuoso. To his teaching I owe many insights into the mechanics of violin playing. The recording equipment was engineered by Volker Staiger with such delicacy as not to hamper in any way the virtuoso's movements. The drawings by Claudia Martin-Schubert demonstrate her graphic skills (Fig. 2 is not a computer plot!) as well as her personal experience in musical performance. Drs. Ad Aertsen, Horst Greilich and Günther Palm were my consultants in matters of physics and mathematics and Shirley Würth put it all together into a manuscript. Last but not least, while I was writing this paper, the presence of Dr Gin McCollum in our department was a source of inspiration and of much constructive discussion on the theory of movement control.

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