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Cerebellar structure and function: Making sense of parallel fibers

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Abstract

Many parts of the brain have to cooperate in a finely tuned way in order to generate coordinated motor output. Parameters of these cooperations are adjusted during early childhood development and years of motor learning later in life. The cerebellum plays a special role in the concert of these brain structures. With the unusual geometrical arrangement of its neuronal elements, especially of parallel fibers and Purkinje cells the cerebellum is a selective and sensitive detector of a specific class of spatio-temporal activity patterns in the mossy fiber system: sequences of excitatory input which 'move' along the direction of parallel fibers at about 0.5 m/s, i.e. the speed of spike conductance in parallel fibers. Precise spatio-temporal neuronal activity patterns have been shown to occur in two major sources of afference to the cerebellum, the neocortex and the sensory feedback system. Based on our own experimental work and the above-mentioned findings we suggest that the cerebellum detects specific spatio-temporal activity patterns which trigger learned cerebellar output related to motor control and which contributes to the control of precise timing of muscle contraction.

PsycINFO classification: 2530
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Skilled movement is admired by a large audience and some sport professionals get extremely well paid for their skills. For their extraordinary performance they need to be able to coordinate muscle contractions on a millisecond time scale while at

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the same time evaluating sensory input and predicting movement of other players or objects. Their superior performance, which sometimes seems so effortless, is the result of many years of training during which different parts of the brain learn to collaborate and fine-tune their outputs to generate smooth and effective movement. The cerebellum seems to play a special role in this process.

The role of the cerebellum in the control of human movements and especially highly skilled movements was first described in great detail by the English neurologist Gordon Holmes (Holmes, 1917, 1939). Holmes' clinical studies on first world war casualties with gunshot injuries restricted to the cerebellum showed that these patients had lost the ability to move properly. Their movements were highly ataxic and they had problems with body posture and balance, comparable to the performance of babies and toddlers. However, the patients did not show any signs of paralysis or muscle weakness nor did they show any obvious signs of psychological disorders. The dominant finding was their disability to perform coordinated movements like the finger-to-nose test, normally performed at ease with eyes shut, but almost impossible for cerebellar patients even under visual control. More recent clinical studies suggest that cerebellar patients have lost the ability to compensate for interaction torques, which inevitably occur in multi-joint movements (Bastian, Martin, Keating, & Thach, 1996) (e.g. movements of the upper arm in one direction will result in movement of the lower arm in the opposite direction if that is not actively compensated for).

Anatomically the cerebellum is very peculiar, compared to the rest of the brain, because the neuronal elements it consists of are arranged in a very strict geometrical order (Fig. 1).

The only excitatory fibers within the cerebellar cortex are the thin, unmyelinated and slowly conducting (0.5 m/s) parallel fibers (Eccles et al., 1967; Heck, 1993), which run in parallel (hence their name) in a latero-lateral direction. The output neurons of the cerebellum are the Purkinje cells, which receive about 175,000 excitatory synaptic inputs (Napper & Harvey, 1988) from the parallel fibers and send their inhibitory output to the cerebellar nuclei (Ito, Yoshida, & Obata, 1964). These, in turn send excitatory efferents to thalamic structures, nucleus ruber, the vestibular system and various brain stem structures and an inhibitory output to the inferior olive (Allen & Tsukahara, 1974).

One of the two cerebellar afference types—the mossy fibers—terminate on the short dendrites of a large number of tiny granule cells ($\sim$5 μm cell body diameter), each of which gives rise to a parallel fiber. The granule cells are so numerous that their number amounts to more than half of all neurons in the central nervous system of mammals (Andersen, Korbo, & Pakkenberg, 1992; Pakkenberg & Gundersen, 1997).

The input to the cerebellum originates mainly from the motor cortex, arriving via the pontine nuclei and delivering information about motor commands, and from the spinal cord-carrying sensory feedback about the ongoing motor output (Brodal, 1981).

The presence of both, information about the intended and the actual motor output makes the cerebellum a structure very likely to be involved in motor learning.

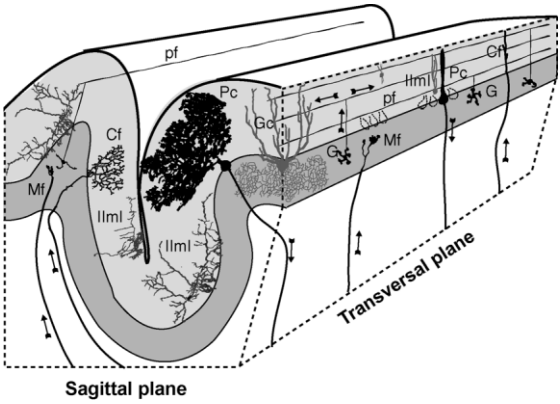

Fig. 1. A 3D scheme of the cerebellar cortex with its neuronal elements. The overwhelming majority of the intrinsic cerebellar cortical axons and dendrites adhere to a strict planar built that yields an anisotropic structure. These structures are embedded in two perpendicular planes shown here (the sagittal and transversal plane). Whereas the Purkinje cell dendritic tree, the axons and dendrites of the molecular layer interneurons (basket and stellate cells) are confined to the sagittal plane, the granule cell axons—the parallel fibers—are oriented in the transversal plane and perpendicular to the latter. Of the two main inputs to the cerebellar cortex, the climbing fibers also lie within the sagittal plane. The other input, the mossy fibers, shows a more intricate branching pattern, which, however, also has tendencies to branch in a sagittal plane. Light gray: molecular layer, dark gray: granule cell layer. Abbreviations: Cf: climbing fiber; IIML: inhibitory interneurons of molecular layer; G: granule cells; Gc: Golgi cells; Mf: mossy fibers; Pc: Purkinje cells; pf: parallel fibers (modified from Eccles, Ito, & Szentagothai, 1967).

It is worthwhile to compare the cerebellum to the other major cortex in the mammalian brain—the neocortex—in order to underline the peculiarities of the cerebellum. The connectivity in the neocortex is dominated by feedback loops. About 80% of all fibers leaving the gray matter re-enter it after traveling some distance in the white matter (Braitenberg & Schüz, 1991). Hence the enormous volume of white matter in the neocortex, contributing the same volume as the neocortex itself (Frahm, Stephan, & Stephan, 1982). There are no intracortical feedback loops in the cerebellum (Braitenberg, Heck, & Sultan, 1997). Here, the white matter consists only of afferent and efferent fibers, which make only a small contribution to the total volume of the structure (25%, Andersen et al., 1992). The neocortical gray matter can be several millimeters thick (Hofman, 1985) whereas the cerebellar cortex measures less than a millimeter in thickness (Andersen et al., 1992). The neocortex consists of two hemispheres, visibly separated by the central fissure but strongly connected by an enormous fiber bundle, the corpus callosum. The cerebellar cortex, instead, is a continuous structure with no interruption along the midline.

Although the neocortex is much larger in volume than the cerebellum, the two structures are more similar when comparing the areas of the two cortices.

As the neocortical hemispheres flatten out to a roundish shape, each with a diameter of about 30 cm (Blinkov & Glezer, 1968), unfolding the cerebellum reveals a very long and narrow surface, reaching a length of about 2 m in humans (Fig. 2) (Sultan & Braitenberg, 1993). In the neocortex the axons whether excitatory or

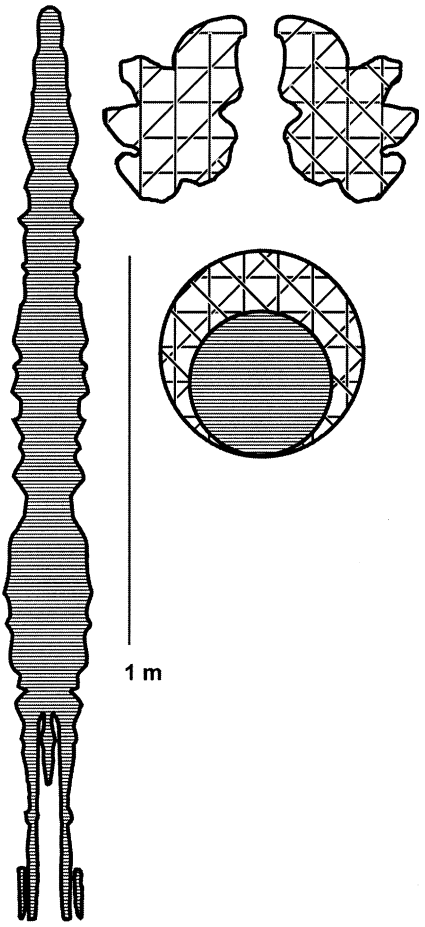

Fig. 2. Comparison of human cerebral and cerebellar cortex areas and outlines. The outline of the unfolded cerebellar cortex is depicted on the left. Typical for all mammals is a singular anterior (upper part of figure) and a tripartite posterior built (lower part of figure). The middle appendage of the tripartite ending corresponds to the caudal vermis. Strikingly different from the cerebral cortex's outline (shown on the upper right of figure, modified from Van Essen & Drury, 1997), is the anterior posterior length of the cerebellar cortex, which corresponds to over 2 m (2.38 m). The areas of the two cortices are shown as two circles on the lower right part of the figure. The cerebellar area equals the area of one and a half hemispheres of the cerebral cortex.

inhibitory project in every direction without any preference (granted a few exceptions). In the cerebellum, however, excitation and inhibition is strictly separated: excitatory parallel fibers all run in the same direction (perpendicular to the long axis of the unfolded cerebellum) and inhibitory fibers grow perpendicular to the direction of parallel fibers (Eccles et al., 1967).

Comparing the surface areas of both cortices across several mammal species, the cerebellum turns out to be on average slightly larger than a single neocortical hemi-

sphere but smaller than both hemispheres taken together (Sultan, 2002). But, because of the extremely dense packing of granule cells, the cerebellum contains about five times more neurons than the neocortex (10×10^{10} vs. 2×10^{10}, respectively) (Andersen et al., 1992; Pakkenberg & Gundersen, 1997).

Thus, taking both the area and the number of neurons as parameters indicative of information processing potential both structures seem to be involved in tasks of comparable complexity. Yet, the very different wiring schemes suggest radically different neuronal processing schemes.

1. A first attempt at a functional interpretation of the parallel fiber system

Because of the unusual geometry of the parallel fibers they were thought to play a central role for cerebellar function (Braitenberg & Atwood, 1958). Probably the most influential theory suggested that the cerebellum would work as a clock and control the timing of muscle contractions. It was suggested that the slowly conducting parallel fibers would play the role of delay lines able to produce delays in the range of hundreds of milliseconds (Braitenberg, 1961; Freeman, 1969). Assuming that action potentials travel along the parallel fibers with a slow but fixed velocity and would excite Purkinje cells along their way, a clock can be postulated that translates time into distance and vice versa. This clock could be useful to determine the time intervals between two successive muscle contractions, e.g. in order to bring a movement to a precise stop. Today, however, there is anatomical and electrophysiological evidence confuting some important assumptions of the theory. Typical time intervals relevant for motor control are several hundred milliseconds long. With a conductance velocity of 0.5 m/s the parallel fibers would need to be 50 mm long to produce a delay of 100 ms. We now know that the parallel fibers are about 5–7 mm long (Harvey & Napper, 1988; Mugnaini, 1983; Pichitpornchai, Rawson, & Rees, 1994), i.e. much too short to produce time delays relevant for motor control.

In the 'clock' idea of cerebellar function a single or maximally two coincident parallel fiber inputs suffice to elicit a spike in a Purkinje cell. Electrophysiological studies have shown that single parallel fibers have only a very weak effect on the postsynaptic firing probability. Experimentors failed to show a spreading of activity along the parallel fibers using sensory stimulation of cerebellar afferences as a test stimulus (Bower, Beermann, Gibson, Shambes, & Welker, 1981; Shambes, Gibson, & Welker, 1978). These findings resulted in the suggestion, that the parallel fibers might not be the major source of excitatory input to the Purkinje cells but that instead the short raising parts of the granule cell axons, which typically establish several synapses on an individual Purkinje cell were responsible for suprathreshold excitation (Llinás, 1982). In this concept the parallel fibers were assigned a modulatory function, i.e. to provide contextual information shaping the Purkinje cells response to input from the raising parts of the granule cell axons. This interpretation, however, leaves several questions unanswered regarding the unusual anatomical arrangements in the cerebellar cortex, such as: Why do the parallel fibers run in parallel? Why are the

dendritic trees of Purkinje cells flat and oriented perpendicular to the parallel fibers? What is the reason for the large number of granule cells, hence the large number of parallel fibers? Why do excitatory and inhibitory fibers grow perpendicularly to each other?

2. The tidal wave mechanism

Within a theoretical framework developed by Braitenberg (Braitenberg, 1983; Braitenberg, 1987; Braitenberg, 1991) the peculiarities of cerebellar anatomy, especially the interaction between parallel fibers and the fan shaped Purkinje cell dendrites play a central role for the function of the cerebellar cortex. The important point of the tidal wave theory is that sequential activation of granule cells will be transformed into synchronous activity by the parallel fibers and that this synchronous activity will excite Purkinje cells (Fig. 3).

A sequential activation of granule cells aligned in the direction of parallel fibers (cells 1–4 in Fig. 3) will result in an apparently "moving" stimulus. If the velocity of the apparent "movement" matches the velocity of spike conductance in parallel fibers the action potentials traveling in the parallel fiber system will be aligned in the plane of Purkinje cells and provide highly synchronized excitatory input. In a series of in vitro and in vivo experiments we were able to show that in fact the cerebellum specifically detects such sequential input and that Purkinje cells are indeed activated by sequential granule cell activation when the sequence moved at the correct speed (Braitenberg et al., 1997; Heck, 1993, 1995, 1999; Heck, Sultan, & Braitenberg, 2001).

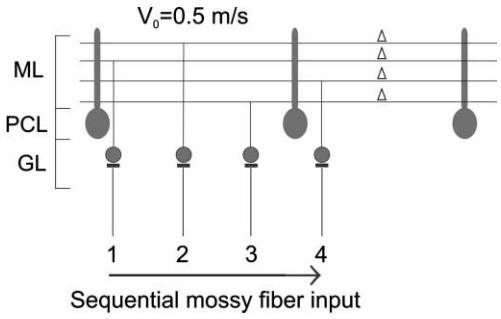

Fig. 3. Schematic transversal view of cerebellar cortex illustrating the generation of synchronous parallel fiber activity by sequential stimulation of granule cells. If several neighboring mossy fibers are activated sequentially as indicated by the numbering (1–4) and the sequence "moves" at the speed of conductance in parallel fibers (V_0) the individual action potentials (triangles) elicited in the granule cells (small gray circles) will line up in a plane parallel to the plane of Purkinje cell dendrites and provide a highly synchronous excitatory synaptic input. (Purkinje cells are drawn with gray oval somata with dendrites in the molecular layer.) If the velocity of the apparent movement of the input sequence deviates from V_0 spikes on the parallel fibers will be less synchronized. Consequently their effect on Purkinje cell activity will be reduced accordingly. ML: molecular layer; PCL: Purkinje cell layer; GL: granular layer.

The tidal wave mechanism offers explanations for several open questions—some of them mentioned above—about cerebellar anatomy. The parallel arrangement of the excitatory fibers is a prerequisite for the arrangement of spikes within a single plane in response to sequential input. Only neurons with flat dendrites—like those of Purkinje cells—oriented parallel to that plane of spikes will perceive a strong synchronous input. Neurons with 3-dimensional (3D) dendrites would receive an asynchronous synaptic input as the spike wave front traverses the volume of their dendrite. The tidal wave mechanism uses many synchronized parallel fibers to drive Purkinje cell activity. Thus, the weakness of individual parallel fiber-Purkinje cell synapses provides a threshold separating successful from unsuccessful input sequences.

Where could sequential activity patterns eliciting tidal waves of activity in the cerebellum originate? Highly precise spatio-temporal activity patterns exist in both major sources of input to the cerebellum: the neocortex (Abeles, Bergman, Margalit, & Vaadia, 1993; Riehle, Grün, Diesmann, & Aertsen, 1997) and in sensory feedback (Gray, Perciavalle, & Poppele, 1993; Kolb, Rubia, & Bauswein, 1987a,b; Osborn & Poppele, 1989a,b). With the necessary temporal precision provided by these inputs, the spatial positioning of synapses in order to correctly arrange a time sequence of spikes into a moving sequential input could happen during development and learning by mossy fiber sprouting and pruning (Sultan, 2001). Each tidal wave would be elicited by neocortical activity pattern together with sensory feedback, both inputs properly intertwined both in space and time to result in a single, ordered sequence of mossy fiber activity (Fig. 4).

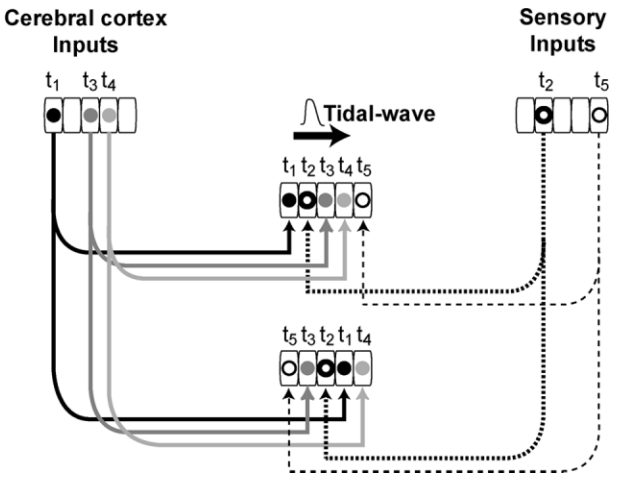

Fig. 4. The basic idea of the tidal wave is shown in this figure. Mossy fiber inputs arising from two sources (cerebral cortex inputs mediated via the pontine nuclei and sensory inputs) converge unto single folia to form patterns of spatio-temporal inputs. In some folia (here with sequence $t_1 \rightarrow t_2 \rightarrow t_3 \rightarrow t_4 \rightarrow t_5$) the relative positions of the mossy fiber inputs yields a sequential temporal pattern. This pattern then allows for the build-up of the tidal wave in the parallel fibers, provided that Δt between any two sequential mossy fiber inputs are of the right magnitude.

Fig. 5. A scheme of the unfolded human cerebellar cortex with numerous locations where sequential mossy fiber inputs could give rise to a tidal wave in the parallel fiber system. The individual mossy fiber inputs are shown as gray rectangles (not to scale). Each line or sequence of mossy fiber inputs (read from left to right or vice versa) could give rise to a tidal wave activation of a beam of parallel fibers. The width of such a beam (from top to bottom) we define to be the average distance between neighboring Purkinje cell bodies, i.e. $\sim$50 μm. Based on the cerebellar cortex's length and the width of a beam the human cerebellum consists of about 50,000 beams, only a fraction of which is shown in the sketch (1/500). The number of possible tidal waves could be in the order of 10 higher if we assume that each line contains more than one tidal wave.

Based on the average distance between neighboring Purkinje cells (~50 μm) and the average overall length of the human cerebellum (~2.3 m) we estimate a total number of parallel fiber "beams" (Eccles et al., 1967) or equivalently the number of independently active rows of Purkinje cells to be between 40 and 50 thousands. This calculation (based on the assumption that a "beam" is about 50 μm wide) gives the lower limit of the number of possible tidal wave locations in the cerebellum. It is plausible to assume that each beam, which may measure several centimeters in length in humans—hosts several tidal wave locations—each one only a few parallel fiber length long. This could increase the total number of tidal wave sites to several 100 thousands in humans. Each tidal wave site would be activated during a specific phase of a movement by the corresponding neuronal activity pattern consisting of contributions from cortical motor commands and sensory feedback (Heck, 1996) (Fig. 5).

Movement is a dynamic process. Therefore, motor control requires fast and reliable analysis of movement dynamics in order to generate neuronal commands to correctly continue and finish the movement. We suggest here that the cerebellum analyses dynamic aspects of movement by detecting spatio-temporal activity patterns in the mossy fiber system, which correspond to a defined phase of a specific movement. Mossy fibers contributing to these patterns convey online sensory feedback (although delayed) of the ongoing movement to the cerebellum or reflect motor related commands issued by the neocortex. Mossy fiber input patterns hence continuously change along with the ongoing movement. The exact timing and sequence of the patterns would depend on the trajectory and the time course of the movement. Through the tidal wave mechanism a specific and learned subset of spatio-temporal patterns trigger cerebellar output by activating Purkinje cells. This output would ultimately contribute to the selection of muscles and the timing of their activation. During almost any coordinated body movement large synergies of muscles need to be controlled simultaneously. Along the rostro-caudal axis of the cerebellum many movement related sequences of input activity could be detected independently allowing the synchronous control of large groups of muscles.

The tidal wave mechanism described here relates the anatomical peculiarities of cerebellar architecture to function. An important question, however, which has to be addressed in the future, is whether and when sequential activity in cerebellar cortex can be observed in relation to behavior.

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