The cerebellum and timing: Lessons from mormyrids

J. Meek
Department of Anatomy and Embryology, Faculty of Medicine, University of Nijmegen, 6500 HB Nijmegen, The Netherlands. j.meek@anat.kun.nl

Abstract: Mormyrid teleosts have Purkinje cells with palisade dendrites, which probably represent coincidence detectors of parallel fiber activity. Their existence strongly supports the ideas of Braitenberg et al. on cerebellar function. However, the organization of mormyrid granule cells and parallel fibers suggests that a key to cerebellar function is not in interactions within one wave, but between two opposite tidal waves.

Braitenberg et al. present strong arguments in favor of the idea that the detection and generation of sequences must be a key to cerebellar function, and explain that this is presently the only theory fully accounting for the regular cerebellar geometry. Cerebellar geometry reaches its climax in mormyrid teleosts, which have the relatively largest cerebellum of all vertebrates (Nieuwenhuyse & Nicholson 1967) and Purkinje cells with a dendritic palisade pattern. This means that the spiny dendrites of mormyrid Purkinje cells are all oriented parallel to each other, perpendicular to the cerebellar surface (Meek & Nieuwenhuyse 1991; Fig. 1). Since climbing fiber input is restricted to the cell bodies and proximal dendrites in mormyrids (Meek & Nieuwenhuyse 1991), palisade dendrites are a cerebellar specialization exclusively involved in the processing of parallel fiber (and related stellate cell) input. Their significance can only be explained by assuming that Purkinje cells are coincidence detectors of parallel fiber activity. In that case, mormyrid Purkinje cells would be optimally tuned for the detection of very precisely defined patterns of parallel fiber activity (Meek 1992a; Meek & Nieuwenhuyse 1991). This is entirely in line with the ideas of Braitenberg et al., and consequently the presence of a palisade pattern in mormyrids strongly supports their hypothesis that the detection of synchronous or coincident parallel fiber activity is a major, if not the main function of cerebellar Purkinje cells.

In the mammalian cerebellum, synchrony or coincidence of parallel fiber activity at the level of the Purkinje cell dendritic tree can only be achieved by specific sequential mossy fiber input patterns that evoke tidal waves of parallel fiber activity. However, this is not the situation everywhere in the mormyrid cerebellum, since this structure contains configurations where granule cells are located lateral to the molecular layer not underneath the layer of Purkinje cells, giving rise to parallel fibers without any T-bifurcation (Meek 1992b; Fig. 2). The situation in the lobus transitorius (l.t.) is particularly interesting, since parallel fibers arise in this cerebellar subdivision from two populations of granule cells, located at the right and left side of the molecular layer (Fig. 2). This configuration may be considered as an optimal device to detect small time differences in the mossy fiber inputs to the left and right granule cell mass, and suggests that the detection of coincidence of parallel fiber activity waves conducted in opposite directions is a major function of Purkinje cells (Meek 1992a). In my opinion, the theory of Braitenberg et al. should be adapted at this point. It exclusively considers synchrony in the activity of parallel fibers conducting signals in the same direction, thus accounting maximally for only 50% of all parallel fiber input to any Purkinje cell (Braitenberg et al., sect. 14, para. 4). Obviously, in the mammalian cerebellum each Purkinje cell is tuned to two - and not one - tidal waves, one running from right to left and one in the opposite direction. Coincidence of these two tidal waves will have especially strong effects on Purkinje cells. Extending the physiological experiments of Heck to two opposite tidal waves would conceivably confirm this point. So, the detection of sequences is probably a very important feature of cerebellar function, but a full theory should consider particularly the interactions between two opposite tidal waves, and not only those within a single wave. This unravels but half of the truth and many miss the most crucial aspect of cerebellar organization.

A less important lesson from mormyrids deals with the time domain of the detection of sequences. Braitenberg et al. mention in section 13, paragraph 1, that a major problem with a timing function of the cerebellum has always been that the average length of mammalian parallel fibers allows for delays of maximally 10 msec, whereas the movements regulated by the cerebellum typically take at least 200 msec. They suggest that the complete width of the cerebellar cortex should be considered, which indeed would allow for the processing of tidal waves lasting for up to 200 msec in mammals. However, this does not hold for mormyrids or other teleosts, where the cerebellum consists of a single parasagittal zone of 0.5 to 2 mm width (Meek et al. 1992) and where all parallel fibers are as long as this total cerebellar width (Fig. 2). Such cerebella may only detect and process time differences of maximally about 5 msec (Meek 1992a), and any unifying theory should not only account for the processing and significance of time differences of 100 msec or more, but also for smaller ones in the msec range.

Figure 1 (Meek). Sagittal view of a mormyrid Purkinje cell.

Figure 2 (Meek). Schematic transverse views of cerebellar configurations in mormyrids and mammals. Stippled and dotted are granule cells, open circles are Purkinje cell bodies, and horizontal lines are parallel fibers. Valv. = valvula cerebelli; l.t. = lobus transitorius cerebelli; and C1 = cerebellar lobe C1.