# Partition of the Human Cerebellum in Sensory-Motor Activities, Learning and Cognition

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**ABSTRACT:** The circuitry of the cerebellum is quite well understood. The computation takes place in the cerebellar cortex, which functions in synchronized strips to provide excellent timing signals to the cerebral cortex and the spinal cord. The cerebellar cortex is also the site where error signals from other parts of the central nervous system are incorporated. For voluntary limb movements the cerebellular cortex is important for the timing of the innervation of the agonist and antagonist anterior horn neurons. It is also important for the temporal order of and precision in the execution of motor programs. As will be apparent, the cerebellum is not only a computer taking care of motor programs.

**RÉSUMÉ: Répartition dans le cervelet des activités sensitivomotrices, d'apprentissage et de cognition.** Des études récentes du cervelet humain au moyen de traceurs ont révélé que le cervelet n'est pas impliqué seulement dans des activités sensitivomotrices localisées principalement dans le lobe antérieur, mais aussi dans des activités motrices non sensitives. Ces dernières sont actuellement classées comme étant cognitives. Les activités cognitives et les modifications des activités sensitivomotrices dues à l'apprentissage semblent se produire principalement dans le lobe postérieur.

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The output from the Purkinje cells goes to the cerebellar nuclei deep in the cerebellum. Humans have four nuclei, of which the dentate is the most recently developed and by far the largest. The human dentate nucleus consists of a phylogenetically older part, the magnocellular portion and phylogenetically recent part the parvocellular part.[4] The axons intervating the dentate nucleus comes from the lateral part of the cerebellar hemispheres. A smaller intermediate zone send axons to the small globose and emboliform nuclei and the midzone, vermis, sends axons to the fastigial nucleus.

The afferents from the motor cortex and the somatosensory cortex plus the afferents from the spinal cord are somatotopically organized. The cerebellar computation does not disturb this somatotopy. Recordings from single neurons in the dentate nucleus have shown that the dentate neurons to 50% discharge before the start of voluntary movements and that $^2/_3$ of the neurons which are movements related also fire to sensory stimuli, i.e., a light tone or stretch of a muscle in a reaction time paradigm. Only $^1/_5$ of the movement related neurons fire exclusively related to movements.[5]

The efferents from the magnocellular portion of the dentate nucleus go to the red nucleus. The efferents from the parvocellular portion goes to the VLa, VLp and VPL nuclei of thalamus.[6] From here the cerebellar output reaches the cerebral cortex. The output from the globose nucleus reaches the Darkschevitch nucleus in the higher brain stem, and that from the emboliform nucleus reaches the CM intralaminar nucleus of thalamus.[6] The fastigial nucleus is related to centers for eye movements (superior colliculus) and the spinal cord and lower brainstem.

From this, one would expect the human cerebellum to be engaged in sensory-motor tasks, but also in generation and control of eye movements. Table 1 shows the tasks giving rise to increases in regional cerebral blood flow (rCBF) or regional cerebral metabolism (rCMR) in the cerebellum. So far nobody has reported decreases in rCMR or rCBF. The tasks comprise motor tasks, sensory-motor tasks, but also and perhaps unexpectedly, purely cognitive tasks and thinking.

## The Anterior Lobe of Cerebellum

Voluntary movements of the fingers or the hand, either as part of a motor paradigm or as part of a somatosensory exploration of objects increase rCBF and rCMR in the lateral part of the anterior lobe of cerebellum (Table 1). $Ca^{2+}$ channel studies in man revealed the neurons depolarize here during the task.[7]

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**Table 1: Tasks Which Produced Changes in rCBF and rCMR in the Cerebellum**

| Task | Site | Side | Authors |
|---|---|---|---|
| Vibration | LAL | I | Fox et al. 1985c[8] |
| Flex-ext hand | LAL | I | idem |
| Finger sequence | LAL | I | Fox et al. 1985b[14] |
| Saccades no target | V | | idem |
| Motor sequence | LAL | I | Seitz et al. 1990[9] |
| Motor sequence learning | LAL | I | idem |
| Tactile learning | LAL | I | Roland et al. 1987[15] |
| | LPL | B | idem |
| Tactile recognition | LAL | I | Roland et al. 1991[16] |
| Somatosensory discrim | LAL | I | Seitz et al. 1991[10] |
| — | LPL | B | idem |
| — | Dentate | I | idem |
| Preparation for reaching | LAL | B | Decety et al. 1992[17] |
| Route finding | LPL | B | Roland et al. 1987[15] |
| Social philosophical speech | | R | Pawlik et al. 1987[13] |
| Repeating words shown | VLA, LAL | R | Raichle 1990[12] |
| Word association | VLA | | idem |
| | LPL | B | idem |
| Visual discrimination | VLA | | Gulyás et al. 1991[18] |
| Spontaneous speech | LA | B | Heiss et al. 1990[19] |

LA: lob ant LP: lob post L: lateral R: right
I: ipsilateral B: bilateral V: vermis

Fox et al.[8] showed that it was the exact same site of the anterior lobe which increased rCBF when the hand was moved and when it was vibrated. Another way to illustrate the overlapping somatotopical arrangement of the somatosensory and somatomotor afferents to the anterior lobe is to subtract the activation caused by the performance of the motor sequence test[9] from that of somatosensory discriminations of shape.[10] By such a subtraction the activation of the anterior lobe cancels out.[10]

The rCBF and rCMR changes here are not related to the frequency of movements, at least not during learning. During learning of a motor task, the cerebellar changes were restricted to the anterior lobule. The rCBF remained unchanged despite a doubling of the frequency of finger movements during the course of learning.[9] Thus there was a higher relative metabolic cost per finger movement in the early phase of learning.

Still within the anterior lobule of cerebellum, but localized to the vermis is the spot activated when the eyes are moving. One might think that the cerebellar increases in visual discrimination and route finding with the eyes closed were due to a higher frequency of eye movements during the tasks, but the frequency of eye movements did not increase from the control state in these tasks. So the vermis activation cannot be explained by eye movement frequency only.

## The Posterior Lobe of Cerebellum

The lateral part of the posterior lobe is a rather large area and undoubtedly it consists of many different functional fields. Tactile learning increases the rCMR and rCBF in the posterior lobule. This increase is not due to learning of the exploratory finger movements, since these movements are not changed in the adults.[11] The same fields are activated also when subjects discriminate the shapes of rectangular paralellepipeda, but in this case the rCBF or rCMR does not undergo any modulation.[10] Thus the modulation of the initially large rCBF and rCMR increase is related to the learning of the sensory information. There is no such modulation of posterior lobe rCBF in visual learning. That the posterior lobe of cerebellum participated in learning is not surprising, but that it participates in learning of somatosensory information was unexpected.

Even more unexpected were several consistent studies showing that the posterior lobule participates in cognitive activities such as thinking[15] and verbal encoding. The cortical parts activated seem to be more lateral than those engaged in tactile learning and somatosensory discrimination.[10,11] The engagement of cerebellum in language is not related to the formation of the motor programs for speech. This is evident from the fact that word association, but not word repetition activates the posterior lobule (reference[12] and Table 1). In the study of subjects speaking about a social philosophical subject[13] it was only stated that the cerebellum is activated, but not which part was active.

This engagement of cerebellum in cognition was already pointed out in a few studies of patients with lesions of the posterior lobes.[14] Saskai also reports a patient who could not keep the target of his intended action in mind after a cerebellar lesion.[20]

## Functional Cerebellar Sectors

Although traditionally regarded as a motor structure, the cerebellar cortex is activated by not only motor tasks, but also in sensory tasks and situations in which the brain activity is neither sensory nor motor – that is during pure cognitive activity. The PET method provides accurate localization of the cerebellar cortical sectors which are engaged in these different sensory, motor and cognitive tasks. Like the basal ganglia the cerebellum is another example of a subcortical structure parcellated into motor, sensory-motor and cognitive sectors most likely defined by the cerebral cortical inputs the cerebellar cortex receive. However since the borders between the intermediate zone and the lateral zones are not revealed in the living human cerebellum, it is at present only possible to relate the activations to the gross anatomy of the cerebellum. Consequently, the activation can only be allocated to either vermis or the lateral zones of the anterior and posterior lobule.

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