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Cerebellum does more than recalibration of movements after perturbations

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Abstract: We argue that the function of the cerebellum is more than just an error-detecting mechanism. Rather, the cerebellum plays an important role in *all* movements. The bias in (re)calibration is an unfortunate restrictive result of a very successful and important experiment. [SMITH, THACH]

The target articles in this issue provide a superb up-to-date overview of the neuroanatomy and neurophysiology of the cerebellum. However, relatively little attention has been paid to studies on the role of the cerebellum in various motor tasks and on the implications of these studies.

One of the working hypotheses about cerebellar function was based on the idea of an error-detecting mechanism, which could somehow recalibrate the system in order to eliminate any motor errors. This provided the basis for models on the cerebellum by Marr (1969) and Albus (1971). This hypothesis received further support from the observation that (re)calibration after perturbation of the motor system (usually induced by lesions) is not possible when the cerebellum is not active (Optican & Robinson 1980).

As already pointed out in the target article by SMITH there is good evidence that the cerebellum does more than simply (re)calibrate the motor system. For example, cerebellar lesions also give rise to abnormal arm movements when no learning or (re)calibration is required (Becker et al. 1990; Diener et al. 1993; Hallett et al. 1975; Terzuolo et al. 1973). This suggests in our view that the cerebellum is essential not only for adaptive recalibration, but also for normal motor functions.

The statement that cerebellum plays a role both in (re)calibration of the motor system and in normal movements can be most convincingly illustrated for the oculomotor system. Recalibration of the saccadic system can easily be imposed in adaptation experiments in which a visual target appears which serves as the goal of a saccadic eye movement. There is a well known paradigm in which the visual target is displaced further from the start position during the saccadic eye movement. As a consequence, the amplitude

of the saccadic eye-movement is too small to reach the *new* target. The subjects are never consciously aware of the displacement during the saccade because of the well known phenomenon of saccadic suppression of visual information during saccades. After a few of these saccade-triggered displacements, the amplitude of the saccade gradually increases in order to adapt to the intra-saccadic displacement. This adaptation is confined to a limited area around the adapted saccade vector. Frens and van Opstal (1994) demonstrated that after visually induced adaptation, auditory-evoked saccades are also adapted to the visually induced displacement.

Since the superior colliculus (SC) plays an important role in the generation of saccadic eye movements, Goldberg et al. (1993) investigated the role of the SC in the adaptation process. Neurons in the deeper layers of the SC reveal a burst of activity for saccadic eye movements with a particular direction and amplitude. The amplitude of this burst of activity decreases when the direction or amplitude of the saccade deviate more from the optimal saccade amplitude and direction. The range of saccadic eye movements, for which a cell is active is called the cell's movement field. Goldberg et al. found that SC saccade-related cells revealed the same burst-like activity after adaptation if the adapted saccade was no longer in its original movement field. This implies that the range of visual targets, which elicit saccades, differs from the movement field for these cells. They suggested that some system, parallel or downstream of the SC, modifies the neuronal signal from the SC in order to make it suitable for the required adapted saccade. More specifically, they suggested that the cerebellum might be involved. This hypothesis was supported by the finding that lesioning of the cerebellum prevented saccadic adaptation (Goldberg et al. 1993). Surprisingly, electrical stimulation in the SC *after* adaptation elicited saccades with the same amplitude as was observed *before* the adaptation. These results were interpreted as suggesting (1) that the superior colliculus programs saccades in terms of visual location of the target, not the physical amplitude; and (2) that the cerebellum, which does not receive sensory input about visual target position during electrical stimulation, is responsible for the calibration of the properties of the oculomotor plant. This implies that the cerebellum plays an important role for all saccadic eye movements, not only after adaptation. This is well in agreement with the observation that lesioning of the cerebellum also affects normal limb and eye movements.

Recently, Melis and van Gisbergen (1995) found that target displacements during electrically-induced saccades in the SC give rise to adaptation also. At least as important was their finding that after adaptation for saccades induced by electrical stimulation, adaptation also occurs in visually elicited saccades. Their results agree with the hypothesis by Goldberg et al. (1993) that the SC activity codes visual target displacement and that the adaptation for the plant occurs later, downstream of the SC. The main conclusion is that the adaptation center apparently receives both sensory input as well as input of motor commands.

These experiments raise the question of whether a similar model can be proposed for limb movements. For example, it has been shown (Ashe et al. 1993; Georgopoulos et al. 1984) that neurons in primary motor cortex (M1) may be active after presentation of a visual target for arm movements, even when the arm movement does not yet occur. More particularly, if the monkey is trained to move in a direction 90 degrees rotated from the visual target, the population vector in M1 rotates to the final target position before a movement is initiated (Georgopoulos & Massey 1987). These observations suggest that motor cortex codes a "desired" movement direction, rather than actual movement direction and that the properties of the effector system are accounted for by a system parallel or downstream of motor cortex. Although this may seem to be a speculative hypothesis, it is an obvious hypothesis based on the experimental evidence, which is open to falsification.

How an important observation can mislead us. Until the early

eighties the main view on the function of reflexes (both the well known tendon reflex or short latency reflex and the long-latency reflex) was that their main function was to correct for external perturbations of posture or movement. The important observation that large reflex activity was induced by fast lengthening of a muscle gave rise to the notion that the main function of reflexes was to correct for external perturbations (for a review see Houk & Rymer 1981). Later studies have shown that although reflexes play an important role in compensating for external perturbations (the present view is that in general they cannot provide complete compensation), they also figure in normal movements such as walking (Stein 1991). In summary, reflexes are part of the normal activity in the motor system. What happened in the study of reflexes is that a very important and successful experimental observation unfortunately placed too much emphasis on a single aspect of reflexes.

In our view a similar development may be found with regard to the function of the cerebellum. One of the first studies on cerebellum demonstrated its important role in recalibration of movement commands. This was a significant finding, but does not eliminate other possibly important functions of the cerebellum. There are enough observations to indicate that the cerebellum plays a role in natural movements and that cerebellum does more than just recalibrate movement commands. This is also implied in the model by Kawato and Gomi (1992), who consider the cerebellum as an adaptive parallel fine-tuning device to adjust for the complex properties of the effector system.

A comparison between cerebellar activity and neuronal activity in primary, supplementary, and premotor cortex did not demonstrate clear differences in neuronal activity during learning and learned or automatic movements (Raichle et al. 1994). Based on this finding THACH concludes that many of the current hypotheses about cerebellar function are due to erroneous extrapolation of specific experimental results to human motor performance following artificial investigators' instructions and spurious correlations. We fully agree with this conclusion and we share with him the opinion that for most movements cerebellum is necessary for adequate motor performance, not only to correct for perturbations.