

The Relevance of Sensory Input for the Cerebellar Control of Movements

M. JUEPTNER,* S. OTTINGER,* S. J. FELLOWS,† J. ADAMSCHESKI,* L. FLERICH,* S. P. MÜLLER,‡ H. C. DIENER,*
A. F. THILMANN,† AND C. WEILLER*

*Department of Neurology and ‡Department of Nuclear Medicine, University Clinic, Hufelandstrasse 55, 45122 Essen, Federal Republic of Germany; and †Department of Neurology, Fachklinik Rhein-Ruhr, Auf der Rötisch 2, 45219 Essen, Federal Republic of Germany

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The performance of a motor task not only requires subjects to plan, prepare, and initiate but also to monitor how a movement is performed. We used positron emission tomography to examine to what extent the human cerebellum is involved in controlling motor output or sensory input from movements in normal subjects. In the first study, we compared the active performance of a motor task (flexion and extension of the right elbow) to the passive execution of the same movements. Passive movements were driven by a motor with the arm fixed in a guide hinge. Active movements (compared to rest) elicited increases of rCBF mainly in the ipsilateral neocerebellar hemisphere and vermis of the posterior lobe. During passive movements, almost identical parts of the cerebellar hemispheres and vermis were activated (compared to the rest condition). The direct comparison of active and passive movement conditions revealed a small activation of the neocerebellar hemisphere of the posterior lobe and cerebellar nuclei ipsilateral to the movement. Approximately 90% of cerebellar neuronal activity was related to sensory input. In the second study, we compared the execution of a free selection joystick movement task to a condition in which subjects simply imagined the movements. The execution of movements (compared to rest) was associated with increases of rCBF in the ipsilateral neocerebellar hemisphere and vermis of the posterior lobe. During movement imagination, a small part of the ipsilateral cerebellar hemisphere and vermis of the posterior lobe was activated (compared to rest). The increase of rCBF during movement imagination accounted for only 20% of the signal seen during movement execution. Our results indicate that the neocerebellum may be much more concerned with sensory information processing than has been considered previously.

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INTRODUCTION

Using positron emission tomography (PET) for the measurement of regional cerebral blood flow (rCBF) we have recently investigated the functional anatomy of

visually guided limb movements (Jueptner *et al.*, 1996). Normal subjects performed a visual tracking task under two different conditions. In the first condition, subjects used a computer mouse to draw straight lines on a computer screen (DRAW). After three seconds of continuous line elongation a tone sounded, the screen was cleared, and subjects had to draw another line in any direction. The movement parameters (direction, distance, velocity) were stored by the computer. They were used in the second condition in which the same lines were played back, one at a time. Subjects were now required to maintain the mouse pointer at the end of the lines that slowly disappeared from the end (copy). Thus, the same movements were performed in both tasks. However, in the second condition subjects had to be more accurate when tracing along given, i.e., previously generated lines. The neocerebellar cortex, cerebellar nuclei, and neocerebellar vermis of the posterior lobe were the only structures in the brain which were more active during line tracing than during new line generation (copy-draw).

During scanning, all movements were performed in the absence of visual control over the moving arm. Therefore subjects had to rely on sensory input from visual information, proprioceptive receptors (primary muscle spindle afferents and tendon organ afferents), and cutaneous afferents to guide their movements. In two follow-up experiments, we were therefore interested in analyzing the relative contribution of sensory input and motor output control to the cerebellar control of movements.

The first study was planned to analyze the relative contribution of sensory input to the cerebellar signal seen during movement execution. More specifically, we were interested in the following: (i) Is the human cerebellum activated by sensory input from passive movements? (ii) What parts of the cerebellum are involved in processing sensory information? (iii) What is the local and spatial extent of activation elicited by passive movements and (iv) is cerebellar activity more related to motor output (active part of movements) or sensory input processing (passive movements)?

In the second study, we tested to what extent the human cerebellum is involved in movement planning. We used a paradigm recently described by Stephan *et al.* (1995): during movement execution, subjects had to move a joystick in any of the four possible directions when triggered by a pacing tone. During movement imagination, subjects simply performed the movements in their heads. Again, we analyzed whether cerebellar activity was more related to motor output control (imagination, i.e., planning of movements) or to movement execution.

MATERIALS AND METHODS

Subjects and Experimental Design

Regional cerebral blood flow (rCBF) was examined as an index of neuronal activity (Jueptner and Weiller, 1995) in twelve healthy volunteers (six in each study) aged 21–31 years (mean = 25.3 years). None of them had a history of neurologic or psychiatric diseases; none of them took any medications. Approximately 30 min prior to scanning, subjects were acquainted with the task and performed 8 to 10 test trials on each experimental condition. All subjects gave written informed consent prior to the examination. The study was approved by the Ethics Committee of the University of Essen.

In the first study, scans were performed under the following three conditions: (a) in the baseline condition (rest) subjects kept their eyes closed. A metronome produced tones at a frequency of 1 Hz to control for auditory input as needed in the active movement condition. Subjects were instructed to ignore the tones. (b) In the passive movement condition, the subject's elbow was fixed to a guide hinge. A motor was used to induce sequential flexions and extensions (amplitude of 90°) of the elbow at a constant velocity (identical to the active movements). One movement of 90° amplitude (flexion or extension) was completed in 1 s. Subjects were instructed to relax their arms during this task. The metronome produced tones at a frequency of 1 Hz as in the other conditions. (c) Active movements were performed with the subject's arm fixed to the guide hinge (active). Elbow flexions were performed against gravity with the arm reaching a 90° upright position at the end of the flexion. Subjects were instructed to perform the movements at a constant velocity as in the passive movement task. The movements were triggered by the metronome at the same frequency. Each condition (rest, passive, and active movements) was repeated four times in a balanced way (i.e., ABC CBA ACB BCA).

To test whether voluntary muscle contractions can be detected during the two movement conditions, we recorded offline EMG activity from the biceps and triceps muscles in three subjects using surface electrodes and a 10 Hz–1 kHz filter. EMG activity was

recorded from the biceps and triceps muscles of the right arm.

In the second study, scans were performed under the following three conditions: (a) In the baseline condition ("rest") subjects kept their eyes closed. A computer was used to produce tones at a frequency of 0.6 Hz. Subjects were instructed to ignore the tones and refrain from moving their right hand which kept the joystick in the neutral position. (b) In the imagining condition ("imagine"), the pacing tones were produced at the same frequency. Subjects kept the joystick in the neutral position. They were instructed to *imagine* joystick movements in one of the four possible directions in their head without moving their hand. (c) When triggered by a pacing tone (frequency of 0.6 Hz) subjects had to actively move the joystick in one of the four possible conditions and return to the neutral position ("execute"). The joystick was then kept in this neutral position until the next pacing tone sounded. Each condition was repeated four times in a balanced way (i.e., ABC CBA ACB BCA).

To test whether subjects did exert any voluntary muscle contractions during the imagining task, we recorded offline EMG activity from the biceps, triceps, supinator, and pronator teres muscles in two subjects using surface electrodes and a 10 Hz–1 kHz filter.

Data Acquisition

For each subject, 12 scans were performed. Subjects lay in a supine position with eyes closed in a darkened room. Head position was maintained by use of an individually molded styropor headrest to minimize involuntary head movements during the scans.

Dynamical scans were performed with a CTI ECAT 953-15 camera (CTI, Knoxville, TN) covering an axial field of view of 5.4 cm. The camera was tilted to include the entire cerebellum. Radioactivity was administered as a slow bolus injection (over 30 s) of H₂¹⁵O through a venous line in the left arm. Emission data were corrected for attenuation by the tissues of the head using a transmission scan, which was performed prior to the activation scans. During each scan, 3 ml of radiolabeled water was applied containing 20 mCi of ¹⁵O. Dynamic PET scans were collected over a period of 70 s; the paradigm was started 20 s prior to data acquisition and continued for 90 s. Any increase in the amount of radioactivity in a specific region reflects an increase in regional cerebral blood flow (Fox and Mintun, 1989; Mazziotta *et al.*, 1985), which in turn is coupled to synaptic neuronal activity (Jueptner and Weiller, 1995).

Data Analysis

All calculations were performed as previously described (Jueptner *et al.*, 1995); the scans were corrected for involuntary movement artifacts using realignment

to the first corrected image (Woods *et al.*, 1992; Friston *et al.*, 1995). All images were transformed into the standard anatomical space (Friston *et al.*, 1995; Talairach and Tournoux, 1988) and filtered with a low-pass Gaussian filter ($15 \times 15 \times 9$ mm in x, y, z dimensions) to increase the signal-to-noise ratio (Friston *et al.*, 1995).

Differences in global blood flow between subjects and conditions were removed by analysis of covariance (Friston *et al.*, 1995). Pixel-by-pixel comparisons were performed using t -statistics to reveal significant differences in rCBF between conditions ($P < 0.05$, corrected for multiple comparisons). Results are displayed as statistical parametric maps showing the areas of significant increase of rCBF (Friston *et al.*, 1995).

MRI scans were obtained and processed as described previously (Jueptner *et al.*, 1995). The group MRI scan served as a template onto which the average PET data were superimposed for exact anatomical localization of activations.

RESULTS

EMG Recordings

In the first study, EMG recordings from biceps and triceps muscles showed a typical activation pattern during active elbow movements. During passive movements, no EMG activity could be recorded. Figure 1 shows data from a representative single subject illus-

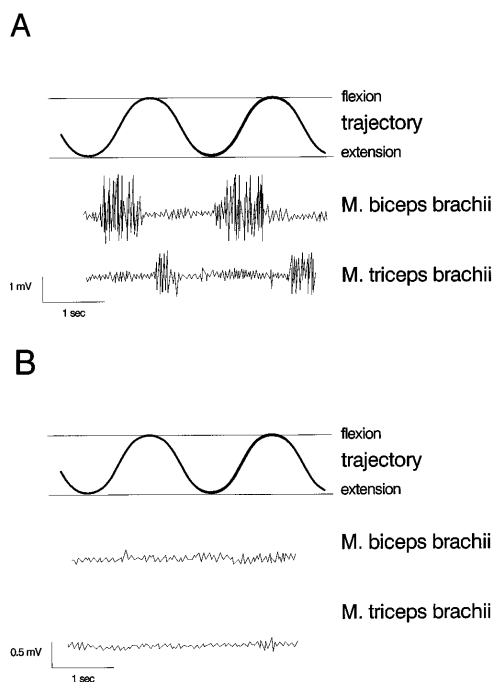


FIG. 1. EMG recordings from the biceps and triceps muscles of a single representative subject. Active (A) and passive (B) movements of the elbow were performed at a frequency of 0.5 Hz. EMG activity was recorded using surface electrodes and a 10 Hz–1 kHz filter.

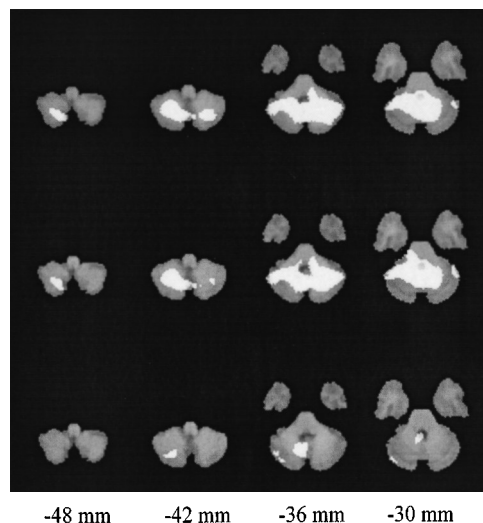


FIG. 2. Increases of regional cerebral blood flow during active and passive movements of the right elbow. The results from the PET experiment (significant increases are shown as white spots) were superimposed onto a group MRI for a more detailed anatomical information. Top row: increases of rCBF during active movements compared to rest (active vs rest). Middle row: increases of rCBF during passive movements compared to rest (passive vs rest). Bottom row: increases of rCBF during active compared to passive movements (active vs passive). The left side of the image corresponds to the right side of the brain. Numbers indicate the level of the axial planes relative to the intercommissural (AC-PC) line.

trating the absence of significant muscular activity in the passive movement task.

In the second study, EMG recordings from biceps, triceps, supinator, and pronator teres muscles showed a typical activation pattern during movement execution. During imagination of movements, no EMG activity was recorded.

Increases of rCBF Related to Active and Passive Movements

When subjects performed active movements of their right arm, significant increases of rCBF were observed in the ipsilateral neocerebellar hemisphere of the posterior lobe (active vs rest) which also extended to the contralateral side. The maximum increase of rCBF reached 3.2% in the right neocerebellar hemisphere and 5.4% in the neocerebellar vermis. The area of activation comprised 5419 voxels. The data of this comparison are illustrated in the first row of Fig. 2, which presents the significant increases of rCBF in the active movement task superimposed onto the group MRI for exact anatomical localization.

During passive movements of the right elbow (passive vs rest), significant increases of rCBF occurred in the identical parts of the cerebellum, i.e., in both neocerebellar hemispheres of the posterior lobe—with a maximum in the right, ipsilateral neocerebellar hemi-

sphere—and in the neocerebellar vermis of the posterior lobe. The maximum increase of rCBF reached 5.0% in the right hemisphere and 4.8% in the vermis. The area of activation comprised 5507 voxels and slightly extended into the more anterior parts of the neocerebellar hemispheres. The second row of Fig. 2 illustrates the significant increases of rCBF in the active movement task superimposed onto the group MRI for exact anatomical localization.

When comparing active and passive movements directly (active vs passive), significant increases of rCBF were found in a restricted volume (671 voxels) of the ipsilateral neocerebellar hemisphere, cerebellar nuclei, and vermis of the posterior lobe. The increase of rCBF in the neocerebellar hemisphere reached a maximum of 3.0%. The peak increase of rCBF in the neocerebellar vermis of the posterior lobe was 3.3%. The data of this comparison are illustrated in the third row of Fig. 2. The exact anatomical localization of activations are summarized in Table 1.

Decreases of rCBF Related to Active and Passive Movements

Functional neuronal activity and regional cerebral blood flow are closely related to each other (Jueptner and Weiller, 1995). Increases of rCBF mainly reflect increases in (pre-)synaptic activity in a population of neuronal cells irrespective of their excitatory or inhibitory functions. On the other hand, decreases of rCBF indicate decreases of neuronal activity and thus a disengagement of brain areas in a certain task.

During the active performance of the motor task, decreases of regional cerebral blood flow occurred in the medial and lateral prefrontal cortex, the lateral tempo-

ral cortex bilaterally, and in the left medial temporal cortex. These data are summarized in Table 2. In the same areas, decreases of rCBF also occurred when the movements were performed passively (Table 2). However, these decreases were smaller than those seen during the active performance of the task (Table 2).

Increases of rCBF Related to Movement Execution and Imagination

During free selection of joystick movements, significant increases of rCBF were observed mainly in the ipsilateral neocerebellar hemisphere of the posterior lobe (execute vs rest, Fig. 3). The maximum increase of rCBF reached 3.9% in the ipsilateral neocerebellar hemisphere and 3.8% in the cerebellar vermis of the posterior lobe. A volume of 4589 voxels was activated above threshold.

During movement imagination (imagine-rest), significant increases of rCBF were restricted to a small area of the ipsilateral neocerebellar hemisphere and vermis of the posterior lobe. The peak increase of rCBF reached 4.7% in the hemisphere and 6.5% in the vermis. A volume of 1206 voxels was activated above threshold. Further details are given in Table 3. The findings are illustrated in the lower part of Fig. 3, which shows the significant increases of rCBF superimposed onto the group MRI.

Decreases of rCBF Related to Movement Execution and Imagination

During execution of freely selected joystick movements, decreases of regional cerebral blood flow occurred in the temporal (peak coordinates $-2, 2, -22$),

TABLE 1

Comparison of Active Movements, Passive Movements, and Rest Condition: Foci of Significant Increases of rCBF in the Cerebellum during the Movement Tasks

Site of cerebellar activation	Extent of area activated (rel. to AC-PC plane)	Talairach coordinates of peak activation	% increase in normalized rCBF	Size of activated area ^a
I. Active vs rest				
Hemisphere (R)	-48 to -20 mm	26, -60, -34	3.2	5419
Hemisphere (L)	-42 to -26 mm	-26, -58, -40	4.7	5419 ^b
Vermis	-48 to -14 mm	-4, -68, -36	5.4	5419 ^b
II. Passive vs rest				
Hemisphere (R)	-48 to -20 mm	24, -60, -34	5.0	5507
Hemisphere (L)	-42 to -26 mm	-40, -58, -36	6.2	5507 ^b
Vermis	-48 to -14 mm	6, -50, -28	4.8	5507 ^b
III. Active vs passive				
Hemisphere (R)	-42 to -30 mm	24, -74, -42	3.0	183
Vermis	-36 to -16 mm	-8, -66, -34	3.3	488

^a Expressed in number of coherent voxels activated above threshold.

^b Identical numbers since only one coherent block of activated voxels was detected.

and medial prefrontal (peak coordinates $-2, 56, 6$) cortices bilaterally. In the same areas, decreases of rCBF also occurred when the movements were imagined (peak coordinates $8, -4, -20$ and $8, 58, 0$, respectively). However, these decreases were smaller than those seen during movement execution. Decreases of rCBF were observed in the medial temporal and medial prefrontal cortices for the direct comparison of imagine and execution conditions (imagine vs execute).

DISCUSSION

The role of the cerebellum in the control of movements is only poorly understood. While it has been known for many decades that the cerebellum is concerned with movement "coordination" (e.g., Holmes, 1917), little is known about the exact role of the cerebellum in motor control. We were interested to see whether the cerebellum is more involved in the control of movements *before* any voluntary action has occurred or *while* movements are being performed. In the first case, the cerebellum may be concerned with the determination of movement parameters like output to alpha- and gamma-motoneurons specifying duration of muscle contraction, direction, force, or velocity of movements (for reviews see Ito 1984; Thach *et al.*, 1992). In the second case, it may be concerned with control of feedback (sensory information processing) from ongoing

TABLE 2

Comparison of Control and Movement Tasks: Foci of Decreases of rCBF

Area activated	Extent of area activated (rel. to AC-PC plane)	Talairach coordinates of peak activation	% increase in normalized rCBF
I. Active vs rest			
Prefrontal cortex			
Lateral (L)	-4 to $+12$ mm	$-30, 40, 4$	4.9
Medial (L)	$+4$ to $+20$ mm	$-8, 46, 14$	3.2
Temporal cortex			
Lateral (R)	-30 to -12 mm	$52, -26, -26$	5.9
Lateral (L)	-32 to -16 mm	$-58, -44, -18$	5.8
Medial (L)	-24 to -12 mm	$-38, -20, -18$	3.2
II. Passive vs rest			
Prefrontal cortex			
Lateral (L)	0 to $+12$ mm	$-30, 44, 4$	4.1
Temporal cortex			
Lateral (R)	-30 to -16 mm	$52, -30, -24$	2.6
Lateral (L)	-28 to -20 mm	$-52, -42, -22$	1.9
Medial (L)	-16 to -4 mm	$-32, -20, -8$	2.7
III. Active vs passive			
Prefrontal cortex			
Lateral (R)	$+8$ to $+16$ mm	$18, 46, 12$	2.9
Lateral (L)	$+8$ to $+20$ mm	$-30, 40, 18$	2.5
Medial (L)	$+12$ to $+20$ mm	$-4, 44, 18$	2.8

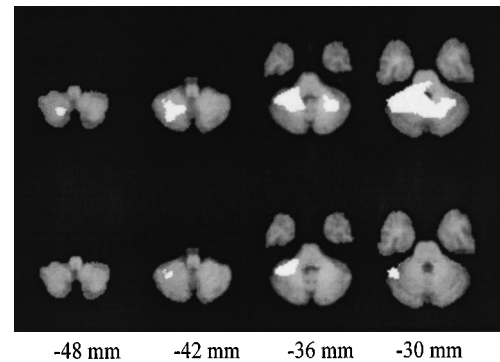


FIG. 3. Increases of regional cerebral blood flow during movement execution and imagination. The results from the PET experiment (significant increases are shown as white spots) were superimposed onto a group MRI for a more detailed anatomical information. Subjects performed joystick movements in any of four possible directions when triggered by a pacing tone. Top row: increases of rCBF during movement execution compared to rest (execute vs rest). Bottom row: increases of rCBF during movement imagination compared to rest (imagine vs rest). The left side of the image corresponds to the right side of the brain. Numbers indicate the level of the axial planes relative to the intercommissural (AC-PC) line.

movements to ensure the exact execution of a motor task (for reviews see Ito, 1984; Stein and Glickstein, 1992; Thach *et al.*, 1992).

Two studies were performed to test both hypotheses in normal human subjects. We were especially interested to analyze the *degree* of cerebellar activation in these tasks to see whether the cerebellum is primarily involved in controlling movement output parameters or controlling sensory input.

Active and Passive Movements

Passive movements lead to activation of muscle spindle afferents (primary muscle spindle afferents, group Ia fibers, and secondary muscle spindle afferents, group II fibers) and cutaneous receptors (for reviews see Ito, 1984; Rothwell, 1994). Animal experiments have shown that these afferents inform the cerebellum about many aspects of movement execution, e.g., joint position, direction and velocity of movements (Ito, 1984; Rothwell, 1994; Bauswein *et al.*, 1983; Berretta *et al.*, 1991; Bosco and Poppele, 1993; Ishikawa *et al.*, 1972; Kolb *et al.*, 1987a,b; Murphy *et al.*, 1973). It has been shown that the cerebellum uses this proprioceptive feedback to optimize movements (Ito, 1984; Stein and Glickstein, 1992; Thach *et al.*, 1992). In humans there has been a rather limited number of studies concerned with cerebellar sensory processing (Grill *et al.*, 1994; Ivry and Keele, 1989; Jueptner *et al.*, 1995, 1996). While these data suggest that the cerebellum is involved in processing sensory information, they do not reveal the functional relevance of this process.

Our data show that passive movements induce increases of rCBF in the same parts of the human

TABLE 3

Comparison of Movement Execution and Imagination to the Control Condition: Foci of Significant Increases of rCBF in the Cerebellum during the Movement Tasks

Site of cerebellar activation	Extent of area activated (rel. to AC-PC plane)	Talairach coordinates of peak activation	% increase in normalized rCBF	Size of activated area ^a
I. Execute vs rest				
Hemisphere (R)	-50 to -16 mm	38, -56, -26	4.7	4589
Hemisphere (L)	-40 to -24 mm	-22, -58, -30	3.6	112
Vermis	-44 to -12 mm	2, -56, -20	6.5	4589 ^b
II. Imagine vs rest				
Hemisphere (R)	-42 to -16 mm	34, -52, -38	3.9	1206
Vermis	-24 to -12 mm	14, -56, -16	3.8	1206 ^b
III. Execute vs imagine				
Hemisphere (R)	-50 to -16 mm	20, -54, -28	6.2	3534
Hemisphere (L)	-40 to -24 mm	-28, -52, -28	3.7	3534 ^b
Vermis	-44 to -12 mm	2, -58, -22	5.6	3534 ^b

^a Expressed in number of coherent voxels activated above threshold.

^b Identical numbers since only one coherent block of activated voxels was detected.

neocerebellar hemisphere as active movements. The local extent (percentage increase of rCBF at a specified location; see Table 1) and spatial extent (size of activation as determined by the number of significant voxels) of activation due to passive movements were almost identical to those for the active movements. Although we did not explicitly analyze the nature of the signal seen during passive movements (e.g., by electrical recordings from sensory nerve fibers or recording from cerebellar neurons), the above-mentioned animal experiments suggest that the neocerebellar cortical activation during the passive movement condition reflects sensory information processing. The direct comparison of active and passive movements revealed that only 12% of neuronal activity (671/5419 voxels) was more related to the active execution of a movement. These findings suggest that the cerebellum may be much more concerned with sensory information processing than with motor output control. This hypothesis is in accordance with findings reported by others (e.g., Bower, 1995; Grill *et al.*, 1994) but contradicts many previous studies which have postulated that the cerebellum primarily controls movements via computation of output parameters to alpha- and gamma-motoneurons such as duration of muscle contraction, direction, force or velocity of movements (Fortier *et al.*, 1989; Gorassini *et al.*, 1993; Thach *et al.*, 1992).

Imagining Movements: Set of Instructions

In the second study, we used positron emission tomography as a tool to analyze brain functions in the absence of apparent actions (imagining movements). Stephan *et al.* (1995) emphasized that precise instructions and good cooperation by subjects are of special

importance in such experiments. In the present study we therefore used the same instructions for all subjects, in the same way as described by Stephan *et al.* (1995). As in their study, we used surface EMG to monitor for activity in the relevant muscles. Typical EMG activation patterns were observed during movement execution while there was no change in EMG activity during movement imagination.

The Cerebellum and Movement Imagination

The performance of a motor task requires subjects to plan, program, initiate, and execute movements (Stephan *et al.*, 1995). The concept of a movement plan or motor program was derived from the observation that well-trained fast actions are executed too quickly to be dominated by sensory feedback (Keele, 1968). Although most movements require more than 100 ms and allow spinal and transcortical feedback to contribute, a neural representation of an entire complex action (so-called motor program) is still considered to be prepared before response onset (Inhoff *et al.*, 1989).

Stephan *et al.* (1995) analyzed two components of motor planning, i.e., motor imagination and preparation. These authors reported that the entire motor system which was active during movement execution was also activated during movement imagination with the exception of the primary sensorimotor and adjacent premotor and parietal cortices which were not activated during movement imagination. However, these authors used a camera with an axial field of view of 10.5 cm and did not visualize the cerebellum. Decety *et al.* (1990) analyzed the effects of movement imagination on cerebellar blood flow. These authors used a rather complex paradigm: imagination of tennis serving in

combination with silent counting. Changes of rCBF were observed in both cerebellar hemispheres and vermis (Decety *et al.*, 1990). There were several problems with this study: (i) the authors did not correct for global flow changes, (ii) they used a region of interest analysis (iii) which was performed on a single slice, and (iv) the two conditions being compared differed in more than one parameter, i.e., changes in rCBF might well have been due to differences in silent counting and not to imagination.

Therefore, our second study was planned to test whether the human cerebellum is involved in movement planning in an established motor paradigm (Stephan *et al.*, 1995) which is simpler than the one described by Decety *et al.* (1990). We tried to visualize areas of cerebellum involved in planning and analyze the extent of activation relative to movement execution. Our results demonstrate that movement imagination was associated with increases of rCBF in the ipsilateral neocerebellar hemisphere and vermis of the posterior lobe. These results are in accordance with physiological studies in animals and humans (for reviews see Diener and Dichgans, 1992; Thach *et al.*, 1992) which demonstrated the involvement of the neocerebellar hemispheres in movement planning.

However, in our study only a small portion of neocerebellar activity, i.e., 20% (1206/5795 voxels) of neuronal activity, was related to movement planning. This result supports the finding from the previous experiment (active and passive movements) in that the cerebellar activity is only minimally related to movement planning which reflects motor output control (Stephan *et al.*, 1995).

Is the Cerebellum a Sensory Organ?

If sensory information processing represents an important cerebellar function, it should be possible to (i) separate sensory from motor functions within the cerebellum, (ii) demonstrate sensory functions in the absence of a motor task, and (iii) show that sensory information processing is carried out for different input modalities (proprioceptive, acoustic, visual, etc.).

Using positron emission tomography in normal human subjects we have recently demonstrated that sensory information processing can be separated from a motor task within the cerebellum (Jueptner *et al.*, 1995). We required subjects to estimate differences of time intervals. A first, so-called standard interval was defined by two tones. A second (test) interval was presented after a short delay. Subjects had to lift their index finger if the test interval was shorter than the standard interval. The middle finger was lifted if the test interval was longer. In the control task, subjects had to alternate between index and middle finger movements to ensure that the same movements were performed in both conditions. When finger movements

were compared to a baseline reference condition, increases of blood flow were observed in the ipsilateral cerebellar hemisphere and vermis. Estimation of time intervals (compared to the control task) was associated with an increase of rCBF in the cerebellar vermis and adjacent hemispheres of the anterior lobe. Thus, within the cerebellum sensory information processing could be isolated from the motor control function.

In a follow-up study, we required subjects to compare the velocity of paired moving stimuli on the dorsum of the subject's right hand. We showed that this process (sensory information processing) involved the cerebellum even in the absence of motor output (Jueptner *et al.*, 1996). Apart from showing cerebellar sensory information processing in the absence of a motor task, the two studies cited here revealed that sensory information processing is carried out for different input modalities.

In summary, our results suggest that sensory information processing may represent an important aspect of the cerebellar control of movements. On the other hand, control of motor output seems to play a much less important role.

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