

Comparing Motion- and Imagery-Related Activation in the Human Cerebellum: A Functional MRI Study

Andreas R. Luft,* Martin Skalej, Alexander Stefanou, Uwe Klose, and Karsten Voigt

Department of Neuroradiology, University of Tübingen, 72076 Tübingen, Germany



Abstract: Cerebellar activation during execution and imagination of a finger movement was compared. Functional magnetic resonance imaging was used to detect cerebellar activation during execution and imagination of an untrained self-paced finger-to-thumb movement (left and right hand separately). The four fingers were opposed to the thumb in changing sequences freely chosen by the subjects. The activation maps of 10 right-handed healthy subjects were averaged after transformation into a common coordinate space. Averaged activation maps revealed strong motion-related bilateral activation in the anterior lobe of the cerebellum and in the paravermal regions of the posterior lobe. Ipsilateral activity predominated significantly. Compared to motion, imagination of the same task produced lower signal changes, and foci were more variable in position and strength. The averaged activation maps showed activity in the same regions as in motion. Activation in the posterior cerebellar lobe was more prominent extending into the lateral hemispheres. Ipsilateral dominance was significant for right-hand imagery. The left-hand task only showed marginally stronger ipsilateral activation. The activation pattern observed during execution of the finger-to-thumb movement is in agreement with theories of functional cerebellar topography. For imagery, activation at a comparable location may reflect common functionality, e.g., motor preparation and/or timing. Additional activation in the lateral hemispheres may be related to an imagery-specific function. *Hum. Brain Mapping 6:105–113, 1998.* © 1998 Wiley-Liss, Inc.

Key words: magnetic resonance imaging; echo-planar-imaging; brain mapping; imagination; movement



INTRODUCTION

Psychological, electrophysiological, and functional brain mapping studies suggest that the performance of a task and its imagination share common neural substrates [Berthoz, 1996; Cunnington et al., 1996; Decety, 1996; Jeannerod and Decety, 1995; Lang et al., 1996; Porro et al., 1996; Stephan and Frackowiak, 1996].

Visual perception involves roughly the same areas in the brain as visual imagery [Farah, 1989]. Roland and Friberg [1985] found activity in higher visual cortices during visual imagination. Accordingly, execution and imagination of a motor task are assumed to involve similar circuitry [Jeannerod, 1995]. Roth et al. [1996] and Leonardo et al. [1995] reported activation of the motor cortex during the ideation of movement. Neuropsychologic studies which showed that motor tasks can be trained by imagination [Pascual Leone et al., 1995] support this assumption.

The role of the cerebellum in imagery is far less studied than the role of the motor cortex. Cerebellar

*Correspondence to: Andreas R. Luft, Department of Neuroradiology, University of Tübingen, Hoppe-Seyler-Str. 3, 72076 Tübingen, Germany. E-mail: aluft@gris.uni-tuebingen.de

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activation during motor imagery was reported in several studies, using different functional brain mapping techniques and stimulation paradigms (positron emission tomography (PET) [Decety et al., 1994; Jueptner et al., 1997; Parsons et al., 1995], and single photon emission computed tomography (SPECT) [Ryding et al., 1993]). Motor imagery, which can be interpreted as an incomplete motor program terminated before execution, is a valuable paradigm for characterizing the role of the cerebellum in the motor process, especially with respect to its recently suggested role in sensory processing [Gao et al., 1996; Jueptner et al., 1997] and higher motor function (e.g., planning, initiation) [Bonneto-Kyriacou et al., 1995; Botez et al., 1989; Diener and Dichgans, 1992; Higgins, 1987]. Additionally, studying imagery in the cerebellum may uncover some of the brain's functionality involved in motor imagery.

Using functional magnetic resonance imaging (fMRI), we compared execution and imagination of a complex hand movement in their effect on cerebellar activity. While most motor studies use regular finger-to-thumb tapping, our task consisted of a self-paced sequence of opposing fingers 2–5 to the thumb. The subjects changed the sequence to avoid effects of training and automatism. This paradigm was designed to elicit a high degree of motor timing and planning. The pattern of cerebellar activity in 10 healthy volunteers was averaged after registration in a common coordinate space. The results demonstrate congruencies and differences of activation between imagery and motion.

MATERIALS AND METHODS

Subjects and MR protocol

Using a conventional 1.5T scanner (Magnetom Vision, Siemens, Erlangen, Germany), we examined 10 healthy, right-handed volunteers (mean age, 26.5 years) after obtaining informed consent. Handedness was assessed using the Edinburgh inventory [Oldfield, 1971]. For each paradigm, 48 measurements were performed in 4 cycles of baseline and stimulation phases (6 measurements per phase). Twelve measurements were acquired per cycle, using a two-dimensional echo planar sequence (matrix size, 256×192 ; FOV = 270 mm; slice thickness, 4 mm; gap, 1 mm; $TE_{\text{eff}} = 100$ msec, 25 slices) in coronal orientation. The scan time was 72 sec for each phase. The first measurement of each phase was excluded to omit overshoot and undershoot effects. The sections were aligned parallel to a line through the posterior commissure and the obex, to allow registration in a common coordinate space (see below). For anatomical correlation, T1-

weighted spin echo images were acquired after every second paradigm. A cushion with a head-shaped cutout was used to minimize motion artifacts. The subjects were instructed to keep their eyes closed during image acquisition.

Paradigms

The motion task consisted of finger-to-thumb opposition in changing sequence (e.g., 2-3-5-4, 2-2-3-4-4-5, 2-4-3-5; frequency, 3–5 Hz) and was performed with the right and left hand separately. The subjects chose and varied the rhythm themselves (the change in sequence was done every 12 sec, triggered by the noise of the measurement). The individual performance was supervised and recorded using the scanner's proprietary video system. Subsequently, the same movement was imagined. In the sequence of experiments, right-hand movement preceded right hand imagery, followed by left-hand movement and imagination. The subjects were instructed to avoid counting or semantic thought (e.g., thinking of the words "thumb" or "index" finger) during imagination. Motion and imagery tasks were trained for 10 min outside and 10 min inside the MR machine before the first experiment was started. After the session the subjects were asked to estimate the frequency of the imagined movement and to describe the method of imagination as dominated by "visual" or "motor" thought. Explicitly, the subjects were asked whether they "predominantly saw the movement in front of their mind's eye" or whether they "predominantly felt the movement."

In a pilot study, muscle activity in the forearm was monitored electromyographically in 5 of the subjects performing the imagery task outside the scanner.

Postprocessing

Activated pixels were extracted using a modified Z-score method [Klose et al., 1996]. Baseline and stimulation phases were averaged for every slice position. The resulting maps were subtracted. Subsequently, a noise map was calculated (= standard deviations of intensities at every pixel position over time). Areas of activation were extracted by defining thresholds for subtraction and noise maps. Additionally, a kernel was used to filter clusters (with a diameter of 2 mm) rather than solitary pixels. For verification, the "averaged" signal-time course of all pixels in a cluster was plotted and screened. Foci which did not match the expected on-off pattern but still passed the Z-score filter (e.g., due to noise or movement related signal changes) could hence be

excluded. All other foci were rated according to their (averaged) signal gain over all stimulation phases (rating 1; 3–3.8%; rating 2, 3.9–4.6%; rating 3, 4.7–5.4%) (Fig. 1). The reason for this grouping was the limitation of our homemade software system for intersubject averaging, which only allowed limited differentiation between summed activation for every coordinate (limited by the number of colors).

Localization of activation

All extracted foci were registered using a cerebellar coordinate system (Fig. 2). The system consisted of two symmetrical boxes, each enclosing one cerebellar hemisphere. The medial limits of the boxes were aligned for the lateral boundaries of the vermis (indentation between vermis and tonsil). Each box was divided into 8 partitions in x- (horizontal) and 10 partitions in y-direction (vertical). In z-direction, the boxes were partitioned according to slice positions. As stated above, the slices were aligned for the posterior commissure-obex line. Pilot measurements indicated that this line was relatively invariable in relation to landmarks in the cerebellum [Luft et al., 1998].

In practice, the two grids were adjusted in position, size, and rotation for a coronal slice through the midcerebellum. The adjusted grids were copied to consecutive sections, keeping their relative position to the image origin. The coordinates of the foci of activation could then easily be determined.

Averaging of activation maps

For every coordinate, the signal course ratings (1–3, see above) of all individual foci were summed. The resulting map therefore reflected the signal strength and the reproducibility of activation. To test for lateralization, four quadrants were analyzed (right and left anterior lobe, and right and left posterior lobe; Fig. 4, maps at 3 cm). Individual activation in every quadrant was averaged. The resulting variables (one for each quadrant) were tested for significant difference using two-sided paired t-tests. Accordingly, activation in motion vs. imagery was tested for significant difference. To quantify the variability of activation, the center of every focus was determined and variability coefficients were calculated for the coordinate values. Absent activation was not considered in the calculation of the variability coefficient.

RESULTS

The motor task evoked a constant pattern of activation (Fig. 3) in all subjects (variability coefficient of

location: $V_{\text{right}} = 0.073$, $V_{\text{left}} = 0.064$). Activation was present in the anterior lobe of the cerebellum. It predominated ipsilaterally in relation to the moving hand ($P_{\text{left}} < 0.01$, $P_{\text{right}} < 0.05$) (Fig. 4a,c: sections at 3–5 cm, upper quadrants). The strong ipsilateral focus was present on 3–4 neighboring sections (1.5–2 cm in z-extension). Activity in the posterior lobe was confined to the medial aspect of the hemispheres (Fig. 4a,c: sections at 3 and 4 cm, lower quadrants, and section at 2 cm). Posterior lobe activation showed significant ipsilateral predominance only for the left-hand task ($P < 0.01$). Foci in the vermis were rare (Table I). Supracerebellar activation was found in the contralateral primary motor cortex (M1). Infrequently, activation was observed in the ipsilateral M1 during left-hand movement (3 cases) [compare Colebatch et al., 1991; Kim et al., 1993]. Bilateral signals were consistently detected in the premotor, somatosensory, and temporal cortices, and rarely in the thalamus (2 cases) and the basal ganglia (3 cases).

The estimated frequency of the imagined movement was 2–5 Hz, which was equal to or slower than the frequency of the executed movement (Table II). All subjects described their method of imagination as dominated by visual thought (although they did not exclude “feeling the movement”). None of the 5 subjects who underwent electromyography showed muscle activity during ideation. Compared to motion, activation in imagery was more variable in presence and location (Table I, $V_{\text{right}} = 0.1$, $V_{\text{left}} = 0.081$). The average signal gain between rest and stimulation was smaller (3.6%, as compared to 4.5% in motion). In the anterior lobe and the medial part of the posterior lobe where motion produced its greatest activation, significant activation was observed in the majority of subjects (Table I). Activation was significantly greater in the ipsilateral hemisphere for right-hand imagination ($P < 0.05$). For the left-hand task, only a trend towards ipsilateral dominance was observed (Fig. 4d, section at 3 cm). Activity in the posterior lobe was more pronounced in imagery than in motion. It extended into the lateral cerebellar hemispheres (Fig. 4b, 2–4 cm; Fig. 4d, 2–4 cm). Extracerebellar activity was noted in the temporo-parietal association cortex and in occipital areas corresponding to V5, which is associated with visual motion processing [Zeki, 1978]. The premotor areas and the somatosensory cortex showed bilateral activation. Minimal activity was detected in 3 subjects in both areas M1 [compare Leonardo et al., 1995]. One left-hand imagery experiment had to be interrupted due to technical reasons.

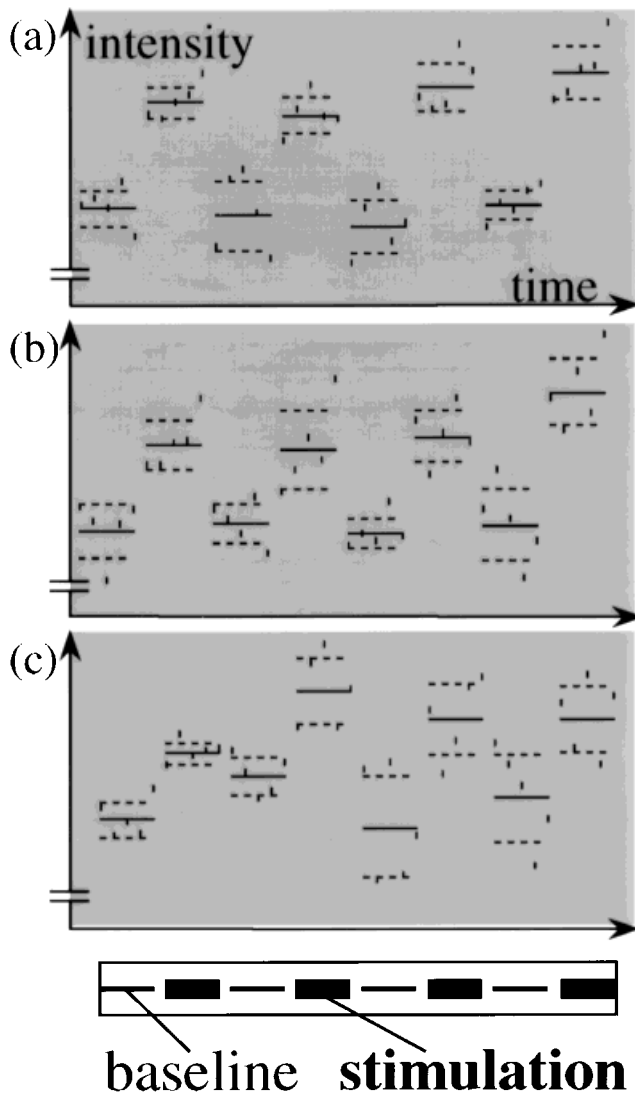


Figure 1.

Signal course patterns. Typical patterns of the signal-time course are demonstrated, reflecting the on-off pattern of the stimulation paradigm. To produce these plots, intensities of all pixels in a cluster of activated pixels were averaged for each (baseline/stimulation) phase. Solid lines indicate the mean intensities of five consecutive measurements (the first measurement of each phase was excluded), while dashed lines represent 1 standard deviation above and below the mean. **a:** Observed in the ipsilateral anterior lobe of a subject moving the right hand. The mean signal amplitude (difference between stimulation and baseline) was 5.3% of the averaged baseline signal. Similar signal-patterns were rated highest (= 3) on a scale from 1–3, reflecting the strength of activation (see text). **b:** Derived from a contralateral activation in the anterior lobe with a mean signal of 4.1%. A rating of “2” was assigned. Note the tendency of the signal to increase inside each stimulation phase. This effect was observed infrequently at varying sites in the cerebellum. **c:** Signal-time course of an activation in the paravermal posterior lobe. With mean signal difference of 3.7%, the rating “1” was assigned.

DISCUSSION

Intersubject variability in activation is a problem for studies investigating the functional topography of the human brain, especially when tasks such as imagery are used, which cannot be objectively controlled. Imagination may vary among individuals. Additionally, the experimental setting of fMRI induces different mental states (e.g., agitation, excitement, or fear), which may have variable (and unknown) effects on brain activation. These factors can only be overcome by averaging the patterns of activation in a number of individuals. Before averaging, the individual activation has to be registered in a common coordinate space to account for the anatomical variability. No standard cerebellar coordinate system exists for the posterior fossa (the system of Talairach et al., which is commonly used for the cerebral hemispheres, does not cover posterior fossa structures [Talairach and Tournoux, 1988]). We therefore used an orthogonal coordinate space aligned for the posterior commissure-obex line. These landmarks proved to be less variable with respect to posterior fossa anatomy than the anterior commissure-posterior commissure line [Luft et al., 1998], which is the baseline of the Talairach system. The insufficiency of this and probably every system to precisely “normalize” individual anatomy may add to the variability observed in the location of foci (blurred foci on the averaged map in Fig. 4). For statistical comparison, we therefore evaluated activation in four regions corresponding to rough functional compartments, to account for local anatomical variability.

Additionally, the lack of motion correction in the present study may add to spatial variability (as well as to statistical significance of the detected focus). Head motion is probably greater when the subject is moving the hand. Therefore, this artifact would only diminish the difference in the variability between the two tasks. The punctual activation during the motor task may even be more sharply circumscribed than found in our study.

The results of the motion experiment agree with known cerebellar topography and connectivity. The strong ipsilateral activation in the anterior lobe reflects the organization of the spinocerebellar pathways, which project from the spinal cord to the anterior cerebellum without crossing the midline. Contralateral activation is somewhat more difficult to interpret, but may be related to the minority of afferent fibers, which cross the midline (anterior spinocerebellar tract). It may also reflect signals from ipsilateral cortical areas (i.e., premotor cortices and sensory cortices), where activation was detected. Compared to the somatotopical maps de-

TABLE I. Number of subjects showing activation in a particular ROI*

ROI	Motion			Imagery		
	Right (of 10)	Left (of 10)	Both (left and right)	Right (of 10)	Left (of 9)	Both (left and right)
A-IPSI	10	10	10	10	7	7
A-CON	10	10	10	8	9	7
P-IPSI	10	10	10	9	6	6
P-CON	6	6	2	4	9	5
Vermis	1	3	1	2	2	1
IH	0	0	0	7	7	5

* A-IPSI/CON, anterior lobe, ipsi-/contralateral cortex; P-IPSI/CON, posterior lobe, ipsi-/contralateral cortex; IH, lateral hemisphere; ROI, region of interest.

scribed by Snider and Stowell [1944], activation is present in both maps, i.e., the anterior lobe and the posterior lobe map. These areas of activation were rather stable among subjects (high intensity peaks in Fig. 4).

In contrast, activation in imagery was more variable in position, intensity, and size. This variability can be interpreted in different ways. It may reflect individual differences in method and performance of imagery. The method may vary between visual imagination, motor, or semantic thought [Annett, 1995]. The variability may also be understood as interindividual differences in cerebellar functional topography.

A disadvantage of our study is that subjects were not able to perform executed and imagined movements at the same rate. External pacing was avoided for two reasons. First, the paradigm should require autonomic timing in which the cerebellum may be involved [Braitenberg, 1967]. In addition, external pacing in a fixed frequency would bias the comparability of different individuals (for some subjects the frequency would be too high, for others too low, depending on individual motor skills). The difference in frequency may cause the weaker activation detected during imagination. However, it is not clear whether the rate of a repetitive movement has an influence on cerebellar activation [Blinkenberg et al., 1996; Sadato et al., 1996].

Another possible explanation for the weaker signal during imagery is the lack of somatosensory feedback to the cerebellum. Jueptner et al. [1997] found that active and passive movements produced almost identical cerebellar activation, suggesting that about 90% of the activity is related to somatosensory input. In a second experiment, the authors studied the mental rehearsal of a joystick movement and found only small activity in the ipsilateral hemisphere and posterior lobe. The posterior lobe involvement is consistent with our findings. However, we detected more widespread activation over both cerebellar hemispheres, with overlap to the foci of motion. This discrepancy may be related to the variability in cerebellar activation during imagery (the authors examined 6 subjects). More likely it reflects the different nature of both imagery tasks. While Jueptner et al. [1997] investigated an acoustically paced and freely selected (in any of four directions) joystick movement, we asked the subjects to oppose the four fingers to the thumb in a self-paced, self-chosen, and changing pattern. Both tasks share the element of free selection. However, a major difference is that our subjects had to rely on their own pacing. A second difference is the greater importance of sensory feedback in our task. During execution, correct performance of the sequence of finger-to-thumb movements depends on monitoring the touch-signals. They serve

TABLE II. Judgments of method and frequency of imagined movement*

Subject	1	2	3	4	5	6	7	8	9	10
Method (predominantly)	v	v	v	v	v	v	v	v	v	v
F_{motion} (Hz)	4	3	4	4	3	4	5	4	4	5
$F_{\text{imagination}}$ (Hz)	3	2	4	3	2	4	3	3	3	4

* v, visual; F, frequencies.

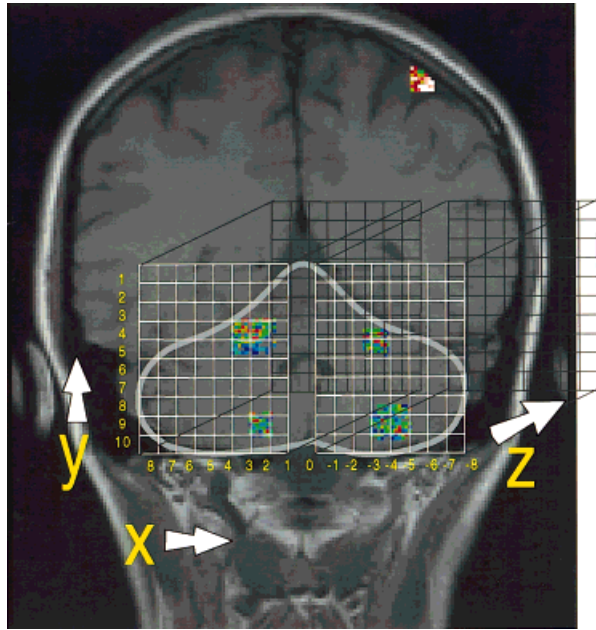


Figure 2.

Cerebellar coordinate system. A two-dimensional coordinate system consisting of a 10×17 grid (horizontal \times vertical) was used to normalize for individual anatomy. The grid was adjusted in height and width for a coronal section through the anterior cerebellum and copied to consecutive sections, keeping its position relative to the origin of the image. The orientation of the coronal slices was defined by a line through the posterior commissure and the obex. Registration in the common coordinate space allowed interindividual averaging of activation.

as important feedback signals as long as the sequence is untrained. Training was prevented by changing the pattern. In imagery, such sensory feedback may be “simulated” by the brain to coordinate the movement (see below).

Activation in the medial parts of the hemisphere observed in motion and in imagery may reflect a common functionality (e.g., motor preparation or timing) which is required for both tasks. Ryding et al. [1993] did not detect medial activation in a SPECT study in which subjects imagined a complex motor task (playing tennis). Again, the discrepancy may result from different paradigms (imagination of tennis is probably more visually dominated, especially with the subject in supine position), technique (measuring blood flow changes in SPECT and oxygenation effects in fMRI), or resolution.

Consistent with the SPECT study, we recorded activation in the lateral cerebellar hemisphere during imagery, whereas motion was lacking activity in these areas. This activity may reflect an imagery-specific

function of the cerebellum. Beyond the assumption that motion and imagery share the same neural processes and substrates, studies have postulated the involvement of additional functionality in imagery [Grafton et al., 1996]: these may be inhibitory processes to terminate the motor program before execution [Berthoz, 1996; Leonardo et al., 1995]. It may reflect sustained (“circulating”) motor representations when the motor program awaits execution [Jeannerod, 1995]. More likely, motor imagery may involve retrieval of sensory impressions from memory [Annett, 1996] or visual imagination of motor actions [Annett, 1995; Decety and Ingvar, 1990]. These functions point towards sensory processing, which has been discussed as a function of the lateral cerebellum [Allen et al., 1997]. Gao et al. [1996] observed stronger activation in the dentate nucleus (which is the output nucleus of the lateral cerebellum) during sensory discrimination tasks than during fine motor control tasks. Besides somatosensory components, visual components may be important [Parsons et al., 1995]. Which modality dominates is unclear, although our subjects put more emphasis on visual thought.

Sensory input from different modalities may converge to form a spatial working memory with a major role in motor imagery. Middleton and Strick [1994] found evidence for connections of the lateral cerebellum to prefrontal area 46 in primates. Area 46 is known to be involved in spatial working memory. Although the present work contains no proof, it supports such interpretations. Further studies will be required to fully clarify all the mechanisms involved.

CONCLUSIONS

Our study shows that execution as well as imagination of a self-paced, self-planned, and self-initiated hand movement evokes reproducible cerebellar activation in fMRI. Imagery and motion were found to share common cerebellar circuitry: still imagery produced additional activation, which may reflect a higher demand for the cerebellum as compared to motion. The medial cerebellum seems to play a role in execution as well as preexecution steps of the motor program, since it is activated in imagery and motion. The response of the lateral cerebellum during imagery may reflect an imagery-specific function.

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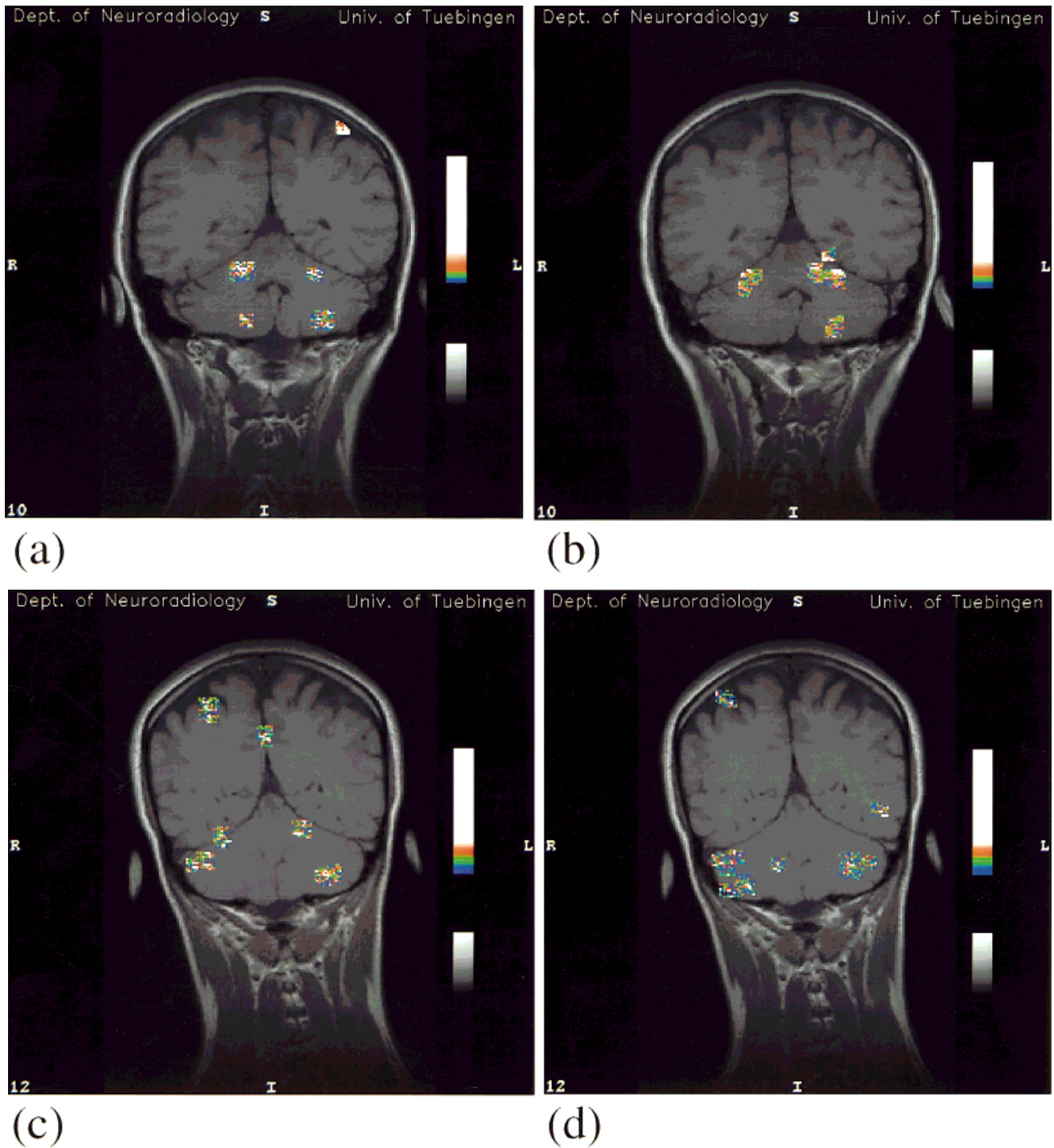


Figure 3. Individual activation maps superimposed on conventional spin-echo images show typical patterns of cerebellar activation during execution (**a**, right hand; **b**, left hand) and imagination (**c**, right hand; **d**, left hand) of a self-paced, self-planned, and self-initiated finger-to-thumb movement.

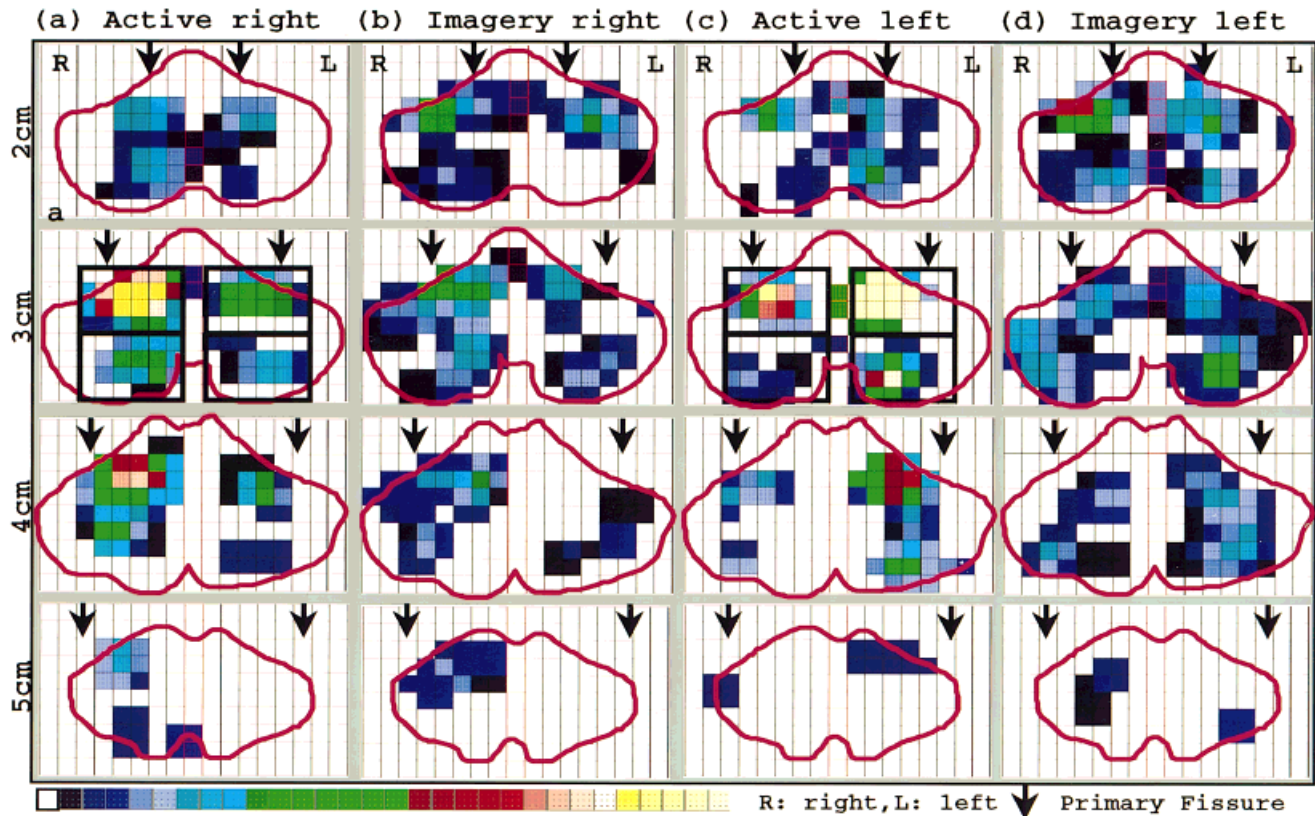


Figure 4.

Averaged activation maps. Averaged activation maps of corresponding (coronal) sections through the cerebellum illustrate the mean responses of 10 subjects. To compute these maps, every pixel of the coordinate grid (see Fig. 2) was initially set to zero (= white). For each focus hitting a specific pixel, this pixel's color grade (increasing from left to right in the bar in the lower left corner) was increased by the rating of the focus (see Fig. 1). One step in color represents an increase by 3 units. The arrow pointing to the superior surface of the cerebellum indicates the intersection of the primary fissure. The position of each section is measured from the posterior edge of the cerebellum (= 0 cm). **a**: Maps of right-hand movement task demonstrate four areas of activation (highlighted on the 3-cm section: upper quadrants, anterior lobe; lower quadrants, posterior lobe) in the anterior and posterior cerebellar lobes, showing marked ipsilateral dominance. Most activity is

confined to an area medial to the primary fissure (sections at 3–5 cm) in the upper quadrants (= anterior lobe). Activity in the posterior lobe (lower quadrants and section at 2 cm, behind the primary fissure) is focused close to the midline. **c**: Comparable activation for left-hand motion. Lateralization is inverse, showing a predominant activation of the left cerebellum. **b,d**: Activation during imagination. In general, activity is not as focused as in motion (low-colored pixels) and covers a larger area, which reflects higher interindividual variability. The four foci observed during motion show (lesser) activity in imagery. Ipsilateral dominance is evident on the 3-cm sections (significant only for right-hand imagination). Compared to motion, the posterior lobe shows more activation. Lateral hemisphere activation is evident on sections at 3 cm and 2 cm.

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