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Changing Brain Networks for Visuomotor Control With Increased Movement Automaticity

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Floyer-Lea, A. and P. M. Matthews. Changing brain networks for visuomotor control with increased movement automaticity. *J Neurophysiol* 92: 2405–2412, 2004; 10.1152/jn.01092.2003. Learning a motor skill is associated with changes in patterns of brain activation with movement. Here we have further characterized these dynamics during fast (short-term) learning of a visuomotor skill using functional magnetic resonance imaging. Subjects ($n = 15$) were studied as they learned to visually track a moving target by varying the isometric force applied to a pressure plate held in the right hand. Learning was confirmed by demonstration of improved performance and automaticity (the relative lack of need for conscious attention during task execution). We identified two distinct, time-dependent patterns of functional changes in the brain associated with these behavioral changes. An initial, more attentionally demanding stage of learning was associated with the greatest relative activity in widely distributed, predominantly cortical regions including prefrontal, bilateral sensorimotor, and parietal cortices. The caudate nucleus and ipsilateral cerebellar hemisphere also showed significant activity. Over time, as performance improved, activity in these regions progressively decreased. There was an increase in activity in subcortical motor regions including that of the cerebellar dentate and the thalamus and putamen. Short-term motor-skill learning thus is associated with a progressive reduction of widely distributed activations in cortical regions responsible for executive functions, processing somatosensory feedback and motor planning. The results suggest that early performance gains rely strongly on prefrontal-caudate interactions with later increased activity in a subcortical circuit involving the cerebellum and basal ganglia as the task becomes more automatic. Characterization of these changes provides a potential tool for functional “dissection” of pathologies of movement and motor learning.

INTRODUCTION

Neurological diseases affecting movement frequently alter motor automaticity, the ability to perform a task accurately without exerting full attention. Automation with skill development allows general attentional resources to become available for other tasks (Doyon et al. 1998). As automaticity increases, it therefore becomes easier to perform a second, attention-demanding task simultaneously. In principle, impairment of automaticity could arise from dysfunction in any of several brain regions within the network involved in motor control. Specific definition of the functional anatomical loci for changes in the control of more automatic learned motor behaviors could contribute to the development of strategies for enhancement of recovery after brain injury.

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Several studies already have begun to characterize functional changes in a wide network of brain regions that are involved in learning to perform a novel sequence of movements. During the early stages of learning a simple motor task, the dorsolateral prefrontal cortex (DLPFC) and premotor cortex are relatively active (Ghilardi et al. 2000; Grafton et al. 1992, 2002; Jueptner et al. 1997). The ipsilateral lateral cerebellar cortex also is active early in skill learning (Eliassen et al. 2001; Jenkins et al. 1994; Penhune and Doyon 2002). Increased activation in the cerebellar dentate nucleus and basal ganglia characterizes later stages of motor-sequence learning (Doyon et al. 2002). The importance of subcortical structures is highlighted by the observation that lesions of either the cerebellum or basal ganglia impair automatic (implicit) performance without affecting explicit knowledge of the motor sequence (Doyon 1997). However, technical limitations have prevented more detailed definition of the dynamics of relative activity changes across the brain during short-term motor skill acquisition and, specifically, their relation to the development of automaticity of movement. Also, although correlations of brain activity changes with performance have been made, the relevance of these changes to automaticity has not been explored.

Here we have characterized brain activity changes with short-term visuomotor learning in greater detail than has been possible previously. We also have related these time-dependent changes to changes in performance and movement automaticity. To do this, a tracking task was used in which subjects tracked a continuously changing, visually presented target by varying the force exerted on a pressure sensor held in the right hand. This task is initially highly attentionally demanding but rapidly becomes highly automatic as performance improves. We explicitly measured the increase in automaticity of the task after learning by using a dual-task paradigm outside the scanner.

METHODS

Volunteers

Fifteen healthy right-hand-dominant subjects participated in this study (mean age: 25.4 yr; range: 20–31 yr; 8 women, 7 men). All gave informed consent according to a protocol approved by the local research ethics committee.

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Image acquisition

Data acquisition was performed on a 3 Tesla Varian Inova MRI system, using a multislice gradient-echo EPI sequence [repetition time (TR): 3,000 ms, echo time (TE): 30 ms, 21×6 mm axial slices providing whole-brain coverage, field of view: 256×192 mm², matrix: 64×64). Four “dummy” scans were added at the beginning of the image sequence to reach steady-state magnetization. A T1-weighted structural image also was acquired for each subject with a notional resolution of $1.5 \times 1.5 \times 3$ mm³ (IR 3D Turbo Flash, TR: 30 ms, TE: 5 ms, inversion time (TI): 500 ms, flip angle 15° , FOV: 256×256 , matrix: 256×256) to allow functional image registration for precise localization of activations and to define individual regions of interest.

Paradigm

Subjects held a magnetic resonance (MR) compatible pressure sensor in their right hand between the thumb and fingers (Fig. 1). The arm was held in a semi-pronated position, supported by an armrest, and secured to prevent arm or wrist movement. As the arm and wrist were held immobile, subjects used the muscles of the thenar eminence and the finger flexor muscles to perform the task. The movement was isometric. Subjects viewed a large screen on which the movement sequence was presented from a distance of 2 m by means of prism glasses.

Two vertical bars were shown on the screen during the experiment. The target pressure, which the subject was required to match, was cued by the height of a red bar on the left-hand side of the screen. A second blue bar on the right-hand side of the screen gave a continuous measure of the subject's response. Each subject was instructed to maintain the two bars at equal heights on the screen at all times. For both the target and response bars, increased pressure increased the level of the bar on screen. The force applied to the pressure sensor was sampled at 100 Hz and projected to the screen at the maximum refresh rate of the projector (50 Hz) so that there was no discernible lag between a response by the subject and the on-screen feedback. The software used to present the experiment was written in C++ by A. Floyer-Lea.

The tracking error, calculated as the difference between the target and response forces and measured as a percentage of each subject's maximum voluntary contraction, was recorded throughout the experiment with a sampling rate of 100 Hz. The mean absolute tracking error was calculated for each repeat of the sequence; but this infor-

mation was not available to the subject. The pressure applied by subjects during rest also was recorded to confirm that subjects did not move their hand during this period.

The experiment was implemented as a block design with blocks of force tracking alternating with blocks of a visually matched rest condition. Instructions were shown on screen for 3 s immediately before each tracking and rest block. Each tracking block consisted of a 1-s warm-up period in which the target force increased linearly from zero to the initial value of the sequence followed by four repeats of the 8-s pattern. The warm-up period prevented an increased error on the first sequence of each block. The tracking pattern was not shown during the rest periods; instead subjects were shown a sinusoidal moving pattern, attention to which was intended to prevent mental rehearsal of the pattern to be learned during the rest block. The matched learning and rest blocks lasted 70 s and each experiment includes 10 of these blocks, giving a total experimental duration of 11 min 40 s. The maximum, minimum, and median force exerted by the subject during each block were recorded to confirm that these parameters remained constant throughout the experiment.

Prior to scanning, each subject was trained outside the scanner for a period of 10 min on a randomly varying tracking sequence. Tracking performance over this period was measured to ensure that subjects achieved and maintained a stable baseline performance level before the start of the learning experiment. All subjects were able to perform the task easily. Immediately prior to each scanning session the force level required was calibrated to require a maximum force equal to 75% of each subject's maximum voluntary contraction to equalize task difficulty across subjects.

Measurement of automaticity

To explicitly assess improvements in automaticity which occurred during learning, a separate dual-task experiment was carried out outside the scanner. Ten of the subjects who were trained on the tracking task also trained in a serial subtraction task involving verbally counting backward from 99, 100, or 101 to 0, 1, or 2, respectively, in steps of 3 as quickly as possible. Training was performed until there was no further improvement in the total time necessary for completing the task over three successive trials. In a quiet room, these subjects then engaged in a dual-task paradigm, performing the visuo-motor tracking task and the subtraction task (at 75% of their maximum rate, paced by an auditory metronome cue) together. An observer recorded the number of counting errors during each trial, while the tracking error was recorded as described in the preceding text. Subjects performed the tracking task with a novel sequence for 1 min, followed by the dual-task paradigm for 1 min (baseline). They then practiced the novel sequence using the same protocol that was used for short-term visuomotor task learning during the scanning sessions. After this learning period, they were tested again on both the tracking task alone and on the dual-task paradigm as at baseline. Increases in automaticity of the tracking task were assessed as a decrease in the interference between the two tasks, measured from the change in error rates when the tasks were performed together before and after short-term learning of the tracking task.

Data analysis

The analysis was carried out using tools from the FMRIB Software Library (www.fmrib.ox.ac.uk/fsl). The following prestatistics processing was applied: motion correction (Jenkinson et al. 2002), spatial smoothing using a Gaussian kernel of full-width half-maximum 5 mm, and nonlinear high-pass temporal filtering (Gaussian-weighted LSF straight line fitting, with $\sigma = 50.0$). Statistical analysis was carried out using the general linear model (GLM) with local autocorrelation correction (Woolrich et al. 2001). Registration of EPI functional images to high resolution and into standard space (Talairach

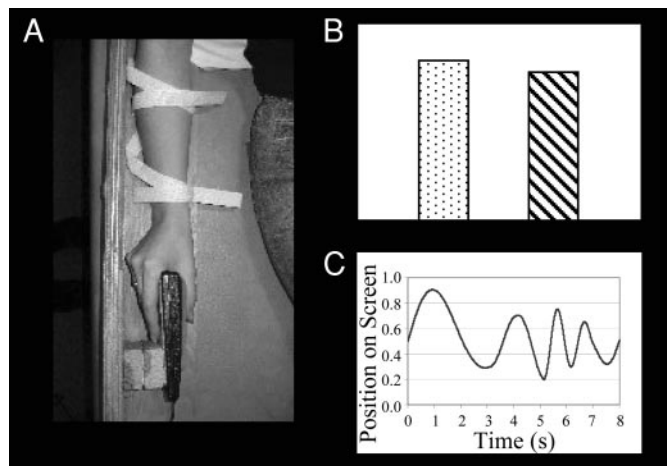


FIG. 1. A: positioning of the force sensor and a subject's arm and hand. B: representation of the screen displayed to subjects in the scanner. The left bar showed the target and the right bar showed the subject's response. Subjects had to try to keep the height of the right bar as close as possible to that of the left bar at all times. C: response target of the sequences learned by the subjects.

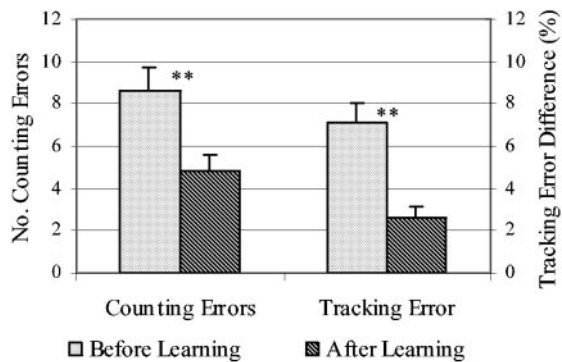


FIG. 2. Increase in automaticity over time. After learning, subjects were able to perform better on a secondary verbal subtraction task. Performing the secondary task also had less effect on their tracking performance, showing that the tracking task required less conscious attention after learning.

and Tournoux 1988) was carried out using an affine transformation with 12 df (Jenkinson and Smith 2001).

Group random effects analysis was performed. Z (Gaussianized T/F) statistic images were corrected for multiple comparisons using cluster detection, with clusters determined by $Z > 2.3$ and a corrected cluster significance threshold of $P = 0.05$ (Forman et al. 1995; Friston et al. 1994; Worsley et al. 1992). Activation maps were overlaid on the group mean high-resolution image, and the anatomical location of clusters was reported using macroscopic anatomical boundaries approximating the cytoarchitecture (Crespo-Facorro et al. 2000; Geyer et al. 2000).

The data from each subject were divided into two sections, early and late, on the basis of each subject's behavioral results. The early section was defined as the period during which the subject showed a reduction in tracking error of $>0.25\%$ on each block and late as the period after they had attained stable performance. To identify regions of interest for further analysis, learning was modeled within the GLM as a linear trend over the early period. A linear trend was chosen for the model as it is sensitive to a wide variety of time-dependent activation patterns in the brain. Areas of learning-correlated change were defined as those that showed changes in activation over the early period that correlated with the linear model and then showed no significant further changes in the late period. The instruction periods and the subject-movement parameters were included within the GLM to model out the signal attributable to these factors but were not included within the contrasts of interest.

The whole-brain group analysis was used to define areas that were functionally significant during learning of this task, and a further region of interest (ROI) analysis was conducted on these areas. ROIs were created by anatomically defining the significant clusters within the group learning-correlated random effects image and then registering these clusters to the functional data in each subject. The mean percentage signal change across all voxels within each ROI over every experimental block was found for every subject individually. From this, a mean group time course across the whole experiment was calculated.

A laterality index (LI) was also calculated to explore relative hemispheric changes in cortical motor regions. An anatomical ROI was created for each subject that included the primary motor cortex, premotor cortex and the supplementary motor area (SMA) and pre-SMA. This ROI was defined to include the cortex from the anterior bank of the central sulcus to a point midway between the central sulcus and the anterior limit of the frontal lobes. The mean percentage signal change within the ROI was found for each hemisphere, and the LI was calculated according to the following formula: $LI = (\text{contralateral signal change} - \text{ipsilateral signal change}) / (\text{contralateral signal change} + \text{ipsilateral signal change})$. Consequently, LI values ranged from +1, indicating completely contralateral activation

through to -1, indicating ipsilateral activation, with 0 signifying an even bilateral spread.

RESULTS

Behavioral results: evidence for learning and increased automaticity

Subjects performed a novel tracking task alternating with a matched perceptual task in serial blocks through the trial period. The performance in each tracking block was measured as the mean absolute tracking error. This short-term motor-skill learning is associated with an increase in automaticity of performing the task, defined as a reduction of the error and increased speed of a simultaneous attentionally demanding task. Automaticity was assessed specifically using a dual visuomotor tracking and verbal subtraction task with subjects outside of the magnet ($n = 10$, Fig. 2). After learning the visuomotor tracking sequence, the mean number of errors in the subtraction task decreased from 8.6 ± 3.6 to 4.8 ± 3.0 (SD) errors (paired t -test $t = 2.85$; $P < 0.01$).

The increase in tracking error caused by the counting task (i.e., the tracking error in the dual task paradigm minus the tracking error on the force tracking task alone) decreased from 7.1 ± 2.5 (mean \pm SD) before learning to 2.8 ± 1.4 after practice equivalent to that used for the fMRI task below (paired t -test $t = 3.98$; $P < 0.01$).

All subjects showed performance improvement between the first and last blocks when the task was performed in the imaging experiment (t -test, $P < 0.03$ for every subject). After initial rapid increases in tracking accuracy, stable, improved performance was achieved after between four and seven trial blocks (median: 5 blocks). The maximum, median and minimum levels of force applied by the subjects did not change significantly over the course of the experiment (Fig. 3).

Tracking task-related activation

In a contrast with the perceptually matched rest periods, the tracking task was associated with activation in a widespread network of brain regions (Table 1). Activation was found in the

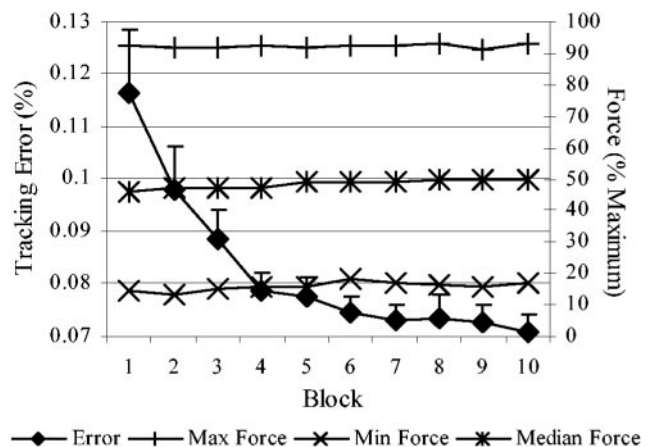


FIG. 3. Mean tracking error on each block across all subjects together with the average maximum, median, and minimum force applied by the subjects. While the error decreases over the course of the experiment, the normalized force parameters remain constant, suggesting that the activation changes detected were due to improvements in tracking performance and not a result of changes in motor output.

TABLE 1. *Brain regions activated by the tracking task*

Region of Interest	Brodmann's Area	Maximum Activated Voxel (Z)	MNI Coordinates (x, y, z)
Left primary motor cortex	4	7.37	-30, -15, 58
Right primary motor cortex	4	4.45	30, -22, 54
Left primary sensory cortex	1	6.37	-38, -26, 58
Supplementary motor area	6	5.31	-6, -8, 54
Pre-supplementary motor area	8	4.46	-2, 12, 56
Left premotor cortex	6	6.36	-38, 6, 52
Right premotor cortex	6	4.49	-28, -2, 58
Prefrontal cortex	46	4.86	-32, 20, 38
Frontal pole	10	5.54	-15, 49, 20
Cingulate motor area	24	5.42	-6, 0, 44
Left intraparietal sulcus	7	5.45	-28, -42, 60
Right intraparietal sulcus	7	3.44	34, -42, 56
Left insula	27	4.49	-42, 8, 2
Right insula	27	2.65	46, 12, 0
Left cerebellum	N/A	3.52	-26, -4, -24
Right cerebellum	N/A	5.43	34, -20, -42
Left thalamus	N/A	5.55	-12, -26, 4
Right thalamus	N/A	2.74	10, -22, 0
Left striatum	N/A	3.64	-26, 2, 2
Right striatum	N/A	3.44	30, 8, 2

Random Effects, $Z > 2.3$, $P < 0.01$ corrected.

primary sensorimotor and premotor cortices bilaterally (with greater activation in the hemisphere contralateral to the hand moved), supplementary motor areas [Brodmann's area (BA) 6 and 8], prefrontal cortex (BA 46), frontal pole (BA 10), cingulate motor cortex (BA 24), thalamus, and basal ganglia. Activation also was found bilaterally in the cerebellar cortex and deep cerebellar nuclei with relatively greater activation in the cerebellar hemisphere ipsilateral to the hand moved.

Changes in brain activity were associated with improved tracking performance

Tracking performance and automaticity are related in this short-term learning paradigm. To define brain regions in which activity changes with the development of greater automaticity in movement, we tested for tracking performance-related changes by defining regions that showed time-dependent changes during the early phase of motor learning when changes were greatest. Decreasing activation over time was found in the frontal pole, left prefrontal cortex, bilateral primary sensorimotor cortex, left intra-parietal cortex, and the supplementary motor area, along with the caudate nucleus and Crus I and II of the right cerebellum. Decreasing activity also was found along the medial wall; but the precise anatomical localization of these changes was somewhat variable between subjects. Analysis of individual data sets indicated that this activity included contributions from centers of activation in the SMA/pre-SMA (12/15 subjects), the adjacent region of the superior frontal gyrus (11/15 subjects), and the anterior cingulate cortex (11/15 subjects). Increasing activity was found in the right dentate nucleus and in the left ventral putamen and thalamus. Changes in these regions were then measured over the full time course of the experiment using a ROI approach (Fig. 4A).

Dynamic changes in primary motor cortex activation

Decreasing activation was found bilaterally in the hand area of the primary motor cortex (Yousry et al. 1997) as perfor-

mance improved. Analysis of the mean (over all subjects) time course of significantly activated voxels within the precentral sulcus (Fig. 4, A and B) confirmed that primary motor cortex activation decreased monotonically toward baseline levels over the course of the experiment. The relative decrease was greater in the right hemisphere (ipsilateral to the hand moved); substantial activation (mean signal intensity $>1.5\%$) was maintained in the left primary motor cortex (contralateral to the hand moved) throughout the experiment. The hemispheric lateralization of activation in the cortical motor areas thus also became progressively left-shifted: the mean laterality index moved from a relatively bi-hemispheric ($0.08 + 0.11$) to a predominantly contralateral pattern ($0.22 + 0.08$) over the course of the experiment. This pattern was consistent between individual subjects; an increase in the laterality index was measured in comparisons of the final with initial trial blocks for 13/15 subjects (χ^2 , $P < 0.01$).

Dynamic changes in prefrontal and parietal cortex activation

Early decreases in activation were seen in the DLPFC (BA 46), frontal pole (BA 10) and in the IPS, (BA 40; Fig. 4, C-F). The DLPFC showed a rapid decrease in activation, reaching a stable, minimum value by the fifth trial block, approximately when performance reached an asymptote with a relative increase in movement automaticity. Activation in the frontal pole had a similar time course, showing an initial rapid decrease through the first five practice blocks to reach a relatively constant level maintained until the end of the experiment. The activation time course in the midline SMA structures was significantly different during this early period (ANOVA; $P < 0.05$). SMA activity did not begin to decrease until the DLPFC activation reached its minimum activity. Activation in the IPS showed a gradual decrease through the experiment.

Dynamic changes in activation of subcortical gray matter

There were two distinct patterns of activation change in subcortical gray matter over the course of the experiment (Fig. 5). The left caudate showed a progressive decrease in activation in the first five blocks (cf. DLPFC and frontal pole changes in Fig. 4). Activity in the right cerebellar cortex (Crus I) also decreased during task learning. There was a strong correlation between decreases in right cerebellar cortical activation and decreases in tracking error ($r^2 = 0.94$, $P < 0.01$). A different pattern of relative activation change was found in the right dentate region, the left thalamus and the left putamen. Activity in all three regions increased throughout the period that performance improved and then remained relatively stable.

DISCUSSION

We have characterized dynamic changes in brain activation associated with improved performance and greater automaticity for execution of a visually guided motor tracking task. Subjects were trained on the task prior to scanning until stable performance was reached and thus were familiar with the general demands of the task and the equipment they were using before the start of the experiment. The specific tracking pattern was novel, however. The high tracking error at task onset suggests that accurate performance initially was attentionally

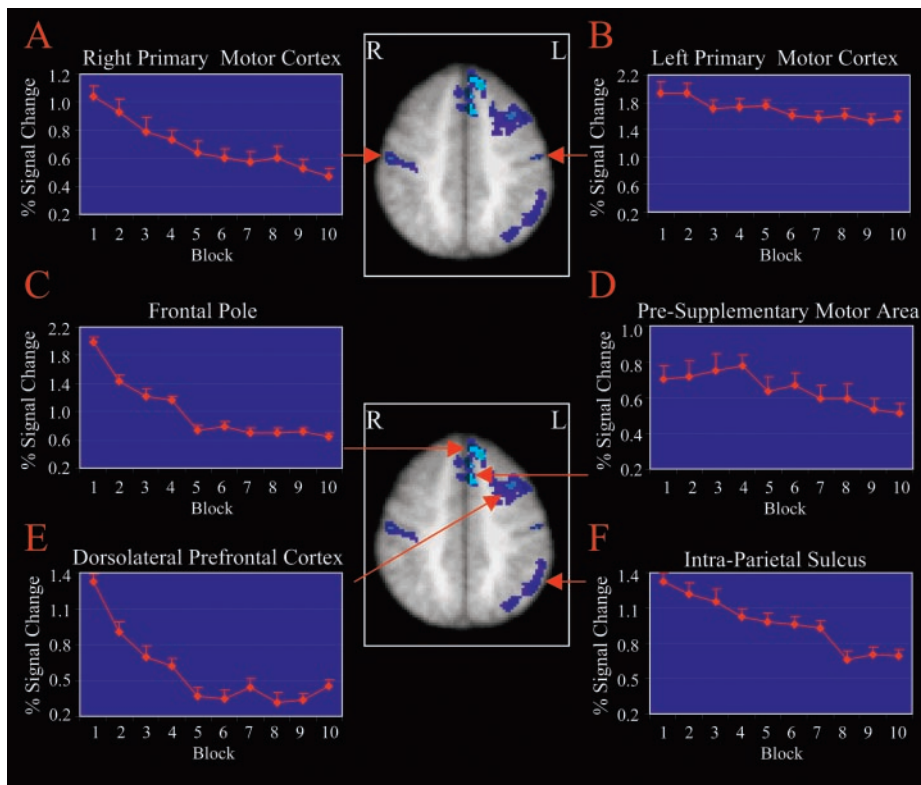


FIG. 4. Cortical areas of activation that correlate with the improvement in task performance together with their time courses (group random effects image, $z < 2.3$, $P < 0.01$, corrected). Areas that showed an increase in activation are shown in red, whereas those areas that showed a decrease in activation are shown in blue. At the start of the experiment, the level of activation is similar in the right (A) and left (B) motor cortex. Although both sides show a decrease in activation over the course of the experiment, the right hemisphere shows a more significant decrease than the left hemisphere, so that by the end of the experiment the activation is almost completely left-lateralized. The dorsal lateral prefrontal cortex (DLPFC) and pre-SMA show contrasting time courses. The DLPFC (E) shows initially high activation that drops off sharply, reaching baseline levels before the early learning phase is complete. The pre-SMA (D) shows an initial increase in activation before decreasing, reaching a peak at the time when activation in the DLPFC has declined. The frontal pole (C) has a time course closer to that of the behavioral learning itself, whereas the intraparietal sulcus (IPS, F) shows a more sustained decrease that continues into the postlearning phase.

demanding. This was confirmed by the behavioral interference observed in the dual-task experiment, a measure of task automaticity. As performance on the tracking task improved, automaticity increased. The mean force parameters did not change throughout the course of the experiment, so the activation changes described are not due simply to changes in the subjects' motor output but must reflect changes in mechanisms of motor control.

Activity in the primary motor cortex decreased with learning

The task involved fast learning (Karni et al. 1995). As previously reported with other examples of the fast motor learning, activation decreased in the primary motor cortex as performance improved (Toni et al. 1998). This early decrease of activity in the motor cortex may be due to increasingly specific afferent input to the primary motor cortex as the movement pattern becomes better defined. The decrease was greatest in the hemisphere ipsilateral to the hand moved. Previous studies also have suggested that novel or more difficult motor tasks involve activation of ipsilateral motor cortex as well as in the hemisphere contralateral to the hand moved (Chen et al. 1997; Rao et al. 1993).

Prefrontal circuit is engaged in the initial period of learning

Our observation that the DLPFC and the frontal pole (BA 10) are active in early stages of learning the tracking task extends prior lesion and functional-imaging studies. Patients with prefrontal cortex lesions are impaired in both verbal and visuomotor sequence learning (de Guise et al. 1999). The role of PFC appears specific for aspects of learning as subjects with prefrontal damage are unimpaired on a tracking task that does

not involve learning a specific sequence of movements (Gomez et al. 2002). In functional-imaging studies of learning, the prefrontal cortex is activated primarily when subjects learn new motor sequences (Jenkins et al. 1994) and thus may be involved in the acquisition or encoding of explicit knowledge of the task (Hazeltine et al. 1997). The prefrontal cortex also is connected to the cerebellar cortex; in monkeys, area 46 neurons project via the pons to Crus II of the cerebellum, which in turn projects back to area 46 via the dentate and thalamus (Kelly and Strick 2003).

Our results also showed decreases in caudate activity over a similar time course to the prefrontal cortex activity changes. This correlated activity and the strong anatomical connectivity between prefrontal cortex and caudate (Yeterian and Pandya 1991) is consistent with the hypothesis that development of the type of complex, integrated motor plan necessary for rapid and accurate performance of complex movements is mediated in part by activity in the striatum, which has strong afferent input from both the SMA and the premotor cortex (Alexander et al. 1986).

Activity in a cerebello-thalamo-striate network increases as learning progresses

The cerebellum showed regionally distinct patterns of activity change over the course of motor learning. The ipsilateral cerebellar cortex (Crus I and II) was most active initially, with a subsequent progressive decrease. In contrast, activation in the ipsilateral dentate nucleus increased during the early period. A similar pattern of activation changes previously was seen in studies of motor adaptation (Nezafat et al. 2001) and with a sequence learning paradigm (Doyon et al. 2002), although

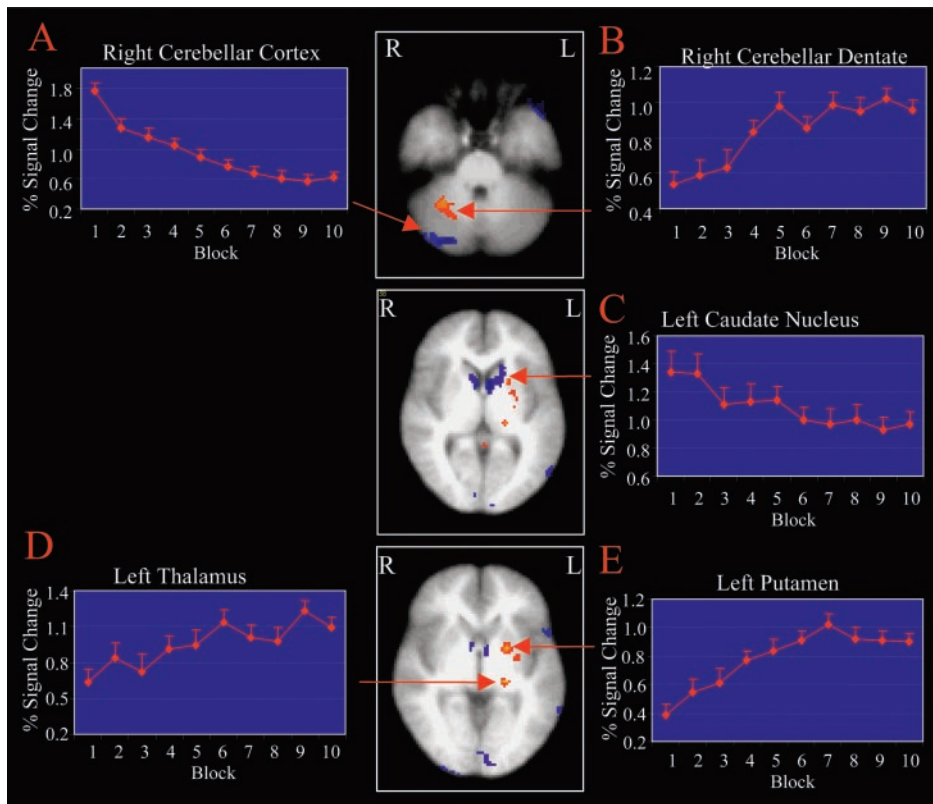


FIG. 5. Subcortical areas of activation that correlate with the improvement in task performance, together with their time course (group random effects image, $Z < 2.3$, $P < 0.01$, corrected). Areas that showed an increase in activation are shown in red, whereas those areas that showed a decrease in activation are shown in blue. The right cerebellar cortex (A) shows a decrease in activation that closely follows the decrease in tracking error by the subjects. In contrast, the right dentate nucleus (B) shows an increase in activation that continues into the postlearning phase, which is mirrored by a similar but more modest increase in activation of the left thalamus (D) and striatum (E).

these studies did not define the time course of activation changes well.

The fMRI signal predominantly reflects relative presynaptic activity (Attwell and Iadecola 2002; Logothetis et al. 2001). Our data therefore imply that the cerebellar cortical input regions (from the cortico-ponto-cerebellar and spinocerebellar tracts) are most active early in learning with activity in the output nucleus of the dentate subsequently increasing to a plateau [likely with a later relative decrease (Doyon et al. 2002)]. Early stages of motor learning may be associated with experience-induced plasticity at granule-Purkinje cell synapses within the cerebellar cortex with later changes at the mossy fiber synapses within the deep cerebellar nuclei (Mauk 1997; Mauk et al. 2000). A component of the more stable activity in the dentate nucleus may reflect input related to the control of tracking accuracy from matching of a forward model for the movement sequence to afferent feedback reflecting performance (Miall et al. 2001).

Cerebellar lesions and basal ganglia dysfunction (e.g., with Parkinson's disease) reduce forms of implicit motor learning (Martin et al. 1996) and the automaticity of execution of a sequence of movements (Doyon et al. 1998). We found similar signal intensity time courses in the cerebellar dentate nucleus, the thalamus, and the putamen. The correlation between these changes, the time of relative stabilization of performance gains and increased automaticity, is consistent with the notion that the development of movement automaticity is associated particularly with increased input into the cerebellar dentate and the putamen. Projections from these structures influence cortical motor control regions including the premotor cortex, SMA, and primary motor cortex, where output from the two circuits could be integrated.

Activity in the supplementary motor area shows biphasic changes with learning

As found in our study, previous work also has shown that the SMA is active in the early and intermediate stages of learning (Sakai et al. 1998) and movement planning (Deiber et al. 1996) or when a previously learned sequence is executed (Gerloff et al. 1997). Its functions have a critical role; damage to the SMA impairs procedural motor learning (Ackermann et al. 1996). Our work did not define a simple relationship between performance accuracy and activity, emphasizing the functional complexity in this region. There are distinct functional subdivisions within the pre-SMA/SMA region. Together with the pre-SMA, SMAr may have a role in early stages of movement representation and planning (Cunnington et al. 2002; Stephan et al. 1995; Tyszkla et al. 1994). The SMAC may have a more direct role in movement control. There are direct spinal projections from SMAC, for example (Dum and Strick 1992). However, the SMA receives primarily proprioceptive input from sensory afferents stimulated by passive movements (Radovanovic et al. 2002), and some SMA neurons behave as if contributing to the discrimination of somatosensory signals (Romo et al. 1993).

Stable activity in the intra-parietal cortex

Although there was a monotonic decrease in magnitude, the IPS showed substantial activation throughout the period of our experiment. Increases in activation in the IPS between early and intermediate learning phases have been described during visuomotor learning of a finger-movement sequence with a later decrease after the full movement sequence was defined (Sakai et al. 1998; Toni et al. 1998). Together, this evidence suggests that the IPS contributes to the control of movement by

processing visuomotor transformations (Rushworth et al. 1997). The IPS is part of the dorsal visual system that processes spatial information (Ungerleider and Mishkin 1982), and in monkeys, activity in this region is related to motor intention and preparation (Mazonni et al. 1976). IPS activity may reflect transformation “load” related to the movement sequence complexity or length.

Conclusions

This study of fast learning in a visuomotor task extends previous work with better definition of the relative time courses of activity changes in interacting brain regions. We found evidence consistent with the involvement of distinct functional subsystems at different stages of learning. The initial learning phase in which there is greater conscious attention to the task was associated with greatest activity in widely distributed regions with prominent prefrontal cortex involvement. As the attentional demands decreased with greater task automaticity, activity increased in a dentato-thalamo-striate circuit.

The importance of prefrontal “executive” regions early in learning suggests that formulation of the cognitive demands of aspects of the task in terms of a spectrum of attention and automaticity may be useful for understanding the underlying brain activity changes in conjunction with the more commonly employed notions of “explicitness” or “implicitness.” The more attention-demanding early phase of learning shows brain activity patterns corresponding to those found with more “explicit” motor-learning tasks (Jueptner et al. 1997). The more automatic phase of the learning paradigm here corresponds to patterns found with more “implicit” tasks (Hazeltine et al. 1997). With this framework, learning paradigms such as this may allow functional “dissection” of pathologies of motor control and their responses to treatments.

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