

# The mind of expert motor performance is cool and focused

John Milton,\* Ana Solodkin, Petr Hlušík,<sup>1</sup> and Steven L. Small

Department of Neurology and Brain Research Imaging Center, The University of Chicago, IL, USA

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**Extraordinary motor skills required for expert athletic or music performance require longstanding and intensive practice leading to two critical skills, a level of maximal performance that far exceeds that of non-experts and a degree of privileged focus on motor performance that excludes intrusions. This study of motor planning in expert golfers demonstrated their brain activation during their pre-shot routine to be radically different than in novices. The posterior cingulate, the amygdala–forebrain complex, and the basal ganglia were active only in novices, whereas experts had activation primarily in the superior parietal lobule, the dorsal lateral premotor area, and the occipital area. The fact that these differences are apparent before the golfer swings the club suggests that the disparity between the quality of the performance of novice and expert golfers lies at the level of the organization of neural networks during motor planning. In particular, we suggest that extensive practice over a long period of time leads experts to develop a focused and efficient organization of task-related neural networks, whereas novices have difficulty filtering out irrelevant information.**  
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## Introduction

We have all marveled at the extraordinary motor skills displayed by expert athletes, dancers and musicians (Milton et al., 2004a). Not only are their movements precise and reproducible, their quality is smooth and effortless. Compared to novices, highly trained individuals performing the same task exhibit a number of differences including a reduction in the variability of repeated skilled movements (Davids et al., 2006; Milton et al., 2004b; Pelz, 2000), reductions in muscle activation (Lay et al., 2002), and a decrease in

the overall volume of brain activation together with a relative increase in the intensity of activation of specific brain regions necessary for the execution of the task (Jancke et al., 2000; Münte et al., 2002, 2003; Ross et al., 2003; Schlaug, 2001). Taken together these observations have led to the hypothesis that experts exhibit a relative economy of motor planning both at the level of central neural programs and subsequent motor unit activation (Hatfield et al., 2004; Haufler et al., 2000; Lay et al., 2002).

Another striking characteristic that distinguishes expert from novice is the consistency of the expert's performance over a much wider range of environmental conditions (Fitts and Posner, 1973). Indeed, skill levels manifested in novices under practice conditions are not predictive of performance levels under 'game conditions' (Fairweather, 1999; Fitts and Posner, 1973; Landin et al., 1993). Moreover, the well-known phenomena of "choking", i.e. the sudden and catastrophic deterioration of skills in an appropriately stressful environment (Beilock and Carr, 2001; Linder et al., 1999), provide strong evidence that factors other than those involved in the refinement of motor programs must be involved in determining performance in a given situation, such as those related to the management of limited cortical resources, e.g. conscious attention (Beilock et al., 2002; Broglio et al., 2005; Brown and Jahanshahi, 1998; Cabrera and Milton, 2004) and working memory (Beilock and Carr, 2005; Beilock et al., 2004).

Behavioral studies have drawn attention to an important association between performance, i.e. the ability to maintain skill level under stressful situations, and the quality of the preparatory period that precedes the movement. This preparatory period has been most extensively studied in archers, rifle shooters, and golfers where it is called the "pre-shot routine". Consistency and reproducibility of the pre-shot routine have been suggested to be among the most important differences that distinguish expert from novice in these sports (Feltz and Landers, 1983; Hatfield et al., 1984; Hatfield and Hillman, 2001), in contrast to other sports, for example goal kicking in rugby (Jackson, 2003), in which no association between temporal consistency of the pre-shot routine and performance has been observed. Investigations using electroencephalography (EEG) have provided insights into the cortical psychophysiology of expert performance in terms of asymmetries in hemispheric and regional cortical activations (Crews and Landers, 1993; Hatfield et al., 2004; Haufler et al., 2000). How-

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\* Corresponding author. Present address: Joint Science Department, The Claremont Colleges, W. M. Keck Science Center, 925 North Mills Ave., Claremont, CA 91711, USA.

E-mail address: [jmilton@jsd.claremont.edu](mailto:jmilton@jsd.claremont.edu) (J. Milton).

URL: <http://faculty.jsd.claremont.edu/jmilton/> (J. Milton).

<sup>1</sup> Present address: Departments of Neurology and Radiology, Palacky University, Olomouc, Czech Republic.

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ever, the neural substrates involved in tasks related to focusing conscious attention and working memory, for example the basal ganglia and limbic structures (Ravizza and Ivry, 2001), are located deep to the cortical surface and hence their activation cannot be directly monitored using EEG with scalp electrodes (Davidson, 2004). On the other hand, both cortical and sub-cortical neural networks are accessible to study using functional magnetic resonance imaging (fMRI) (Ross et al., 2003).

A distinguishing feature between golf and other sporting activities is its pace: whereas in most sports the athlete is continually caught up in the action and has little time to think, in golf there is ample time for contemplation. Consequently the performance of the golf shot, particularly in novices, is heavily influenced by what the golfer was thinking about before the shot is performed (Gallwey, 1981; Rotella, 1995). Despite the fact that expert golfers have repeated the same task over and over for years, the length of their pre-shot routine is not dramatically shorter than that of experienced novices, as might be expected, but is about the same as novice golfers in practice situations, and minimally longer during competition (Boutcher, 1987; Douglas and Fox, 2002). Since novices and experts need about the same amount of time to prepare each shot, we hypothesized that differences in performance are most likely related to differences in the organization of the involved neural networks during this preparatory period. For example, since novice golfers are in the cognitive stage of learning there might be increased participation of cerebellum (Boyden et al., 2004) and basal ganglia (Graybiel, 2005; Seger, 2006), whereas difficulties experienced filtering out relevant information might be associated with activation of limbic and paralimbic structures, such as the posterior cingulate (Tracy et al., 2003). Assessing activity in these structures is particularly important for assessing the economy of central motor programs since it has been suggested that under appropriate circumstances inputs from these structures can disrupt activation of cortical motor programs thereby altering muscular contraction and hence influencing performance (Cotterill, 2001; Pochon et al., 2002). Thus, the basic neurobehavioral questions are: what neural systems are active during this motor preparation period and what are the differences that correlate with the differences in performance? We used fMRI to compare the neural networks of novice and expert golfers during their pre-shot routine. We observed that whereas the neural networks of expert golfers are focused and efficiently organized those of novices are not.

## Methods and materials

### Subjects

Studies were carried out on six expert golfers and seven novice golfers. All subjects were female and were right handed females according to the Edinburgh Handedness Inventory (Oldfield, 1971). They all played golf right-handed. Two criteria were used to classify golfers as novice or expert (Fairweather, 1999; Milton et al., 2004b): (1) golf skill as evidenced by handicap; and (2) ability to maintain golf skill in tournament play. The expert golfer group consisted of six members of the Ladies Professional Golf Association (LPGA): five were participants in the 2000 U.S. Women's Open and one was a former tour professional (average age 35; range 22–48). Six out of the seven novice golfers were beginners with fewer than 2 years golfing experience (handicap range 26 to 36+). Although the remaining novice golfer was more skilled and experienced (handicap 5.8), she experienced difficulty in

maintaining her skill level under stressful conditions, such as during tournament play. The average age of the novice golfers was 30 (range 21–42). Motor imagery abilities were assessed using previously published questionnaires that had been adapted for golfers (Wonder and Donovan, 1984; Vealey, 1986). Since there were no significant differences between the novice and expert golfers with respect to these measures, they were not used for further analysis.

This study was approved by the Institutional Review Board of the Biological Sciences Division of The University of Chicago in accordance with the currently applicable U.S. Public Health Service Guidelines. All participants provided written informed consent for all research testing.

### Behavioral task (pre-shot routine)

Subjects were placed in the scanner and head movement was restricted with foam rubber pillows. Electrostatic headphones (Resonance Technologies, Northridge, CA) were wrapped around the ears. A Macintosh computer with the PsyScope psychological software system (Cohen et al., 1993) was used to present the stimulus material to the subjects. During functional imaging, the subjects viewed a collection of photographs, consisting of either a golf green and pin (active condition) or a non-golf scene containing a vertical object (e.g. a flag pole) (control condition). For the golf scene, the participant was told to perform her pre-shot routine for a shot to the observed pin. She was also informed that the pin was 100 yards away and that there was no wind. When the subject was ready for the shot, she was asked to flex the right index finger once as a surrogate for the golf swing. All participants were interviewed afterwards regarding their activities during these trials, and all included participants reported active motor planning and imagery. One professional, not included in this report (i.e. a seventh professional golfer), was not compliant during the scan and was excluded from the study. The finger flexion allowed us to measure the duration of each self-paced pre-shot routine as the time between when the image was shown and the index finger moved.

The purpose of the non-golf scenes was to control for the effects on brain activation of visual perception and eye movement. The golfer was asked to focus on the centrally placed vertical object. Since the internal timing inherent to the golfer's pre-shot routine could not be reproduced by this control task, the subject was asked not to move their index finger while viewing a non-golf scene. The golf and non-golf scenes were randomly selected from a large pool of images, and a given scene could be viewed at most once. The experiment was performed in three runs each consisting of 30 trials randomized to include 15 golf scenes and 15 control scenes. Each scene was presented for 18 s. Thus each run took 9 min (30 scenes times 18 s per scene=540 s) to complete.

### Brain imaging

Whole-brain MRI data were acquired with a 1.5 T Signa Scanner (GE Medical Systems, Milwaukee, WI) and a standard quadrature GE head coil. Twenty-four contiguous 6 mm axial slices were obtained starting from the vertex through the bottom of the cerebellum. Blood oxygen level dependent (BOLD) data acquisition used a single-shot gradient echo ( $T_2^*$ -weighted) spiral sequence (TR=3 s, TE=35 ms, flip angle=60°) to provide 3.4×3.4 mm resolution over a 24 cm field-of-view (FOV) (Noll et al., 1995). During analysis, these images were re-sampled to 1.875×1.875 mm, for a total single voxel size of 21 mm<sup>3</sup>

(1.875 mm × 1.875 mm × 6 mm). Structural T<sub>1</sub>-weighted images were acquired both within the same imaging planes (500 ms TR, 16 ms TE, spin echo pulse sequence) and with a high-resolution 3D SPGR sequence to provide anatomical reference.

### Statistical analysis

#### Within-subject analysis

Functional images were spatially registered in three-dimensional (3D) space by Fourier transformation of each of the time points and corrected for head movement, using the AFNI software package (Cox, 1996). The high-resolution 3D T<sub>1</sub>-weighted image was registered to the reference T<sub>2</sub>-weighted (BOLD) image. Voxel-by-voxel statistical analysis of the extended single trials used a general linear model deconvolution technique (Dale, 1999; Serences, 2004). We modeled the hemodynamic response to each of the two conditions with a linear combination of five time-shifted delta functions, one TR (3 s) apart. Additionally, we used fifteen regressors of no interest — a constant, linear, and quadratic trend for each of the three runs and six motion estimate vectors, obtained from the spatial alignment procedure.

The significance of the model fit to the voxel-wise data was assessed using a randomization approach. In particular, we performed a Monte Carlo simulation (Forman et al., 1995) with 10,000 iterations to establish a single voxel statistical threshold ( $1.0 \times 10^{-5}$ ), given the minimally acceptable cluster size of none voxels (189 mm<sup>3</sup>) and the desired whole-brain alpha level ( $p \leq 0.05$ ).

Having separately modeled the response during the active and control trials, we used two post hoc tests (general linear contrasts) to identify those voxels in which the hemodynamic response differed significantly between active and control conditions when compared at each time point. The first post hoc contrast included the fitted hemodynamic response from the initial 9 s of the 18-second trial and the second contrast used the full modeled response (due to modeling constraints, only 15 s out of the 18-second trial were modeled). Because of the delay and slow rise of the hemodynamic response (5–9 s from onset of stimulus or initiation of a particular behavioral/neural process to the peak of the hemodynamic response), even the full modeled response will predominantly reflect the motor planning and preparation processes of the pre-shot routine rather than preparation and execution of the simple finger movement which occurs towards the end of each active trial. Data reported in Figs. 1–3 and Table 2 are from the 15-second contrast.

#### Between subject analysis

For comparisons of brain activation between subjects we used a region of interest (ROI) approach, as we have done previously (Bhimani et al., 2006; Solodkin et al., 2001, 2004). We take this approach to minimize the effects of anatomic and functional variability between individuals (Brett et al., 2002; Uylings et al., 2005) and the inconsistent correlation between surface anatomy and cytoarchitectonics (Uylings et al., 2005). Before the study was conducted, fourteen specific ROIs per hemisphere were selected (Table 1). In addition to ROIs related to the known neuroanatomy of human motor control (Solodkin et al., 2001), we included ROIs anticipated to be involved in visually guided voluntary motor tasks (Rizzolatti et al., 2001), e.g. OCC, SPL, LPMCd, as well as those related to the golfer's reaction to stress (Beilock et al., 2004; Linder et al., 1999), e.g. LIMBIC. The goal of the regional analysis was to determine whether or not

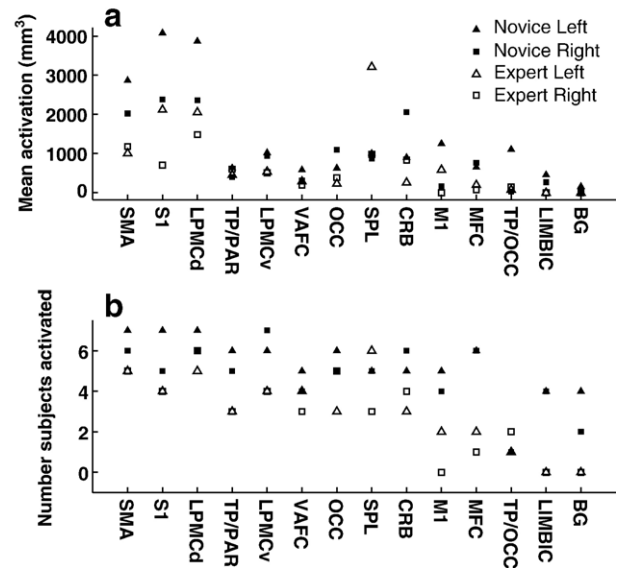


Fig. 1. (a) Mean volume of activation within each ROI for novice and expert golfers during the pre-shot routine contrasted with the control task. The contrast is based on 15 s from the start of the trial. (b) The number of golfers in whom a significantly activated voxel cluster was detected within an ROI during the pre-shot routine contrasted with the control task.

these predetermined ROIs were activated during the pre-shot routine and, if so, compare the ROIs activated between novice and expert golfer. These two effects, i.e. whether or not an ROI contains a significantly activated voxel cluster and the total volume of activated voxels in an ROI, constitute independent observations.

#### Regions of interest

The significantly activated voxel clusters were manually assigned to the ROIs listed in Table 1 using anatomic T<sub>1</sub>-weighted images. The assignment of a significantly activated voxel cluster to an ROI was made using anatomical criteria (Solodkin et al., 2001) by three of the authors who were blinded as to the golf status of the subject (JM, AS, SLS). Only one of the investigators (PH) was aware of the skill level of the subjects during the analysis and was not involved in this phase of the analysis. The anatomical landmarks used to delimit the ROIs were as follows: the hand area of M1 was defined as the anterior bank of the central sulcus as determined by the location of the knob (Yousry et al., 1997). The posterior corner of the lateral edge of the precentral gyrus was the boundary between M1 and the lateral premotor cortex (LPMC). The LPMC was defined as the area between M1 posteriorly and a line at the level of the coronal plane through the anterior commissure, bounded inferiorly by the inferior edge of the frontal lobe. LPMCd was the region of LPMC located in the upper two-thirds of the distance between the top of the brain and the lateral fissure. The ventral portion of LPMC (LPMCv) was the region of LPMC located in the lower one-third of this distance. The LPMCv defined in this way also includes Brodmann's area 44. There are two reasons for combining these areas into one region: (1) LPMCv is more aligned with area 44 than with LPMCd from a cytoarchitectural viewpoint (Kotter et al., 2001; Petrides and Pandya, 1994; Rizzolatti et al., 2002), and (2) previous studies

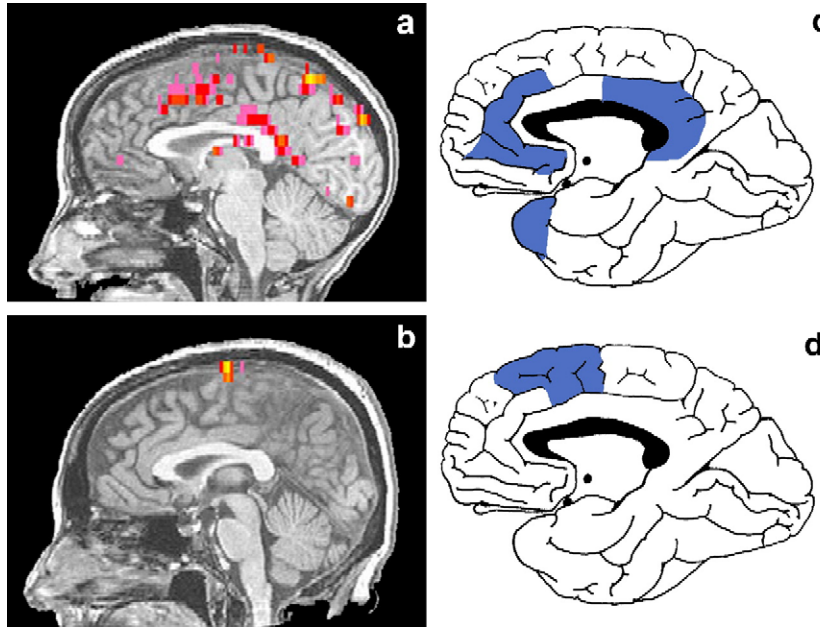


Fig. 2. Brain activation derived from 15 s from the onset of the pre-shot routine — control task for (a) a novice and (b) an expert golfer. In each case, the golfer shown represents the one whose overall brain activation was closest to the group mean. The color code gives the  $F$  values for the  $F$ -test of those voxels significantly different between the active and control tasks: red ( $6.63 < F < 10$ ), orange ( $10 \leq F < 25$ ), yellow ( $F \geq 25$ ), where  $F=6.63$  correspond to the whole-brain corrected significance level ( $p=0.05$ ). The right hand side shows a schematic representation to summarize those brain regions which were activated during the pre-shot routine for the two groups of golfers: (c) novice golfers activated the limbic regions including the cingulate and temporal pole and (d) expert golfers activated the supplementary motor region.

suggest contiguity of function across these two areas in some motor behaviors such as imitation (Rizzolatti and Arbib, 1998; Rizzolatti et al., 2001). S1 was defined as the postcentral gyrus and posterior bank of the central sulcus along the same inferior–superior and lateral extents as M1. The supplementary motor

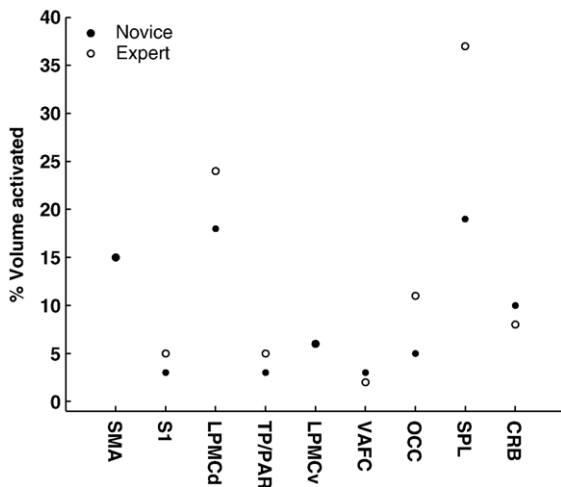


Fig. 3. Proportion of the total volume of brain activation attributed to each ROI during the pre-shot routine of novice (●) and expert (○) golfers when contrasted with the control task over the period of 15 s from trial onset. Only those ROI are shown for which at least three golfers had at least one significantly activated cluster. For each golfer the volume of activation within a given ROI was combined for the left and right hemisphere and then divided by the total volume of brain activation observed for that golfer. In the figure this fraction is represented as a percentage.

cortex, the pre-supplementary motor cortex and the cingulate motor area were combined into a single SMA region. The boundary of the supplementary motor cortex was the medial region of the hemispheres superior to the dorsal bank of the cingulate sulcus along the same anterior–posterior extent as LPMCD. The pre-supplementary cortex was defined as the medial region bounded posteriorly by the anterior commissure plane and limited anteriorly by a coronal plane at the level of the genu of the corpus callosum as described previously (Picard and Strick, 1996, 2001). The cingulate motor area was limited dorsally by the dorsal bank of the cingulate sulcus, inferiorly by the corpus callosum, and posteriorly by the coronal plane of the posterior commissure. The superior parietal lobule (SPL) was defined as the region immediately posterior to S1 and bounded by the occipito-parietal sulcus posteriorly, by the boundary to the temporal lobe laterally, and the intraparietal sulcus inferiorly. The temporo-parietal region (TP/PAR) was limited dorsally by the lateral sulcus, ventrally by the superior temporal sulcus, posteriorly by the intraparietal sulcus, and anteriorly by the temporal pole; the pre-frontal region (pFR) was limited posteriorly by the superior supraorbital sulcus and ventrally by the inferior supraorbital sulcus; the medial pre-frontal region (MPF) was limited ventrally by the inferior frontal sulcus and posteriorly by the lateral premotor area; the limbic lobule was limited by the cingulate sulcus dorsally except in the most frontal region where the limit was the superior supraorbital sulcus, and ventrally by the presence of the *corpus callosum*; the posterior limit of the temporal pole was established by the presence of the superior and inferior temporal sulci. The occipital cortex (OCC) was limited medially by the parieto-occipital sulcus and in the lateral surface of the brain by an imaginary line between the parieto-occipital sulcus and the occipital notch.



Table 1  
Anatomical regions of interest

Name	Abbreviation	Areas included	Brodmann's number
Medial premotor	SMA	Supplementary motor area, pre-supplementary area, cingulate motor	6 m, 24c
Somatosensory	S1	Primary somatosensory, secondary somatosensory, posterior insula	1, 2, 3, 5
Lateral premotor cortex dorsal	LPMCd	Lateral premotor cortex dorsal	61
Temporo-parietal areas	TP/PAR	Superior temporal gyrus, middle temporal gyrus, inferior parietal lobule	21, 22, 39, 40
Inferior frontal areas	LPMCv	Lateral premotor cortex ventral, inferior frontal gyrus	61, 44, 45
Ventro-anterior frontal cortex	VAFC	Orbital frontal areas, frontal pole	8, 10–12, 47
Middle frontal cortex	MFC	Middle frontal gyrus	9/46, 46
Temporo-occipital areas	TP/OCC	Posterior parahippocampal gyrus, fusiform gyrus	20, 36, 37
Superior parietal lobule	SPL	Superior parietal lobule, intraparietal sulcus	7
Cerebellum	CRB	Cerebellum	
Primary motor area	M1	Primary motor cortex	4
Basal ganglia	BG	Caudate, putamen	
Limbic areas	LIMBIC	Limbic lobule, posterior cingulate, temporal pole amygdala, extended amygdala	23, 29, 31, 32, and 38
Occipital	OCC	Occipital lobule	17–19

### Regional volumes of activation

Within each ROI, the volumes of activation of significantly activated voxel clusters were calculated. When the pre-shot routine activated multiple noncontiguous clusters within the ROI, these clusters were summed to give the volume of activation of the ROI.

### Group comparisons

We used three measures to compare brain activation of novice and expert golfers during the pre-shot routine: (1) overall brain activation volume; (2) numbers of ROIs activated per golfer; and (3) volume of activation within a given ROI, expressed as a percentage of overall brain activation for a given golfer. A Student's *t*-test was used to determine whether there were significant differences between overall brain activation volume and between the volume of activation of a given ROI between the novice and expert golfers during the pre-shot routine (see also legend to Fig. 1). Since it was observed that not all golfers activated a given ROI, we used a Fisher's exact test to determine if significant differences existed between the number of novice and expert subjects who activated a given ROI. Whereas changes in overall brain activation are related to the overall efficiency of the neural network to perform the task, the latter two measures are related to changes in the functional structure of the involved neural networks.

## Results

The mean length of the pre-shot routine was not significantly different between expert golfers (mean = 13.6 s, range 8.5–16) and

the novice golfers (mean = 10.3; range 4.7–17 s,  $p = 0.064$ , one-sided *t*-test). The novice group included two golfers with less than 6 months playing experience whose pre-shot routine lasted about 5 s. Short pre-shot routines are typical for beginning golfers (Crews and Boucher, 1986).

### Experts have reduced overall brain activation

We observed that all significant brain activations during the pre-shot routine of novice and expert golfers only occurred in a priori selected ROIs. As observed previously during motor imagery of the golf swing (Ross et al., 2003), the overall volume of activation during the pre-shot routine was significantly lower for the expert golfers ( $p < 0.001$ ; Table 2). Fig. 1a shows that this difference between brain activation of novice and expert golfers is also seen on a regional level, with one exception (SPL). These differences in brain activation could not be accounted for by differences in the length of the pre-shot routine.

### Only novices activate basal ganglia and limbic areas

Fig. 1b shows the number of golfers who exhibited a significantly activated voxel cluster within a given ROI. Whereas activation was detected within certain ROIs for all golfers regardless of skill level (e.g. LPMC, IPS), the occurrence of activation within other ROIs was considerably more variable. Particularly striking is the observation that no expert golfer activated limbic regions ( $p < 0.0002$ ; Fisher's exact test) or BG ( $p < 0.02$ ) during the pre-shot routine. In contrast, 6/7 of the novice golfers activated limbic regions and 5/7 activated the basal ganglia

Table 2

Comparison of the number of regions of interest (ROI) and volume of activation for novice and expert golfers during their pre-shot routine contrasted to the control task

Hemisphere	Novice golfer ( $n = 7$ )		Expert Golfer ( $n = 6$ )	
	Number of ROI's activated	Brain activation ( $\text{cm}^3$ )	Number of ROI's activated	Brain activation ( $\text{cm}^3$ )
Left	11 (6–13) <sup>a</sup>	23.1 (5.2–30.7)	7 (1–12)	13.2 (0.9–24.2)
Right	9 (4–12)	16.4 (4.6–31.5)	7 (3–9)	8.5 (1.3–14.4)
Left+Right	20 (13–22) <sup>b</sup>	39.5 (16.3–71.7) <sup>c</sup>	12 (4–21) <sup>b</sup>	22.3 (2.2–38.7) <sup>c</sup>

<sup>a</sup> Data shown as mean (range).

<sup>b</sup> A number of ROIs activated were significantly higher for novice golfers ( $p < 0.05$ ; Student's *t*-test).

<sup>c</sup> Total volume of brain activation was significantly higher for novice golfers ( $p < 0.05$ ; Student's *t*-test).

(all activated either LIMBIC or BG, or both). The basal ganglia activated in the novice golfers included the putamen (5/7 novice golfers) and the caudate nucleus (2/7 novice golfers). Three other ROIs had an increased response rate in novice golfers: MPF ( $p < 0.004$ ), TP ( $p < 0.02$ ), and M1 ( $p < 0.02$ ).

Fig. 2 summarizes the regions located on the mesial surface of the hemisphere which contained significantly activated voxel clusters during the pre-shot routine of novice and expert golfers. The left side of the figure compares the fMRI of the novice (upper) and the expert (lower) golfers whose overall brain activation during the pre-shot routine was nearest to the group mean. The right hand side of the figure shows a schematic representation of those areas in which significantly activated voxel clusters were detected. The limbic regions activated in the novice golfers included the posterior cingulate area (4/7) and the basal forebrain–extended amygdala area (6/7).

Solely on the basis of activation of the limbic and basal ganglia regions it was possible for a blinded investigator to correctly identify 6/6 of the expert golfers and 7/7 of the novice golfers. The novice who did not activate the limbic regions was the most inexperienced golfer and was also the golfer who exhibited the greatest activation of the basal ganglia.

#### *Experts have increased activation of SPL–LPMCd–OCC*

Fig. 3 compares the proportion of the total brain activation during the pre-shot routine attributed to each ROI (combined left and right hemisphere) for novice and expert golfers. Only those ROIs are shown for which at least three golfers exhibited activation. It is evident that the relative proportion of activation in the LPMCd, SPL, and OCC ROIs for expert golfers during the pre-shot routine is higher than seen for novice golfers.

## Discussion

Our observations suggest that experts have a precise and efficient neural network for specialized motor planning that integrates visual information with motor commands. However, since novices are still in the process of motor learning, the comparable motor planning network is more diffusely organized. As part of learning this difficult motor task, limbic areas such as the posterior cingulate area might contribute to the establishment of specialized networks by teasing out relevant from non-relevant information. Thus the activation seen for novice golfers in these regions likely relates to the fact that these golfers have not yet mastered this complex task and have difficulties filtering out the relevant sensory and cognitive information needed to plan a successful golf shot. This may also explain why the basal ganglia were activated in novice golfers, but not in experts (Middleton and Strick, 1994; Packard and Knowlton, 2002).

A possible interpretation of the activation seen in limbic regions of novices could suggest that the “emotional content” during the pre-shot routine is higher in this group than in experts (Davidson, 2004). Certainly, fear and anxiety contribute to the deterioration in performance observed when athletes are placed in stressful situations (Linder et al., 1999) and this may be the case to some extent in our novices. However, there are two observations that strongly argue against this as a primary interpretation.

First, in our experiment, no golfer reported a stressful experience during the study, and both groups of golfers were equally naive to the scanner environment. Thus it is difficult to

conclude that the activation of amygdala and basal forebrain areas for novice golfers was because they were more anxious or fearful than the experts. Activation of the amygdala–basal forebrain complex in novice players may relate to the control of autonomic changes known to occur during the pre-shot routine. Autonomic responses have been reported to occur in a graded fashion and correlated to effort during imagined movements (Decety et al., 1991; Oishi et al., 2000). One component of the pre-shot routine includes imagery of the movement to be executed. Since the amygdalar complex is the interface between cortical areas (including limbic areas) and autonomic centers (Benarroch, 1993; Gray, 1993; Ghashghaei and Barbas, 2002), it is possible that its activation was seen as a consequence of increased effort exerted by the novices.

Second, the regions of the limbic system activated include regions not exclusively associated with control and regulation of emotions (Davidson, 2004), namely the posterior cingulate gyrus (Fig. 3). Previous studies have emphasized an inverse relationship between activation of the posterior cingulate and the extent to which complex motor skills have been mastered, i.e. the lower the motor skill, the higher the posterior cingulate activation (Jancke et al., 2000; Puttemans et al., 2005). However, the fact that even the most skilled novice golfer activated the posterior cingulate area implies that this cannot be the sole explanation. This observation is consistent with the observation that activation of posterior cingulate occurs in good learners who may be highly skilled, but who have not yet automatized performance (Tracy et al., 2003). In addition, when corrected for total brain activation, activation of CRB, a brain region important for motor learning (Boyden et al., 2004), was not significantly different between novices and expert (Fig. 3). The posterior cingulate area activated in the novice golfers included a number of Brodmann’s areas (23, 29, 30) (Vogt et al., 2001) that extend together and curve around the splenium of the corpus callosum (Petrides and Pandya, 1999) to terminate in the cingulo-parahippocampal isthmus (Ding et al., 2003). Hence, these regions can be considered the interface between the cingulate areas, the parahippocampal region, and the visual cortices. Due to this strategic location and its connectivity patterns (with pre-frontal areas as well as anterior cingulate, superior temporal sulcus, the hippocampal complex and visual areas), the posterior cingulate region has been associated with functions such as working memory, encoding of visuomotor tasks and extrapersonal space, topokinetic and topographical memory, dynamic relocation of spatial attention, and global attention (Morris et al., 1999; Petrides and Pandya, 1999; Vogt et al., 2000; Mesulam et al., 2001; Raichle et al., 2001; Vogt et al., 2001).

Novice golfers activated LIMBIC and BG, but no expert golfer had statistically significant activation in these two regions. This consistent difference between golfers suggests that the role of LIMBIC and BG must relate to a difference in an invariant component of motor planning that differs between the two levels of expertise. In view of the functions of the posterior cingulate region we suggest that, unlike the experts, novice golfers have difficulty filtering diverse stimuli to obtain the most useful information for planning the shot. This interpretation resonates strongly with the verbal information provided by the participants after completing the experiment. Only the novice golfers raised many questions concerning, for example, whether the distance given to each of the holes was similar (the various pin positions had been laser sighted to the same distance within an accuracy of about one foot) and whether there was wind and the direction it was blowing (they had been told

to assume that there was no wind). Thus the novices were actively participating in the task, but seemed unnecessarily preoccupied with details that were irrelevant for the required task. A similar conclusion has recently been obtained in the context of students who performed poorly solving problems in mathematics (Beilock et al., 2004). Consistent with this line of reasoning is the observation that more novice golfers activated MFC than expert golfers (Fig. 1). Activation of MFC is anticipated to be greatest in subjects whose actions are based on conscious choices (i.e. novices) than in subjects whose actions are automatic (i.e. experts) (Firth et al., 1991). A similar explanation has been used to explain the increase in EEG power observed over temporal regions between novices and experts (Hatfield et al., 2004; Haufler et al., 2000). However, although our fMRI studies show a tendency for activation to be higher in the temporal regions of novices (Figs. 1 and 3), these differences between novice and expert were not statistically different.

The regional differences in brain activation between novice and expert golfers during the pre-shot routine were not limited to the limbic and basal ganglia. A striking finding is the reciprocal relationship between activation in the posterior cingulate gyrus (Figs. 2 and 3) and in the cortical regions involved in visual spatial tasks (SPL, LPMCd, OCC) (Fig. 1b). Novice golfers have significant activation of the posterior cingulate region but far less activation in SPL–LPMCd–OCC. The opposite pattern is seen for expert golfers: none of these golfers activated the posterior cingulate region, yet the relative contribution of SPL–LPMCd–OCC in terms of total activation was much higher than for the novices. A recent postulate implicates the posterior cingulate and precuneate regions for the maintenance of global, rather than selective attention (Shulman et al., 1997; Raichle et al., 2001). A lack of attentional focus in novices could help explain their overall brain activation pattern, which contrasts with the highly selective motor system activation in the experts.

Preferential activation of SPL–LPMCd–OCC has been observed in subjects who attend to goal-directed movement tasks that are visually triggered (Rizzolatti et al., 2001), but not in golfers who mentally image their golf swing without their usual pre-shot setup routines (Ross et al., 2003). The fact that proportional activation in visual cortices is different for novice and expert golfers indicates that the differences seen in the activation of SPL–LPMCd are not due to differences in sensory input since both groups received the same visual stimuli (i.e. not forward). This suggests that the increased activation for OCC seen for expert golfers might reflect a backward process from cortical association areas forming neural networks involved in motor imagery (Solodkin et al., 2004). Motor imagery has been proposed to be an essential part of motor preparation (Jeannerod and Decety, 1995; Cunnington et al., 1996; Johnson, 2000). However, the role of activation of M1 during motor imagery has been difficult to ascertain: consistent activation has been observed during kinetic motor imagery, but not during visual motor imagery (Solodkin et al., 2004). Thus it is not possible to determine whether the difference in M1 activation between novice and expert golfers (Fig. 1) was related to differences between the efficiency of motor programs or differences in the type of imagery used during the pre-shot routine.

Although there might be some concern that the index finger movement could affect our results, there are several reasons why we believe that this does not play a role in the findings. First is that the single index finger movement was present in both groups of participants, and thus should not affect the group comparison.

Second is that the finger movement occurred at about 12 s, and thus the peak hemodynamic effect would be manifested 4–6 s later (i.e. at 16–18 s), which is after the portion of the response that we have analyzed. To verify this, we compared the amount of activation detected by the first post hoc contrast (initial 9 s) to that revealed by the second post hoc contrast (15 s out of the 18-second trial). On this comparison, both the total brain activation volume and the regional responses of M1 and SMA activation increased when the full modeled response was considered. However, the increase in M1 and SMA was smaller than the increase in overall brain activation for both novice and expert golfers suggesting that the effect of the index finger movement is indeed small.

In summary, our studies demonstrate a number of important differences between brain activation in novice and expert golfers. First, our studies show that the motor programs of experts are more efficiently organized, i.e. they require less energy to execute (Ross et al., 2003). A similar conclusion has been inferred using electroencephalographic (EEG) techniques (for a review see Hatfield et al., 2004). However, it must be emphasized that the EEG is primarily a measure of neuronal synchrony not of neuronal activation (Ebersole and Milton, 2003; Nunez, 1981). Second, our studies show that, although experts and novice activate many of the same cortical regions, experts have increased activation in cortical regions important for visuomotor transformations.

Third, and perhaps most importantly, our studies demonstrate that novice golfers, presumably in the cognitive stage of learning, activate structures that are not activated in experts, namely BG and LIMBIC. An unsolved problem is the effect of activation of BG and LIMBIC on the performance of existing neural motor programs. On long time scales, structures included in BG and LIMBIC are thought to be important for learning (Graybiel, 2005; Seger, 2006). However, on the short time scales involved in the execution of a single golf shot, their effects are not known. Indeed it has been suggested that over-activation of these structures could negatively impact the motor unit activations programmed by the central motor programs. For example, under appropriate circumstances some components of the neural motor networks appear to be able to influence muscular contraction by denying the motor areas of cortex sufficient activation, a concept that has been referred to as “conditionally permitted movement” (Cotterill, 2001; Pochon et al., 2002). For example, activation in cerebellum, primary sensory cortex and the basal ganglia inhibits the activation of primary motor cortex (Cotterill, 2001) whereas activation in limbic and paralimbic areas decreases activity in cortical cognitive areas involved in motor planning and reward (Pochon et al., 2002).

From a pragmatic point of view the importance of studies that compare experts to novices is to develop insights that can be used to better educate and train the relatively unskilled. What are the rate limiting steps for the development of expertise: the time it takes to develop efficient motor programs and/or the time it takes to learn to filter relevant from irrelevant information? Spatial reduction of participating neural networks with expertise likely decreases the complexity of dynamic motor control, allowing for improvement in the consistency of motor performance. Hence the activation of BG and LIMBIC regions in novice would be expected to decrease performance because the complexity of dynamic motor control has been increased. The activation of posterior cingulate in novices is consistent with neuropsychological investigations suggesting that the novices experience difficulty filtering out irrelevant information. Would educational

strategies that place greater emphasis on enabling students to sort irrelevant from relevant information translate into achieving higher skill levels more quickly? It is possible that fMRI studies in concert with a controlled teaching protocol would lead to the development of more effective strategies for improving student performance. Such performance-based educational strategies could be applicable more widely to those who are trying to regain motor skills lost after focal brain injury, such as stroke or other neurological disease.

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