

When Planning Fails: Individual Differences and Error-related Brain Activity in Problem Solving

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The neuronal processes underlying correct and erroneous problem solving were studied in strong and weak problem-solvers using functional magnetic resonance imaging (fMRI). During planning, the right dorsolateral prefrontal cortex was activated, and showed a linear relationship with the participants' performance level. A similar pattern emerged in right inferior parietal regions for all trials, and in anterior cingulate cortex for erroneously solved trials only. In the performance phase, when the pre-planned moves had to be executed by means of an fMRI-compatible computer mouse, the right dorsolateral prefrontal cortex was again activated jointly with right parahippocampal cortex, and displayed a similar positive relationship with the participants' performance level. Incorrectly solved problems elicited stronger bilateral prefrontal and left inferior parietal activations than correctly solved trials. For both individual ability and trial-specific performance, our results thus demonstrate the crucial involvement of right prefrontal cortex in efficient visuospatial planning.

Keywords: individual performance, neuroimaging, planning, problem solving, Tower of London, trial correctness

Introduction

There has been considerable interest in the neuronal processes underlying complex, high-level cognitive processes such as problem solving (Nichelli *et al.*, 1994; Prabhakaran *et al.*, 1997, 2001; Christoff *et al.*, 2001; Chen *et al.*, 2003; Atherton *et al.*, 2003) or planning (Dagher *et al.*, 1999; Lazeron *et al.*, 2000; Rowe *et al.*, 2001; Cazalis *et al.*, 2003; Schall *et al.*, 2003; van den Heuvel *et al.*, 2003). However, both individual differences in planning ability and item-related processes due to correct and incorrect problem solution may have a great influence on these processes, and have often not been considered in previous studies. In a recent notable exception to this (Cazalis *et al.*, 2003), post-hoc classification of participants into standard and superior problem-solvers revealed different activation patterns during planning; however, these differences may have been due to either ability- or item-related processes, or to a combination of both. Similar concerns apply to another recent study (van den Heuvel *et al.*, 2003) where only correctly solved trials were included in a correlation analysis of task complexity with brain activation during planning.

This possible confound of planning-related and performance- and item-related processes becomes apparent when considering the literature on neuronal processes elicited by errors in speeded-response tasks (e.g. Go-NoGo or flanker tasks; Falkenstein *et al.*, 1991; Gehring *et al.*, 1993). Recent fMRI studies showed that performance errors are accompanied by a characteristic pattern of activity in the rostral anterior and the posterior cingulate, the insular cortex, and the intraparietal

sulcus (Menon *et al.*, 2001; Ullsperger and von Cramon, 2001). Although the tasks used in such studies usually require rapid motor responses, and can thus not be directly compared to problem solving tasks, the question remains whether error-related processes at least partly contribute to the overall patterns of brain activation observed during higher-order cognitive tasks.

In the present study, we thus examined the influence of both problem-solving ability (between-subjects) and error-related processing (within-subject) on brain activation elicited by problem solving. Participants were recruited ranging from very poor to very good problem-solvers, based on scores in pilot testing. The problem set used was constructed to ensure that good problem-solvers would commit at least some errors, and that poor problem-solvers would still be able to solve a substantial number of trials correctly. As planning task we chose the Tower of London (ToL; Shallice, 1982), to obtain optimal comparability with previous studies. This task allows the precise determination of a cut-off value where participants start to fail finding a correct solution. Moreover, the ToL task consists of a mental preplanning and a movement execution phase. The use of an MRI-compatible computer mouse allowed us to examine cognitive processing during the motor realization of problem solving for the first time ever in an fMRI-study.

Materials and Methods

Participants

Two months before the imaging session, 59 students were assessed regarding their performance in the ToL task. Selection of participants for the imaging study was based on this testing in order to ensure a wide and equally distributed variety of individual performance. Another criterion for selection was that both good and poor performers were able to solve six move problems in a defined predetermined time window, without significant differences in planning time for good and poor performers. The mean \pm SD preplanning time for good performers was 13451 \pm 4790 ms, and for poor performers 15864 \pm 2590 ms. These times did not differ reliably ($P = 0.17$).

Finally, 22 right-handed students (12 male, 10 female; aged 22.5 \pm 3.5 years) with normal or corrected-to-normal vision (contact lenses) and normal audition participated in the imaging experiment. None of the volunteers had any history of neurological or psychiatric disorders, or of significant drug abuse. All subjects gave informed consent prior to participation in the study, and all procedures complied with both university and hospital ethical approval (research project no. 35/2001). Participants were paid €25.

MRI-compatible Computer Mouse

This special, wedge-shaped mouse (ESINOMED GmbH, Prutting) has a small joystick which is operated with the thumb to move the cursor across the screen. At the front side of the mouse, a touch-sensitive button allows the selection of a ball with the index finger, while a second touch uncouples the ball from the cursor.

Cognitive Paradigm

Participants were administered a computerized version of the Tower of London (ToL; Shallice, 1982). In this version, the goal state is presented in the upper field of the screen, while participants operate on the start state in the lower half of the screen by moving the balls with the computer mouse. Participants were told to transform the start state into the goal state while following three rules: (i) only one ball may be moved at a time; (ii) a ball cannot be moved when another ball is lying on top of it; and (iii) three balls may be placed on the tallest peg, two balls on the middle peg, and one ball on the shortest peg. For all problems, the minimum number of moves was indicated on the screen. In addition to the description of the ToL, participants received instructions to (i) always plan ahead the optimal solution to a given problem first and (ii) only thereafter to start moving the balls. The problem set employed in the present imaging study (see Appendix) ranged from four- to six-move problems. Problems differed from those used in the preliminary testing session. Concerning problem structure, only structurally unique problems (Berg and Byrd, 2002) with a single path for achieving an optimal solution were selected. Across the levels of minimum number of moves, ToL problems were counter-balanced according to the following global problem parameters: the ambiguity of goal hierarchy and the patterns of subgoal generation (Kaller *et al.*, 2004). In addition, existence and number of suboptimal alternatives were also controlled for. Furthermore, problems featuring specific parameters (e.g. counterintuitive subgoal moves, alternative goal moves) were not included in the problem set. Controlled selection of an individual iso-form (Berg and Byrd, 2002) for each selected structurally unique problem ensured for all problems that within the sequences of the first as well as the last three moves, 95.8 and 97.9% of the inherent two-move sequences were unique, respectively. This was done in order to prevent potential learning of state-move contingencies across problems.

The final problem set comprised 24 ToL problems (eight four-, five-, and six-move problems each). Since task difficulty and cognitive demands also vary within the particular levels of minimum number of moves according to structural problem parameters (Kaller *et al.*, 2004), the systematic item selection applied in the present study allowed for a controlled increase of problem difficulty ranging from very easy four- to very difficult six-move problems.

Regarding the performance measure, empirical problem difficulty was estimated for each problem and found to reflect closely the variety in problem difficulty especially for problems with the same minimum number of moves. For every participant, individual performance was then calculated on the basis of the empirical problem difficulty of the correctly solved trials.

Experimental Design

Four stimulus conditions were applied in a blocked design: a problem solving condition and three different baseline conditions (rest, visual and motor).

The problem solving condition consisted of an initial planning phase and a subsequent movement execution phase. Participants were instructed first to solve the ToL problem mentally and to repeat the trial in mind if they found a solution before the end of the planning phase which lasted 24 s and was followed by a movement execution phase of 32 s. Within the latter, the cursor appeared in the middle of the screen and participants were asked to execute the movements according to their preplanned solution.

In the rest condition, participants were instructed to look at a black cross in the middle of a gray screen. The visual reference condition was implemented to control for the effects of visual stimulation by presenting two identical tower structures in the upper and lower half of the screen. Participants simply had to match for slight differences in the brightness of the color of the balls without performing any response. In the motor reference condition, subjects were requested to assemble and disassemble the tower structures in the lower half of the screen in a simple, predetermined way avoiding any self-generated planning strategies. Each of the three baseline conditions was presented eight times, with each presentation lasting 24 s.

During the imaging session, the arrangement of the four conditions was pseudo-randomized according to the following restrictions: (i) a problem solving condition must not be followed by another problem

solving condition with the equal minimum number of moves; (ii) a baseline condition must not be followed by the same baseline condition. For every participant, the assignment and order of the 24 ToL problems was randomized. However, to avoid differences of general task difficulty between participants due to unequally distributed sequences of particularly demanding problems, the frequencies of four-, five-, and six-move problems were counter-balanced within the session. For the first six problems, two four-, five-, and six-move problems each were randomly selected from the item pool; for the second six problems, another two four-, five-, and six-move problems each were randomly selected from the pool of the remaining 18 problems, and so on.

Experimental Procedure and Imaging Techniques

Prior to the neuroimaging experiment, experimental procedures were practised outside the scanner in order to ensure that participants were familiar with the fMRI-compatible computer mouse and the experimental conditions. First, subjects practised with the mouse on three-move ToL problems for approximately half an hour. Afterwards, participants were introduced to the four different experimental conditions and practiced for ~10 min.

Imaging was performed on a 1.5 T whole-body MR scanner (MAGNETOM Vision, Siemens Medical Systems, Erlangen, Germany). Using a magnet-compatible video beamer, stimuli were projected onto a screen mounted on the rear of the scanner bore. Visual images were viewed via a mirror system placed on the standard head coil. To avoid excessive motion, neck and side pillows were used to fix participants' heads in the coil. During scanning, participants responded with their right hand using the fMRI compatible computer mouse.

Functional images were collected with a gradient-recalled echo-planar imaging (EPI) sequence, allowing the sampling of 30 parallel slices effectively covering the whole brain ($T_R = 4.12$ s, $T_E = 60$ ms, FOV = 256×256 mm, FA = 90° , 4×4 mm in-plane resolution, 4 mm slice thickness, 0.4 mm interslice gap). A total of 484 functional image volumes were collected lasting ~33 min. Four rest scans were collected at the beginning in order for T1-effects to stabilize, and these images were excluded from further analysis. At the end of the experiment, a sagittal T1-weighted magnetization-prepared rapid-acquisition gradient echo (MP-RAGE) image of the entire brain (160 slices, $T_R = 40$ ms, $T_E = 6$ ms, FA = 40° , FOV = 256×256 mm, voxel size = $1 \times 1 \times 1$ mm) was acquired for purposes of co-registration and normalization during image preprocessing.

Image Preprocessing

All fMRI data were processed and analyzed using the SPM99 software (Wellcome Department of Imaging Neuroscience, London, UK). Functional and anatomical images were reoriented in such a way that the anterior commissure corresponded to the origin of the three-dimensional standard coordinate system used in SPM99. The functional images were realigned with respect to the first image of each run, using the realignment procedure of SPM99. The mean image and all other functional images were then co-registered with the anatomical image volume collected for each subject. Parameters for spatial normalization were determined from the anatomical image volumes and applied to the respective subject's co-registered functional image volumes. A new set of normalized functional images was created for which the original spatial resolution of the EPI volumes was interpolated from $4 \times 4 \times 4$ mm to a voxel size of $2 \times 2 \times 2$ mm. The realigned and normalized images were finally smoothed with a 6 mm full width at half maximum (FWHM) Gaussian kernel. Areas were labeled using the nomenclature of Talairach and Tournoux (1988) and Brodmann (1909) by use of the Talairach Daemon (Lancaster *et al.*, 2000).

Model Specification and Statistical Inference

Single-subject data were modelled with a box-car function convolved with a canonical hemodynamic response function, removing low-frequency noise with a high-pass filter. The function contained the appropriately placed models of the hemodynamic response for the three baseline conditions, and for four-, five-, and six-move problems in the planning and movement execution phases. For analysis of trial-correctness, six-move problems were further differentiated into correctly and erroneously solved trials. The six sets of realignment

parameters were included in the model to account for undesired effects of head movements. Single-subject contrast images were then set up for all planning and movement execution conditions, using the respective four-move planning or execution phase as reference.

For group analyses, the single subject contrast images were entered into SPM99 random effects models, using simple t-tests for categorical comparisons and simple regression for assessing the correlation of individual performance scores and change in hemodynamic activity. Given the engagement of many different processes and the extended time-scale of measurement in the blocked design, all inferences were performed at cluster level ($P < 0.05$, corrected for multiple comparisons across the whole brain; Friston *et al.*, 1996).

Results

Behavioral Data

Inside the scanner, participants solved 94% (range 7-8) of four-, 77% (range 4-8) of five-, and 57% (range 2-7) of six-move problems. The numbers in parentheses indicate the number of correctly solved trials out of eight possible. Subjects' overall performance ranged from 24 to 81% on the weighted performance score. To ensure that participants in the pilot study showed similar performances compared to those tested in the scanner, a correlation analysis was carried out, which revealed highly reliable results ($r = 0.68$; $P < 0.001$). There was no significant difference in movement execution time between good ($20\,682 \pm 1829$ ms) and poor problem solvers ($21\,861 \pm 1981$ ms; $P = 0.163$).

Planning-related Brain Activations

To limit large-scale brain activation to units relevant for complex planning, and to compare different levels of difficulty, we analysed the brain activity elicited by complex six- versus easy four-move problems. On average, ~ 50% of the six-move problems were solved correctly, providing an adequate number of trials for examination of individual performance level, trial correctness and their interaction. In contrast, four-move prob-

lems were solved by nearly all participants and thus serve as an adequate reference condition.

Figure 1a shows the overall brain activation of six- versus four-move problems during the planning phase. Significant bilateral activations can be seen in the prefrontal cortex, in lateral and mesial parietal regions, in the cingulate cortex, the basal ganglia, thalamus, and cerebellum.

Individual Performance Level

Regression analyses revealed a linear positive relationship between individual performance level and strength of activation of the right dorsolateral prefrontal cortex (BA 9, 10), with the main extension in the right middle gyrus (Fig. 2a; Table 1). Better problem-solvers also showed increased activation in right superior temporal and inferior parietal regions (BA 22, 40). No regions showed a significant negative relationship with performance.

Trial-correctness

No significant voxels were found when comparing the brain activation elicited by incorrectly and correctly solved problems, in both directions. We did not find any significant activations at a threshold of 0.001 uncorrected, either. Additional direct comparisons of correctly and erroneously solved six-move problems (without being contrasted to four-move problems) also failed to reach significance.

Combining Individual Performance Level and Trial-correctness

Analyses were performed using the following models: Correctly and erroneously solved problems were separately correlated with performance level, to test for either positive or negative relationships with brain activation. During erroneously solved trials, we found a strong positive relationship of performance level and activation of the anterior cingulate cortex bilaterally (BA 32) and the medial wall of the prefrontal cortex bilaterally. These activations were slightly more pronounced in the right hemisphere, and extended into the dorsal prefrontal cortex (BA

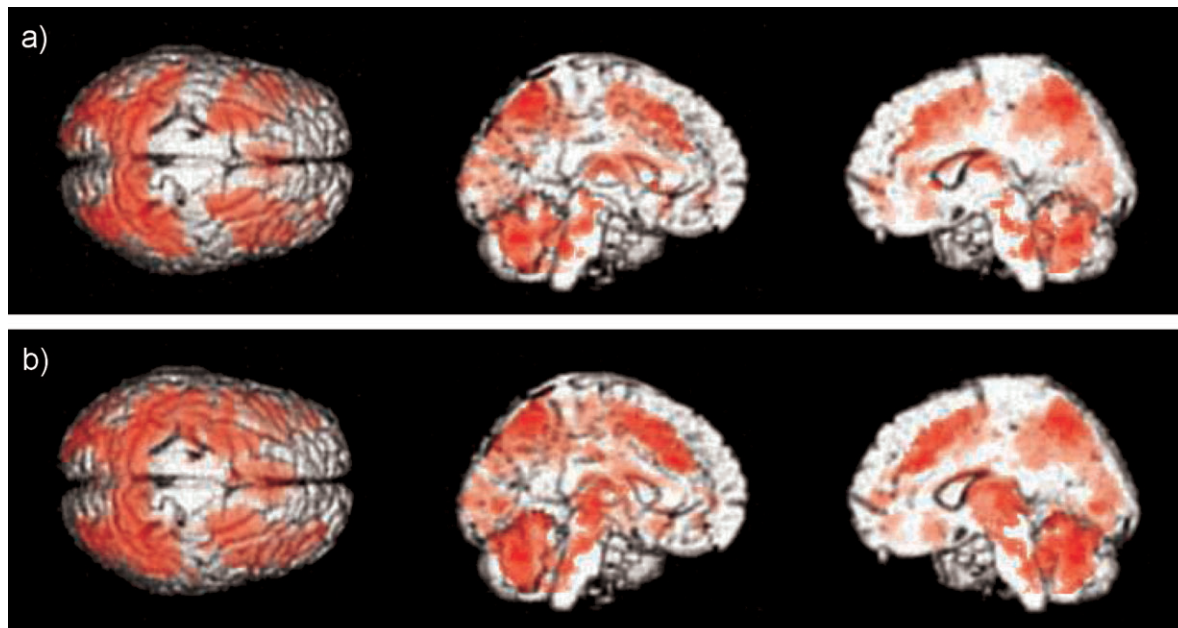


Figure 1. Surface-rendered projections on a representative atlas brain (SPM99) of areas of significant activation differences (six- minus four-move problems) during (a) planning phase and (b) movement execution phase ($Z > 3.0$).

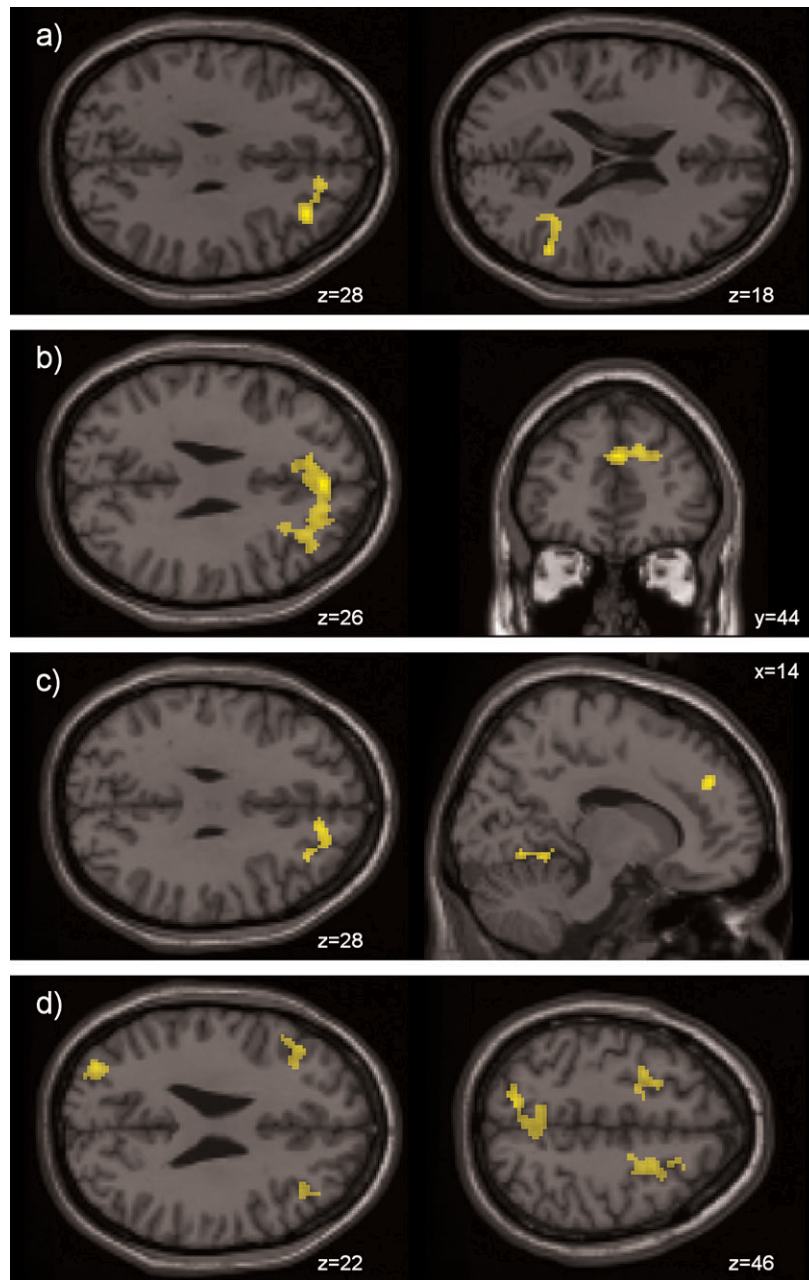


Figure 2. (a) Increase of activation with better performance in the planning phase; (b) increase of activation with better performance during erroneous trials in the planning phase; (c) increase of activation with better performance during movement execution; and (d) significant differences in activation of erroneous versus correctly solved trials during movement execution.

9; Fig. 2*b*, Table 2). No negative relationship between performance level and brain activation was found. For correctly solved trials, performance level was significantly positively correlated with activation in the right posterior thalamus, more precisely in the pulvinar, while no negative relationships were observed.

Movement Execution-related Brain Activations

The overall activation patterns of movement execution are shown in Figure 1*b*. As expected, in comparison to the planning condition, additional activations were detected in the left precentral gyrus and in the midbrain. In analogy to the planning conditions, all subsequent analyses were carried out on the activations elicited by six- versus four-move problems.

Individual Performance Level

When correlating performance level with brain activation during the execution phase, significant activation peaks emerged in the right dorsolateral prefrontal cortex (BA 9; Fig. 2*c*, Table 3) and in the right parahippocampal and lingual cortex (BA 30, 19). No significant negative relationships were observed.

Trial-correctness

When subtracting incorrect from correct solutions during movement execution, a significant difference in activation maxima (cluster size 326 voxels) was found in the border between the posterior cingulate and the precuneus ($x = 0$, $y = -42$, $z = 34$; BA 23, BA 29–31). In contrast erroneously solved

Table 1

Areas activated with better performance in the planning phase

| Cluster | | Activation peaks within cluster | | | | | | |
|---|------|---------------------------------|-------------------------|----|-----------------------|-----|----|---------|
| Region | Size | L/R | Anatomical location | BA | Talairach coordinates | | | Z value |
| | | | | | x | y | z | |
| Prefrontal cortex | 151 | R | Middle frontal gyrus | 9 | 34 | 36 | 26 | 4.4 |
| | | R | Medial frontal gyrus | 9 | 16 | 44 | 24 | 3.8 |
| Inferior parietal and superior temporal regions | 175 | R | Superior frontal gyrus | 10 | 24 | 42 | 24 | 3.1 |
| | | R | Superior temporal gyrus | 22 | 38 | -44 | 17 | 4.1 |
| | | R | Supramarginal gyrus | 40 | 53 | -48 | 21 | 3.9 |
| | | R | Inferior parietal lobe | 40 | 38 | -42 | 24 | 3.8 |

Table 2

Areas activated with better performance during erroneous trials in the planning phase

| Cluster | | Activation peaks within cluster | | | | | | |
|-------------------|------|---------------------------------|------------------------|----|-----------------------|----|-----|---------|
| Region | Size | L/R | Anatomical location | BA | Talairach coordinates | | | Z value |
| | | | | | x | y | z | |
| Cingulate cortex | 162 | L | Cingulate gyrus | 32 | -6 | 14 | 40 | 3.8 |
| | | R | Cingulate gyrus | 32 | 8 | 16 | 40 | 3.6 |
| | | R | Medial frontal gyrus | 6 | 4 | 12 | 46 | 3.5 |
| Prefrontal cortex | 564 | R | Medial frontal gyrus | 9 | 4 | 44 | 24 | 4.7 |
| | | R | Medial frontal gyrus | 9 | 16 | 44 | 25 | 3.8 |
| | | R | Superior frontal gyrus | 9 | 36 | 36 | 28 | 3.8 |
| | 260 | L | Superior frontal gyrus | 8 | -18 | 20 | 41 | 4.0 |
| | | L | Middle frontal gyrus | 6 | -26 | 10 | 53 | 3.7 |
| | | L | Superior frontal gyrus | 6 | -14 | 16 | 47 | 3.5 |
| 264 | R | Middle frontal gyrus | 8 | 34 | 19 | 38 | 3.8 | |
| | R | Middle frontal gyrus | 9 | 26 | 23 | 32 | 3.7 | |
| | | R | Middle frontal gyrus | 9 | 28 | 31 | 35 | 3.5 |

Table 3

Areas activated with better performance during movement execution

| Cluster | | Activation peaks within cluster | | | | | | |
|--|------|---------------------------------|------------------------|-------|-----------------------|-----|----|---------|
| Region | Size | L/R | Anatomical location | BA | Talairach coordinates | | | Z value |
| | | | | | x | y | z | |
| Prefrontal cortex | 136 | R | Superior frontal gyrus | 9 | 16 | 44 | 29 | 4.1 |
| | | R | Middle frontal gyrus | 9 | 30 | 38 | 24 | 3.3 |
| Inferior medial occipito-temporal cortex | 189 | R | Lingual gyrus | 19 | 8 | -49 | -4 | 3.9 |
| | | R | Lingual gyrus | 19 | 14 | -62 | -2 | 3.6 |
| | | R | Parahippocampal gyrus | 19/30 | 20 | -55 | -2 | 3.3 |

trials elicited more activation than correctly solved trials in the prefrontal cortices (BA 6, 8, 9, 46) bilaterally and in the left precuneus (BA 31), extending from the superior occipital and middle temporal gyrus to the inferior parietal cortex (BA 19, 39; Fig. 2d, Table 4).

Combining Individual Performance Level and Trial-correctness

During erroneously solved trials, we found a significant positive relationship of performance level with activation of the right medial and dorsolateral prefrontal cortex (BA 9, 10), and of posterior cortical areas including the cerebellum and the lingual and parahippocampal gyri (BA 19, 30; Table 5). No significant negative relationships were detected. We found no significant positive or negative relationships of performance level and brain activation for correctly solved trials.

Discussion

In the present fMRI-study, we examined the impact of both problem-solving ability (between-subjects) and error-related

Table 4

Significant differences in activation between erroneous versus correctly solved trials during movement execution

| Cluster | | Activation peaks within cluster | | | | | | | |
|----------------------------------|------------------------|---------------------------------|--------------------------|------------------------|-----------------------|-----|-----|---------|-----|
| Region | Size | L/R | Anatomical location | BA | Talairach coordinates | | | Z value | |
| | | | | | x | y | z | | |
| Prefrontal cortex | 579 | R | Middle frontal gyrus | 6 | 26 | 10 | 44 | 4.3 | |
| | | R | Middle frontal gyrus | 8 | 24 | 18 | 49 | 3.9 | |
| | | R | Middle frontal gyrus | 9 | 36 | 32 | 24 | 3.8 | |
| | | 307 | L | Middle frontal gyrus | 9 | -46 | 25 | 28 | 3.9 |
| | | | L | Superior frontal gyrus | 9 | -34 | 35 | 33 | 3.8 |
| | | | L | Middle frontal gyrus | 46 | -44 | 30 | 22 | 3.6 |
| | | 245 | L | Middle frontal gyrus | 6 | -24 | 6 | 44 | 4.0 |
| L | Superior frontal gyrus | | 6 | -24 | 10 | 51 | 3.9 | | |
| L | Frontal lobe, subgyral | | 6 | -24 | 3 | 57 | 3.8 | | |
| Superior medial parietal cortex | 313 | L | Precuneus | 7 | -2 | -57 | 54 | 4.2 | |
| | | L | Precuneus | 7 | -14 | -63 | 51 | 4.1 | |
| | | L | Precuneus | 7 | -8 | -50 | 52 | 3.5 | |
| Parieto-temporo-occipital cortex | 190 | L | Precuneus | 31 | -22 | -73 | 22 | 4.8 | |
| | | L | Superior occipital gyrus | 19/39 | -32 | -76 | 26 | 4.7 | |
| | | L | Middle temporal gyrus | 19 | -40 | -78 | 24 | 2.9 | |

Table 5

Areas activated with better performance during erroneous trials during the movement execution phase

| Cluster | | Activation peaks within cluster | | | | | | |
|--|------|---------------------------------|------------------------|----|-----------------------|-----|----|---------|
| Region | Size | L/R | Anatomical location | BA | Talairach coordinates | | | Z value |
| | | | | | x | y | z | |
| Prefrontal cortex | 273 | R | Medial frontal gyrus | 9 | 6 | 48 | 25 | 4.0 |
| | | R | Superior frontal gyrus | 10 | 26 | 42 | 26 | 4.0 |
| | | R | Middle frontal gyrus | 9 | 34 | 36 | 28 | 3.9 |
| Inferior medial occipito-temporal cortex, cerebellum | 301 | R | Cerebellum/culmen | - | 4 | -49 | -6 | 4.2 |
| | | R | Lingual gyrus | 19 | 14 | -49 | -4 | 3.5 |
| | | R | Parahippocampal gyrus | 30 | 10 | -41 | -3 | 3.1 |

processing (within-subject) on brain activation elicited by problem solving. For the first time ever, an fMRI-compatible mouse enabled us to obtain 'real' performance data on a problem solving task, in contrast to the usually employed forced-choice decision tasks in which correct solutions may be obtained by simply guessing (Cazalis *et al.*, 2003; Newman *et al.*, 2003; van den Heuvel *et al.*, 2003). Although our results are generally in line with studies reporting extensive prefrontal, parietal, cingulate, striatal and cerebellar brain activity during the Tower of London task (Dagher *et al.*, 1999; Newman *et al.*, 2003; Schall *et al.*, 2003; van den Heuvel *et al.*, 2003), they demonstrate the crucial involvement of right dorsolateral prefrontal cortex in all components of higher-level problem solving (e.g. planning and movement execution), both in terms of overall activity and in relation to individual performance level. In contrast, other neuronal structures such as right inferior parietal cortex or anterior cingulate cortex seem involved in more specific components of problem-solving (e.g. error-processing). In the following section, the results will be discussed with respect to the approaches applied.

Individual Performance Level

In the planning condition, better problem-solvers showed an increased activation in the right dorsolateral prefrontal cortex (DLPFC) as well as in the right superior temporal and inferior parietal regions. The activation in the frontal cortex reached its maximum at the mid-dorsolateral part of the prefrontal cortex

(BA 9), even though the activation extended into the medial wall. This pattern is well in line with previous neuroimaging (Owen *et al.*, 1996), patient (Burgess *et al.*, 2000), animal lesion (Petrides, 1994), and computational modeling studies (Newman *et al.*, 2003), which suggest a strong role of right dorsolateral prefrontal cortex in the generation of plans for complex visuospatial tasks (Dagher *et al.*, 1999; van den Heuvel *et al.*, 2003). As direct evidence for this claim, our study shows a relation of right dorsolateral prefrontal cortex activity and performance level during planning, supporting the view that right DLPFC function is a critical determinant of planning efficiency. Note that simple subtraction analysis of difficult and easy problem-solving trials revealed bilateral DLPFC activation. Thus, the left prefrontal cortex seems to be generally involved in planning, but does not seem to determine the planning performance in healthy adults. Cazalis *et al.* (2003) reported that superior performers on the Tower of London task showed a significantly more spatially extended activation in the left dorsolateral prefrontal cortex than did standard performers. When we checked for the left prefrontal dorsolateral brain activation, we detected a cluster (cluster size 16; $x = -32$; $y = 36$; $z = 32$) that was the homologue to the right dorsolateral activation in the regression analyses. However, this cluster did not reach significance even at an uncorrected level ($P = 0.19$).

The central role of right DLPFC activation for planning performance is further underlined by our finding of a significant relationship to performance level during movement execution. The activation maximum for this condition is comparable to the right prefrontal activation in the planning condition, but the cluster extends into the medial wall of BA 9 and BA 10. Note that previous studies have never assessed brain activation during the execution of pre-planned movements; however, computational models suggested that left prefrontal cortex should be primarily involved in the execution of a problem (Newman *et al.*, 2003).

In addition to right DLPFC, other regions showed a context-specific positive correlation with performance level, pointing to a more specific involvement in processes necessitated during phases of problem solving. These regions included right inferior parietal and temporal cortices during planning, and right parahippocampal and lingual gyri during movement execution. It has been proposed that during planning, dorsolateral prefrontal cortex monitors and manipulates information stored in posterior parietal areas, given the extensive connections of both areas (Petrides, 1994; Dagher *et al.*, 1999). In contrast, other theorists state that the right parietal cortex is mostly involved in attention processes, while the left homologue is supposed to be more important for mental imagery processing (Newman *et al.*, 2003). The planning-related increase in right inferior parietal activation in the present study is consistent with both these interpretations, and may reflect more pronounced visuospatial attentional processing, a more intensive recourse on stored visual information needed for the task, or a combination of both (Jonides *et al.*, 1993; Formisano *et al.*, 2002; Sack *et al.*, 2002). In contrast, the engagement of right parahippocampal and lingual gyri during movement execution probably reflects these increased demands on spatial working memory, when the successive spatial positions of single balls have to be recalled and integrated into the overall movement plan. This interpretation is supported by findings that lesions in these structures cause marked spatial memory deficits (Ploner *et al.*, 2000), and that right parahippocampal and lingual gyri seem to respond preferentially to stimuli that depict spatial and topographical information about the

environment (Gorno-Tempini and Price, 2001). Moreover, a recent fMRI study found activation of right parahippocampal regions during a comparable high-level cognitive task, reasoning about spatial relations between geometrical objects (Ruff *et al.*, 2003).

Trial-correctness

In our analysis of planning-related brain activation, we did not find any significant differences for correctly and incorrectly solved problems across participants. While this pattern is certainly surprising, it underlines that the relationship observed between performance level and brain activation during planning is not an artefact of trial-related error-processing, as has been possible in previous studies.

However, during the movement execution phase, incorrectly solved trials elicited more widespread activations than correctly solved problems in bilateral premotor and dorsolateral prefrontal cortex, as well as in the left precuneus and the temporo-parieto-occipital region. These activations resemble the pattern observed during the overall planning condition (Fig. 1a), raising the suspicion that participants simply began to 're-plan' once they recognised they could not solve a problem correctly. Such re-planning should result in longer movement execution times for incorrect than for correct trials, which were confirmed in post hoc analyses (correctly solved trials, mean = 14.2 s; erroneously solved trials, mean = 16.5 s; $P = 0.003$). However, a striking difference to planning-related activation during erroneous movement execution trials was that no significant activations were detected in the right posterior hemisphere, but in the left inferior posterior parietal cortex instead. This may indicate that during execution and re-planning of erroneous trials, increasingly verbal strategies are applied to solve the problem.

Combining Trial-correctness and Individual Performance Level

The combined analysis of individual and item-related performance level revealed that for planning during erroneous trials only, there was a positive relationship between individual performance level and bilateral activation of the anterior cingulate cortex and the medial wall of the prefrontal cortex. Note that during the execution phase, in contrast, we observed similar correlations between performance level and brain activity as in the analysis of all movement execution trials, underlining the specificity of the ACC activation for planning.

Prominent theories (Bush *et al.*, 2000; Botvinick *et al.*, 2001) summarize the functions of the anterior cingulate as relating to response override, underdetermined responding, and error commission. Interestingly, these authors describe the anterior cingulate activation found for planning tasks as being related to competition or conflict among alternative actions. Competition between response alternatives should thus be a key feature of correctly and incorrectly solved trials, and should be present for both superior and inferior problem solvers. This is supported by the results of the comparison of difficult six-move and easy four-move problems. However, our data also suggest that the cingulate additionally plays a crucial role during planning for erroneous trials, specifically for good problem-solvers.

One might argue that better problem-solvers are aware of their disability to solve a problem, and try to resolve this conflict with special strategies expressed in the additional activation

of the anterior cingulate. Interestingly, the awareness of the existing conflict and the additional effort to solve the problem does not seem to succeed, since cingulate activity was only observed in erroneously solved trials. Alternatively, the activation pattern we observed might not be directly associated with the notion of an error, but rather might reflect the ongoing efforts to correct it by re-planning. In this context, the ACC may either signal the need for further resource allocation, or participate in the resolution of a conflict between response alternatives when faced with uncertainty in the problem-space (Bush *et al.*, 2000; Botvinick *et al.*, 2001; Ruff *et al.*, 2001).

Irrespective of these hypotheses for why only good problem solvers show additional activation of the ACC during erroneous planning, it is interesting to note that the location of ACC activation found in the present study is different from those locations commonly found in studies of error processing. In speeded motor response paradigms, error-related activation is mostly observed in the motor cingulate area (BA 24c'; Ullsperger and von Cramon, 2001), while the cingulate activity during erroneous trials in our planning condition was located more dorsally, and adjacent to the anterior prefrontal cortex including BA 9. It is well-known that the ACC can be subdivided into several different regions according to preferential processing of emotional, motor or cognitive information (Bush *et al.*, 2000). Error-related processing during higher cognitive functions may thus take place in the segments of the ACC anatomically related to the cortical regions involved in the specific cognitive processes carried out (Stephan *et al.*, 2003). The performance-related activations of the ACC subunit and the right lateral PFC in the present study support such a process-specific model.

Conclusion

Our findings demonstrate that the simultaneous consideration of human planning abilities and item-related error-processing helps to explain a substantial part of the general patterns of brain activation found during problem solving. The most prominent finding of the present study is the general increase of activation in the right dorsolateral prefrontal cortex (especially in BA 9) associated with better individual performance, both during the planning and the execution phase of problem-solving tasks. The general relation of activation of this brain structure to individual performance level was mirrored during planning by right inferior parietal and superior temporal cortex, during problem execution by right parahippocampal gyrus,

and during planning of erroneously solved trials by anterior cingulate cortex. Although left-hemisphere DLPFC and parietal regions were active during the task as a whole, they did not display a relationship with performance level. Thus, consistent with the visuospatial nature of the problems used, efficient problem solving seems essentially determined by right-hemispheric brain structures, most notably the DLPFC.

Interestingly, no significant negative relationships were obtained when correlating brain activation with performance level. One might argue that there is only one alternative to solve a given problem correctly, while there are many ways to bring the problem to an end in a suboptimal manner.

Notes

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Appendix — The Tower of London Problem Set

Across four-, five-, and six- move problems two structural ToL problem parameters (goal hierarchy and search depth) were experimentally manipulated in the problem set while the number of suboptimal alternatives was controlled for. Due to structural properties of the ToL problem space, the latter intention could only be implemented by confounding the number of suboptimal alternatives with search depth (Table A1).

Goal hierarchy concerns the obviousness of goal priority gathered from the structure of the goal state (Kaller *et al.*, 2004). Goal states can be unambiguous (1), partially ambiguous (2) or completely ambiguous (3). *Search depth* is defined as the number of subgoal moves that must be considered in order to gain the first goal-reaching move on the optimal solution path (Spitz *et al.*, 1982). In the ToL, this depends on two prominent subgoal patterns: For the last four moves, one can distinguish optimal solutions that demand sequences of one subgoal move followed by three succeeding goal moves (1) from sequences of one goal move, one subgoal move and two succeeding goal moves (2). Hence, the search depth for the initial goal move varies with the respective subgoal pattern. *Suboptimal alternatives* compete with the optimal solution and allow to solve a problem in one or two additional subgoal moves. In Table A1, the numbers indicate the number of suboptimal alternatives for a given problem. *Start and goal states* are referred to by the Berg and Byrd notation (Berg and Byrd, 2002).

Table A1
The Tower of London problem set

| Structural problem parameters | | Four move problems | | Five move problems | | Six move problems | |
|-------------------------------|--------------|----------------------|-------------------------|----------------------|-------------------------|----------------------|-------------------------|
| Goal hierarchy | Search depth | Start and goal state | Suboptimal alternatives | Start and goal state | Suboptimal alternatives | Start and goal state | Suboptimal alternatives |
| 1 | 1 | 34:11 | 0 | 42:21 | 0 | 11:51 | 1 |
| 1 | 1 | 44:51 | 0 | 63:21 | 1 | 22:41 | 1 |
| 2 | 1 | 24:43 | 0 | 24:64 | 1 | 66:34 | 1 |
| 2 | 1 | 33:54 | 0 | 53:33 | 1 | 42:63 | 1 |
| 2 | 2 | 16:24 | 1 | 14:54 | 2 | 64:43 | 2 |
| 2 | 2 | 32:24 | 1 | 53:13 | 2 | 33:14 | 2 |
| 3 | 2 | 26:45 | 1 | 15:55 | 2 | 56:15 | 2 |
| 3 | 2 | 12:65 | 1 | 45:25 | 2 | 62:35 | 2 |

Note: For an explanation of the structural problem parameters and the start and goal state notation please refer to the text.

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