Mental Rotation Studied by Functional Magnetic Resonance Imaging at High Field (4 Tesla): Performance and Cortical Activation

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Abstract

We studied the performance and cortical activation patterns during a mental rotation task (Shepard & Metzler, 1971) using functional magnetic resonance imaging (fMRI) at high field (4 Tesla). Twenty-four human subjects were imaged (fMRI group), whereas six additional subjects performed the task without being imaged (control group). All subjects were shown pairs of perspective drawings of 3D objects and asked to judge whether they were the same or mirror images. The measures of performance examined included (1) the percentage of errors, (2) the speed of performance, calculated as the inverse of the average response time, and (3) the rate of rotation for those object pairs correctly identified as “same.” We found the following: (1) Subjects in the fMRI group performed well outside and inside the magnet, and, in the latter case, before and during data acquisition. Moreover, performance over time improved in the same manner as in the control group. These findings indicate that exposure to high magnetic fields does not impair performance in mental rotation. (2) Functional activation data were analyzed from 16 subjects of the fMRI group. Several cortical areas were activated during task performance. The relations between the measures of performance above and the magnitude of activation of specific cortical areas were investigated by anatomically demarcating these areas of interest and calculating a normalized activation for each one of them. (3) We used the multivariate technique of hierarchical tree modeling to determine functional clustering among areas of interest and performance measures. Two main branches were distinguished: One comprised areas in the right hemisphere and the extrastriate and superior parietal lobules bilaterally, whereas the other comprised areas of the left hemisphere and the frontal pole bilaterally; all three performance measures above clustered with the former branch. Specifically, performance outcome (“percentage of errors”) clustered with the parieto-occipital subcluster, whereas both the speed of performance and the rate of mental rotation clustered with the right precentral gyrus. We conclude that the mental rotation paradigm used involves the cooperative interaction of functional groups of cortical areas of which some are probably more specifically associated with performance, whereas others may serve a more general function within the task constraints.

INTRODUCTION

Shepard and his colleagues pioneered a series of tasks involving mental rotation of visual images (Shepard & Metzler, 1971; Shepard & Cooper, 1982). Typically, subjects are shown two asymmetric figures and are asked to judge whether they are of the same or of mirror image configuration. The salient and consistent finding has been that the response time (RT) for a correct judgement is a linear function of the angular difference between the two figures. This suggests that an image of the figure is being mentally rotatated to be superimposed on the reference figure for the judgement to be made, a suggestion that has been strengthened by various manipulations of the task (see Shepard & Cooper, 1982). The results of these manipulations also indicated that rotating images are passing through intermediate positions in a continuous fashion (“analog” type). This hypothesis was supported by the results of neurophysiological experiments in behaving monkeys in which a rotation of a neural population measure (i.e., the neuronal population vector) in the motor cortex was observed in a motor variant of the mental rotation.
paradigm (Georgopoulos, Lurito, Petrides, Schwartz, & Massey, 1989; Lurito, Georgakopoulos, & Georgopoulos, 1991).

Studies of the neural mechanisms of behavior using functional brain imaging have commonly been aimed at identifying the areas “activated” in a given task, that is areas that show a statistically significant change in blood flow (e.g., in positron emission tomography (PET)) or in a metabolic signal (e.g., blood oxygenation level dependent (BOLD) activation in fMRI). With respect to mental rotation (Shepard & Metzler, 1971), such analyses have singled out the parietal cortex as the cortical area most consistently and prominently activated during task performance (Cohen et al., 1996; Petrides, Alivisatos, & Evans, 1994; Tagaris et al., 1994). Although this categorical approach to functional brain imaging is very useful, it leaves a lot to be desired. For example, it is obvious that mental rotation (or any other task) is hardly the function of a single brain area but usually involves the cooperative interaction of a number of brain areas. Although some of these areas can be identified by the categorical approach, this approach does not address explicitly the interaction among these areas. Moreover, this interaction can be important even when each area may not show a statistically significant change by itself. Therefore, new approaches are needed to address this issue.

A different issue concerns the relation between brain activation and behavioral performance. Most functional neuroimaging studies treat behavioral tasks as qualitative variables: Different tasks lead to different functional activation maps, and inferences about behavior are usually made by assessing the qualitative differences in these maps, for example, whether a new area is activated when a specific task manipulation is introduced. Again, this is a very useful approach, but it would also be important to relate quantitatively levels of activation to specific performance measures. Attempts in that direction have been made recently in PET (Dettmers et al., 1995) and fMRI (Tagaris et al., 1996a) studies. Ideally, one would like to determine the relations between performance measures and the covariation among brain areas, since it is this covariation that captures the cooperative activation underlying task performance; an attempt to solve this problem is made in the present study. Finally, it is unknown how high magnetic fields may affect cognitive performance. A main objective of this study was to determine how performance in 3-D mental rotation may be affected in the 4 Tesla magnet.

RESULTS

Performance

Percentage of errors. The percentage of errors decreased with practice, over the period spanned by the five sessions tested (Figure 1). This effect of practice (see “Methods”) was statistically significant ($p = 0.037$, $F$ test, repeated measures ANOVA). Neither the group nor the sex factors nor any interaction terms were significant.

Speed of performance. The speed of performance increased with practice (Figure 2). This effect of practice was statistically significant ($p < 10^{-4}$, $F$ test, repeated measures ANOVA). Neither the group nor the sex factors or any interaction terms were significant.

Rate of rotation. Although the rate of rotation tended to increase with practice (Figure 3), no statistically significant effects were observed.

Functional Activation

Statistically significant functional activation was observed in each area examined, in at least one subject. The areas most consistently activated across subjects included the superior parietal lobule (SPL) and the occipital cortex, bilaterally. An example is shown in Figure 4.

Hierarchical Tree Modeling

The results of a hierarchical tree-modeling analysis (see “Methods”) are shown in the dendrogram of Figure 5. The tree fitted accounted for 77.6% of the variance ($R^2 = 0.776$). This indicates that the fit was very good.

The following features can be seen. At the first level, two large branches [1.0, 2.0] were distinguished. In general, branch I comprised right hemispheric structures, bilateral SPL and occipital cortical areas, and all three performance measures. In contrast, branch II comprised left hemispheric structures and, bilaterally, the frontal pole but no performance measures. These results indicate that branch I is the most important one for the mental rotation task. The fine features of this branch are as follows.

Branch I splits into two branches (Figure 5): the upper one [1.1] comprises the right precentral gyrus, parieto-occipital areas, and the three performance measures, whereas the lower one [1.2] comprises two right anterior (medial and superior) frontal areas. The short length of the stem [1.0] indicates that these two branches have little in common. We now follow branch [1.1]. This branch splits into two branches: The upper one [1.1.1] comprises parieto-occipital areas and the performance outcome (percentage of error) [1.1.1.2], whereas the lower one [1.1.2] comprises the right precentral gyrus [1.1.2.1], the speed of performance, and the mental rotation rate; these two performance measures are parts of a separate subbranch [1.1.2.2].

DISCUSSION

Methodological Considerations

One of the major objectives of this study was to investigate the relations between performance in mental rota-
Figure 1. The percentage of errors in performance is plotted against the session number (see text). The vertical bars indicate 1 SEM. \( N = 24 \) and 6 for the MRI and control groups, respectively.

Figure 2. The speed of performance (see text) is plotted against the session number. Conventions are as in Figure 1.
Figure 3. The rate of mental rotation (see text) is plotted against the session number. Conventions are as in Figure 1.

three to two. This allowed that the activation observed during the task period might include effects stemming from the mental reconstruction of a 3-D object, in addition to its mental rotation. We deemed this a lesser evil than allowing the possibility of mental rotation during the control period. More importantly, in the tree analysis that we performed (see below), the rate of mental rotation was an independent variable by itself, which allowed the association of the mental rotation process with cortical areas independently of other processes.

Since there are several performance measures and several brain areas, the relations between these two sets of variables are best investigated using multivariate analyses. With respect to performance, we chose three meas-

Figure 4. Functional activation map (see text) of the superior parietal lobule during mental rotation in one subject. The distance of the three consecutive slices from the anterior-posterior commissure level is 63, 53, and 43 mm, from left to right, respectively. The green lines demarcate the area (superior parietal lobule) used for the calculation of the normalized activation. R and L denote the right and left side of the brain, respectively.
ures that cover different aspects of performance in mental rotation, namely, performance outcome (estimated by the percentage of errors), performance speed (estimated by the inverse of the average response time), and mental rotation per se (estimated as the rate of mental rotation, see “Methods”). With respect to fMRI, we used a measure based on a normalized change in the intensity of the signal in an area of interest. This is a continuous measure of intensity rather than one based on the count of voxels deemed activated. The latter involves the choice of a threshold based on some statistical test of significance (e.g., t test) applied on a voxel-by-voxel basis and using a threshold that may differ among subjects. The present approach avoids decisions on thresholds. For the normalized activation employed, (a) is a quantitative measure that is not based on any test of significance but instead simply reflects the change in the normalized signal intensity during the task period from that observed in the control period, and (b) is derived in the same way for all subjects. In a previous study (Tagaris et al., 1996a) we found a significant correlation between the activation of the superior parietal lobule and the percentage of errors made during task performance. In the present study we examined the activation of a number of cortical areas in relation to a number of performance measures using the multivariate analysis of additive tree modeling. Our objective was to identify those cortical areas, the cooperative activation of which would relate to specific performance measures.

Performance at High Magnetic Field

The performance of subjects improved with time in both the control and fMRI groups. In fact, the performance of these two groups of subjects did not differ significantly for any of the three performance measures tested. Therefore, we conclude that a high magnetic field does not adversely affect performance in a demanding cognitive task, such as mental rotation.

Functional Brain Activation During Mental Rotation

The neural mechanisms underlying mental rotation of visual objects (Shepard & Metzler, 1971; Shepard &

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Cooper, 1982) are largely unknown. In general, the objective of several studies has been to identify the brain areas involved in the task. For that purpose, electrophysiological methods (Peronnet & Farah, 1989; Pierrot, Peronnet, & Thenevet, 1994; Ruchkin, Johnson, Canoune, & Ritter, 1991; Stuss, Sarazin, Lecch, & Picton, 1983; Wijers, Otten, Feenstra, Mulder, & Mulder, 1989) and techniques measuring changes in regional blood flow (Deutsch, Bourbon, Papanikolaou, & Eisenberg, 1988; Parsons et al., 1995; Petrides et al., 1994; Wendt & Risberg, 1994) have been employed. Two recent studies (Cohen et al., 1996; Tagaris et al., 1994) using fMRI have identified a number of cortical areas involved in this task, including parieto-occipital and frontal areas. Mental rotation is a complicated task that presumably involves imagined motion of visual objects with the ultimate goal of identifying them as the same, or discriminating them as mirror images. This multifaceted operation apparently involves several operations, including encoding of the visual images, presumably rotating them, judging whether they are the same or not, making a discriminatory motor response, etc. It is also obvious that some general processes are involved as well, such as attention. Therefore, it is not surprising that a number of brain areas are engaged in this task, although the mere fact that a certain brain area is activated during the task does not mean that this area is specifically involved in mental rotation per se. We attacked this problem by using specific parameters of task performance as markers by which to identify those cortical areas that would be specifically related to the task. For that purpose, we used three performance measures, namely, percentage of errors made, speed of performance, and rotation rate. Of these, the percentage of errors provides an overall assessment of performance without being specific for any particular process, since an error can be the result of a multitude of factors, from encoding the visual images to making the motor response. Similarly, the speed of performance is also a general measure that reflects how fast subjects processed information, irrespective of success rate. However, unlike the two measures above, the rate of mental rotation is very specific to the presumed operation in this task and, although it is correlated with the speed of performance, in the sense that faster rotation rates will result in higher performance speeds, it captures the essence of the mental rotation task. It is within this conceptual framework that we discuss next the results of the hierarchical tree modeling.

Clustering of Cortical Areas and Performance Measures in Mental Rotation

A major goal of this study was to determine the association between two sets of data, namely, performance measures in mental rotation and functional activation in cortical areas. Since each one of these sets comprises more than one variables, multivariate statistical methods, such as factor analysis, clustering, multidimensional scaling, hierarchical tree modeling, etc. (Green, 1978; Shepard, 1980; Corter, 1996), have to be used. Although all of these methods are used for the analysis of multivariate data, different methods provide different insights into the relations among variables. Therefore, the choice of a particular method depends on the specific objective of a study. In the context of the present work, it is reasonable to assume that mental rotation of visual images is subserved by functional groups of cortical areas that process different aspects of information (see, for example, Kosslyn, 1994). Therefore, a technique should be employed that would identify those functional groups and relate them to the kind of information being processed. In particular, we were interested in three aspects of task performance in mental rotation, namely, the outcome of the performance (estimated by the percentage of errors made), the speed of performance, and the rate of mental rotation that is specific to the process of mental rotation itself. We chose to analyze the data using the hierarchical tree-modeling technique (Corter, 1996), as opposed to, for example, multidimensional scaling, because tree-based techniques portray similarities "as being composed of patterns of shared or unique discrete features of properties," whereas spatial techniques (e.g., multidimensional scaling) portray similarities as "being determined by the differing values of objects on one or more continuous dimensions" (Corter, 1996, p. 49). Since the purpose of this analysis was to identify groups of functionally interrelated areas rather than separate areas along arbitrary dimensions, tree-based techniques seem to be more appropriate for this objective. Factor analysis would also identify functional groups, but tree analysis provides greater detail in the structure of the functional clusters.

The hierarchical tree-modeling analysis yielded a tree that accounted for a good percentage (77.6%) of the variance in the data. There were several clusters that can be discussed under four groups (from top to bottom in Figure 5). The first group (branch [1.1.1] in Figure 5) comprised the performance outcome (i.e., percentage of error) and subclusters of parietal and occipital areas of the right hemisphere, and the superior parietal lobule and occipital (extrastriate) cortex bilaterally. Parietal areas have been implicated in visuospatial processes (Petersen et al., 1994; Haxby et al., 1991; Patzwal, Zanker, & Altenmüller, 1994; de Jong, Shipp, Skidmore, Frackowiak, & Zeki, 1994) and extrastriate visual areas in visual imagery (see Kosslyn, 1994). It is reasonable to suppose that mental rotation involves both of these processes and that both of these processes are crucial for successful performance, hence, the association with performance outcome.

The second group (branch [1.1.2] in Figure 5) comprised the two other performance measures (i.e., speed
of rotation and rate of mental rotation) and only one area, namely, the precentral gyrus of the right hemisphere. This result identifies the right precentral gyrus as the cortical area most specifically related to the essential task parameter of mental rotation rate. It should be noted that this relation cannot be due to simple motor aspects because activation due to movement was factored out by subtracting the signal observed during the control period, which also involved movements.

The precentral gyrus in this study was defined anatomically as the area contained between the central and precentral sulci (see "Method"). Although it definitely comprises the primary motor cortex, it is unclear whether it also comprises part of the premotor cortex. Both motor and premotor areas have been shown to be involved in complex operations in human subjects. For example, areas labeled as premotor have shown activation in studies of working memory using PET (Jonides, Smith, Koepppe, Minoshima, & Mintun, 1993), and the primary motor cortex has been clearly involved in studies of imagined movements using magnetoencephalography (MEG) (Lang, Cheyne, Höllinger, Gerschlagier, & Lindinger, 1996). This last study is particularly important because the localization of changes in the MEG signal is excellent when they originate from banks of sulci, in this case the anterior bank of the central sulcus. Therefore, there is little doubt that primary motor cortex in humans can be involved in complex functions, as also shown by other neuroimaging studies (Karni et al., 1995; Tagaris et al., 1996a). Similarly to the results obtained from human studies, findings from neurobehavioral studies in monkeys, in which the activity of single cells has been recorded during behavior, have documented changes in cell activity in both motor (Georgopoulos et al., 1989; Pellizzer, Sargent, & Georgopoulos, 1995) and premotor (Wise, di Pellegrino, & Boussaoud, 1996) areas during performance of complex tasks. Of particular importance is the involvement of the motor cortex of monkeys in a motor variant of the mental rotation task (Georgopoulos et al., 1989; Lurito et al., 1991). The results of those studies pointed to a role of motor cortex (among, possibly, other areas) in the mental rotation of an intended movement direction. The results of the present and another (Tagaris et al., 1996b) study extend this role to mental rotation of figures. The neural mechanisms of this function remain to be investigated in behaving monkeys.

The remaining groups of areas were not associated with performance itself. This suggests that the role of these areas may be of a more general nature on which we can only speculate based on results of other studies in the literature. For example, the third group (branch [1.2] in Figure 5) comprised the middle and superior frontal gyri of the right hemisphere. These areas, and especially the middle frontal gyrus, have been consistently implicated in spatial working memory (Jonides et al., 1993; McCarthy et al., 1994), and it is reasonable to suppose that the mental rotation task relies on working memory to operate on intermittent images of the 3-D objects shown. Finally, the fourth cluster (branch [2.0] in Figure 5) comprised several areas of the left hemisphere and the anterior frontal areas bilaterally. Specific information concerning the role of these areas could be gained by examining their clustering with performance measures of different tasks or different designs of the mental rotation task.

**METHODS**

**Subjects**

Thirty healthy, right-handed human subjects [19 women and 11 men, age (mean ± SD) 30.1 ± 9.0 years and 31.5 ± 5.5 years, respectively] participated in these experiments as paid volunteers. The study protocol was approved by the University of Minnesota Institutional Review Board and informed consent was signed by each subject. Of these subjects, 6 (control group) performed the behavioral task only outside the magnet, whereas 24 subjects (MRI group) performed the task inside the magnet before and during data acquisition (see below). Of the latter group, valid neuroimaging data (e.g., without motion artifacts) were obtained from 16 subjects [8 women and 8 men, age (mean ± SD) 31.9 ± 9.7 years and 30.5 ± 5.0 years, respectively].

**Mental Rotation Task**

**Behavioral Studies**

All subjects (i.e., both in the control and the fMRI groups) performed the following task. They looked at pairs of perspective drawings of 3-D objects in various orientations. The objects shown were similar to those used previously by Shepard and Metzler (1971) and were generated on a computer screen (Figure 6a,b). Five different objects and five isometric ("mirror") forms of them were used. For each object, seven perspective views were generated by a rotation in depth, around the vertical axis; the rotation angles used were 0, 20, 100, 180, 200, 240, and 320°. From these 70 object views (5 objects × 7 views × 2 isometric forms = 70), 300 pairs were formed. One-half of these pairs consisted of the same object (in different orientations; "same" pairs), whereas the other half consisted of mirror forms ("mirror" pairs). The pairs of the "same" objects were formed in such a way that a clockwise rotation of the right object, as seen from the top of the vertical axis, would bring it into congruence with the left object through the smallest angle. Pairs of all possible angular departures from 20 to 180°, in steps of 20°, were included. During the study, the objects were projected on a screen in a randomized sequence and subjects had to decide, by pushing one of two buttons on a specially designed keypad, whether the

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two objects of the pair projected were the same or mirror images. The subjects used the index and third finger for "same" and "mirror," respectively, and were randomized with respect to the hand used for the response. Each response by the subject was followed by the immediate presentation of the next pair of objects. The maximum time allowed for each pair was 8 sec. We measured the response time and identified whether the response was correct or not.

**fMRI Group**

In these studies there were three periods: a "task" period, which was preceded and followed by two "control" periods (Figure 7). During the task period, subjects in the fMRI group performed the same mental rotation task as above (Figure 6a,b). However, during the two control periods, they looked at pairs of identical 2-D longitudinal rectangles (Figure 6c) and pushed one of the two buttons, as they wished. The objects were projected on a screen (Figure 8) and were visible by the subject with the help of a small mirror, fixed in the interior of the magnet.

**Experimental Design (Figure 9)**

Each subject performed the task five times ("sessions") in two days. For the control group, all sessions were outside the magnet. For the fMRI group, sessions 1 and 2 were outside the magnet, sessions 3 and 4 were inside the magnet but without image acquisition, and session 5 was inside the magnet during image acquisition.

**fMRI Studies**

During the control and task periods successive multislice functional MR images were acquired using a 4 Tesla whole body system with actively shielded head gradients and a homogeneous RF coil [SIS Co. (Sunnyvale, CA) and Siemens (Erlangen, Germany)]. A head support system with a deflatable vacuum pillow was used in order to
Figure 7. Temporal arrangement of the control and task periods and of the MR image acquisition.

Figure 8. Experimental setup in the magnet.
minimize head movements during the experiment. Firstly, sagittal anatomic images were acquired to define the location of the anterior and posterior commissures and to determine the position of slices for functional imaging. Axial multislice T₁-weighted anatomical images were obtained using a turbo-FLASH sequence with 5-mm slice thickness and in-plane spatial resolution of 1.6 × 1.6 mm². For functional imaging, a T₂*-weighted turbo-FLASH sequence was employed (TE = 28 msec, TR = 6 msec, flip angle = 11°) (Hu & Kim, 1993). Interleaved multislice images were collected covering an 8-cm span from the top of the brain (slice thickness = 10 mm, center-to-center interslice distance = 5 mm, N = 15 slices). The in-plane resolution was 3.1 × 3.1 mm². Imaging planes were parallel to the line (Figure 10) defined by the anterior and posterior commissures in a midline sagittal view. The acquisition time for a single slice was 400 msec. However, because of a delay period of 400 msec between slices, the time that was necessary for the collection of all 15 slices was 12 sec. This time interval was the effective temporal resolution in this study. Images were collected continuously during the experiment.

The duration of the experiment was 9 min (3 min for each of the first control, the task, and the second control periods). Fifteen images were collected during the first control, the task, and the second control periods. Possible artifacts due to movement of the head induce spatially interleaved positive and negative alterations in image intensity and are usually generalized and over large areas, including the borders of the brain image. All of our images were screened for such artifacts and the images were rejected if artifacts were present.

**Measures of Performance**

We used the following three measures to quantify the performance of each subject in the task: (1) The percentage of error responses. (2) The speed of performance was calculated as the inverse of the average response time of all trials. Finally, (3) the rate of mental rotation was calculated as the inverse of the slope, b, of the regression of the response time against the angular departure of the objects for trials with "same" pairs and correct responses. The regression equation was:
Response time $= a + b\theta$

where $a$ is the intercept, $b$ is the slope, and $\theta$ is the angular departure.

Demarcation of the Cortical Areas of Interest

The following areas of interest were defined for the right and left hemispheres. Several cortical areas, including primary visual cortex and temporal cortex, were not imaged due to technical limitations (see above).

Occipital cortex (Occ). The demarcation of this area was based on the identification of the parieto-occipital sulcus, in the medial surface of each hemisphere. From that sulcus, a horizontal line to the lateral surface of the hemisphere was drawn. With regard to the rostral limit, care was taken to avoid possible overlapping with the area defined as superior parietal lobule (see below). This area does not comprise the primary visual cortex, which was not included in the volume imaged.

Superior parietal lobule (SPL). The SPL was defined as the area posterior to postcentral sulcus and rostral to the intraparietal sulcus. The appearance of the parieto-occipital sulcus in the medial surface of the hemisphere defined the inferior limit of this area.

Inferior parietal lobule (IPL). This was defined as the area caudal to intraparietal sulcus, posterior to postcentral sulcus, and anterior to the occipital area defined above. The lower limit of this area was defined by the appearance of the posterior part of the Sylvian fissure.

Postcentral gyrus (Poc). This was the area contained between the central and postcentral sulcus.

Precentral gyrus (Pre). This was defined as the area between the central and precentral sulcus.

Superior frontal cortex (SF). This area was demarcated by the precentral sulcus, superior frontal sulcus, and
the midline, starting from the top of the brain, just above the appearance of anterior cingulate. 

**Middle frontal cortex (MF).** This area was defined as the area anterior to precentral sulcus and inferior to SF. The lowest portion was usually at the level of the AC-PC line.

**Anterior cingulate (Ant. Cing.).** This area included the portion of the anterior cingulate that lies rostrally and anteriorly to the anterior commissure. It was not resolved into left and right areas.

**Frontal pole (FP).** This area included the portion of superior frontal gyrus that was below the anterior cingulate.

### Statistical Analyses

**General**

Standard statistical methods (Snedecor & Cochran, 1980) were used to display and analyze the data, including repeated measures analysis of variance (ANOVA), t tests, linear regression, etc. In the ANOVA, there were two between-group factors ("group" and "sex") and one repeated measures within-group factor ("practice", i.e., sessions over time).

### Hierarchical Tree Modeling

The multivariate analysis of hierarchical tree modeling (Corter, 1982, 1996) was used to analyze the data in order to (1) determine functional clusters among the areas of interest and (2) assign the three performance measures above to these clusters. For that purpose, the following steps were employed. (1) Construction of the raw data matrix. This matrix contained the original, raw data. It was a rectangular matrix with dimensions of 16 subjects (rows) × 20 measurements (columns; i.e., normalized activation of 17 areas of interest + 3 performance measures). (2) Construction of the z-transformed data matrix. This matrix had the same dimensions as the one above but the data were z-transformed within each column. This means that the new values were expressed in units of standard deviation and were, therefore, dimensionless. This transformation made the data comparable across measurements and enabled the application of the next step. (3) Construction of 16 proximity matrices, one for each subject. Each one of these matrices was a square 20 × 20 matrix and contained the euclidean distances between the 20 z-transformed values above. The proximity matrices were also symmetric along the main diagonal. (4) Construction of a single, average proximity matrix (Corter, 1996, p. 34). This was a 20 × 20 matrix derived by averaging, cell by cell, the 16 proximity matrices above. (5) This average proximity matrix was then used as input to a hierarchical additive tree-modeling computer program to derive a dendrogram that depicts graphically the results of this analysis. The program used was ADDTREE/P (Corter, 1982) and was kindly provided to us by Dr. James E. Corter.

In the resulting dendrogram, the horizontal distances have an exact interpretation (i.e., of dissimilarity), whereas the vertical ones are arbitrary. Thus, for example, the amount of dissimilarity between two areas equals the sum of the horizontal distances that separate them. Finally, the goodness of fit of the tree solution can be assessed by calculating the coefficient of determination ($R^2$) that provides the proportion of variance accounted for the tree solution. This measure is provided by the ADDTREE/P program above.
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