

Research Report

Individual differences in brain activity during visuo-spatial processing assessed by slow cortical potentials and LORETA

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Abstract

Using slow-cortical potentials (SCPs), Vitouch et al. (*International Journal of Psychophysiology* 27 (1997) 183–199) demonstrated that subjects with low ability to solve a complex visuo-spatial imagery task show higher activity in occipital, parietal and frontal cortex during task processing than subjects with high ability. This finding has been interpreted in the sense of the so-called “neural efficiency” hypothesis, which assumes that the central nervous system of individuals with higher intellectual abilities is functioning in a more efficient way than the one of individuals with lower abilities. Using a higher spatial resolution of SCP recordings, and by employing the source localization method of LORETA (low-resolution electromagnetic tomography), we investigated this hypothesis by performing an extended replication of Vitouch et al.’s study. SCPs during processing of a visuo-spatial imagery task were recorded in pre-selected subjects with either high or low abilities in solving the imagery task. Topographic and LORETA analyses of SCPs revealed that a distributed network of extrastriate occipital, superior parietal, temporal, medial frontal and prefrontal areas was active during task solving. This network is well in line with former studies of the functional neuroanatomy of visuo-spatial imagery. Contrary to our expectations, however, the results of Vitouch et al. as well as of other studies supporting the neural efficiency hypothesis could not be confirmed since no difference in brain activity between groups was observed. This inconsistency between studies might be due to differing task processing strategies. While subjects with high abilities in the Vitouch et al. study seemed to use a visuo-perceptual task solving approach, all other subjects relied upon a visuo-motor task processing strategy. © 2005 Elsevier B.V. All rights reserved.

Theme: Neural basis of behavior

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1. Introduction

The biological bases of intellectual abilities attracted increased research interest in the past years. Genetic influences on brain anatomy and their relationship to intelligence differences have been revealed (see [18] for a review), and a recent structural magnetic resonance imaging study demonstrated detailed insights into how variations of brain structure are related to psychometric intelligence [23]. With respect to brain function, numerous studies reported

negative correlations between intellectual ability and brain activity. Such correlations reflect that individuals with higher intelligence show less overall brain activity and/or activity that is more focused to task-relevant brain areas when processing a cognitive task—a finding that has traditionally been interpreted within the framework of the so-called neural efficiency hypothesis [10]. This hypothesis assumes that the nervous system of individuals with higher intelligence is functioning in a more efficient way than the nervous system of individuals with lower intelligence. The cellular basis for this assumption might be that the functional neural networks (cell assemblies *sensu* Hebb) involved in task processing are smaller and/or interconnected in a more efficient way in more intelligent individuals. Results supporting the neural

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efficiency hypothesis have been obtained using the functional neuroimaging techniques of positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) (e.g., [21,49]; but see also [20] or [17] who report positive correlations). Most studies in support of the neural efficiency hypothesis, however, employed electroencephalographic methods (EEG) (e.g., [25,26,29,36,38,56]). EEG seems to be optimal to assess the efficiency of neural processing since it reflects activity of synchronously activated cell assemblies, and since it provides sufficient temporal resolution to resolve the sometimes fine-grained individual differences in cognitive and neural processing.

Numerous variables affecting direction and size of the relationship between intellectual ability and brain activity have been identified. Variables documented so far are gender [37], personality dimensions such as extraversion vs. introversion [12], the amount of experience with a task [15], but evidently also the neurological and psychiatric status of subjects [22]. A crucial variable affecting the intelligence–activity relationship is the type of cognitive processing that is investigated. Most studies published so far employed tasks that can be solved within a comparably short amount of time (usually <3 s) and that involve strong memory, attention and executive control components. Typical examples are elementary cognitive tasks such as Posner's letter matching or the sentence verification test, which have been repeatedly used by Neubauer and colleagues (e.g., [36,37]). Only few studies so far employed tasks requiring more complex and prolonged cognitive processing which do not primarily put memory or executive control demands upon their subjects. Our group investigated individual differences in the topography of event-related slow cortical potentials (SCPs) during complex and prolonged visuo-spatial imagery in a male sample [56] and in a sample including both genders [29]. Both studies revealed that subjects with lower visuo-spatial imagery ability show higher activity in task-relevant occipital–parietal areas, and that their activity extends more into anterior (mainly medial frontal and medial central) regions. This pattern of results was clearly supporting the neural efficiency hypothesis and extended its scope to the area of more elaborate cognitive processing.

A major limitation of most EEG investigations of the neural efficiency hypothesis – including our own former studies – is their restricted capability to localize the neural generators of the scalp-recorded individual differences. Localizing individual differences, however, would provide more detailed insights into the assumption that larger or more distributed cell assemblies are active in individuals with lower intellectual ability. A number of source localization methods has been developed and validated recently (see [33] for review), but they have only rarely been used in the assessment of ability-related individual differences (e.g., [25]). The present study thus has been designed with three main goals. First, we intended to investigate

whether the formerly observed individual differences in brain activity during visuo-spatial task processing can be replicated. Second, the relationship of ability-related differences to functional neuroanatomy should be assessed with higher spatial resolution of scalp measurements. Third, we aimed to localize the cortical generators of the expected individual differences using the source localization method of LORETA (low-resolution electromagnetic tomography) [43].

2. Materials and methods

The study was performed according to local guidelines and regulations of the University of Vienna, and informed written consent was obtained from all subjects. All experimental procedures, particularly the subject selection criteria, were identical to those described in [56]. Thus, we also only investigated male subjects since ability-related differences of our two former studies [29,56] have been more consistent in males—a finding that has been corroborated in the meantime by other studies [16,37,38]. A number of technical and methodological improvements has been achieved in the present replication. EEG was recorded with much higher spatial sampling (45 instead of 22 EEG electrodes), and individual electrode coordinates were determined for each subject using a photogrammetric head digitizer [4]. This enabled the mapping of SCPs with higher resolution on individual realistic head models [30] and with a more accurate interpolation algorithm [3]. The only (irrelevant, see below) difference to [56] was that the baseline image preceding the presentation of the visuo-spatial imagery tasks slightly differed in half of the trials.

2.1. Subjects

Subjects were selected out of a large pre-testing sample recruited in various undergraduate and graduate courses at the University of Vienna. In this sample, handedness (Annett handedness inventory [1]), visuo-spatial ability (three-dimensional cube test 3 DC [13]), and general verbal ability (word power test [50]) had been determined. Based upon effect size estimates (partial η^2) derived from a re-analysis of the data of [56], a sample size of twenty-seven subjects (14 good, 13 poor performers) was considered to provide sufficient statistical power for the present study (see below, Discussion). All subjects were right-handed healthy males who were selected according to their 3 DC score in the following way: subjects whose score fell into the first quartile of the male student norm were assigned to a group of poor performers, and subjects with scores in the fourth quartile of the norm were classified as good performers. This procedure yielded a between-subjects design with two experimental groups that reliably, validly and significantly differed in their ability to solve the tasks used during SCP recordings.

2.2. Task paradigm

The task paradigm was identical to the one used in Vitouch et al. [56]. Tasks had been adapted (dichotomized) from the 3 DC test and consisted of two blue cubes with white figural objects (triangle, dots, squares, arrows etc.) on each of their three visible faces; cubes were simultaneously presented on black background (Fig. 1). 3 DC tasks allow the assessment of visuo-spatial imagery with increased intra- and interindividual homogeneity since they fulfill the criteria of the Rasch model [45]. Tests conforming to this probabilistic test model yield unidimensional assessments of cognitive abilities, implying that identical cognitive operations are triggered with all items as well as in different groups of subjects. This is in contrast to several 2-dimensional letter or object comparison tests in which some of the items do not require mental rotation of stimuli [7,8], or in which some subjects predominantly use verbalization instead of visuo-spatial strategies. Although such intra- and interindividual differences in processing strategies are still possible with Rasch-homogeneous task material, they are known to be considerably reduced. Furthermore, 3 DC tasks show only minimal practice-related changes in processing strategy.

Each trial consisted of a baseline image presented before a task stimulus. Trial presentation was subject-paced. Subjects had to indicate whether the two cubes could be identical or not by pressing one of two response buttons (answers: “yes, cubes could be identical” or “no, cubes could not be identical”). Answering immediately replaced the task stimulus with the baseline image. All buttons were pressed using the dominant right hand. Subjects were informed using the written instruction of [56] to have ample time to solve each item, but to answer as soon as they were convinced to have found the solution. The reason for using unrestricted item presentation times was that the instruction to answer as quickly as possible evokes cognitive processes not specifically attributable to the cognitive task [19]. In addition, it has been shown that a speeded instruction affects individual differences in SCPs [30].

One hundred items were presented in two blocks, each containing 50 items. The only difference between blocks was the baseline image: in block 1, the baseline image

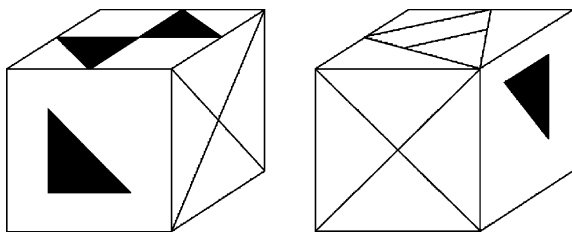


Fig. 1. Black and white sample of the tasks used in this study. Subjects had to decide whether the two cubes could be identical (which is the case for the sample shown).

consisted of a fixation cross; in block 2, two empty blue cubes (with no white edges and no objects) were presented in addition to this cross. The reason for using different baseline images is outside the scope of this paper. The sequence of blocks was counterbalanced across subjects. Since statistical analyses of LORETA and SCP topographies revealed no significant differences between blocks (even when the statistical threshold was lowered to $P \leq 0.30$), all 100 trials were used for averaging in order to increase the signal-to-noise ratio.

2.3. EEG recording

EEG was recorded using a multi-channel DC amplifier with high baseline stability and an input impedance of 100 G Ω . Signals were sampled at 3 kHz (250 Hz downsampling for digital storage) and recorded within a frequency range from DC to 30 Hz. Vertical (electrodes above and below right eye) and horizontal eye movements (electrodes on left and right outer canthi) were recorded in order to eliminate artifacts related to eye movements and blinks. All electrodes were mounted on small plastic adapters that had been individually fixed to the subject's scalp and skin using collodion or adhesive tape. The skin at each recording site was slightly scratched using a sterile single-use needle [44] to minimize skin potential artifacts and to ascertain electrode impedances that were homogeneous, stable and ≤ 1 k Ω . Impedances were measured for each electrode by a manual impedance meter before the experiment. Electrodes and adapters were filled with degassed electrode gel (Electro-Gel, Electro-Cap International, Inc., Eaton/OH, USA). Electrodes had been filled with the gel at least 1 h before application to allow for stabilization of the electrode potential. A sterno-vertebral reference [51] was used in order to obtain a true non-cephalic recording reference. Although a linked mastoid reference was used in [56], this difference is irrelevant because re-referencing to linked mastoids yielded virtually identical SCPs and SCP topographies, and because CSD maps and LORETA analyses are independent of the recording reference. Thus, all data reported in this paper are referenced to the sterno-vertebral reference. EEG was recorded from 45 electrodes evenly distributed across the scalp surface. Electrode application was aided by an application cap, whose positions lay close to the following coordinates of the 10–20 electrode system: Fpz, AF3, AFz, AF4, F7, F5, F3, Fz, F4, F6, F8, FC5, FC3, FCz, FC4, FC6, A1, M1, T7, C5, C3, Cz, C4, C6, T8, M2, A2, CP5, CP3, CPz, CP4, CP6, P7, P5, P3, Pz, P4, P6, P8, PO3, POz, PO4, O1, O2, Iz. The fact that electrodes did not exactly match the 10–20 coordinates will be indicated in the remainder of the text by an apostrophe. Three-dimensional coordinates of these electrodes and of nasion, inion and the two preauricular points were determined using a photogrammetric head digitizer and used in SCP mapping [4].

2.4. EEG analysis

Eye movement and blink artifacts were eliminated offline using a linear regression approach with channel-specific correction coefficients. EOG coefficients were determined in EOG-calibration trials (see [56] for a detailed description). In order to determine blink coefficients, time windows containing blinks were identified using a template matching procedure. Using these time windows, blink correction coefficients were calculated for each EEG channel using linear regression. Blink correction based on these coefficients was then performed in those time windows where a blink had been identified by the template matching procedure. In addition, all EOG- and blink-corrected trials were visually screened to exclude those containing artifacts, and to exclude trials in which EOG and blink correction had not been satisfactory.

Following artifact screening, stimulus-onset linked averages were computed for each subject with the baseline being the mean amplitude of the 200 ms epoch preceding task presentation. In addition, response-linked averages (with the same pre-stimulus baseline) were computed to evaluate activity related to response execution. Stimulus- and response-linked SCP and current source density (CSD) maps were calculated using an analytical interpolation algorithm [3]. CSD (or surface Laplacian) transformation yields reference free maps and attenuates low spatial frequencies (“smearing”) introduced into the scalp topography due to volume conduction and thus provides a more precise estimate of the epicortical surface potential distribution [40]. SCP and CSD averages were visualized on individually reconstructed head shapes that had been reconstructed using analytical spline interpolation of the 3D electrode and landmark coordinates acquired by the photogrammetric head digitizer [31]. Grand mean averages of the pooled sample were mapped using the mean electrode coordinates of all subjects. The following six components were analyzed: N1, MRP, SCP2 to 5. N1 and MRP (motor response potential) were used to validate individual SCP topographies and LORETA results. N1 is the first prominent negative peak ($>5 \mu\text{V}$) observable over the occipital–parietal region after task presentation. It is one of the first endogenous ERP components, has a well-known topography and is thought to reflect neuronal activity in primary and higher order sensory projection areas (visual cortex in the present case) [48]. Based on visual inspection of individual and grand mean maps and waveforms, N1 was defined as the highest negative SCP amplitude at electrode POz occurring in a time window from 100 to 300 ms after task presentation. The MRP component was computed as the mean amplitude 100 ms before task response. The topography of this component is also well known [9] and reflects motor preparation and movement planning. Activity thus was expected in medial premotor areas (medial Brodmann area BA 6/supplementary motor area SMA) and in lateral premotor areas (BA 6), with the latter showing

left-hemispheric lateralization due to the right handed responses. Components SCP2 to SCP5 were used to analyze brain activity related to task-specific cognitive processing. SCP components were computed as mean amplitudes of 1800–2000 ms (SCP2), 2800–3000 ms (SCP3), 3800–4000 ms (SCP4), and 4800–5000 ms (SCP5) after task presentation.

Greenhouse–Geisser corrected repeated-measures ANOVAs with factors GROUP (2 levels) and LOCATION (45 levels) were performed for raw amplitude and z-normalized values [24]. Linear contrasts were used to test a-priori hypotheses based on the results of Vitouch et al. [56] who observed the most prominent activity differences over the parietal, the medial frontal and the medial central region. All contrasts were calculated with specific error variances, in order to take into account violations of the sphericity assumption inherent to repeated measures designs [5]. In addition, Pearson correlations of component SCP5 with pre-test scores of the word power test, the percentage of correctly answered items (percentage correct), and median response time were calculated.

2.5. Low-resolution electromagnetic tomography (LORETA)

The LORETA-KEY software package (<http://www.unizh.ch/keyinst/NewLORETA>), version 03, was used for all source localization analyses. LORETA calculates inverse solutions by identifying the smoothest of all possible 3-D current density distributions that would explain the surface potentials. Solution space of LORETA is restricted to cortical and hippocampal gray matter, with gray matter defined via a reference brain from the Montreal Neurological Institute (MNI). The smoothness constraint gives LORETA its name and results in “blurred-localized” images of 3 D current density with $7 \times 7 \times 7$ mm voxel sizes. While the LORETA algorithm is supposed to preserve the location of maximal activity of point sources, it introduces some degree of spatial dispersion into the resulting current density images [42]. The electrophysiological rationale for applying the smoothness constraint is the observation that neighboring cortical neurons usually are simultaneously and synchronously active. In addition, synchronous activity is a prerequisite for measuring electrical potentials on the scalp surface. While there is some debate about introducing such a constraint [32], numerous studies support the usefulness and validity of LORETA in localizing generators of scalp-recorded potentials [34,41,55]. LORETA is a distributed source modeling method based on the minimum-norm approach. As such, it does not require assumptions about the number, localization, configuration or extent of neuronal sources. Using a combination of fMRI and SCPs, it was revealed that a distributed network of brain areas with activity clusters of considerable spatial extent is involved in processing the items used in our study [32]. Thus, LORETA was considered an ideal method to accurately localize this distributed network of activities. Electrodes A1, A2 (pre-auricular points), M1, and M2 (left and right mastoids) were

excluded from LORETA analyses since LORETA assumes electrodes lying on the scalp surface. As the higher bone thickness and density at theinion violates the assumption of a homogenous bone thickness in the three-shell spherical head model used by LORETA, electrode Iz was also excluded. Individual electrode coordinates of the remaining 40 scalp electrodes were transformed to the surface of the standardized MNI-brain. Using these coordinates, transformation matrices with no over-smoothness (i.e., with the standard smoothing factor) were computed for each subject [42]. LORETA current density estimates were computed for all six components. Statistical analyses of group differences were performed using statistical non-parametric mapping (SnPM; [39]) implemented in the LORETA software. Group differences were assessed by calculating independent-samples *t* values for every voxel, and thresholded at a significance level of $P \leq 0.05$. The significance threshold was based on a permutation test with 5000 permutations, using log-transformed LORETA values but no subject-wise normalization (since the latter would have attenuated possible differences in the amplitude of activity). For a descriptive analysis of resulting brain images, grand mean LORETA averages were calculated and visually analyzed. Talairach coordinates, anatomical structures and Brodmann areas were determined using the LORETA software for cluster maxima $\geq 0.03 \mu\text{V}/\text{mm}^2$ and $\geq 0.01 \mu\text{V}/\text{mm}^2$ for the SCP components and the N1 component, respectively. A lower amplitude was chosen for N1 because this component evoked lower scalp amplitudes and current density values than the SCP components.

3. Results

Debriefing revealed that all subjects were motivated and goal-oriented during task processing. This is also reflected in the EEG data which were of good quality: on average, only 22% of trials had to be discarded due to artifacts, resulting in a mean of 78 trials (range: 43–96) available for averaging. Data of one subject had to be excluded due to excessive movement artifacts. Another subject was excluded because generators of N1 were not localized to posterior (parietal or occipital) brain areas, and because MRP

generators were not localized to motor areas. Thus, a final sample of 14 good and 11 poor performers remained for the analyses. This sample is slightly larger than the 12 vs. 8 good and poor performers analyzed in [56].

3.1. Behavioral data

Table 1 contains performance and pre-test results of the analyzed sample. Statistical analyses revealed that good and poor performers significantly differed with respect to 3 DC scores (being a direct result of the subject selection criteria; Mann–Whitney *U* test, $P < 0.001$), WPT scores (Mann–Whitney *U* test, $P < 0.001$), the percentage of correctly answered items ($t(1,23) = 5.035$, $P < 0.001$), and median response time (Mann–Whitney *U* Test, $P = 0.028$). Groups did not differ with respect to age ($t(1,23) = 0.318$, $P = 0.754$). Correlations of 3 DC and WPT ($r = 0.662$, $P < 0.001$), of 3 DC and percentage correct ($r = 0.749$, $P < 0.001$), and of WPT and percentage correct ($r = 0.742$, $P < 0.001$) were significant. Median response time did not correlate significantly ($P > 0.141$ for all correlations) with any of the other behavioral parameters (3 DC: $r = -0.209$, WPT: $r = -0.277$, percentage correct: $r = -0.303$). Except for the significant difference in WPT scores (and a correspondingly lower correlation of WPT and 3 DC scores, $r = 0.21$) and a generally longer response time in both groups in the present study, the same pattern of results was obtained in [56]. Note, though, that the group difference of around 3 s in median response time was similar in both studies.

3.2. Time-course and topography of SCPs

Fig. 2 shows grand mean SCPs for selected channels. After phasic negative and positive deflections (N1 and P3) with mean latencies around 200 ms and 400 ms, negative SCPs with an almost linear increase developed over occipital, parietal, medial central and medial frontal regions. The highest negative SCP amplitudes were observed in medial occipital–parietal electrodes: Grand mean amplitudes (pooled sample) for electrodes POz' and Pz' were $-13.09 \mu\text{V}$ and $-13.02 \mu\text{V}$, respectively. CSD maps of the N1 component showed a topography dominated by a single distinct current sink over the medial occipital–parietal

Table 1
Behavioral results of the present study and of [56]

Study	Group	3 DC mean (std)	WPT mean (std)	Age mean (std)	% correct mean (std)	Response time median (range)
Present study	Good	16.6 (.5)	35.4 (.9)	23.1 (2.3)	91.1 (5)	13 (7.7–19.9)
Present study	Poor	5.6 (2.9)	33.8 (.8)	23.5 (2.7)	75.6 (9.3)	16.3 (9–24.3)
Vitouch et al.	Good	16.2 (0.8)	36.2 (1.6)	24.3 (2.1)	93	10.2
Vitouch et al.	Poor	5.4 (2.4)	35.8 (1.9)	23.6 (2.9)	77	13.4

Mean and standard deviations for pre-test results and performance data in the present study and in Vitouch et al. [56]; group: good vs. poor test performers (score falling either in 1st or 4th quartile of 3 DC test norm); 3 DC: 3 DC score (possible range: 0–17); WPT: Word Power Test score (possible range: 0–42); % correct: percentage of correctly answered tasks; response time: response times, median and range of the median response times of subjects. Standard deviations for % correct and response time were not provided in [56].

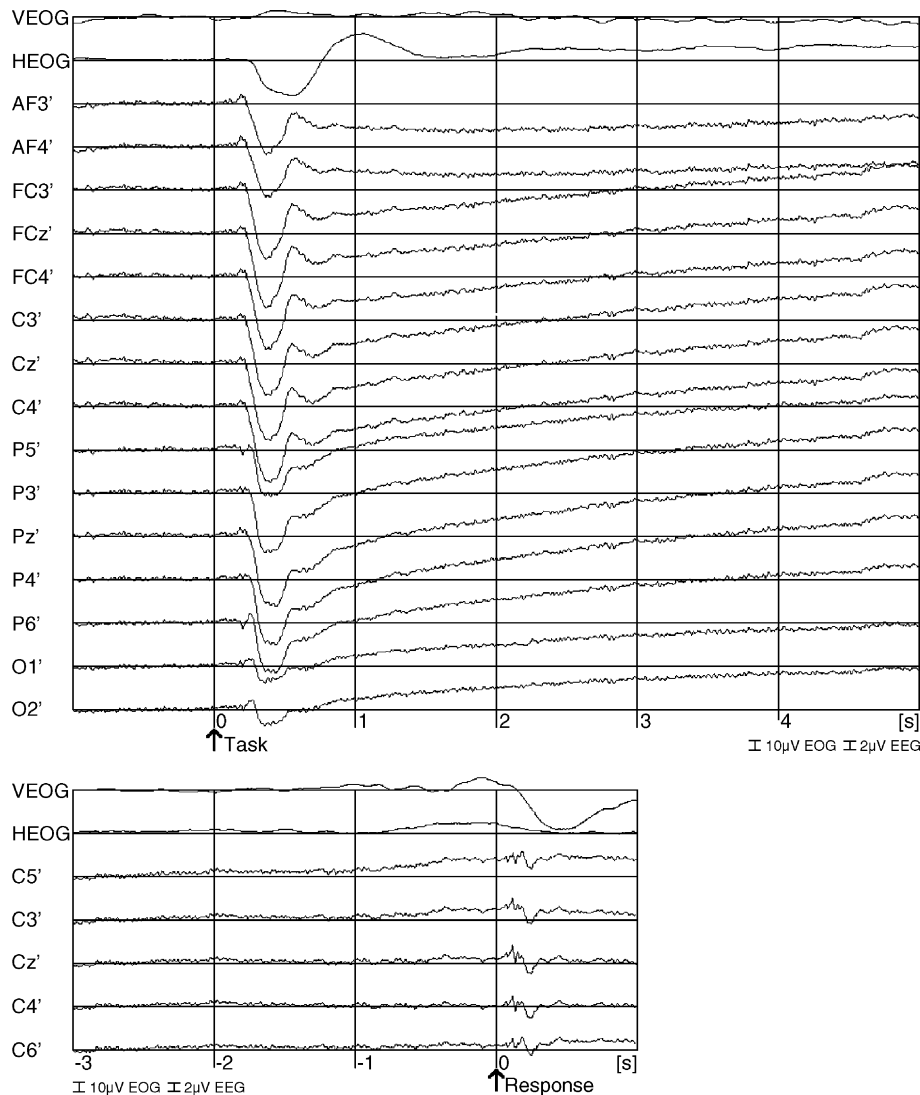


Fig. 2. Stimulus-linked (above) and response-linked (below) grand mean SCP waveforms of selected channels showing task- and response-related activity changes. Task presentation and task answering are marked by arrows.

region (maximal grand mean amplitude at electrode POz': $-5.86 \mu\text{V}$). This sink is consistent with neural activity in primary and secondary visual areas. Maps of the SCP components related to task-related cognitive processing (SCP2 to SCP5) revealed topographies that were dominated by current sinks over the parietal and the fronto-central cortex (Fig. 3). Analysis of the time-course of activity shows that the parietal current sinks appeared around 800 ms after task presentation and then showed an almost linear amplitude increase. The same linear increase was evident for the fronto-central sinks, which showed a slightly higher onset latency of around 1100 ms post stimulus. In addition to these occipital and parietal sinks, maps of the MRP component revealed a clearly lateralized current sink over the lateral central region and a distinct current sink over the medial fronto-central scalp.

Statistical analyses of SCP2 to SCP5 using repeated-measures ANOVAs revealed no significant main effect of GROUP ($P > 0.30$ for all components), and no

significant interaction GROUP \times LOCATION (irrespective of whether raw amplitude data or z-normalized values were used in the ANOVAs, $P > 0.40$ for all components). None of the a priori linear contrasts was significant either: medial frontal region (electrodes F3'/Fz'/F4'/FC3'/FCz'/FC4', component SCP5): $P = 0.604$, medial central region (C3'/Cz'/C4', SCP5): $P = 0.491$, medial parietal region (P5'/P3'/Pz'/P4'/P6', SCP5): $P = 0.926$, and occipital–parietal region (OP3'/Opz'/OP4'/O1'/O2', SCP5): $P = 0.473$. Vitouch et al. [56] observed differences of up to $10 \mu\text{V}$ in group-specific grand mean amplitudes in numerous electrodes. Fig. 4 shows that such differences are clearly absent in our study, with the majority of mean amplitudes being virtually undistinguishable. However, some electrodes showed at least small differences of around $2\text{--}3 \mu\text{V}$ (e.g., C4': $-6.166 \mu\text{V}$ vs. $-9.208 \mu\text{V}$ in good and poor performers, respectively). In order to assess whether these differences are significant, we performed t tests for independent

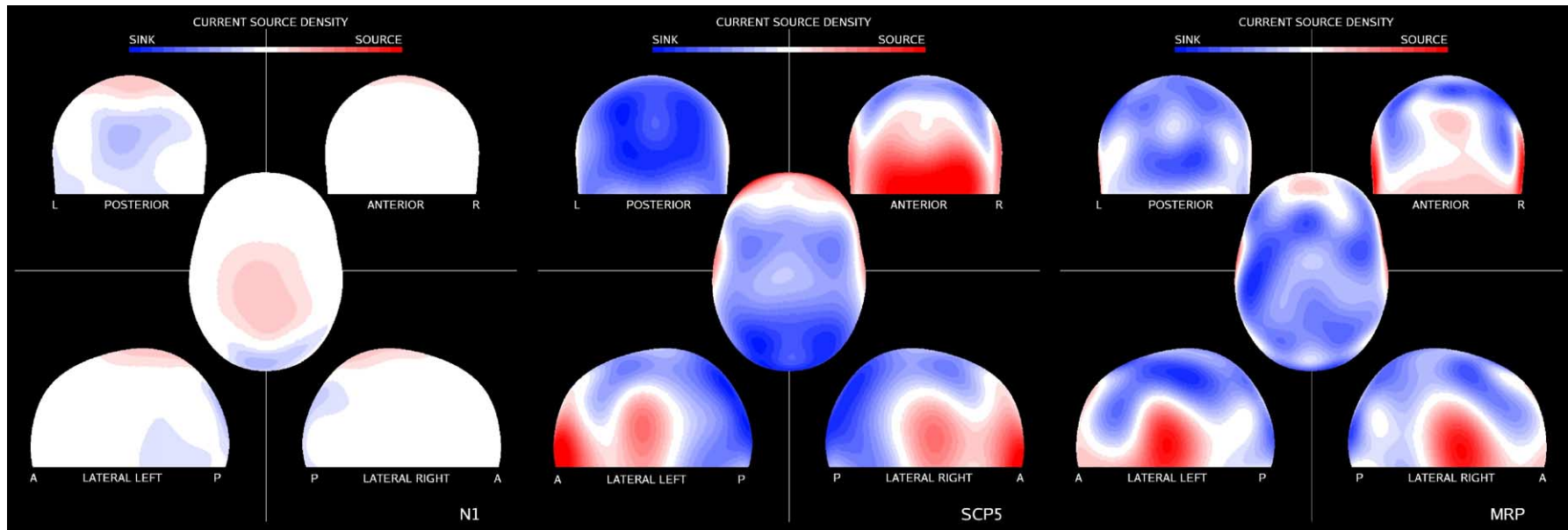


Fig. 3. Color-coded grand mean CSD maps of components N1, SCP5 (mean CSD values 4.8 to 5 s after task presentation), and MRP (mean CSD values 100 ms before task response). Current sources are coded in red and current sinks are coded in blue. While the N1 component is dominated by a single occipital–parietal sink, SCP5 reveals a distributed network of brain areas to be involved in task processing, including parietal and frontal areas. MRP shows a clearly left-lateralized sink over the lateral central region, reflecting activity in motor areas related to button pressing with the right hand.

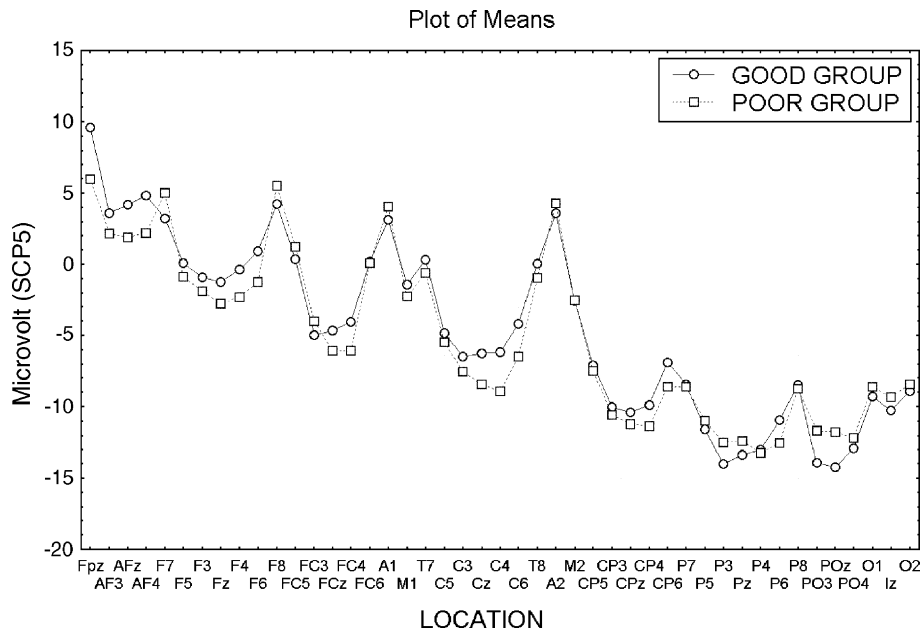


Fig. 4. Group-specific grand mean plot of component SCP5 for all EEG electrodes. Circles/solid lines: good performers, squares/dotted lines: poor performers. None of the electrodes shows relevant mean differences between groups. This absence of mean differences is confirmed by *t* tests of single electrodes, which take into account the variance of the means, but did not reveal any significant difference.

samples for all 45 electrodes of component SCP5. Even when the significance threshold was lowered to $P \leq 0.10$, none of these tests was significant. The largest *t*

value was observed for electrode PO4' ($t(1,23) = 1.589$, $P = 0.126$). However, since good performers showed a higher negative SCP amplitude ($-14.5 \mu\text{V}$ vs. -10.53

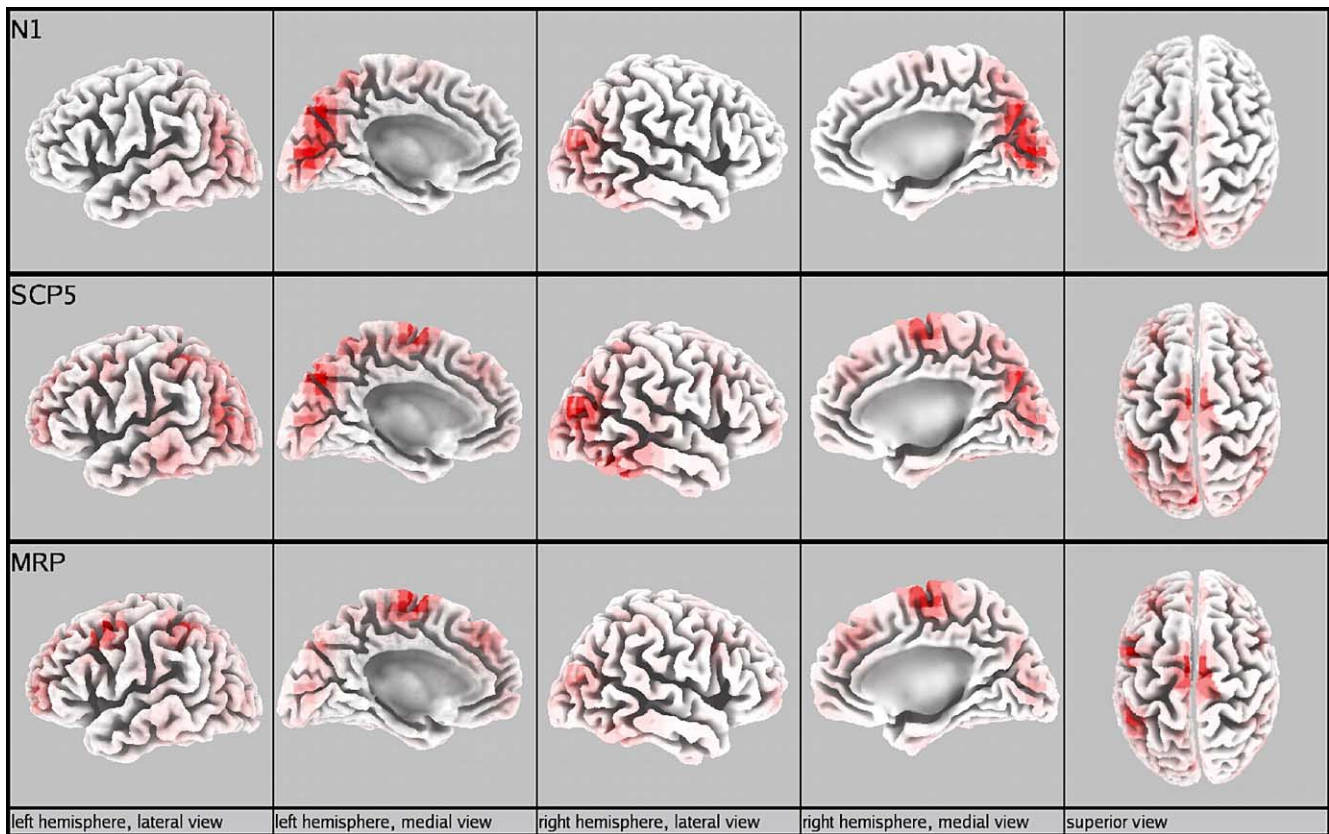


Fig. 5. Maximum intensity projection images of grand mean current density (LORETA) averages for components N1, SCP5 and MRP. While N1 is dominated by maxima in extrastriate occipital and parietal cortex, SCP5 reveals activity clusters in a number of cortical regions, including visual (occipital and superior parietal) and premotor (lateral and medial) areas. Note that current density in lateral premotor areas is clearly left-lateralized for component MRP.

μV), this difference was opposite to the expected negative correlation between ability and brain activity.

Correlating performance parameters and WPT scores with SCP amplitudes also did not yield significant results. For parameter median response time, the highest correlation was observed for electrode CPz' ($r = 0.285$, $P = 0.167$; longer response times correlating with less negative amplitudes); for percentage correct, the highest correlation was observed with electrode POz' ($r = -0.359$, $P = 0.078$; higher percentage correct correlating with more negative amplitudes). The highest correlation between WPT and SCPs was observed for electrode Cz' ($r = 0.262$, $P = 0.197$; higher WPT values correlating with less negative amplitudes).

A recent study [38] obtained results confirming the neural efficiency hypothesis only after subjects had participated in a training session. In order to investigate whether the absence of individual differences in our study can be explained by training effects, a post hoc analysis was performed to assess whether performance data and SCPs from the first and the second task block significantly differed. To this end, repeated-measures ANOVAs with factors ORDER (1st vs. 2nd block), GROUP and LOCATION were calculated for component SCP5. Neither the main effects (GROUP, ORDER) nor any of the interaction terms were significant. The largest effect was observed for the interaction ORDER \times LOCATION ($F(44,1012) = 1.518$, $P = 0.15$). All other interactions had P values >0.30 .

3.3. LORETA analyses

The grand mean (groups pooled) of the N1 component revealed extended activity in posterior brain regions, with the global maximum being localized in medial parietal lobe (precuneus, BA 7, Talairach coordinates of the

maximum: $x = -3$; $y = -74$; $z = 36$). Additional local maxima were observed in occipital and temporal areas (see Fig. 5 and Table 2). As for the MRP component, the global current density maximum was located in medial frontal cortex (-3 , -11 , 64 ; BA 6, supplementary motor area SMA), and clear lateralization of activity was observed in lateral premotor cortex (lateral BA 6, -45 , 3 , 50 ; current density of corresponding left and right activity clusters $0.11 \mu\text{V}/\text{mm}^2$ vs. $0.05 \mu\text{V}/\text{mm}^2$, respectively) and in left inferior parietal lobule (-45 , -46 , 50 , BA 40). Grand mean averages of SCP2 to SCP5 revealed a very similar network of clusters for all components, with activity being dominantly localized in areas responsible for higher-order visual and spatial processing. In all components, the global maximum of activity was located in a large cluster extending from middle temporal to middle occipital gyrus (right BA 39/BA 19; Talairach coordinates of maximum for SCP5: 46 , -47 , 15). The second highest maximum was located in precuneus (-3 , -74 , 36 , BA 7), and the third highest activity was located in SMA (-3 , -11 , 64 , medial BA 6). Additional activity clusters (see Table 2) were identified around the border of middle temporal and occipital lobe (BA 37, extending into fusiform gyrus; BA 39), occipital cortex (BA 17 and BA 19), inferior parietal lobule (BA 40) and middle frontal gyrus (BA 9 and BA 10). When groups were compared using SnPM, no significant difference was obtained for any of the four SCP components, even when the significance threshold was lowered to a value of $P \leq 0.20$.

4. Discussion

The aim of the present study was to confirm the finding [56] that subjects with higher visuo-spatial ability show less

Table 2

Anatomical area, Talairach coordinates, and Brodmann area of grand mean activity clusters with maxima $\geq 0.03 \mu\text{V}/\text{mm}^2$ for component SCP5 and $\geq 0.01 \mu\text{V}/\text{mm}^2$ for component N1

	Anatomical area	x	y	z	Brodmann Area	Current density ($\mu\text{V}/\text{mm}^2 \times 10^{-2}$)
N1	Precuneus	-3	-74	36	7	1.40
	Cuneus	4	-81	8	17	1.37
	Middle temporal gyrus	46	-74	15	39	1.25
	Middle temporal gyrus	-45	-74	15	39	1.08
	Precuneus	-3	-60	57	7	1.07
	Middle temporal gyrus	53	-53	-13	37	1.02
SCP5	Middle temporal gyrus	46	-74	15	39	4.10
	Precuneus	-3	-74	36	7	3.95
	Medial frontal gyrus	-3	-11	64	6	3.83
	Middle temporal gyrus	53	-53	-13	37	3.66
	Middle temporal gyrus	-45	-74	15	39	3.41
	Inferior parietal lobule	-45	-46	50	40	3.41
	Precuneus	-10	-53	64	7	3.25
	Cuneus	4	-81	8	17	3.17
	Middle frontal gyrus	-31	38	36	9	3.09
	Middle frontal gyrus	-38	52	8	10	3.7
	Inferior parietal lobule	39	-46	50	40	3.07
	Middle occipital gyrus	-31	-88	8	19	3.04

cortical activity during processing of a visuo-spatial imagery task than subjects with lower ability. In addition, we intended to extend this finding by recording SCPs with higher spatial resolution, and by applying a source localization method to identify the cortical generators of individual differences. In contrast to our expectations, no activity differences between groups could be found. However, results for the whole sample are well in line with evidence concerning the functional neuroanatomy of spatial cognition and visuo-spatial imagery (e.g., [32,52]).

4.1. Topography and tomography of visuo-spatial processing

Topographic and tomographic analyses revealed that task processing evoked activity in a widely distributed network of brain areas. This network was dominated by activities in extrastriate areas of the dorsal and ventral stream (parietal and temporal lobes, respectively). Additional activity was found in medial premotor cortex, as well as in occipital, temporal and prefrontal cortical areas. It was expected that the spatial transformations (mental rotation/tilting) required by 3 DC items predominantly activate areas of the dorsal visual stream (superior parietal lobe). Ventral stream activity (inferior and middle temporal gyrus) was also expected, reflecting perception and representation of the objects on the cubes' faces. Premotor areas such as SMA and lateral premotor areas are known to contribute to the imagined rotation of graspable objects [47,54]. Such an imagined (or mental) rotation was also required by the task material we used. In general, the inverse solution of LORETA provided valid results. Except for one subject who was excluded from the analyses, the N1 component was correctly localized to cortical areas involved in visual perception. Localization of the MRP component additionally supported the validity of LORETA: The current density maximum was localized to SMA, and clearly left-lateralized activity was obtained in lateral premotor areas (lateral BA 6). Specific support for the validity of the present results can also be derived from another study by our group [32] in which we assessed neural activity during processing of 3 DC-derived items via a combination of fMRI and SCPs (in good performers only). Time-courses and topography of SCP maps of that study were virtually identical to those of the present study. Notably, LORETA identified activity in similar areas as fMRI. The main finding of fMRI was a large activity cluster in bilateral parietal cortex, with the maximum located in superior parietal cortex (BA 7). Additional activity was identified in occipital cortex (BA 18 and BA 19), dorso-lateral prefrontal cortex (BA 9/46), insular cortex, and in medial and lateral premotor areas (lateral and medial BA 6). LORETA also revealed activity in the parietal lobe (though with a more posterior maximum as fMRI), as well as in occipital cortex and in SMA (see Fig. 5 and Table 2). The most obvious difference to fMRI results is the localization of maximal current density in inferior and middle temporal cortex. One

reason for this discrepancy might be that the whole epoch from task presentation until response was modeled in the fMRI analyses. In contrast, LORETA exploited the higher temporal resolution of SCPs by calculating source localizations at specific earlier latencies. At these latencies, object encoding (i.e., analysis of the objects on the cubes' faces) is more dominant. This probably results in higher activity in ventral stream areas representing "what" rather than "where" information processed by parietal areas [53].

4.2. Individual differences

While brain activity of the whole sample was well in line with our hypotheses and former results, neither the topographic analysis of SCPs nor LORETA revealed differences in brain activity between groups. No significant correlation between SCPs and performance measurements (median response time and percentage correct) was obtained either. Note, though, that a number of prerequisites for observing ability-related differences has been met. First, pre-selection using a valid and reliable psychometric measure yielded groups considerably differing in their ability to solve the task used in the EEG experiment. The success of this procedure is also supported by distinct differences in performance measurements. Second, the experimental design we implemented is particularly valid to investigate individual differences in brain activity, since identical cognitive processes were required in the EEG experiment and in the determination of subjects' abilities. This is in contrast to most other studies of the neural efficiency phenomenon. In most of these studies, psychometric intelligence is correlated with brain activity during processing of tasks not requiring the same cognitive operations as those required by the intelligence measurements. Finally, since individual differences in brain activity seem to be more consistent in male samples, we investigated only male subjects.

Data quality, sample size, differences in verbal intelligence, time pressure, and training effects do not provide valid explanations for the absence of individual differences in our replication. Data quality was high and group-independent results were in line with a number of former studies. Single outliers also did not "contaminate" the grand mean results since all topographies and tomographies were individually validated, with components N1 and MRP serving as sensory and motor "gold standards" for which clear hypotheses concerning brain activity existed. Based on this validation, only one subject had to be excluded from the analyses.

While sample size always is a relevant factor in between-subjects designs, it does not explain the lack of significant differences in the present study. SCPs of the two groups were virtually undistinguishable, and even contrasting individual electrodes did not reveal any relevant (nor significant) activity difference (see Fig. 4). In order to get an approximation of the power in the present analyses, we performed a "post hoc" power analysis combining the data from [56] and

the sample size of the present study. This analysis was performed using the mean group difference at electrode Cz' of [56] (since the highest difference between groups was observed at this electrode in [56]), group-specific standard deviations of [56], and the final sample size (14 and 11 subjects) of the present study. Type I error was set to 0.05, assuming a one-tailed *t* test for independent samples as the analysis method. The analysis revealed a power value of 0.935, indicating high power in the present analyses.

Several arguments suggest that the difference between groups in verbal intelligence (and the differences in correlations across studies between WPT and 3 DC) also does not provide a good explanation for the lack of individual differences. First, no significant or relevant correlations between WPT scores and SCPs were obtained. Second, although statistical analysis indicated a significant difference between scores, this is rather due to very little statistical variation of the group scores than to a relevant difference in mean WPT scores. In addition, it should be noted that all subjects in this study as well as in [56] showed scores in the upper percentiles of the WPT measurement range (which ranges from 0 to a maximum of 42 points). Thus, the very small mean difference of only 1.6 points should not be considered a *relevant* difference—in particular when comparing this small difference with the large difference in 3 DC scores resulting from pre-experimental selection. Third, WPT scores indicate higher general intelligence (in fact, WPT scores have been used in this study to obtain a rough estimate of general IQ). According to the neural efficiency hypothesis, this should have resulted in an even *larger* group difference in brain activity in the present study, where good performers showed significantly higher WPT scores. However, the opposite was the case, since the highest correlation at electrode Cz' was positive and thus indicated that higher WPT scores correlated with higher brain activity over the corresponding region. Therefore, we consider it highly unlikely that the difference in WPT scores between studies can explain the lack of brain activity differences in the present study.

Since time pressure affects individual differences in SCPs [30], it might be speculated that such time pressure was exerted upon subjects. We concede that experimenter effects cannot be completely eliminated in EEG experiments since they always require some kind of interaction between experimenter and subjects. However, the same standardized written instruction as in [56] was used, explicitly giving subjects ample time to solve each task. Also, the experimenters were well aware of the fact that time pressure affects results. In addition, response times in the present study were generally about three s longer than in [56]. Training effects can also be excluded as an explanation, since the separate analysis of trials collected in the first and the second block of the experiment revealed no significant differences.

Despite a number of precautions has been met, the results of the present study are inconsistent with earlier findings confirming the neural efficiency hypothesis, as well as with

the study we attempted to replicate [56]. None of the just now discussed confounds can explain this discrepancy. However, currently available empirical and theoretical evidence suggests two additional accounts for the differences between our own and former results. These accounts are necessarily speculative, and mutually non-exclusive. The first account refers to the type of cognitive processing required by the tasks used in our study. 3 DC items require extended visuo-spatial processing, but have comparably low working memory and executive control demands [13]. Most studies revealing robust support of the neural efficiency hypothesis used tasks predominantly tapping into substantial memory, attention and executive control demands. For example, Neubauer's group [16] recently confirmed the neural efficiency hypothesis using a variety of short-term and working memory tasks. Other groups (e.g., [21,26]) predominantly report inverse relationships between brain activity and ability when using reasoning tasks (assessed by, for example, the Advanced Progressive Matrices test APM; [46]). Reasoning tasks invoke substantial working memory and executive function demands, and reasoning tests are regarded as a measure of general fluid intelligence (gF). Along with metacognition (the ability to reflect upon ongoing mental processes), executive control of working memory is thought to be an important component of gF [6,17]. Recent analyses suggest that the negative ability–activity relationship is more robust when test scores of fluid rather than of crystallized intelligence are used [16,35]. With respect to the 3 DC, estimates of the common variance of a reasoning test of fluid intelligence [11] and the 3 DC range – depending upon the analysis approach – from 20 to 50% [2,14]. It might thus be hypothesized that the neural efficiency phenomenon is more robust (and, thus, more likely to be replicated) with tasks having high loadings on fluid intelligence. This increased robustness is most likely due to the higher memory and executive function demands of tests of fluid intelligence.

Another explanation for the difference between studies is related to the task solving strategies used by our subjects and those of [56]. A number of functional neuroimaging studies (e.g., [27,28]) suggests that subjects can employ at least two dominant strategies when solving mental rotation tasks: a visuo-perceptual strategy and a visuo-motor strategy. While the former mainly relies upon processing of three-dimensional visual information in more caudal higher-order visual areas (such as the posterior inferior parietal sulcus and parieto-occipital sulcus ([27,28]), the visuo-motor strategy predominantly involves areas involved in action planning and action simulation (such as the superior parietal lobe, and, most notably, lateral premotor areas such as the dorsal part of lateral premotor cortex). It has been shown that strategy selection can be influenced by the (implicit or explicit) instruction of subjects, as well as by their gender and/or ability. Kosslyn and colleagues [28] demonstrated using PET that differences in the (implicit) instruction of subjects resulted in activity of different neural

networks. This was interpreted as a difference in processing strategies evoked by the different instructions (see also [57]). Using fMRI, Jordan et al. [27] revealed that men and women who have been matched for their performance level used a vastly overlapping network of brain areas when solving different types of mental rotation tasks. However, according to the authors' interpretation, men seemed to rely more upon a more basic visuo-perceptual network (with higher activity in left inferior parietal and in right parieto-occipital sulcus), while women's activity was more in line with a visuo-motor strategy since they showed higher activity than men in superior parietal and dorsal lateral premotor areas. Note that men also showed higher activity in left primary motor cortex, which might be related to explicit motor imagery, though. Substantial differences between men and women were also found in [52], with men showing more parietal activity and women showing higher activity in right inferior frontal gyrus. However, performance levels between males and females differed, and differences in brain activity might thus have been related to differences in task-specific abilities.

This cumulating evidence about two dominant processing strategies made us hypothesize that different processing strategies have also been used by the subjects in our study and in [56]. Closer inspection of the current source density (CSD) maps indicates that this might have been the case. Subjects with high and low abilities in the present study as well as subjects with low abilities in [56] showed a CSD topography indicating substantial activity in medial and lateral premotor areas (see Figs. 3, and 4 of [56])—with the higher resolution of the present study allowing identification of bilateral and clearly separated current sinks over the lateral fronto-central scalp region. In contrast, subjects with high ability in [56] only show a (rather weak) current sink over the medial fronto-central scalp, and no substantial activity over the lateral fronto-central scalp region. In addition, CSD maps indicate a more posterior activity maximum in those subjects. This suggests that occipital–parietal activity was generated in more inferior and posterior cortical areas than parietal activity of the other subject groups. The latter show CSD sinks with a more dorsal–anterior focus, indicating activity in superior parietal lobe. Except for the primary motor activity, this pattern of results resembles the one observed for males and females in [28]. It might thus be tentatively concluded that the main difference between studies is the predominant use of a visual–perceptual processing strategy in the group of subjects with high ability in [56], while both groups of the present study and the subjects with low ability in [56] seemed to predominantly rely upon a visuo-motor strategy. It should also be noted that although differences in task processing strategies are generally reduced with Rasch-homogeneous task material such as the 3 DC, they can never be completely excluded in any kind of cognitive task.

On a more general level, our data suggest that the neural efficiency hypothesis seems to hold only when subjects use

differing (and possibly more or less efficient) task solving strategies, and/or when tasks requiring substantial memory and executive function loads are used. Future studies should thus attempt to use tasks having different loads on memory and executive function, and group comparisons should be controlled for the use of different processing strategies.

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