Neurophysiological factors in human information processing capacity


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Summary
What determines how well an individual can manage the complexity of information processing demands when several tasks have to be executed simultaneously? Various theoretical frameworks address the mechanisms of information processing and the changes that take place when processes become automated, and brain regions involved in various types of information processing have been identified, as well as sequences of events in the brain. The neurophysiological substrate of human information processing capacity, i.e. the amount that can be processed simultaneously, is, however, unresolved, as is the basis of inter-individual variability in capacity. Automation of cognitive functions is known to increase capacity to process additional tasks, but behavioural indices of automatization are poor predictors of processing capacity in individuals. Automation also leads to a decline of brain activity in the working memory system. In this study, we test the hypothesis that processing capacity is closely related to the way that the brain adjusts to practice of a single cognitive task, i.e. to the changes in neuronal activity that accompany automatization as measured with functional MRI (fMRI). Using a task that taxes the working memory system, and is sensitive to automatization, performance improved while activity in the network declined, as expected. The key finding is that the magnitude of automatization-induced reduction of activity in this system was a strong predictor for the ability to perform two different working memory tasks simultaneously (after scanning). It explained 60% of the variation in information processing capacity across individuals. In contrast, the behavioural measures of automatization did not predict this. We postulate that automatization involves at least two partially independent neurophysiological mechanisms, i.e. (i) streamlining of neuronal communication which improves performance on a single task; and (ii) functional trimming of neuronal ensembles which enhances the capacity to accommodate processing of additional tasks, potentially by facilitating rapid switching of instruction sets or contexts. Finally, this study shows that fMRI can provide information that predicts behavioural output, which is not provided by overt behavioural measures.

Keywords: working memory; information processing capacity; fMRI; individual variation; multitasking; automatization

Abbreviations: ACC = anterior cingulate cortex; AUT = automatization; CT = control task; DLPFC = dorsolateral prefrontal cortex; fMRI = functional MRI; NT = novel task; PT = practised task; WM = working memory

Introduction
Humans are generally not very good at conducting multiple tasks simultaneously. Driving a car, for instance, becomes more difficult when the driver conducts a demanding telephone conversation. Several factors are known to affect multitasking ability, such as experience with the individual tasks (e.g. driving) and task characteristics. These are, however, not sufficient to explain why some individuals are better at multitasking than others (Richardson, 1996). Interference of multiple tasks is generally attributed to competition of the information processing requirements of each task for the limited capacity of working memory (WM), the central processing system (Baddeley et al., 1974; LaBerge...
et al., 1974; Shiffrin et al., 1977; Logan 1988; Shallice et al., 1996; Garlick, 2002). Multitasking typically becomes easier when the tasks are practised, as has been shown with measures of performance (reduction of reaction time and errors). One would expect that individuals who benefit the most from practice would also perform better at multitasking, but there is surprisingly little evidence from psychometric studies in the literature to support this.

Functional neuroimaging has elucidated some aspects of information processing, including multitasking (e.g. D’Esposito et al., 1995; Passingham, 1996; Klingberg, 1998; Bunge et al., 2000). Studies involving good and bad performers, or patient populations, provide evidence that brain activity characteristics and performance are correlated when subjects perform a WM task (e.g. Callicott et al., 1999; Rypma et al., 1999), by using functional MRI (fMRI) to assess the neurophysiological correlates of brain functions on an individual basis (Ramsey et al., 1996). The underpinnings of information processing capacity have, however, received little attention, and call for another approach. In this study, we utilize the potential of fMRI to investigate the neurophysiological mechanisms underlying individual variability in processing capacity.

Two main theoretical frameworks provide a basis for addressing the neurophysiological basis of information processing capacity, i.e. one that addresses executive functions, and one that addresses learning. The core feature of executive functions is generally conceptualized in terms of a WM system that regulates the flow of information involved in a given task or context (i.e. the nature of information and of the relevant end product of processing). Theories on WM stress the significance of a central executive (Baddeley and Hitch, 1974) or supervisory attention system (Shallice and Burgess, 1996) for the limitations in processing capacity. The existence of such a system, and its role in multitasking, has been corroborated by means of primate (Goldman-Rakic, 1995) and neuroimaging techniques (D’Esposito et al., 1995; Klingberg, 1998; Adcock et al., 2000; Bunge et al., 2000). Most of these studies (except for that of D’Esposito et al., 1995) suggest that there are multiple, albeit overlapping, systems for information processing (depending on stimulus type and features), and that there is no region that is specifically associated with multitasking. Rather, different tasks appear to compete for the same set of regions, including dorsolateral prefrontal cortex (DLPFC), anterior cingulate cortex (ACC) and parietal cortex, indicating that these regions may play an important role in the limited capacity to process information. The early works of Shiffrin and Schneider (1977), Logan (1988) and LaBerge and Samuels (1974) emphasized the significance of automatization of cognitive processes for processing capacity. Automatization follows when certain types of tasks are practised, and leads to a plastic change in the way information is processed, resulting in two measurable behavioural changes: performance becomes more accurate and faster, and it becomes easier to conduct additional tasks concurrently. Shiffrin and Schneider (1977) argued that processing capacity may be determined by the ability to automate cognitive processes by means of which demands on the limited resources are reduced. Neurophysiological studies on automatization indicate that it leads to a reduction of the spatial extent of brain activity (Garavan et al., 2000; Jansma et al., 2001), and to enhanced connectivity between task-specific brain structures (Buchel et al., 1999). Similar effects have been described in non-human primate studies on perceptual or motor systems (for a review see Gilbert et al., 2001), but the underlying mechanisms appears to apply to WM systems as well (e.g. Rainer et al., 2000). A recent study with schizophrenic patients in which a dissociation between performance and reduction of brain activity in an automatization paradigm was presented (Jansma et al., 2001) generated the notion that the effect of practice on extent of brain activity may be independent of the effect on speed and accuracy of processing.

In this study, we test the hypothesis that information processing capacity is determined by the neurophysiological adaptation in the WM system during automatization. The experiment involved three parts, i.e. a training session to accomplish automatization of cognitive processes involving WM, an fMRI scanning session to acquire neurophysiological measures of automatization, and a dual-task cognitive test session to assess information processing capacity. To measure automatization, we used a task based on Sternberg’s item recognition paradigm (Sternberg, 1966; Jansma et al., 2001). This task (denoted AUT) involves memorizing sets of consonants, and deciding whether subsequently presented letters belong to the set or not. The task has two versions, i.e. a practised version with a fixed set (PT) and a novel version with a variable set (NT) (Fig. 1). The second task, used during the dual-task session, was an auditory tone discrimination task, where subjects had to detect and count brief tones that differed in pitch from a baseline tone. This task addresses
Areas are obtained from the location of voxels with the highest $Z$-value. MNI-305 coordinates are shown for the five regions where activity during NT is significantly increased compared with CT. The coordinates $x$, $y$ and $z$ represent the location of the voxels with the highest $Z$-value in the group map. Corresponding names and Brodmann areas are obtained from the location of voxels with the highest $Z$-value.

### Table 1: Regions of working memory-related brain activity

<table>
<thead>
<tr>
<th>Region</th>
<th>Brodmann area</th>
<th>Number of voxels</th>
<th>$x$</th>
<th>$y$</th>
<th>$z$</th>
<th>Maximum Z-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left dorsolateral prefrontal cortex (L-DLPFC)</td>
<td>9/46</td>
<td>181</td>
<td>−41</td>
<td>5</td>
<td>31</td>
<td>9.23</td>
</tr>
<tr>
<td>Left superior parietal cortex (L-SPC)</td>
<td>7</td>
<td>157</td>
<td>−33</td>
<td>−62</td>
<td>47</td>
<td>8.36</td>
</tr>
<tr>
<td>Anterior cingulate cortex extending into superior frontal gyrus (ACC)</td>
<td>24/6</td>
<td>89</td>
<td>−5</td>
<td>5</td>
<td>59</td>
<td>8.73</td>
</tr>
<tr>
<td>Right superior parietal cortex (R-SPC)</td>
<td>19</td>
<td>49</td>
<td>34</td>
<td>−66</td>
<td>43</td>
<td>7.58</td>
</tr>
<tr>
<td>Left fusiform gyrus (L-FUG)</td>
<td>37</td>
<td>16</td>
<td>−37</td>
<td>−50</td>
<td>−20</td>
<td>4.96</td>
</tr>
</tbody>
</table>

WM, while avoiding interference with visual processing and response generation. A measure of information processing capacity was obtained with a dual-task paradigm, with the two described tasks. Dual tasks are often used to assess processing capacity, which is inferred from the drop in performance when comparing execution of a single task with execution of the two concurrent tasks (Fisk et al., 1987; Baddeley et al., 2001; Logan et al., 2001). The improvement of performance on the AUT and the change in brain activity following practice were compared with the negative effect of adding a second task on performance of the first task.

### Methods

#### Subjects

Twelve right-handed healthy volunteers (seven male, five female, mean age 24 years) participated in this fMRI experiment after signing an informed consent approved by the Ethics Committee of the University Medical Center of Utrecht.

#### Tasks

The AUT task has the following basic format (see also Jansma et al., 2001). A set of five consonants is shown for 5340 ms (the target set). After this, a series of 10 consonants is displayed in sequence (Fig. 1). A new set of five consonants is then shown, followed by 10 new trials presented with an interval of 2670 ms. Subjects were instructed to memorize the target set and subsequently press a button as quickly as possible when a consonant belonged to the target set (50% were targets). Two experimental tasks were administered, which differed only with regard to the target set(s): a novel task (NT) and a practised task (PT). In the PT, one and the same set was used repeatedly. In the NT, the composition of the target set was changed after every run of 10 trials. The target set and set of non-targets for the NT were chosen from the 10 remaining consonants that were not used for the PT. During the training session, which lasted 21 min, only the PT was presented, in five series of 100 stimuli. During and after scanning, both tasks were presented, in eight epochs of 10 stimuli each. In the scanner, an additional reaction time control task (CT, same numbers of epochs and stimuli) was included, during which subjects had to press the button as quickly as possible when the symbol $\leftrightarrow$ appeared (i.e. with a random stimulus interval with a mean of 5340 ms), as well as rest periods of equal epoch duration. The sequence of the three tasks and rest periods was randomized. Reaction time for all correctly identified targets and accuracy for all stimuli were measured. The tasks contained equal numbers of targets. The critical feature of this experimental design is that it measures automatization, i.e. the difference between NT and PT, without the complication of learning effects within the scan session (Jansma et al., 2001).

The second task, presented during and after scanning, involved detection of tones with a higher or lower pitch than the baseline tone. The difference in pitch was determined individually before the experiment, by adjusting it until the subject detected 80% of the deviant tones. The 200 ms tones (16% deviants randomly distributed) were presented bi-aurally with a variable interstimulus interval (mean 1.0 s). During scanning, subjects responded to deviant tones (to verify that the attentional demand was equal for all subjects, i.e. ~80% correct) in epochs of 29 s, alternated with resting epochs of equal duration. The tone task was administered after the AUT task in the scanner, not simultaneously. During the dual-task session, subjects had to count the deviant tones silently, and report the count after each series of 25 stimuli (corresponding to the 10-trial epochs of the AUT task), instead of giving a motor response for each target, to prevent interference with the motor response to the AUT task. In all tasks after scanning, the inter-trial interval for the AUT target was 2500 ms, with a stimulus duration of 1500 ms. Due to different stimulus presentation rates and durations for the two tasks, tones and AUT stimuli frequently coincided. However, only on three occasions did a deviant tone and an AUT target coincide (i.e. three of the 64 deviant tones coincided with the onset of AUT target stimuli). Thirteen deviant tones occurred in the first 1000 ms of AUT targets (virtually all AUT target responses occurred within that period). Given that the deviant tones required no response, target coincidences most probably did not cause interference of response generation. The stimulus sequence in the dual task is shown in Fig. 2.
fMRI data acquisition and analysis

For fMRI, a three-dimensional technique was used (navigated PRESTO) that measures BOLD signal changes (Ramsey et al., 1998). For the AUT task, a single run of 384 scans was acquired over a period of 17 min (for scan parameters see Jansma et al., 2001). Scanning started 5340 ms before the task, to compensate for the delay in onset and peaking of the BOLD response. Each epoch (target set plus 10 trials) spanned 12 scans and lasted 32 s. Data analysis consisted of three stages. First, after motion correction, statistical activity maps were generated for each subject, for each of the three tasks (NT, PT and CT each compared with the rest condition, excluding scans obtained during presentation of the letter sets) by means of multiple regression (Worsley et al., 1995). Secondly, these maps were smoothed (full width half maximum; FWHM 8 mm) and normalized into standard MNI-305 space (Collins et al., 1994), and were analysed for the whole group, contrasting the NT with the CT and using Z-statistics (for details see Jansma et al., 2001). This contrast eliminated activity that was not directly involved in WM, and yielded several regions of activity at a threshold of Z = 3.88 (P < 0.0001 uncorrected) with a cluster size of at least 10 voxels. Thirdly, for each of the active regions, a mean activity score was obtained for NT and PT for each subject, by averaging Z-values across all contained voxels for each subject. These final variables were entered into the analysis of variance (ANOVA) for repeated measurements with practice (NT and PT) and region (listed in Table 1) as within-subject factors. The predictive value of practice-induced changes in brain activity for processing capacity was tested by adding the increase in errors on the AUT (dual versus single task) as a covariate.

For the tone task in the scanner, the same scan parameters were used as for the AUT task, but with 26 slices. Activity was assessed by contrasting scans acquired during the tone task with scans acquired during rest periods of equal duration. Data analysis was similar to that of the AUT task (t > 3.88, cluster size = 10 voxels). This part of the scan session only served to locate the brain regions involved in the tone task.

Results

Automatization and the working memory system

To identify the WM system, individual activity maps contrasting the NT with the CT were combined into a group map. Five regions in frontal, parietal and visual cortex

Fig. 3 Brain regions involved in working memory. The areas involved in working memory (in colours) are superimposed on the averaged anatomical image. Five of the 30 slices are shown, for display of the five regions that emerged from the group contrast between NT and CT, i.e. left fusiform gyrus (I-FuG, green), left superior parietal cortex (l-SPC, dark blue), right superior parietal cortex (r-SPC, pink), left dorsolateral prefrontal cortex (l-DLPFC, red) and anterior cingulate cortex extending into superior frontal gyrus (ACC, light blue). The numbers above the slices indicate the MNI-305 Z-coordinates. Slices are in radiological orientation (left side is right hemisphere, and vice versa). In these five regions, brain activity declined with practice. The bars in the graph represent levels of activity during NT and PT, relative to the rest state. Details of these regions are listed in Table 1. Bars on the right represent brain activity levels averaged across the five regions. Activity is given in arbitrary units (a.u.). *Analysis of variance, main effect of practice P < 0.001.
reached significance (Table 1, Fig. 3), and were used for further analyses. All subjects showed an improvement in reaction time \([t(11) = 6.1, P < 0.001]\) and error rate \([t(11) = 2.4, P = 0.03]\) with practice (NT versus PT), confirming that automatization had occurred (Shiffrin and Schneider, 1977). ANOVA of fMRI data revealed an overall decrease of activity due to practice, NT versus PT \([F(1,10) = 176.4, P < 0.001]\), that did not differ between the regions (interaction \(P > 0.4\)), replicating earlier studies of Jansma et al. (2001), but also of others who used a different paradigm (Buchel et al., 1999; Garavan et al., 2000). Signal reduction in the group-wise analysis was most probably due to a decrease in the extent of active brain tissue (i.e. neurophysiological ‘trimming’), as the numbers of active voxels within the five regions, obtained from the individual subject’s unsmoothed activity maps, was reduced by 77% (NT versus PT). Practice-induced reduction of the spatial extent of brain activity has also been reported in other studies (Buchel et al., 1999; Gilbert et al., 2001). There was no association between improvement in reaction time (NT versus PT) and magnitude of activity reduction, either over all regions \([F(1,10) = 0.48, P = 0.50]\) or in any particular region [interaction \(F(4,40) = 0.51, P = 0.7\)], confirming the previous study (Jansma et al., 2001). Non-human primate studies provide evidence that improved performance is associated with enhanced, more selective and sensitive responding of particular neurons to stimulus presentation (Rainer and Miller, 2000; Gilbert et al., 2001), which may go unnoticed in the fMRI signal if metabolic rate does not change. The activity pattern of the tone task overlapped with that of the AUT task only in the ACC and left DLPFC (Fig. 4).

**Fig. 4** Overlap of brain regions activated by the automatization and the tone task. Composite brain activity maps for the AUT task and for the tone task. The regions that were active during the AUT task are shown in red (also shown in Fig. 2) and those active during the tone task in blue. Overlap (yellow) was found exclusively in the I-DLPFC and the ACC. Regions activated additionally during the tone task included right operculum/insula, left and right auditory cortex and left anterior prefrontal cortex. The numbers above the slices indicate the MNI-305 Z-coordinates. Slices are in radiological orientation (left side is right hemisphere, and vice versa).

**Fig. 5** Performance on the tasks. The results are shown for the AUT task under three conditions: in the scanner (SCAN), after scanning when only the AUT task is performed (SINGLE) and when the second task is added (DUAL). The graphs display reaction time to targets (only correct responses), and the numbers of errors (missed targets plus responses to non-targets). Performance on an additional reaction time control task (CT) administered in the scanner is also shown as a reference for the extent of practice. \(t\) test \(P < 0.05, *P < 0.001, **P < 0.001.\)

**Dual-task performance**

After the scan session, the AUT task was repeated, once alone and once simultaneously with the tone task. The effect of the tone task on performance on the AUT task reflects processing capacity of the WM system. ANOVA with practice (NT versus PT) and task (single versus dual task) as within-subject factors revealed that reaction time was not affected by the additional task (main effect \(P = 0.30\) and interaction \(P = 0.8\); Fig. 5). This indicates that the two tasks did not compete for perceptual processing or motor response generation (Fisk et al., 1987). Error rate, however, increased significantly
during both NT and PT \( [F(1,11) = 19.4, P = 0.001; \text{Fig. 5}] \). The increase in error rate was not significantly different for NT and PT (interaction \( P = 0.20 \)), and therefore the mean error rate was used for further analysis. The absence of a differential effect on NT and PT is most probably due to the limited period of practising (see Schneider et al., 1982). The fact that reaction time on the PT was longer than on the (conceptually highly automated) CT indicates that complete automatization was not achieved yet. Importantly, the practice-induced improvement in performance during the AUT task (in any of the sessions) did not correlate with the drop in performance during multitasking \( (P > 0.4, \text{see also Fig. 6A and B}) \), indicating that the behavioural measure of automatization did not predict information processing capacity.

To examine whether errors on the AUT task were associated with deviant tones, we compared the number of errors (misses and false alarms) that occurred within a window of 3 s around deviant tones with the number of errors that would fall within those windows by chance, for each subject separately (estimation was based on the error rates for each subject). The difference was significant (Wilcoxon signed rank test for two related samples, 12 subjects, \( P = 0.026 \)), indicating that more AUT errors in the dual task occurred within 1.5 s of a deviant tone than would be expected by chance.

**Working memory activity and dual-task performance**

Finally, the fMRI data were compared with error rates on the AUT task (dual minus single task) in an ANOVA with the latter as covariate. The covariate (error rate increase) interacted significantly with practice \( [F(1,10) = 15.2, P = 0.003] \). The effects of practice and error rate increase did not vary significantly across regions (interaction effects, \( P > 0.4 \)). Across subjects, the mean change in signal due to practice (averaged across regions) was negatively correlated \( (r = -0.78, P = 0.003) \) with the error rate increase, indicating that a large decrease of activity predicted a small increase in error rate in the dual-task session, and vice versa (Fig. 6C). Given that the practice period was relatively brief, and that complete automatization was not achieved in this paradigm, individual differences in brain activity reduction may reflect differences in the duration of practice that is required to achieve full automatization. This interpretation is supported by the fact that when reduction of brain activity was expressed as the proportion relative to the difference between NT and CT \( [(\text{NT} - \text{PT})/(\text{NT} - \text{CT})] \), the correlation was still significant \( (r = -0.58, P = 0.05) \).

**Discussion**

The results show that practice-induced reduction of brain activity in the WM system, which we argue reflects neurophysiological trimming, predicts the difference in performance when comparing a single task with a dual task. As dual-task paradigms are thought to assess information processing capacity (Fisk et al., 1987; Baddeley et al., 2001; Logan and Gordon, 2001), this finding may be relevant for the mechanisms by which the brain copes with multiple simultaneous tasks. The effect of trimming on processing capacity may be interpreted in terms of a practice-induced disengagement of neurons whose action is not relevant for mapping the correct response onto the given stimulus (Buchel et al., 1999; Rainer and Miller, 2000; Gilbert et al., 2001). When the task is novel, i.e. when direct coupling between a stimulus and response has not, or cannot, be achieved, it appears that a relatively large number of neurons is recruited to process multiple features of the stimulus (Rainer and Miller, 2000; Gilbert et al., 2001). When, however, the coupling is made possible by the nature of the task, and is achieved by means of practice, it may be that only those neurons whose action is necessary for generation of the correct response remain involved, whereas those whose action is irrelevant disengage from stimulus processing (Gilbert et al., 2001). The present study provides new evidence that the behavioural significance of this postulated disengagement may relate to a liberation of processing resources.

The dual task itself provides some clues about how multitasking is facilitated by practice of one task. The dual task requires continuous monitoring of visual and auditory stimuli, each associated with a different context, and involves frequent switching of the instruction sets. Most of the AUT errors in the dual task occurred within 1.5 s of a deviant tone, indicating that these tones caused a switch of contexts that resulted in more errors on the AUT task. If indeed the dual task is processed in a serial manner, then it seems plausible that the ability to disengage neurons rapidly from a task benefits performance by reducing switch cost (Kimberg et al., 2000; Baddeley et al., 2001). We argue that the ability to disengage neurons from the AUT task in some way relates to the ability to switch from one context to another, which could explain the relationship between trimming during practice, and information processing capacity as measured with dual-task performance. This is supported by the fact that both tasks activated, and potentially relied on, the ACC and left DLPFC regions (Fig. 4), reflecting competition for the WM system that coordinates action within certain contexts (Klingberg, 1998; Baddeley et al., 2001; Bunge et al., 2000). Given that the dual-task paradigm required rapid switching between contexts, the (individual-specific) degree or speed of trimming may facilitate dual tasking by enabling rapid reassignment of the neuronal resources to either task.

The finding that the degree to which activity is reduced does not correlate with improvement of performance on the AUT task suggests that neurophysiological trimming does not affect the ‘streamlining’ of stimulus–response mapping that follows practice. Streamlining refers to the enhancement of efficiency, and the reduction of processing time, of judging whether or not a stimulus is a member of the target set. The
underlying mechanism is thought to involve either a shift from computational mapping to retrieval from long-term memory (Strayer et al., 1990), or enhancement of communication within one and the same network (e.g. LaBerge and Samuels, 1974). The present study does not distinguish between these two mechanisms (the hippocampus, associated

Fig. 6 Measures of automatization and dual-task performance. The graphs show the relationship between measures of automatization. On the vertical axis, the increase in the number of errors on the AUT task due to the additional task is shown. A large value reflects a large negative effect of the second task on AUT performance (errors during the dual task minus errors during the single task). (A) The horizontal axis represents the difference in errors (misses and false alarms) on the single AUT task (NT minus PT). There is no correlation with dual-task performance. (B) The difference in reaction time to targets in the single AUT task (NT versus PT) is also not correlated with dual-task performance. (C) The horizontal axis represents the reduction of brain activity in the network (NT minus PT). A larger value reflects a large reduction of brain activity. The graph shows the predictive value of the reduction of brain activity within the working memory network following practice of the AUT task, for the ability to maintain performance when a second task was added (dual task). A large decrease of brain activity predicts a small increase in errors, i.e. a large capacity to accommodate an additional task, and vice versa.
with long-term memory, was not included completely in the imaged brain volume, precluding the possibility of tracking changes in that region), but it does support the notion of a gradual change, as PT still activated the WM system. The principal finding of the present study pertains to the individual differences in the transition from controlled to automated cognitive actions. Whether information processing involves a shift to long-term memory (and accordingly to regions associated with that function) or not is therefore not critical for the objective of the present study. Nevertheless, the question of whether activity shifts after practice is in itself an important one, deserving further research.

The finding that there was no significant difference in the effect of the tone task on NT and PT performance is most likely to be the result of the fact that the practice period was too short to achieve complete automatization (see Schneider and Fisk, 1982). However, the specific combination of tasks for the dual-task paradigm may also contribute. (Schneider and Fisk, 1982). Reaction time on correct responses during the AUT task was not affected by the tone task, and this may be due to the fact that the two tasks did not compete directly for resources associated with stimulus processing (e.g. Fisk et al., 1987). Apparently, there was also no notable competition for maintenance of verbal material (i.e. the target set, and the count of deviant tones). The tasks more probably competed for resources associated with coordination of information within contexts (i.e. executive function, see Della Sala et al., 1995), causing switching between contexts to be the primary source of the dual-task effect. One might expect a stronger differential effect of the second task on performance on NT and PT if both tasks would compete for the same stimulus processing resources, such as modality-specific WM or temporary storage of (encoded) stimulus properties, for instance when the tasks involve processing of different features of the same stimuli (e.g. Strayer and Kramer, 1990) or when stimuli are of the same sensory modality. In that case, a large degree of streamlining might predict a large difference in the effect of dual tasking on the PT versus on the NT, and vice versa. At any rate, the choice of tasks for the dual-task paradigm may have been important for revealing the effect of trimming on processing capacity.

Various groups have also examined associations between brain activity and performance on tasks that involve WM, and report that better performance is associated with more brain activity (particularly DLPFC) (e.g. Brewer et al., 1998; Wagner et al., 1998; Ramsey et al., 2002), although the reverse findings have also been reported (e.g. Rypma et al., 2000). The fact that in the present study improvement of performance is associated with a decline in brain activity does not disagree with those studies, because the experimental design and concepts are quite different. In essence, this study associates the change in activity over time (practice) within subjects with performance on a different (dual) task, whereas other studies associate activity with WM performance directly across subjects. The difference is in fact evident within this study, as we also observed a negative correlation between NT activity in left DLPFC (NT – CT) and number of errors on NT during the scan session (r = −0.85, P < 0.001). However, NT activity was correlated neither with the practice-induced drop in activity (NT – PT), nor with dual-task performance, indicating that NT activity did not predict the neurophysiological effect of practice or processing capacity. Thus, it appears that WM activity predicts performance of tasks that involve controlled processing, but there is little evidence that it can predict effects of practice or processing capacity.

This study confirms our hypothesis that the proficiency of individuals to handle multiple cognitive tasks simultaneously is closely associated with the neurophysiological benefit from practice of a single task. We argue that the reduction of brain activity in the WM system following practice may reflect neurophysiological trimming, which in turn facilitates switching between multiple contexts. Knowing the factors that play a role in this mechanism may prove to be useful in enhancing human cognitive capacities, or in elucidating the bases of cognitive deficits in psychiatric patients. Further research is required to assess what mechanisms are at play in trimming, i.e. whether neurons disengage by themselves, perhaps as a response to unsatisfactory feedback, or whether they respond to top-down regulation by means of active inhibition. Also, further studies are necessary to assess generalizability to other dual-task paradigms, as the present paradigm was specific in terms of different sensory modalities and requiring switching between contexts. Finally, this study shows that fMRI can provide a measure that predicts behavioural output, which is not provided by behavioural measures.

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References


