When two tasks are performed simultaneously, performance often deteriorates, with concomitant increases in reaction time and error rate. Three potential neurophysiological mechanisms behind this deterioration in performance have been considered here: (i) dual-task performance requires additional cognitive operations and activation of cortical areas in addition to those active during single-task performance; (ii) two tasks interfere if they require activation of the same part of cortex; and (iii) cross-modal inhibition causes interference between two tasks involving stimuli from different sensory modalities. Positron emission tomography was used to measure regional cerebral blood flow (rCBF) during performance of an auditory working memory (WM) task, a visual WM task, both WM tasks (dual task) and a control condition. Compared to the control condition, the auditory and visual WM tasks activated sensory-specific areas in the superior temporal gyrus and occipital pole respectively. Both WM tasks also activated overlapping parts of cortex in the dorsolateral prefrontal, inferior parietal and cingulate cortex. There was no separate cortical area which was activated only in the dual task, and thus no area which could be associated with any dual task specific cognitive process such as task-coordination or divided attention. Decrease in rCBF in one WM task did not overlap with the areas of rCBF increase in the other WM task. However, an inhibitory mechanism could not be ruled out, since the rCBF increase in sensory specific areas was smaller in the dual-task condition than in the single-task conditions. The cortical activity underlying WM was to a large extent organized in a non-sensory specific, or non-parallel, way, and the results are consistent with the hypothesis that concurrent tasks interfere with each other if they demand activation of the same part of cortex.

Introduction

Why does performance deteriorate when two tasks are performed simultaneously? Dual-task performance has been studied thoroughly in cognitive psychology, but the neurophysiological basis of the deterioration in dual-task performance remains largely unknown. In this study three different, but not mutually exclusive, hypotheses about the neurophysiological basis for dual-task performance will be considered.

Psychological studies have suggested that dual-task performance demands some cognitive process, such as task coordination, in addition to those required for single tasks (Sverko et al., 1983; Ackerman et al., 1984; Fogarty, 1987). Task coordination per se could require activation of cortical areas in addition to those activated during single-task performance. This is supported by the results of D’Esposito et al. (1995), who found that dual-task, but not single-task, performance activated the prefrontal and cingulate cortices. Suboptimal functioning of brain areas necessary for task coordination could lead to a deterioration in performance during dual-task performance (Baddeley et al., 1986). The single tasks used in the previous dual-task study by D’Esposito et al. (1995) were characterized as not demanding working memory (WM). In the present study we instead used WM tasks as single tasks and tested the hypothesis that concurrent performance of two WM tasks would similarly induce activation of prefrontal and cingulate cortical areas that was not induced by performing either task alone.

Another psychological explanation for dual-task interference is that concurrent tasks interfere with one another because they compete for some limited resource (Broadbent, 1957; Kahneman, 1973; Wickens, 1980; Friedman et al., 1982). A plausible neurophysiological hypothesis is that two tasks which depend on activation of the same part of the cortex at the same time will interfere. A previous study indicated that WM tasks with stimuli from different sensory modalities activate overlapping parts of the cortex (Klingberg et al., 1996). In contrast, it has been suggested that brain activity underlying WM is organized in an entirely sensory specific, or parallel, fashion (Goldman-Rakic, 1988; Wilson et al., 1993), which would imply that overlap in activity cannot be the basis for interference between WM tasks with memoranda of different modalities. In the present study, we tested if WM tasks with memoranda from different sensory modalities produce overlapping activity, since such anatomical overlap could be the source of the interference between the two tasks.

A third hypothesis of dual-task interference was also considered. In tasks requiring selective attention to a sensory modality, the regional cerebral blood flow (rCBF) increases in the part of cortex processing the attribute being attended to. It has also been reported that the rCBF can decrease in parts of cortex processing a non-attended modality (Haxby et al., 1994; Kawashima et al., 1995; Shulman et al., 1997). Such decrease could be due to cross-modal inhibition, which in turn could be a source of interference during dual-task performance. Therefore the present study examined whether or not the decreases in rCBF in one WM task overlapped with the areas of increased rCBF in the other WM task.

Methods and Materials

Tasks

The tasks were performed as previously described (Klingberg and Roland, 1997). In the visual WM task, a circular field on a computer screen changed in luminance between one of six high luminance levels – the target levels – and a baseline luminance level. The 1.00 s stimulations at target luminance levels were separated by 2.00–5.00 s delays with baseline luminance (Fig. 1). The subjects were asked to compare each target luminance level with the previous one, and to respond if the current luminance level was lower than the previous; no response was required when there was a change from a lower to a higher luminance.

In the auditory WM task (Fig. 1), a series of high-pitched tones – the target tones – of different frequencies were presented. Target tones were separated by a temporal intervals of 2.00–5.00 s, during which a low-pitched tone – the baseline tone – was presented. The duration of the target tones was 1.00 s. The subjects were asked to compare each target
Computer screen 100 cm from the subjects. The subject’s peripheral diameter, which was presented against a black background on a computer monitor, was fixed at

A. Stimulus presentation in the single auditory and visual WM tasks. In the auditory WM task a tone changed in frequency. The subjects continuously compared each tone with the previous one (comparison indicated with arrows) and pressed a button if the tone was lower than the previous one. Stimulation of baseline luminance during the auditory task. Not perform any task.

B. Stimulus presentation in the dual task, where the auditory and the visual tasks were performed simultaneously.

tone with the previous target tone, and to respond only if the last target tone was lower in frequency than the previous one.

In the dual-task condition, the auditory and visual WM tasks were performed simultaneously. The onset of a target tone in the auditory task was always separated by at least 1.00 s from a target luminance level in the visual task, and vice versa. The response to stimuli thus did not coincide for the auditory and visual tasks. The delay period between stimuli, which is the period when the subjects are required to keep sensory information on-line, overlapped between the auditory and the visual task.

In the control condition, the subjects only received passive auditory and visual stimulation at the baseline frequency and luminance. They watched the screen and held the computer mouse in their hand, but did not perform any task.

In order to have both auditory and visual stimulation in all four conditions, we presented an unchanging auditory tone of baseline frequency during the visual WM task, and an unchanging visual stimulation of baseline luminance during the auditory task.

### Stimuli

The visual stimulus consisted of a white, circular field of 15 cm in diameter, which was presented against a black background on a computer screen 100 cm from the subjects. The subject’s peripheral visual field was shielded by a cone which was attached to the screen and around the eyes of the subject. The minimum and maximum luminance values were within 4–18 cd/m². The interstimulus ‘baseline’ of luminance was fixed at ~3 cd/m². The auditory stimuli were tones presented through a pair of earphones. The minimum and maximum frequencies were within 650–780 Hz. The ‘baseline’ frequency was fixed at 550 Hz.

The day before positron emission tomography (PET) scanning, each subject was tested on all three tasks (auditory WM, visual WM and dual task). The stimuli levels were adjusted so that the subjects would achieve a $d'$ of ~5 in the non-simultaneous tasks. This measure of accuracy takes into account both hits and false alarms (Green and Swets, 1966). A $d'$ of 5 is approximately equivalent to a probability-of-hit minus probability-of-false-alarm of 0.70. When the stimulus levels in the single tasks had been calibrated, exactly the same stimulus levels were used in the dual task.

Reaction time was recorded by a computer and was defined as the time from the onset of the stimulus to the pressing of a button. Correct responses occurring within 2.00 s were counted as a ‘hit’. The subjects pressed the left button on a computer mouse with their right index finger when responding to visual stimuli, and pressed the right button with their right middle finger when responding to auditory stimuli. Responses on non-target trials (when the stimulus was higher in luminance or frequency than the previous stimulus) were registered as false alarms.

### Subjects

Seven male volunteers, aged 22–37 years (mean 27.9) participated in the experiment. The subjects were all right-handed and none had a history of neurological disease. Informed consent was given by all the subjects and the study was approved by the Ethics Committee and the Radiation Safety Committee of the Karolinska Hospital.

### PET Scanning and Data Treatment

Scans of rCBF were obtained with a CTI-Siemens ECAT EXACT HR scanner in three-dimensional mode. Subjects received a bolus injection of 16 mCi of $[^{15}O]$butanol before each PET scan. Each condition was repeated three times in a semi-randomized balanced order, with a total of 12 scans for each subject. An automatic sampling system measured the radioactive tracer concentration in the radial artery every 1 s during the scans. The tasks started at the time of injection of the bolus, and scanning started at the time increased radioactivity was detected in the brain, ~10 s later. The rCBF was calculated by the autoradiographic method (Meyer, 1989), on the basis of data collected during the first 50 s of scanning. Reconstructed images were smoothed with a three-dimensional Gaussian filter with 8 mm full-width half-maximum. In an initial analysis it was found that there was no significant difference in global CBF among any of the four conditions. Global CBF was then scaled to a mean of 50 ml/100 g/min. The rCBF images from each individual were transformed to the same spatial coordinates using the algorithm of Woods et al. (1992), and then anatomically standardized using the magnetic resonance image (MRI) of each subject and a computerized brain atlas (Roland et al., 1994). The MRIs were also anatomically standardized and PET activations were superimposed on the mean reformatted MRI for localization of the activations. The rCBF from all scans were evaluated with a general linear model (Friston et al., 1995). Task, repetition and subject were included as factors in the design matrix. We contrasted auditory WM versus control, visual WM versus control and dual task versus control, dual task versus auditory WM and dual task versus visual WM. Thresholds for statistically significant changes in rCBF were evaluated with the permutation method described by Holmes et al. (1996). One thousand permutations were performed, and a level of significance was chosen which gives an omnibus probability of $P < 0.05$ of having one or more false positive clusters within the brain ($t > 2.8$, cluster size >960 mm$^3$).

### Results

#### Performance

In the dual task, the subjects responded with different buttons for the auditory and visual stimuli. Reaction times and $d'$ for the visual and auditory stimuli could thus be recorded separately. Mean reaction times and $d'$ values are shown in Table 1.

A four-way ANOVA was performed on the reaction time data and on the $d'$ values from both the two single tasks and the dual task, in order to evaluate the effects of modality (auditory versus visual), task (single versus dual task), subject (1–7) and repetition (1–3). For the $d'$ values, there was no significant effect of modality ($F = 0.03$, $df = 1, 73$, $P = 0.86$) or repetition ($F = 2.5$, $df = 2, 73$, $P = 0.10$), but a significant effect of task ($F = 6.02$, $df = 1, 73$, $P = 0.02$) and subject ($F = 26.4$, $df = 6, 73$, $P = 0.01$).

### Table 1

<table>
<thead>
<tr>
<th></th>
<th>Reaction time (ms ± SEM)</th>
<th>$d'$ (±SEM)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Auditory WM</td>
<td>1005 (±72)</td>
<td>3.18 (±0.23)</td>
</tr>
<tr>
<td>Visual WM</td>
<td>1163 (±138)</td>
<td>3.02 (±0.32)</td>
</tr>
<tr>
<td>Dual task</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Auditory responses</td>
<td>1217 (±85)</td>
<td>2.48 (±0.29)</td>
</tr>
<tr>
<td>Visual responses</td>
<td>1210 (±86)</td>
<td>2.50 (±0.30)</td>
</tr>
</tbody>
</table>
The right prefrontal cortex was strongly activated in all three tasks. In the visual WM task, the right prefrontal activation was separated into two clusters, but the pattern of activation was similar in all three tasks (Fig. 2). All tasks activated the left middle frontal gyrus and the left insula/frontal operculum. In the dual task the activation in the insula/frontal operculum was extended as one cluster laterally into the posterior part of the inferior frontal gyrus, and superiorly into the left middle frontal gyrus. In the single tasks, this activation was detected as separate clusters: the auditory WM task activated the insula plus the posterior part of the inferior frontal gyrus close to Broca’s area, and the visual WM task activated the insula plus the left middle frontal gyrus. The visual task and the dual task also activated a part of cortex corresponding to the left frontal eye-field (x = −38, y = −2, z = 51–53) (Fox et al., 1985; Paus, 1996).

The cingulate cortex was also activated in all three tasks. The center of gravity for the activation (x = 0, y = 16, z = 46) was located in the upper bank of the cingulate sulcus, although the extent of the activation was not confined to this region. The location of the center of gravity corresponds to the location previously found in two previous WM studies (x = 5, y = 20, z = 48) and (x = −6, y = 12, z = 50) (Klingberg et al., 1996, 1997). In these studies, narrower filters were applied to the PET data, and the cingulate activations were then confined to the upper bank of the cingulate sulcus.

### Changes in rCBF in Overlapping Areas

The auditory and the visual WM tasks activated overlapping parts of the cortex. To analyze how the rCBF changed in these overlapping areas during dual-task performance, VOIs were defined as the voxels that were significantly activated in all three tasks relative to control. These VOIs were located in the right prefrontal cortex, left middle frontal gyrus, left insula/frontal operculum, cingulate cortex and bilaterally in the inferior parietal cortex. The mean rCBF change in all the overlapping areas during single task performance was 6.3 ± 0.4 ml/100 g/min, and during dual-task performance 7.1 ± 0.5 ml/100 g/min. The difference, 0.79 ml/100 g/min, was 13% of the single-task rCBF, and was not significant (P = 0.10 two-tailed t-test).

### Dual Task Compared to Single Tasks

Dual task minus visual WM resulted in significant activity in the right superior and middle temporal gyrus, corresponding to the...
Figure 2. Areas of significant rCBF increase relative to control are superimposed on the MR image which was used for anatomical standardization. Significantly activated voxels that were located within 15 mm of the surface of the brain are projected onto the brain’s surface.
location of the activation which was significant in auditory WM minus control and dual task minus control (Table 2). Dual task minus auditory WM showed bilateral activation of the occipital cortex and cerebellum in locations corresponding to the activations which were significant in both visual WM minus control and dual task minus control (Table 2).

Decreases in rCBF

Significant decreases in rCBF relative to control are listed in Table 3. The areas showing decreased rCBF during the visual WM task were compared, voxel by voxel, with the activations in the auditory WM task, and vice versa. No deactivations in the visual WM task overlapped with increases in the auditory WM, and no deactivations in the auditory WM task overlapped with increases in visual WM minus control. In the VOI analysis described above, no decrease in the occipital VOI was detected in the auditory task, and no decrease in the temporal VOI was detected in the visual WM task.

**Discussion**

**Activations in the Single WM Tasks**

The auditory and visual WM tasks activated sensory-specific cortical areas in the temporal and occipital lobe respectively. In addition, both tasks activated overlapping areas in the prefrontal, cingulate and inferior parietal cortex. These activations were thus not specific for the sensory modality of the memoranda. In the present study, the WM tasks differed from the control in several aspects in addition to WM demand. However, in a previous study (Klingberg et al., 1996), the same WM tasks as in the present study were compared to go/no-go tasks without WM demand. These go/no-go tasks were matched in difficulty to the

---

**Table 3**

<table>
<thead>
<tr>
<th>Area</th>
<th>Auditory WM Coordinates</th>
<th>Volume (cm³)</th>
<th>Visual WM Coordinates</th>
<th>Volume (cm³)</th>
<th>Dual-task Coordinates</th>
<th>Volume (cm³)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Superior frontal gyrus (L)</td>
<td>−7, 56, 22</td>
<td>9.8</td>
<td>−10, 57, 29</td>
<td>4.7</td>
<td>−7, 46, 22</td>
<td>29.7</td>
</tr>
<tr>
<td>Middle frontal gyrus (L)</td>
<td>−28, 24, 50</td>
<td>2.2</td>
<td>−25, 22, 50</td>
<td>4.7</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subcallosal gyrif frocculate</td>
<td>1, 26, −3</td>
<td>2.4</td>
<td>−4, 18, −4</td>
<td>1.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precentral gyrus (R)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Premotor cortex</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Precentral gyrus (L)</td>
<td>−14, −52, 56</td>
<td>2.2</td>
<td>−4, −30, 63</td>
<td>1.2</td>
<td>−40, −66, 22</td>
<td>7.4</td>
</tr>
<tr>
<td>Postcentral gyrus mesial</td>
<td>−40, −69, 17</td>
<td>11.5</td>
<td>−50, −64, 19</td>
<td>1.3</td>
<td>−39, −61, 27</td>
<td>1.9</td>
</tr>
<tr>
<td>Anterior middle temporal gyrus (R)</td>
<td>54, −4, −17</td>
<td>1.1</td>
<td></td>
<td></td>
<td>55, −4, −17</td>
<td>1.0</td>
</tr>
<tr>
<td>Anterior middle temporal gyrus (L)</td>
<td>−54, −11, −11</td>
<td>2.4</td>
<td>−54, −11, −11</td>
<td>2.4</td>
<td>−54, −11, −11</td>
<td>2.4</td>
</tr>
<tr>
<td>Posterior middle temporal gyrus (R)</td>
<td>40, −71, 11</td>
<td>2.0</td>
<td></td>
<td></td>
<td>40, −70, 10</td>
<td>1.8</td>
</tr>
<tr>
<td>Inferior temporal gyrus (L)</td>
<td></td>
<td></td>
<td>−52, −35, −25</td>
<td>1.0</td>
<td>−52, −35, −25</td>
<td>1.0</td>
</tr>
<tr>
<td>Precuneus</td>
<td>−2, −55, 23</td>
<td>10.2</td>
<td>−1, −56, 23</td>
<td>6.9</td>
<td>−7, 48, 22</td>
<td>9.0</td>
</tr>
<tr>
<td>Medial temporal lobe (R)</td>
<td></td>
<td></td>
<td>−26, −20, −12</td>
<td>1.4</td>
<td>−26, −20, −12</td>
<td>1.4</td>
</tr>
<tr>
<td>Medial temporal lobe (L)</td>
<td></td>
<td></td>
<td>−16, 2, −15</td>
<td>1.8</td>
<td>−16, 2, −15</td>
<td>1.8</td>
</tr>
</tbody>
</table>

See Table 2 for abbreviations.
WM tasks, and controlled for attention towards the stimuli and motor response. In the comparison between detection tasks and WM tasks, the WM demand could be associated with a significant increase in the activation of the prefrontal cortex, inferior parietal cortex and anterior cingulate. In contrast, activity in sensory-specific areas was not specifically related to WM demand (Klingberg et al., 1996).

The role of the prefrontal association cortex in WM is well documented in both non-human primates and humans (Goldman-Rakic, 1987; Fuster, 1989). A fundamental question concerning the prefrontal activity underlying WM is to what degree it is organized in a modality-specific way, and to what degree WM-specific activity is independent of the sensory modality of the memoranda. In the present study we found sensory-specific activation in the posterior part of the prefrontal cortex: the auditory WM task, but not the visual WM task, activated cortex close to Broca’s area, while the visual WM task, but not the auditory WM task, activated the posterior part of the left middle frontal gyrus ($x = -41, y = 24, z = 39$) and cortex which may correspond to the left frontal eye field. Similar findings were reported by Roland (1982). However, the main prefrontal activity in the WM tasks was located more anteriorly in the right dorsolateral prefrontal cortex, and overlapped between the auditory and the visual WM tasks. This overlapping activity is evidence for a non-sensory-specific, i.e. non-parallel, organization of activity in the prefrontal cortex during WM tasks. It should be pointed out that this overlap is detected at a macroscopic level and that it is still possible that different modalities project to different, but interdigitating, columns in the prefrontal cortex. This finding does not necessarily contradict a ventral/dorsal non-spatial/spatial organization of the prefrontal cortex, since it is possible that such organization could cross modalities and exist for both the auditory and visual modality.

The parietal activations were centered in the posterior part of the supramarginal gyrus. The activity extended into the anterior part of the angular gyrus, and probably into the intraparietal cortex, but not into the superior parietal or dorsal occipital

Figure 4. Coronal sections showing prefrontal and inferior parietal activations in the two single WM tasks relative to the control. (A) Auditory WM, $y = 37$; (B) visual WM, $y = 37$; (C) auditory WM, $y = -55$; (D) visual WM, $y = -55$.  

WM tasks, and controlled for attention towards the stimuli and motor response. In the comparison between detection tasks and WM tasks, the WM demand could be associated with a significant increase in the activation of the prefrontal cortex, inferior parietal cortex and anterior cingulate. In contrast, activity in sensory-specific areas was not specifically related to WM demand (Klingberg et al., 1996).

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The parietal activations were centered in the posterior part of the supramarginal gyrus. The activity extended into the anterior part of the angular gyrus, and probably into the intraparietal cortex, but not into the superior parietal or dorsal occipital
cortex. The parietal activations were lateral and inferior to those found in superior parietal and dorsal occipital cortex in studies involving visuospatial attention (Haxby et al., 1991, 1994; Corbetta et al., 1993; Owen et al., 1996b). Thus, the inferior parietal activation observed in the present study does not appear to be part of the dorsal pathway devoted to visuospatial analysis (Ungerleider and Mishkin, 1982; Felleman and Van Essen, 1991). Activation of the inferior parietal cortex, close to the activation in the present study, has been found in several other WM tasks relative to attention-demanding control tasks, independent of the type of stimulus used (Jonides et al., 1993; Petrides et al., 1993; Smith et al., 1995; Klingberg et al., 1996, 1997; Owen et al., 1996a; Cohen et al., 1997). In all these studies, the inferior parietal cortex was coactivated with the dorsolateral prefrontal cortex.

**Activations in the Dual Task**

The total volume of significantly activated cortex was larger in the dual task than in the single tasks. The task-induced rCBF increase in the overlapping areas was also slightly higher in the dual task (7.1 versus 6.3 ml/100 g/min). However, the voxels which were significantly activated only in the dual task did not constitute any separate clusters, but were always part of the clusters which overlapped with the single-task activations. Furthermore, the increase in size was not significant when rCBF in the single WM tasks were subtracted from that in the dual task. There was thus no separate cortical area that was activated only during dual-task performance, and therefore no cortical area could be associated with any cognitive process specific for dual-task performance, such as divided attention (Corbetta et al., 1991) or task coordination (D’Esposito et al., 1995).

In contrast to the present results, a previous study found prefrontal and cingulate areas which were active during dual-task, but not during single-task performance (D’Esposito et al., 1995). Coordinates for the activations were not reported in this study and it is therefore not possible to make a precise comparison between the results of this and other brain-imaging studies. However, activations of the dorsolateral prefrontal and cingulate cortex have been reported in several studies of WM for sensory stimuli (Jonides et al., 1993; Petrides et al., 1993; Smith et al., 1995; Klingberg et al., 1996, 1997; Owen et al., 1996a), and it is clear that the activations of these areas are not specific for dual-task performance. It is possible that the simultaneous performance of two non-WM tasks could cause an increase in WM demand. For example, it cannot be excluded that the stimulus processing or response in one task is delayed while the other task is given priority, thus inducing a WM requirement. Increased WM demand during the initial training on non-WM dual-task performance is also suggested by Detweiler and Schneider (1991). The important difference between the present study and that of D’Esposito et al. (1995) could thus be that we used WM tasks as single tasks while the previous study did not. Further studies will show how the present results can be generalized to other dual-task situations. Our interpretation of the current and previous imaging results (Corbetta et al., 1991; Jonides et al., 1993; Petrides et al., 1993; D’Esposito et al., 1995; Smith et al., 1995; Klingberg et al., 1996, 1997; Owen et al., 1996a; Cohen et al., 1997; Johannsen et al., 1997) is that performing WM tasks induces the activation of several cortical areas, both prefrontal and parietal, but that there is no need to presuppose any areas with activity specific for dual-task performance.

**Cross-modal Inhibition**

The areas of decreased rCBF in one WM task never overlapped with the areas of increased rCBF in the other WM task, a finding that speaks against a cross-modal inhibition hypothesis. Similarly, the VOI analysis failed to support the inhibition hypothesis (Fig. 3). Previous studies have found that selective visual attention is accompanied by a decrease in rCBF in the middle part of the superior and middle temporal gyrus (Haxby et al., 1994; Shulman et al., 1997). A decrease in the middle temporal gyrus was detected also in this experiment, but since it did not overlap with the increased rCBF in the other WM task, there is no evidence that the decrease was of any functional significance, i.e. it did not produce any interference.

The rCBF increase in the sensory-specific areas was higher in the single tasks than in the dual task (Fig. 3). The reason for this difference in increase is unclear, but it is possible that it is the result of inhibitory mechanisms operating in the dual task but not in the single tasks (Ghatan et al., 1998). Further studies, preferably employing other methods, could perhaps provide answers to this question.

**Commonly Activated Areas**

The present study shows that two WM tasks with stimuli from different modalities can activate overlapping parts of cortex (Table 2, Figs 2 and 4). Furthermore, the brain activity was not reorganized during dual-task performance, but the same pattern of activation was present during both single-task and dual-task performance (Fig. 2). From such overlap in activity interference is likely to occur — either because the two tasks depend on activation of exactly the same population of neurons, which could be organized in functional fields (Roland 1993), or the tasks could activate different but interdigitated columns which inhibit each other by local mechanisms (Simons, 1985; Juliano et al., 1989; Welker et al., 1993). It cannot be determined whether the auditory and visual WM tasks depended on activation of the same part of cortex precisely at the same time during dual-task performance; the PET method does not have the temporal resolution necessary to determine this. From single-cell recordings in non-human primates, WM-specific activity in the prefrontal cortex has been characterized as continuous activity during the delays when stimulus information is kept on-line (Fuster and Alexander, 1971; Kubota and Niki, 1971; Fuster et al., 1982; Funahashi et al., 1989; Quintana and Fuster, 1992). Human studies using EEG (Gevins et al., 1996) and functional MRI (Cohen et al., 1997; Courtney et al., 1997) suggest that not only the prefrontal, but also the inferior parietal cortex, exhibit such sustained delay activity in WM tasks in humans. In the dual task, the interstimulus delays overlapped, which means that the subjects had to keep both visual and auditory information on-line at the same time. There is thus reason to believe that the frontal and inferior parietal areas were engaged by the two tasks at the same time, which in turn presumably leads to interference.

Although the present study does not prove that overlapping activity is the physiological basis for interference, the results are in agreement with this hypothesis. This hypothesis is further supported by the observation that practice is associated with a decrease in interference between two tasks, as well as decreases in prefrontal and cingulate activity and thus presumably a decrease in overlapping activation (Jenkins et al., 1994; Passingham, 1996). This hypothesis is also in agreement with a previous study which showed that the overlap in activity, as detected by PET measurement during single-task performance,
can to some extent predict dual-task interference (Klingberg and Roland, 1997).

Notes
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Address correspondence to Torkel Klingberg, Division of Human Brain Research, Department of Neuroscience, Karolinska Institute, Doktorsringen 12, S-171 77 Stockholm, Sweden. Email: torkel.klingberg@neuro.ki.se.

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