

Limitations in information processing in the human brain: neuroimaging of dual task performance and working memory tasks

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Introduction

The human capacity for information processing is limited; for example, we can only retain a limited amount of information in working memory (WM), and when we try to perform several tasks at the same time, performance deteriorates. The neurophysiological basis of these phenomena is largely unknown. This chapter will review neuroimaging results from dual task performance and tasks where WM load is parametrically varied, and discuss whether and how these results could possibly contribute to the understanding of human capacity limitations. The prefrontal cortex is necessary for performance of WM tasks, and the prefrontal cortex has also been in the focus of attention in questions concerning capacity limitations.

In dual tasks, the putative neural activity required to perform two tasks overlap in time. One example is when there is need to retain information in WM related to one task and during that same time also make comparisons and responses about a stimulus in a second task. The interest in dual task studies is partly driven by an interest in general questions about capacity limitations. Requirement of simulta-

neous performance is also part of everyday behavior and cognition, and the ability to simultaneously perform two tasks correlates highly with performance on tests tapping our general ability for understanding and problem solving (Daneman and Carpenter, 1983). Dual tasks have also attracted some interest because they are said to be prototypical 'executive' tasks (Baddeley, 1986). 'Executive functions' is a concept often used to denote functions of attentional control, such as switching or dividing of attention, inhibition, planning, coordination and decision making. It is, however, probably more fruitful to consider these diverse functions separately, rather than referring to 'executive function' as a single entity.

Hypotheses about physiological limitations – evidence from neuroimaging of dual task performance

The results from neuroimaging of dual task performance will be organized around three potential mechanisms of dual task interference (Klingberg, 1998): (i) that there is a dual task specific area, (ii) the overlap hypothesis, and (iii) inhibition as the source for interference.

The scope of this article will be limited to results with positron emission tomography (PET) and functional MRI (fMRI). In functional activation studies, the signal changes most often detected by

PET reflect changes in regional cerebral blood flow (rCBF), whereas the changes detected by fMRI reflect changes in blood oxygenation level (BOLD-contrast). These signals increase monotonically with increased cortical metabolism.

A dual task specific area

It could be hypothesized that simultaneous performance of two tasks demands a more complex organization of brain activity, with cortical areas which coordinate the networks of areas necessary to perform each of the component tasks. Dual task performance would require activation of an additional, spatially separate, cortical area, which is not necessary for performance of either of the component tasks. The more complex network of cortical areas during dual task performance, or sub-optimal functioning of the coordinating function of the dual task area would consequently mean that dual task performance is not as accurate and fast as single task performance. It has, for example, been suggested that elderly adults with Alzheimer's disease have neurological deficits which impair specifically the 'central executive' functioning and that this is the reason why they would be impaired in dual task performance but not in performance of the component task (Baddeley et al., 1986; Baddeley et al., 1991).

In a widely cited study (D'Esposito et al., 1995), it was found that when subjects performed a word classification task and an object rotation task at the same time, there was activation of areas in the prefrontal cortex and cingulate cortex, whereas these areas were not active during single task performance. The results were not only interpreted as evidence for the existence of a dual task specific area, but the authors also suggested that these areas were the neuronal substrates of 'the central executive'. In a later PET study (Klingberg, 1998) subjects performed a non-verbal visual and a non-verbal auditory delayed matching task, first one task at a time and then both WM tasks simultaneously. In contrast with the results from D'Esposito et al., there were no additional areas activated during dual task performance, compared to single task performance (Fig. 1). Differences in task design could possibly have accounted for the

discrepancy; for example, the task used by D'Esposito did not demand any WM. However, Adcock et al. (1999) used exactly the same tasks as were used by D'Esposito et al., measuring brain activity with fMRI, and failed to find activation specific to dual-task performance. In contrast to D'Esposito et al., they also found prefrontal activity in the component tasks. Two later imaging experiments (Bunge et al., 1999; Geva et al., 1999), used dual tasks that are psychometrically well characterized and widely used in the cognitive literature: the listening span task and the computational span task. Again, these studies failed to find any dual-task specific activations; the finding of a dual task specific area is thus in question, with a majority of studies failing to find any such area.

Although most dual tasks do not activate any additional area, the areas that are activated by both single tasks are often more activated when the tasks are performed simultaneously. In the statistical images from a group analysis, this quantitative change is observed as an increase in peak signal intensity, as well as an increase in the extent of the statistically significant signal (however, see the study by Goldberg et al., reviewed in the next section). The physiological basis for this signal change in the dual tasks compared to single tasks could be an increase in metabolic activity in the cortex, or an increase in the extent of metabolically active cortex, or both, because after spatial filtering of the signal, the effect of increases in intensity and increases in extent can have the same effect (Fig. 2). Smoothing results from several steps during image processing; one reason is the sub-sampling that results from the facts that voxels most often only partly overlaps the metabolically active tissue. Smoothing also results from the interpolation during anatomical normalization, and is in addition often applied as a last step in image reconstruction in order to increase signal to noise and to compensate for anatomical differences between subjects when group analyses are performed.

From Fig. 2, it is also evident that after application of a statistical threshold for what one should call a significant signal change, it is possible to interpret a quantitative difference in signal intensity as if the area was not active in one condition and active in another. This threshold

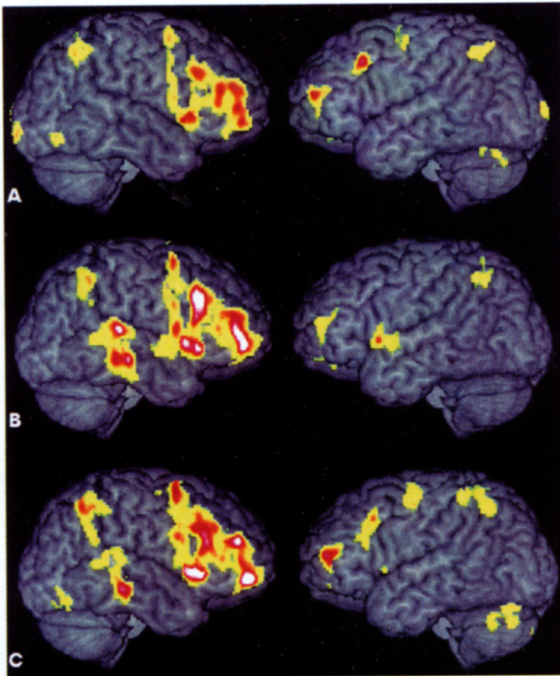


Fig. 1. Activations during single task and dual task performance of WM tasks. A. Auditory working memory minus control. B. Visual working memory minus control. C. Dual task minus control. Dual task activations were the sum of the single task activations, with no additional areas activated. Areas activated in both single tasks, such as parts of the middle and inferior right frontal gyrus, were more active during dual task performance with increases in detected extent (volume of activation) as well as peak intensity of the activation. Areas activated in only one of the single task, such as the auditory cortex, was less active when both WM tasks were performed simultaneously. (adapted from Klingberg (1998)).

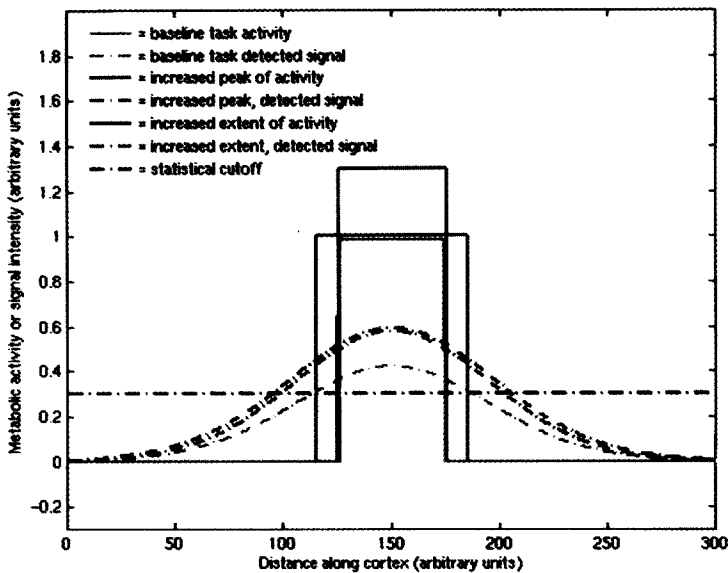


Fig. 2. Idealized model of the effect of filtering upon detection of metabolic changes; the metabolic activation is represented by solid lines. The three metabolic signals have been filtered with the same Gaussian kernel and the filtered signals are represented by the broken lines.

phenomenon could be the explanation for the reported additional dual task areas reported by D'Esposito et al. (1995): the areas activated in the dual task were not specific for the dual task, only slightly more active during the dual task. From Fig. 2, one can see that an increased extent and peak height of the signal in dual task compared to single task condition, could be due to: (i) higher activation or that (ii) a larger part of cortex is active in the dual task. It is unknown whether cortical activations have sharp and fixed boundaries defining the areas of activity (see Roland and Zilles, 1998), or whether the active part of cortex can gradually expand depending on the task requirements.

In a study by Koechlin et al. (1999), subjects were scanned during performance of a WM task, a switching task, and simultaneous performance of both the WM task and the switching task; they found that there was a prefrontal area that was activated only during simultaneous performance of the WM task and the switching task. This result could be interpreted as support for a dual task specific area; however, the pattern of activation was a gradually increased extent in prefrontal activation as the task demand (as measured by reaction time) increased. The results could thus be due to a gradual increase in extent of active cortex, but could also be explained by an increase in signal intensity in the same area, although this signal is not necessarily additive or linear combination of the activity in the component tasks.

An overlap hypothesis

It has repeatedly been suggested that the reason why two tasks interfere is that they compete for some limited resource (e.g. Kahneman, 1973; Wickens, 1980). Although the nature of this resource is seldom specified, the P300 event-related potential has been suggested as one measurement of it (Wickens et al., 1983). It has also been suggested that the degree of interference between tasks is inversely related to the 'functional distance' between the cortical areas activated in the two tasks (Kinsbourne and Hicks, 1978). Roland (1993) related the dual task interference phenomenon to the hypothesis about 'functional fields', and suggested that it would be impossible to perform two

tasks if they use the same 'functional field' (Roland, 1993; Roland and Zilles, 1998).

Klingberg and Roland (1997), proposed that two tasks interfere if they require activation of overlapping parts of cortex at the same time. By combining imaging results and behavioral results, it could be shown that if task A and B have more overlap of activation than task C and D, then there is also more interference between task A and B than between task C and D when the tasks are performed simultaneously. The reason why two tasks would interfere if they produce overlapping activations could be either that they depend on activation of the very same columns in the overlapping region, or that they activate different but inter-digitizing populations of columns, which inhibit each other by interneurons (Juliano et al., 1989; Welker et al., 1993).

The overlap hypothesis would make it possible to predict the degree of dual-task interference between two tasks if one knows the cortical areas activated by the tasks individually; the overlap hypothesis could furthermore be rejected if two tasks interfere without activating overlapping parts of the brain. This was explicitly tested by Klingberg (1998), but the results were consistent with the overlap hypothesis, as are other studies where single task activations were reported (Adcock et al., 1999; Bunge et al., 1999; Koechlin et al., 1999). The overlap hypothesis could also be related to studies showing that practice is associated with decreased interference, decreased cortical activations and thus presumably decreased overlaps in activity between the tasks, although the amount of overlap was not quantified in these studies (Jenkins et al., 1994; Passingham, 1996).

Inhibition and decreased activity during dual task performance

When one pays attention to a stimulus, cortical metabolism increases in the part of cortex processing the features of the stimulus (Roland, 1982); in addition, metabolism can decrease in parts of cortex processing a non-attended modality (Haxby et al., 1994; Kawashima et al., 1995; Shulman et al., 1997). If this decrease in metabolism is associated with active inhibition, one would expect

that this cross-modal inhibition would result in interference between tasks involving stimuli from different sensory modalities. In order to support this hypothesis one would need to show that the decreases in activity in one component task overlaps with the areas that are activated by the other component task, and that this is associated with interference during dual task performance of the two tasks. However, there is yet no evidence for this mechanism, and two explicit attempts to find overlap between activations and deactivations have failed (Klingberg and Roland, 1997; Klingberg, 1998).

What is evident in several dual task situations is that an area that is activated in task A, but not in task B, is less activated when task A and B are performed at the same time. This can be seen for example in auditory cortex (Fig. 1) as well as for sensory specific prefrontal activations such as activation of the frontal eye field in the visual WM task (Fig. 1); this could be taken as indirect evidence of inhibition. An alternative explanation for the decreased activity is a time-on-duty mechanism: selective attention towards a stimulus increases metabolism, and when attention is switched or divided this increase is weaker.

Two studies report decreases in the prefrontal cortex during dual task performance. In one study (Fletcher et al., 1995) there was activation of the prefrontal cortex during performance of an episodic memory task, but when the memory task was performed concurrently with a motor task, the prefrontal activation decreased. Goldberg et al. (1998) similarly found that the prefrontal activity induced by the Wisconsin Card Sorting Task (WCST) decreased when WCST was performed at the same time as subjects repeated aloud words that they heard, at a rate of 1 word every 0.75 s. This decrease could also be evidence of inhibition, but no overlap between activations and deactivations was demonstrated.

Effects of increasing WM load

The question about the physiological basis for capacity limitations can also be approached by studying what happens to cortical metabolism when WM load, i.e. the amount of information that

the subject needs to retain over a short period of time, is increased. One of the most studied WM tasks is the n-back task. In the most common (1-back) version of this task, a series of letters are presented, one letter at time, and the subject is asked to press a button if the presented letter matches the previous letter. WM load can be increased by asking the subject to match each letter to the letter that was presented two letters back (2-back) or three letters back from the current letter (3-back).

When WM load is varied, a majority of studies find that the signal increases monotonically with increasing memory load (Braver et al., 1997; Cohen et al., 1997; Jonides et al., 1997). This monotonic increase is evident in the middle and inferior frontal gyrus, and sometimes also in the parietal cortex and the basal ganglia; as was the case with the dual tasks, the increased load resulted in increased extent of activation as well as increased peak signal intensity. Similar results are found in other WM tasks such as the Sternberg WM-tasks (Rypma et al., 1999) and word recall tasks (Grasby et al., 1994). In the latter task the variation in load was measured over a broader range of loads (3–13 words) and the increase in activity seemed to plateau at the highest loads.

One study, using a slightly different version of an n-back task, found an inverted U-function of metabolism as a function of load (Callicott et al., 1999). The activity in the prefrontal cortex increased from load 0, to load 1 and 2, but then decreased for load 3; the authors interpreted this result as a physiological basis for capacity constraints. However, it is unlikely that there is a metabolic ceiling which is responsible for capacity limitations. When brain metabolism is increased by intense sensory stimulation, rCBF can increase by 50–100% from a resting baseline metabolic level, which is far above the signal increases routinely detected in cognitive paradigms with PET, even at high cognitive loads. Secondly, even if there was an upper metabolic level that constrained information processing, one would expect the amount of information retained as well as the cortical metabolism to approach this limit together in an asymptotic way. In the study by Callicott et al., on the other hand, the total amount of information that

the subjects retained increased from load 2 to load 3, but the brain activity decreased.

How does brain activity differ between subjects with different WM capacities? This was investigated by Jennifer Smith et al. (unpublished data). Subjects were selected based on whether they had a high or low WM capacity, and were then scanned during performance of a 1, 2, and 3-back WM task and a control task. The effect of load reproduced previous findings, with monotonic increases in activity in both prefrontal and parietal cortex as well as basal ganglia. When the two groups were compared, the high WM capacity subjects increased their metabolism less than did the low WM capacity subjects; the interaction between load and group was most pronounced in the right middle and inferior frontal gyrus. The results are in agreement with a study where good and poor dual task performers were scanned during single and dual task performance of the computational span task (Geva et al., 1999). Again, during the higher workload in the dual task situation, poor performers had a higher activation of prefrontal cortex than had the good performers. The difference between subjects with different WM capacities is evidently a difference in the amount of increase in information processing per unit increase in metabolism, the 'gain', which could be used in the tentative units of bits/(mg O₂/min/100 g).

Conclusions

The results of increasing information processing demands is somewhat similar in both WM tasks and dual tasks, with a quantitative increase in activity in several areas, often most pronounced in the inferior and middle frontal gyrus, particularly in the right hemisphere. Although there are conflicting data, a majority of neuroimaging studies do not find any separate cortical area specifically active during dual task performance; nor is there clear demonstration of active inhibition between the component task that could explain the interference during dual task performance. Instead, limited capacity seems to be due to the capacity limitations of single cortical areas, and the overlap hypothesis, i.e. that two tasks depend on activation of the same area, is currently the mechanism that best explains imaging

data of dual task performance. Whether the same mechanisms, with capacity limitation of single areas, could underlie the limitations of WM capacity and dual task performance is unknown.

To proceed in these questions, it is necessary to more precisely characterize the relation between information processing and the signal changes detected with fMRI and PET. Further investigations into these questions, combining the results from fMRI and PET with electrophysiological techniques and comparisons with computational models might be fruitful and could help to use neuroimaging to better understand the limitations on information processing in the human brain.

The results from imaging of dual tasks tell us something about the organization of the prefrontal cortex. A fundamental question is whether the prefrontal cortex is organized in an entirely parallel way, where different sensory modalities are processed in different places and where object information and spatial information are processed in non-overlapping areas, as suggested by Goldman-Rakic (1988) and supported by some imaging results (Courtney et al., 1996). However, repeated studies show that there are, at least at the macroscopic level, areas in the prefrontal cortex that participate in tasks involving different modalities (Klingberg et al., 1996; Klingberg and Roland, 1998; Adcock et al., 1999). This is also in agreement with the existence of multi-modal, or non-modal, prefrontal neurons in non-human primates (Fuster et al., 1982; Pandya and Yeterian, 1985).

Finally, the lack of a dual task specific area shows that although formal description of the dual task suggests that an additional function is needed, in this case a function of coordination, the brain does not solve the problem by activating an additional cortical module. An analogy could be made to the integration of visual information in different areas, where no additional 'binding area' is needed in order to integrate information between areas; integration and coordination can be implemented within the networks of cortical areas.

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