

The central attentional limitation and executive control

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TABLE OF CONTENTS

1. Abstract
2. Introduction
3. The central bottleneck
 - 3.1. The response selection bottleneck
 - 3.2. Bottleneck processing and content-dependent interference
 - 3.3. Practice effects and bottleneck interference
4. Executive mechanisms and bottleneck processing in dual tasks
5. Functional neuroanatomy of dual-task processing
 - 5.1. Neural costs of bottleneck processing
 - 5.2. Task order control and the lateral prefrontal cortex
 - 5.3. The relation of task order control and of other functions to the activity in the LPFC
6. Perspectives
7. Acknowledgements
8. References

1. ABSTRACT

A central attentional limitation is assumed to be one reason why processing costs emerge in situations in which people do two things at once. This limitation causes that processes in two tasks are processed in serial order, if they require simultaneous access to the capacity-limited resource, which is called bottleneck interference. The present article links together recent knowledge about the psychological mechanisms and about the neural implementation of bottleneck interference. First, new findings are reviewed about the location of bottleneck interference in the processing chain, about its relation to the content of the processed information and its dependence on practice. In addition, further new evidence is reviewed that suggests that the bottleneck does not result from a passive occupation of the attention-limited resource by some process. Instead it is suggested that the serial order of processes at a bottleneck results from the involvement of control processes regulating the order of access to the capacity-limited resource. Neuroimaging research suggests that these control processes are associated with activation in regions of the lateral prefrontal cortex, which can be dissociated from the neuro-anatomical implementation of other control functions during dual-task processing.

2. INTRODUCTION

When people perform two tasks concurrently, often large costs emerge, which are reflected by greater processing times and/or larger error rates in the component tasks when performed simultaneously as compared to single-task situations. This has motivated many researchers to propose that there exist serious processing limitations of the cognitive system which expose strong constraints for human behavior. A core assumption holds that a central attentional limitation is an important reason for the emergence of costs in dual-task situations (1-3). As a consequence of this limitation the processing chain of one of two tasks will be interrupted, when the processes of both tasks require simultaneous access to the capacity-limited processing structure – this is called bottleneck interference (but see [4]). In the last 15 years a number of important findings have been reported that shed light on the nature of the bottleneck interference, including its main location in the processing chain, its relation to the content of the processed information and its dependence on practice. While that research suggests generality of bottleneck interference, further new research uncovered the characteristics of those processes that enable the operation of a bottleneck during dual-task processing. In detail, this

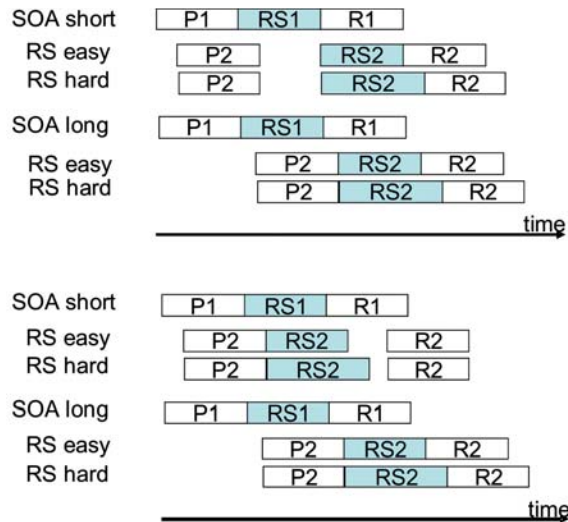


Figure 1. Location of a bottleneck - the effect of a manipulation of the response selection difficulty on response times. P1, P2, RS1, RS2, R1, and R2 = perception stages, response selection stages (blue colored) and motor stages in Task 1 and Task 2, respectively. SOA: Stimulus Onset Asynchrony. Upper panel: The bottleneck is located at the response selection stages. Therefore, at short SOA an interruption emerges in the Task 2 chain before the response selection stage. An increase of the processing time in the RS2 stage leads to an increase of the processing time in Task 2 in the hard compared to the easy condition independently on SOA. This results in an additive pattern of the effects of SOA and difficulty on the response times in Task 2. Lower panel: The response selection stages in Task 1 and Task 2 proceed in parallel and the bottleneck is located after the response selection stages (i.e., at the motor stages). An interruption emerges in the Task 2 chain after the response selection and before the motor stage. An increase of the processing time in Task 2 in the hard compared to the easy condition will be absorbed by the cognitive slack (the interruption) at short SOA. At long SOA there is no cognitive slack and, therefore, the additional processing time in the hard compared to the easy response selection condition will add to the processing time at long SOA. The resulting pattern represents a so-called sub-additive interaction of the difficulty and the SOA effects on the reaction times in Task 2.

research shows that bottleneck interference does not result from a passive occupation of a capacity-limited processing structure by a cognitive process (as it was proposed earlier). Instead the bottleneck mechanism results from the dynamic interaction of basic task processes and of additional executive processes that regulate the order by which the task processes in two tasks will access the attention-limited processing mechanism. These executive processes are associated with additional neural computation mainly in regions of the prefrontal cortex, which is known to be associated with executive functioning. The present review summarizes the main findings of this research.

3. THE CENTRAL BOTTLENECK

While earlier studies used rather complex dual-task paradigms to investigate the influence of capacity limitations on human behavior many recent studies use primarily the highly-controlled dual-task paradigm of the psychological refractory period (3). In that paradigm participants perform two choice reaction time (RT) tasks on the presentation of two stimuli (S1 and S2) presented with a short and variable interval between them (stimulus onset asynchrony [SOA]). As a main finding researchers observed a common pattern of reaction time (RT) functions, which is called the psychological refractory period (PRP) effect. The PRP effect describes the finding that the shorter the SOA, the longer the RT in the second task (RT2) while RTs on the first task (RT1) are often reported to be unaffected.

This effect is interpreted by the assumption of bottleneck interference according to which the processes in Task 2 cannot use the bottleneck stage if it is occupied by the bottleneck processes in Task 1. Consequently the processes in Task 2 will be interrupted for the time of the bottleneck processing in Task 1. The time for the interruption is called the PRP and it leads to a prolongation of the processing time in Task 2, which may be measured as dual-task costs.

3.1. The response selection bottleneck

A number of authors explains the PRP with the assumption of a structural bottleneck at the response selection stage, which can be performed only once at a time because of an attentional limitation of the involved decision component (but see [5, 6] and below). Evidence in favor of that assumption comes from studies that test critical predictions about the potential effects of a difficulty manipulation of certain processes in Task 2 and of the SOA manipulation on the RTs in a PRP task (7-9). As most critical for the localization of a bottleneck is the question whether the difficulty manipulation leads to an additive effect with the SOA or to a sub-additive interaction with the SOA on the RT2. In case of additive effects, the manipulated process is assumed to be subject to bottleneck processing (as is illustrated in Figure 1). By contrast, if the difficulty manipulation leads to a sub-additive interaction with SOA on RT2, then the corresponding process is assumed to proceed in parallel to processes in Task 1 and, importantly, during the bottleneck interruption of Task 2. See Figure 1 and below for the logic of these conclusions.

A number of studies that found additive effects between the SOA and various types of difficulty manipulations of the Task 2 response selection process vote for a bottleneck at the response selection. Additive effects had been found when manipulating the response selection difficulty by varying stimulus-response compatibility (7), by varying the number of response alternatives (9-11) and by varying the number of response repetitions (8). The additive pattern of SOA and difficulty effects on RT2 is interpreted with the assumption of a response selection bottleneck because it is proposed that the additional processing demands in the hard compared to the easy

condition emerge after the PRP in Task 2. As can be seen in Figure 1 (upper panel), in that case RT2 will be prolonged by the same amount of time in the hard compared to the easy condition independently of the SOA between tasks.

One study reported a sub-additive interaction of the response selection manipulation and of SOA on RT2 where the difficulty manipulation led to a smaller difficulty effect at the short compared to the long SOA. In detail, manipulating response selection difficulty by varying the stimulus-response compatibility Schumacher *et al.* (12) found that additive effects between SOA and difficulty in the first two sessions were substituted by a sub-additive interaction in the third practice session. Such findings led some authors (5, 6) to assume that the bottleneck at the response selection is not caused by a structural but by a strategic bottleneck that, importantly, may be avoided under certain conditions. In case of avoidance the response selection processes are assumed to proceed in parallel in the two tasks before the bottleneck. Therefore, additional processing demands in the hard compared to the easy condition should be absorbed into the cognitive slack of the PRP at short SOA (see Figure 1 lower panel).

However, even despite that finding (12) the question whether the response selection bottleneck is really a matter of a strategy is highly controversial because attempts to avoid a bottleneck by manipulating participants' strategies by instruction or by incentives did not succeed (13, 14). Given the overall pattern of findings it seems safe to assume a central bottleneck in situations with low amount of practice (relative to that in [12]) although exceptions from that rule are discussed (15).

3.2. Bottleneck processing and content-dependent interference

The bottleneck concept assumes that interference emerges in dual tasks in a manner which is independent of the specific content of the processed information (2, 3). This assumption had recently been modified on the basis of findings suggesting an additional influence of content-specific interference on the performance in dual tasks. A number of studies reported cross-talk between tasks in which the informational parameters in one task influence the computation of the parameters in the other task (16-21, and see [22] for the influence of the modality of the processed information). This leads to processing advantages in so-called compatible dual-task situations, in which the same or similar computations are required in the two tasks compared to incompatible situations requiring contradicting computations. As an example, Logan and Schulkind (20) report the findings of experiments in which participants are presented with two digits between 1 and 10 as S1 and S2 and are asked to decide whether the presented digits were odd or even. The motor responses (R1 and R2) were key-presses with the left and right hand on S1 and S2. The authors found shorter processing times in both tasks if the digits were either both to classify as even or both as odd (compatible) compared to situations in which the category for S1 (e.g., odd) was incompatible to that for S2 (even).

Of considerable theoretical importance for the notion of a response selection bottleneck is the observation that processing parameters of R2 interact with perceptive (16), lexical (19), and/or motor parameters (17, 18) of Task 1 and via this interaction affect RT1. For example, RT1 is shorter if participants perform a left hand response as R1 and a verbal motor response "left" as R2 (compatible) compared to a situation with a right hand R1 and the verbal answer "left" R2 (19). This is important because according to the response selection bottleneck assumption, parameters of the Task 2 motor response ("left") should not be available before the end of the response selection stages in Task 1 and should not lead to effects on RT1 (19). However, because such effects had repeatedly been observed, the assumption of a response selection bottleneck has recently been modified.

As a solution it has been proposed that the response selection mechanism consists of several sub-processes, i.e. early response activation and late response identification (18, 19, 23, 24), that are to different degree subject to a bottleneck. While the early activation of a memory trace of R2 may proceed in parallel to the response selection in Task 1 and therefore may affect the processes in Task 1 via cross-talk, the final identification of the R2 is assumed to be subject to a bottleneck. Therefore, it proceeds serially to the response selection in Task 1 causing the PRP effect. Schubert, Fischer and Stelzel (24) propose that the activated R2 information is reset at the end of the R1 selection before it can affect the bottleneck stages in Task 2. In particular, they argued that although there may be hints for an early activation of R2 during the PRP, there is no empirical evidence that the activated R2 really survives the influence of the bottleneck processing during Task 1. As evidence against a possible survival, they report findings from an experiment in which response activation processes in Task 2 of a PRP situation were evoked unbeknownst to the participants by the presentation of non-conscious prime stimuli before S2. The decisive question was whether response activation affects RT2 despite a PRP, which would suggest that the evoked response activation survived the influence of the bottleneck between tasks. However, even in a dual-task situation with a dramatically reduced PRP under condition of a short SOA the authors could not find any effects of the non-consciously evoked response activation on RT2. By contrast, under a condition of a long SOA where the Task 2 chain was not interrupted by a PRP, the authors found the non-conscious stimuli to significantly affect the RT2. These findings suggest that a PRP hinders non-consciously evoked response activation to affect R2 through the bottleneck.

3.3. Practice effects in multitasking

A challenging finding for theories assuming a central attentional limitation stems from studies which investigate the influence of practice on dual-task performance. Some of these studies showed a dramatic decrease of the dual-task costs after practice. For example, one study (25) obtained that participants are able to read and understand a short story while writing a dictate with minimal remaining costs after more than 20 weeks of practice. Two further, more recent studies (26, 27)

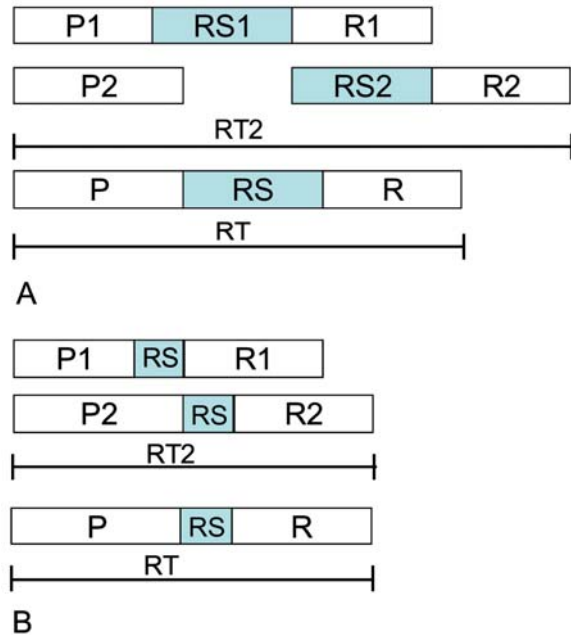


Figure 2. Illustration of practice effects on the processing durations of two tasks and the related dual-task costs. P1, P2, RS1, RS2, R1, R2 = perception, response selection, and motor stages in Task 1 and Task 2. P, RS, R perception, response selection and motor stages in a single task corresponding to Task 2. RT2 reaction time on Task 2, RT reaction time on the single task corresponding to Task 2. The difference between RT2 and RT illustrates the amount of dual-task costs caused by the involvement of a response selection bottleneck in Task 2. Panel A: Hypothetical processing durations in Task 1, Task 2 and the single task at the beginning of practice. Panel B: Hypothetical processing durations in Task 1, Task 2 and the single task at the end of practice. Illustrated is the situation of a latent bottleneck: An unequal practice-related reduction of the duration of the processing stages in Task 1 and Task 2 has caused that the bottleneck stages (RS) in Task 1 and Task 2 do not temporally overlap anymore. In that case, dual-task costs vanish after practice as can be inferred by the comparison of RT2 and RT in panel B (further explanation see text).

replicated this finding with a dual-task situation adapting the PRP paradigm. The participants in these latter studies performed a dual task consisting of an auditory-verbal and a visual-manual choice reaction task both presented at the same time. The authors found no significant (or at least only marginal) differences between the reaction times and error rates in the component tasks of the dual-task compared to that in the single-task situation after 5 (26) or 8 (27) learning sessions.

On the first glance, the finding of zero dual-task costs studies seems to be challenging for the assumption of a structural, immutable bottleneck at the response selection stage. This is so because the fact that both component tasks in (26, 27) involved a response selection stage, would predict that a bottleneck interruption should emerge at least

in one of the two tasks and this should lead to the emergence of dual-task costs even after practice. Moreover, the assumption of an immutable bottleneck seems to suggest that interference effects should be resistant to practice.

However, a number of theoretical analyses and empirical findings show that the findings of zero dual-task costs after extensive practice may indeed not contradict the assumption of a structural response selection bottleneck. For example, a number of studies stressed the role of learning for optimizing attentional functions of the cognitive system (28-30). Learning may cause that a bottleneck is still at work even if it does not lead to the emergence of dual-task costs after long-lasting practice (31-33). In particular, it has been proposed that long lasting practice may lead to a strong and unequal reduction of the response selection (i.e., the bottleneck) stages in the two component tasks. In that case, a so-called latent bottleneck may emerge that represents a particular type of processing architecture during dual-task processing in which attention-limited processing stages are still involved but are scheduled in a way avoiding any temporal overlap between them. Figure 2 shows that in that case no bottleneck-caused interruption of the processing chain is predicted and so no dual-task costs.

A number of findings are consistent with the idea of a latent bottleneck. For example, single-task studies have shown that extended practice leads especially to a decrease of the processing time for the response selection stage (34). Recent neuroimaging findings suggest that this decrease of processing time is accompanied by a practice-related cortical re-organization allowing faster neural pathways from stimulus to motor regions (35). Further studies (31-33) showed that the practice-related decrease of the response selection time represents a major source for the reduction of the dual-task costs in dual-task situations. Additionally, a computational model had been proposed (36) that is based on a production-like processing architecture and assumes serial scheduling of the response selection-related productions in the two tasks after practice. Taken together, these findings are consistent with the assumption that the reduction of the processing time for capacity limited processing stages and their clever scheduling are main causes for the optimization of dual-task performance after practice, though a complete parallel processing can not be excluded (32).

4. EXECUTIVE MECHANISMS AND BOTTLENECK PROCESSING IN DUAL TASKS

An important question concerns the nature of the mechanisms that enable goal-directed behavior in situations in which organisms are hampered by an attentional limitation. Earlier models assumed that the interruption of one of the two task streams results from a rather passive bottleneck in which the processes enter the attentional gate according to their order of arrival (2, 3). Opening and closing of the gate as well as the re-opening of the gate were implicitly assumed to follow an automatic mechanism

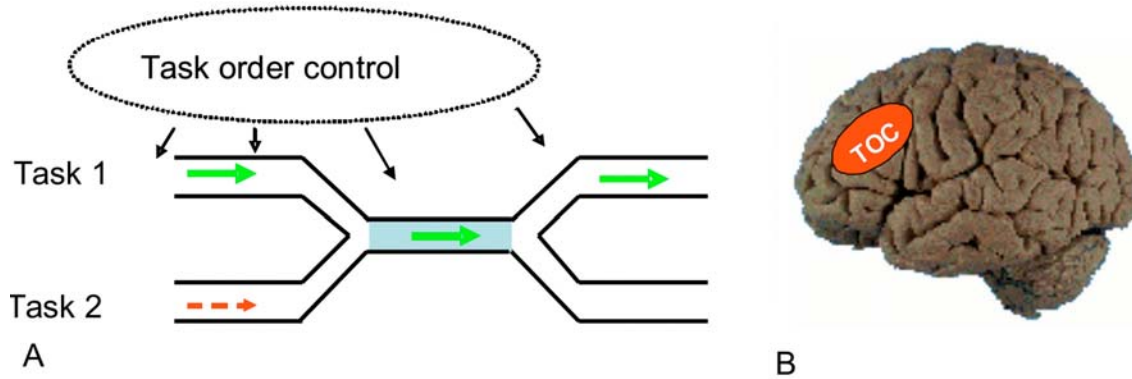


Figure 3. Panel A: Assumption of executive processes (task order control) that regulate the order of processes competing for access to a bottleneck (blue colored box) in dual tasks (5, 36, 38, 46). Panel B: Illustration of the finding that task order control processes (TOC) are associated with activation changes in the lateral prefrontal cortex (41, 53, 72).

which does not result from the involvement of additional processing mechanisms (2).

However, a number of authors suggest that the serial ordering of processes at a bottleneck is associated with the involvement of separate executive processes in addition to the basic task processes. Executive processes are required in task situations in which two task streams compete for access to a capacity limited processing structure (see Figure 3). The existence of such executive processes is not only proposed by authors assuming structural processing limitations (37-40) but also by authors assuming strategic reasons for the emergence of bottleneck interference (5, 6).

Empirical evidence for the existence of executive processes during bottleneck processing comes from different sources, e.g. from neuroimaging studies, from studies in experimental psychology and from studies with persons that are impaired in executive functioning. While the findings of neuroimaging research will be discussed in the next chapter, I will refer to some findings from experimental psychology and from research on persons with impaired executive functions now.

A number of behavioral studies (37, 39, 40) reported evidence about executive order control processes with a specific type of PRP dual tasks. In this paradigm the order of the stimuli (e.g., a tone and a visual character) for the two component tasks varies randomly and unbeknownst to the participants and participants have to perform the tasks according to the order of the stimulus presentation. As an important finding, additional dual-task costs emerge when participants perceive invalid prior information (e.g. a cue) about the expected order of the stimuli for the two tasks (i.e., which one will be the first) compared to a situation in which valid prior information about the order is presented. For example, in DeJong (37) the presentation of an auditory warning stimulus announced that S1 (in the upcoming trial) will be one of two tones, while a visual warning stimulus announced that one of two visual characters will be presented as S1. The finding of higher reaction times (dual-task costs) in the invalid (i.e., visual

pre-cue in case of tone S1) compared to the valid cue condition (auditory pre-cue in case of tone S1) is consistent with the assumption that participants pre-plan the order of the tasks in advance to the trial start. It suggests that additional time-consuming order control processes are required, if the actual order of the stimuli does not correspond with the pre-planned order.

Order control costs do not only emerge if the order of the tasks is pre-cued by information that is delivered by external cues. A recent study (41) has shown that order control costs in an actual trial (N) may emerge even as a result of processes that rely on internal priming of the processing order that is based on the episodic memory trace of the processing order in the previous trial (N-1). In that case, RTs on Task 1 and 2 are elevated, if the order of the component tasks in an actual dual-task trial (N) is opposite to that in the trial N-1, compared to trials in which the order of the two tasks was the same (41).

Together, these findings suggest that participants are able to prepare the order of Task 1 and Task 2 processes in advance at or before the bottleneck according to prior information that is provided either by external cues or by internal information about the expected task sequence. If the actual presentation order of the stimuli does not match the expected (primed) order, additional control processes are necessary in order to re-arrange the task processes.

The mechanisms of order control and of their effects on bottleneck processing has recently been formalized with different types of computational models (5, 21, 39). This helps to link bottleneck theory with models about executive control *in situations* requiring the subsequent alternation (switching) between tasks (42-44). For example, in (39) additional processes are assumed that enable the fast setting of Task 1 processes, their disengagement after the passed bottleneck, and the fast re-configuration of the Task 2 processes after Task 1 processes have finished bottleneck processing. Executive control processes that actively enable bottleneck processing may also be simulated by production-based models (5).

In addition to these findings and theoretical assumptions, further evidence about executive control in PRP dual tasks stems from studies using neuropsychological research approaches (45-49). A particular aim of such studies is to infer the characteristics of executive control in dual tasks by investigating the performance of persons with distinguished difficulties in executive control, e.g. old aged people and patients with close head injury (CHI). For example, two studies (47, 48) showed a specific form of the impairment of the dual-task processing which points to an impaired control of dual-task input processing in these groups of persons. In particular, CHI patients and old-aged people exhibited strong difficulties in sustaining an appropriate processing order of the two tasks at a bottleneck, when the task situation required the processing of a highly-salient visual Task 2 stimulus simultaneously to the processing of an auditory Task 1 stimulus. While young and normal participants are able to schedule the decision on the highly-salient Task 2 stimulus after the decision on the Task 1 stimulus and to process the perception stages of both stimuli in parallel, older people and CHI patients are not able to do so. On the contrary, they are strongly distracted by the presentation of the high-salient visual stimulus. This leads to a short interruption of the Task 1 processing stream and to a strong increase of the RTs in Task 1 and 2 compared to situations with less salient stimuli. Consistent with theories about control deficits in CHI patients and in old-aged people, these findings suggest that efficient control of the serial ordering in PRP tasks requires intact control capabilities of the cognitive system.

In sum, the serial processing order in PRP tasks is not a result of a passive bottleneck but results rather from active control processes. A number of authors assume that these processes are especially required in situations in which two task streams compete for access to a bottleneck. Consistent with this assumption it is proposed that executive control processes regulate the order of the task processes at or before a bottleneck.

5. FUNCTIONAL NEUROANATOMY OF DUAL-TASK PROCESSING

5.1. The neural costs of dual-task processing

The assumption that order control processes are associated with bottleneck processing allows new insights in the findings of neuroimaging studies, a new research area providing rich data about dual-task processing. In particular, the assumption allows formulating several critical predictions about the functional neuroanatomy of dual-task processing. First of all it predicts the observation of so-called overadditive (i.e. additional) neural activity if one compares the neural activity in a PRP dual task with the summed activation of the component tasks. Control of bottleneck processing is involved in dual-task but not in single-task situations and this should, therefore, be reflected by additional neural computations. Second, it predicts that such dual-task-related activation should be found especially in regions of the lateral prefrontal cortex (IPFC) because findings from many studies highlighted the important role of this region for cognitive control.

Consistent with these predictions overadditive neural activation had recently been shown in several neuroimaging studies that compared the fMRI activation in dual-task situations with that in single-task situations (50-54). Overadditive (i.e. dual-task-related) activation had mainly been reported for regions in the left and right prefrontal cortices known to be associated with tasks requiring active interference control (55-58) and with the control of working memory contents (59-63, see [64] for evidence from single-cell studies). Such activation was mostly located in anterior and posterior regions along the inferior frontal sulcus (IFS), which extended into the MFG. Dual-task-related activation was also found in a network of other regions including the intraparietal sulcus, the premotor cortices, and the supplementary motor areas. However, compared to these other regions the observed anterior and posterior parts of the IFS seem to represent regions of the IPFC which are most consistently related with dual-task processing across different studies (50). The specific location of dual-task control in regions along the anterior-posterior axis of the IPFC is consistent with recent findings of (65) and might reflect the extent of a distributed hierarchical prefrontal network of task control in dual tasks.

Many of the studies that reported overadditive activation investigated dual tasks consisting of a combination of two choice RT tasks presented in a PRP-like paradigm (50, 52-54, 66; but see 67, 68). This is different to some other studies which used rather complex component tasks such as reading a sentence and memorizing word information and which did not find overadditive fMRI activation when comparing dual-task with single-task-related activation (69, 70). The use of experimental paradigms that differ with respect to the amount of control about the serial scheduling of the processes in a dual task may represent one reason for the discrepancy in findings between these studies. While the PRP paradigm allows for precise control of the serial scheduling of the processes in the two tasks, complex dual-task paradigms often require a rather loose ordering of the task processes without any temporal adjacency of the bottleneck processes. Because in the latter situation there is no distinguished need for control of task order at or before a bottleneck no additional activation would be expected (53; but see 71 and below).

Although the finding an overadditive fMRI activation in dual tasks compared to single tasks coincides with the assumption of active bottleneck processing additional evidence is required to substantiate an attribution of task order control to the IPFC. This is so because empirical evidence that is based on the logic of subtraction-based fMRI approaches may be confounded by known caveats (68, 71). Therefore, several studies (41, 53, 66, 72) used other approaches to specify the role of the IPFC for dual-task processing as is discussed next.

5.2. Task order control and the lateral prefrontal cortex

Evidence allowing valid attribution of task order control to the IPFC activity was provided particularly by studies that used the methodology of parametric fMRI designs. According to that methodology, a certain process

Central attention limitation and executive control

is associated with a certain brain region, if a difficulty manipulation of that process leads to an activity change in that region.

For example, one study (53) manipulated the difficulty of task order control in different blocks of dual-task trials. In the critical conditions, participants performed a visual-manual and an auditory-manual choice reaction task in close succession. The two tasks were presented in dual-task blocks with either random temporal order of the two component tasks or in blocks with fixed order. In random-order blocks, the task order of the two component tasks changed randomly from trial to trial and participants needed to re-arrange and control the processing order permanently in order to perform the two tasks in the correct temporal order. In fixed-order blocks in which the order of the two component tasks remained the same across the entire block of dual-task trials, the need for task order control is lower compared to random order blocks, albeit still present due to the involved bottleneck.

The increased demands on the computational processes related to task order control led to increased RTs and error rates in random-order compared to fixed-order blocks (37, 40). Even more importantly, when comparing the BOLD signal changes in random-order and fixed-order blocks, the authors found an extended fronto-parietal network with bilateral activation foci in the IPFC (53). Again, the IPFC activation was mainly located in regions surrounding the left and right IFS extending from anterior to posterior portions of this sulcus and dorsally into the MFG (see also Figure 3). These activation foci overlapped closely with the activation foci obtained when subtracting the BOLD signal changes in single-task blocks from those in dual-task blocks. This indicates that activity changes in anterior and posterior parts of the IPFC are associated with active order control during dual-task processing.

The assumption about the role of the IPFC for task order control was further specified by the findings of an event-related fMRI study allowing fine-grained manipulation of the task order control at the level of individual dual-task trials (41; Figure 3). In that study, the BOLD-signal changes in so-called same-order trials were compared with that in different-order dual-task trials which were presented in the same blocks of dual-task trials. While in same-order trials the processing order of the two component tasks in a given trial N was identical to that in trial N-1, the order of the two component tasks was reversed between trial N and N-1 in different-order trials. Consistent with the assumption that task order control may rely on an episodic trace of the task order in the previous trial, RTs and the error rates were elevated in different-compared to same-order dual-task trials. Importantly, the comparison of the fMRI data between different- and same-order trials revealed two activation peaks in parts of the IPFC close to the task order control regions in (53) and to the dual-task-related regions as observed with a subtraction methodology (50).

According to recent conceptions (discussed earlier) task order control represents a mechanism that is

essential for bottleneck processing in general (5, 39, 40), and which is important in random- as well as in fixed-order dual-task blocks. Therefore, the reviewed findings of studies with parametric (41, 53) and with subtraction-based fMRI designs (50, 51, 66) suggest that task order control in dual tasks is associated with activity changes in anterior and posterior parts of the IPFC.

5.3. The relation of task order control and of other functions to the activity in the IPFC

An important question concerns the issue whether task order control can be dissociated from other cognitive functions and their related brain regions in the IPFC. Although the discussed findings and theories point to an association of task order control with the IPFC other cognitive functions during dual-task processing may be associated with these regions just as well. For example, the finding of an overadditive activation in the IPFC when comparing fMRI activation in dual-task with the summed activation in the single-task situations might point to the fact that there were increased demands on task set maintenance in the first compared to the latter condition (68, 71). The load on task set maintenance is far higher in dual-task compared to single-task blocks because of the doubled amount of task set components including the stimulus set, the motor response set, and the number of task rules maintained in working memory during task processing.

Recent findings suggest that the maintenance of the different components of a task set in working memory is served by a network of different brain centers that are distributed across the entire cortex, including its frontal parts. While a number of studies suggest an association of the maintenance of sensory stimuli with various regions in the IPFC other studies have suggested that the maintenance of rather motor-related components of task sets may be associated with increased activity in the premotor cortex as well as with the IPFC (65, 73-78).

Consistent with these findings, a recent study of our group (72) reported a neuroanatomical dissociation of task order control and task set maintenance at least for the motor-related components of the maintained task sets. In that study, the difficulty of both functions was orthogonally manipulated in one and the same fMRI study and the effects of the parametric manipulations on the resulting locations in associated brain regions were assessed. While difficulty of task order control was manipulated by a comparison of random-order and fixed-order dual-task block (53), task set maintenance was varied by a manipulation of the number of S-R rules held to be active during dual-task processing. The participants had to process four possible motor responses in each choice reaction component task in a so-called high-load and two possible motor responses in the low-load condition. The number of stimuli was held constant between the high- and low-load conditions in order to exclude possible confounding influences of the stimulus probability on the expected activated brain regions (79).

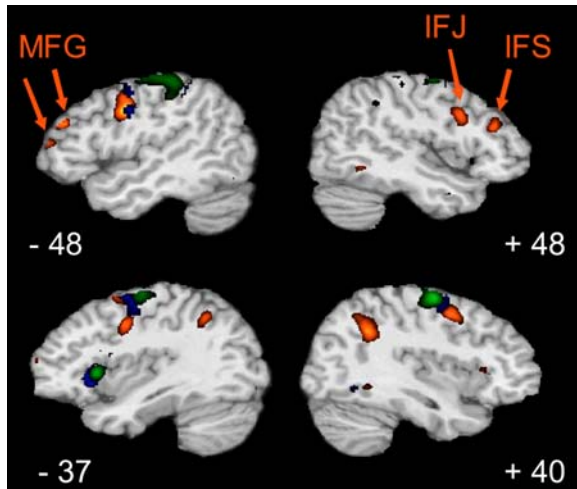


Figure 4. Cortical regions associated with task order control and with task set maintenance, (adapted from 72). Participants performed a dual task under different conditions of task order control and task set maintenance in one and the same fMRI session. Task order control was more difficult in blocks with random order compared to fixed order of the component tasks. Load for the task set maintenance was larger in high- compared to low-load dual-task blocks. While the number of relevant S-R mappings to be held in working memory during dual-task performance amounted to eight in the first, it was four in the latter type of blocks. Red – brain regions affected by the task order control manipulation, green – regions affected when task set maintenance was manipulated, blue – regions affected by both manipulations (i.e. conjunction of task order control and task set maintenance effects). MFG middle frontal gyrus, IFS inferior frontal sulcus, IFJ inferior frontal junction point (for details see 72). Numbers denote X values of the Talairach coordinates. All activations result from a whole brain random effects analysis and are significant at a level of $p < 0.001$ (uncorrected).

As the most important result, cortical activity in the IFS and the MFG was associated with task order control but not with differences in task set maintenance as is illustrated in Figure 4. By contrast, increasing demands on task set maintenance, as manipulated via the number of relevant S-R mappings, were associated with activation changes in the frontal cortex exclusively in the left and right pre-motor cortices and in the left anterior insular cortex. This suggests task order control to be a relevant mechanism of control in dual-task situations that is associated with brain activity in the IPFC and that is dissociable from other functions during dual-task processing.

6. PERSPECTIVES

An important direction of future research concerns the further dissociation of the task order control regions from regions associated with other relevant control mechanisms during dual-task processing, e.g. divided

attention, switching between tasks and others (80-82). A number of studies have shown that the need to alternate between two consecutively performed (i.e., not simultaneously performed) tasks activates brain regions in the posterior IPFC (83, 84), which partially overlap with task order control regions. Several authors, therefore, proposed the posterior IPFC to be associated with mechanisms involved in the preparation of task set information including the fast mapping of stimulus to response information, which is relevant for the response selection in a given task (84-86).

A recent study (87) proposed that the response selection bottleneck is associated with a limited capacity of the neural substrate in the posterior IPFC to maintain a prepared S-R set in an active state. The findings of that study suggest that the temporal duration of the fMRI signal in the posterior IPFC region amounts to the summed processing times of the response selection stages in Task 1 and Task 2 under condition of a short SOA in a PRP task. Consequently, one could assume that the subsequent preparation of two S-R sets (i.e. for Task 1 and for Task 2) is the essential mechanism during task order control which is associated with the observation of the IPFC activation. Note that in this case task-order-control activity in the posterior parts of the IPFC might simply be explained by the mechanism of a subsequent and alternating task set preparation of two task sets (80).

However, a pure break down of task order control to processes of the alternating and subsequent preparation of two task sets one after the other seems not sufficient to explain the task order control activation during dual-task processing. This is because a recent study (71) has shown that the activation of the posterior IPFC in dual-task situations does not simply sum up to the activation associated with the alternating preparation of two task sets. In that study, fMRI activation was compared between single-task and dual-task trials that were presented in one and the same block in random order. While the dual-task trials required simultaneous performance of the two component tasks (A and B together), single-task trials required performance of only one of the two component tasks (i.e., either A or B) presented in unpredictable order. This design ensured that the processing demands in single- and dual-task trials were equalized regarding the preparational demands because participants did not know whether a single-task (A or B) or a dual-task trial would be presented next. In contrast, the processing demands regarding the need to coordinate two simultaneous task streams were present only in dual-task but not in single-task trials. As a result, the authors found increased activation of the IPFC in dual-task compared to single-task trials, which suggests that the need of an active control of two task streams adds to the processing demands related to the pure preparation of the task sets. In addition, the greater amount of activity in dual-task compared to single-task trials and the fact that participants had randomly to alternate between Task A and Task B in the single-task trials suggests that dual-task-related activity in the posterior IPFC is not identical to task-switching related activity of the IPFC.

Although these findings point to differences between the neural implementation of task preparation and task order control, there seem to exist similarities between the neural implementation of the two functions (41, 84). Further experimentation with methodologies like the meta-analytic approach (80) or the orthogonal parametric manipulation of two functions in the same fMRI setting (72, 88) may help to elucidate this issue.

A further issue relates to the question about the specific neural mechanisms the IPFC utilizes in order to exert task order control in dual tasks. It is proposed that the IPFC exerts cognitive control in interference situations by biasing task processing in posterior task-relevant regions (56, 89). For example, Miller (56) assumes task representations in the IPFC to play a decisive role for sending biasing signals in posterior brain regions associated with the processing of stimulus and motor information that is relevant for a present task context.

LPFC-dependent modulation of neural activity in posterior perception-related regions had been shown by studies investigating interference processing in single-task situations (90, 91). For example, Egner and Hirsch (90) investigated the neural implementation of cognitive control with a Stroop task in which participants responded to faces of actors or politicians overlaid by the names of actors and politicians. Category matches between the faces and the names (i.e. both representing an actor) were defined as congruent compared to incongruent conditions. The authors found increased fMRI activation in the fusiform face area (FFA) and an increased degree of the neural connectivity between the FFA area and regions of the dorsal IPFC in so-called high control trials compared to low control trials. High control trials were trials in which the experienced conflict in the previous trial was high and has led to enhanced cognitive control in the actual trial. By contrast, low control trials were trials in which the experienced conflict in the previous trials was low and did not signal the need for enhanced control in the actual trial. The observed findings are consistent with the assumption that the enhanced activation level in the FFA promotes the task processing in the actual task situation and leads to improved performance even under conditions of processing conflicts in incongruent trials (91).

Applied to the situation of dual tasks, where conflict arises between two tasks, this is suggestive for the prediction that the regulation of the processing order of two task streams may result from biasing signals of the IPFC to posterior brain regions associated with S1 and S2. For example, in a situation with a random order dual-task paradigm, biasing signals of the prefrontal cortex may cause that the neural areas for the processing of a stimulus expected to be presented first (i.e. S1) are pre-activated before the start of the dual-task trial. Such pre-activation might stimulate immediate S1 processing in the related sensory region, which would allow advanced processing of S1 compared to S2 and, thus, would cause serial ordering of the task processes.

Careful testing of these and of related assumptions about a potential biasing influence of IPFC activation on posterior brain regions may represent one next challenging step in the investigation of the neural mechanisms of dual-task processing. Uncovering these mechanisms will further help to bridge the gap between the detailed knowledge about basic attentional limitations of the cognitive system and about the brain mechanisms involved in the management and the control of these limitations during goal-directed behavior. In particular, this will not only help to understand the reasons for the tremendous behavioral costs during dual-task processing but also to understand the mechanisms that are associated with the increased neural effort during the performance of multiple tasks.

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