

Research report

Functional neuroanatomy of interference in overlapping dual tasks: an fMRI study

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Abstract

A basic characteristic of the human action and cognition system is the occurrence of interference when participants attempt to perform two tasks at the same time. Such interference has been studied for a long time with so-called overlapping dual tasks, where two stimuli presented in rapid succession require separate responses. As an indicator of interference, reaction times on the second stimulus increase the smaller the interval between both tasks. While most behavioral studies investigated the temporal dynamics of the interference, we focused on the functional neuroanatomy of overlapping dual-task performance by using functional magnetic resonance imaging (fMRI). Participants were asked to perform two choice reaction tasks concurrently [Pashler, Psychol. Bull., 116 (1994) 220–244]. When activation in this overlapping dual-task situation was compared with the summed activation of the single component tasks, activation in the prefrontal, temporal, parietal, and occipital cortices was detected. These data suggest that the processing of the overlapping dual tasks requires an extensive and distributed network of processing centers. However, the main focus of the dual-task-related activation was located in regions surrounding the left inferior frontal sulcus. Based on our findings and on findings of other recent neuroimaging studies, we argue that activation of the left inferior frontal sulcus reflects increased synaptic activity related to the need to manage interfering information in order to determine the appropriate action.

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1. Introduction

Studies on the influence of one task on the performance in another task are of great interest for research on human action and cognition. One important phenomenon is observed in overlapping dual tasks, where separate responses (R1 and R2) are required to two stimuli (S1 and S2) that are presented in rapid succession. In such situations severe dual-task costs emerge that are related to the processing of S2. Usually, reaction times on S2 (RT2) increase dramatically when the interval between both stimuli (stimulus onset asynchrony, SOA) decreases. This increase of RT2 is

often explained by invoking a bottleneck within the processing chain that can be occupied only by one task at a time. Whenever this bottleneck is required by both tasks, S2 processing must be interrupted [72] (see Fig. 1). Such interference is proposed to emerge in nearly all kinds of dual tasks with short intervals between component tasks.

Depending on the locus of their occurrence in the processing chain, different types of dual-task interference have been distinguished (for an overview see Ref. [47]). Thus, researchers distinguish between peripheral interference at the perception stages [7], peripheral interference at the motor stages [33,44] as well as central interference at the response selection stages of RT tasks [42,47,55].

While this functional distinction of different types of interference in overlapping dual tasks is now widely accepted [14,44,47], little is known about the neuro-

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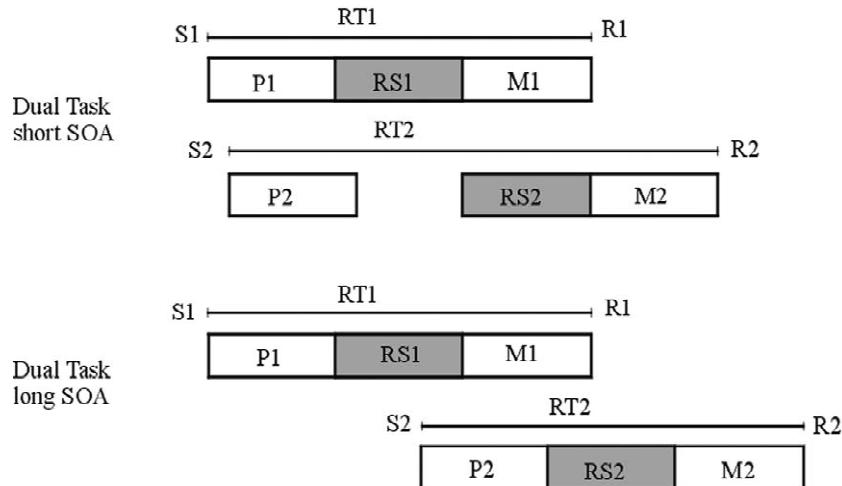


Fig. 1. Illustration of the overlapping dual-task paradigm. Processing diagram of two tasks with the following processes: S1 and S2, stimuli on tasks 1 and 2; R1 and R2, motor reactions on tasks 1 and 2; P1 and P2, perception stages in tasks 1 and 2; RS1 and RS2, response selection stages in tasks 1 and 2; M1 and M2, motor stages on tasks 1 and 2; SOA, stimulus onset asynchrony between the stimuli of tasks 1 and 2; RT1 and RT2, reaction times in tasks 1 and 2. The mechanism of bottleneck interference is illustrated by the interruption of the processing chain of task 2. RT2 decreases with increasing SOA.

anatomical correlates of overlapping dual-task interference in general.

Most studies focusing on the neuroanatomical correlates of overlapping dual-task interference have investigated neurological patients. In these studies, researchers analyzed the impact of specific brain disorders like commissurotomy [30,48], Parkinson's disease [29], or other brain injuries [15] on patients' performance in overlapping dual tasks. While these studies yielded valuable findings about interference processing in the impaired brain, it is unclear to what extent their results may contribute to the understanding of the brain mechanisms that are associated with interference in the normal brain.

Therefore, in the present study we used functional neuroimaging and investigated brain areas of normal participants, which are associated with interference in overlapping dual tasks.

The starting point of our investigation was recent evidence on the neural localization of overlapping dual-task interference obtained in an fMRI study by Herath et al. [28]. In that study, participants performed two simple reaction tasks with the same hand simultaneously upon the presentation of two stimuli with different modalities. Such situations produce peripheral interference solely at the motor stages. This is so because perceptual interference is avoided by using different perceptual modalities, and central interference is avoided by using simple reaction tasks that lack a response selection stage [17,21,25].

As a result, in Herath et al.'s study, severe behavioral decrements in the dual-task condition compared to the single-task condition were accompanied by enhanced activation in posterior portions of the right inferior frontal gyrus (IFG) close to the precentral sulcus. Accordingly,

Herath et al. proposed this cortical region to be related to motor interference in overlapping dual tasks.

Although this study provides important insights into the brain correlates of motor interference it needs to be shown whether its results hold true for other types of interference in overlapping dual tasks as well. In the present study, we aimed at assessing whether the results of Herath et al. [28] may be extended to overlapping dual tasks involving central interference.

In contrast to peripheral motor interference, central interference arises at the response selection stages in two RT tasks [72]. It emerges if participants perform two choice RT tasks simultaneously, which, contrary to simple RT tasks, involve a response selection stage. Experiments with RT measures (Refs. [47,55]; but see Ref. [58]) as well as with evoked potentials [39,46,63] have shown that in such situations a bottleneck arises at the response selection stages of the two tasks.¹ Usually, this results in an interruption of task 2 processing before the response selection stage, which in turn results in an increase of RT2 (Fig. 1).

Central interference strongly differs from the kind of interference involved in the Herath et al. study. This is so

¹A few studies suggest that central interference may disappear after extremely extensive training and the use of especially high demanding training procedures [27,57]. Participants in these studies required about eight training sessions to perform overlapping dual tasks without interference. The authors, therefore, suggest that central interference is a rather strategic phenomenon, which may be overcome with extreme practice (see Ref. [37] for a controversial view). Compared to the extreme training procedures as in Refs. [27,57] the amount of training employed in the present study is by no means sufficient to diminish central interference (see Section 2).

because in situations with central interference the component choice RT tasks require participants to select one response among several competing response alternatives in each task, and consequently, to manage their simultaneous execution. Specifically, such interference was precluded in the Herath et al. study because participants performed two simple RT tasks simultaneously that did not require the selection of different responses.

Actually, the differential involvement of the response selection component is predictive for differences in the functional neuroanatomy of the corresponding tasks. Thus, recent neuroimaging studies [9,18,68,75] suggest that the selection of responses among competing alternatives is associated with increased neural activity predominantly in regions of the left lateral prefrontal cortex. Importantly, these prefrontal regions are typically localized far more anteriorly than the interference-related activation observed in the Herath et al. study.

Thus, a study of Thompson-Schill et al. [68] has shown that the activity in regions surrounding the left inferior frontal sulcus (IFS) increases with increasing numbers of competing alternatives during the selection of appropriate responses. In addition, a number of other neuroimaging studies indicate increased activation in the left lateral PFC in paradigms exhibiting increasing demands on the response selection machinery, e.g. in task switching paradigms [18], in the Stroop-paradigm [75], or in tasks requiring the self-determined selection of action [13,22,31]. In addition, two further studies [9,59] obtained increasing activation in dorsolateral prefrontal regions, which was directly related to the competition between an automatically triggered and a required response in spatial-response compatibility [59] and in the Eriksen-flanker task [9].

Finally, single cell and lesion studies in monkeys indicate an involvement of regions surrounding the sulcus principialis, a candidate homologue of the human dorsolateral PFC, in situations where interfering information has to be maintained and processed in working memory (see Refs. [34,45] for an overview). Based on these findings, we predict cortical regions in the lateral PFC with a predominantly left lateralization to play an important role in overlapping dual tasks requiring the selection and execution of competing response alternatives.

Importantly, such a finding would extend and complement the findings of Herath et al. [28]. This study indicated that the left lateral PFC is not activated in a dual-task situation that, due to the use of simple RT tasks as component tasks, avoids central interference.

In the present study participants were presented with an auditory and a visual choice RT task. These tasks were administered in two separate single-task conditions and in one dual-task condition. In the dual-task condition the stimuli for both tasks were presented with a short variable SOA between stimuli. The use of a short SOA ensured that interference between competing response alternatives

occurred between both tasks [42,47]. Such interference emerges exclusively in the dual-task and not in the single-task conditions. We reasoned that it should be possible to localize brain areas related to this interference by analyzing the emerging dual-task-related activation.

As dual-task-related activation we decided to interpret overadditive (i.e. surplus; [20]) activation in the dual-task condition compared to the sum of activation in the single component task situations. This approach takes into account that dual-task-related activation may not be evident in the recruitment of an exclusively new neural substrate, but may be evident in a more intensive involvement of the neural substrate used for the single tasks [8,16,62].

2. Methods and procedure

2.1. Participants

Eleven right-handed participants (five female, age range from 21 to 27 years, mean age 24 years) took part in this experiment after informed consent was given in written form according to the guidelines of the Max Planck Institute of Cognitive Neuroscience Leipzig and according to the ethical review board at the University of Leipzig, Germany. All participants had normal or corrected to normal vision.

2.2. Tasks

Participants had to perform single-task, dual-task, and baseline conditions in separate blocks.

2.2.1. Single tasks

2.2.1.1. Visual single task (VIS). While lying in the fMRI-scanner, participants viewed a projection screen via a mirror. A trial in the VIS condition started with a blank green screen for 150 ms, followed by a fixation period of 850 ms. During this fixation period, three black squares (each $1.6^\circ \times 1.6^\circ$) were presented, with the middle square containing a green fixation cross ($0.38^\circ \times 0.38^\circ$). The middle square was located at the center of the screen and the two other squares horizontally to the left and right, each with a gap of 0.44° . After the fixation period, one of the three squares (the target) changed its luminance from black to a light gray for 300 ms, while the other two black squares remained on the screen. After the presentation of the target stimulus, the screen was cleared and the participants had to respond during an interval of 1050 ms. Participants had to respond with the right index finger to the left, with the right middle finger to the middle and with the right ring finger to the presentation of the right target square on two separate fMRI-suitable keypads. After responding, either a blank screen or a visual error-feedback was presented for 250 ms.

2.2.1.2. Auditory single-task (AUD). A trial in the AUD condition started with the identical blank screen and fixation period as the visual single-task. After the fixation period, a tone with a frequency of either 300, 600, or 1300 Hz was presented for 300 ms, while three black squares were presented on the screen. After the presentation of the tone the screen was cleared. The participants had to respond to the low tone with their left ring finger, to the middle tone with the left middle finger and to the high tone with the left index finger. Further characteristics of the procedure were identical to the condition VIS.

2.2.2. Dual task (DUAL)

In the DUAL condition, participants had to perform both tasks together. For that purpose, both stimuli (auditory and visual) were presented in rapid succession, separated by the stimulus-onset-asynchrony (SOA). The SOA varied randomly between 50, 125, and 200 ms. Order of stimulus presentation was balanced in separate blocks across the experiment. Thus, in one type of block the auditory stimulus appeared before the visual stimulus, and vice versa in the other type of block. Participants were instructed to respond in the order of stimulus presentation in each block. A special instruction about the upcoming task order (AUD→VIS or VIS→AUD) was given immediately before each block. Participants were instructed to respond to both tasks as fast and as accurately as possible. Furthermore, they were strongly encouraged to respond to both tasks in the order of presentation. This part of the instruction favored the first over the second task during dual-task processing. To ensure equal trial duration under each SOA condition, the time available to respond to the second stimulus was adjusted depending on the SOA. The resulting trial duration was 1050 ms. All other characteristics were identical to the single-task conditions. Altogether, participants performed 70 dual-task trials during the scanning session.

2.2.3. Baseline (BASE)

In the BASE condition participants were presented a blank screen with a fixation cross. No motor or cognitive tasks were required.

2.3. Design

A block design was used, with each block consisting of 10 trials, resulting in 26 s block duration. The blocks were separated by an inter-block-interval (IBI) of 10 s, which also served as an instruction period during which the task in the following block was explained. A session consisted of one run. All conditions were presented seven times, resulting in a total experimental run-time of 16 min and 48 s. The order of the conditions was counterbalanced, such that the probabilities of transitions were best possibly equalized, with the only exception that conditions did not repeat directly. All participants received an identical

stimulus-protocol. One to 3 days before the fMRI-measurement, participants practised the tasks outside the fMRI scanner to become acquainted with the task conditions (practice session). In the practice session, participants were presented with 120 dual-task and 140 single-task trials. The dual-task practice trials consisted of six blocks, in which the visual–manual task was presented as the first task and the auditory–manual task as the second task, and six blocks with the reversed order of tasks. The low number of practice dual-task trials should avoid dual-task learning, which might have enabled the participants to perform the dual-task without central interference. This was necessary because a few studies (Refs. [27,58]; but see Ref. [37]) have shown that under conditions of extremely extensive dual-task learning and under conditions of special dual-task learning situations central interference may disappear (see also Footnote 1).

2.4. MRI technique

Imaging was carried out at the Max-Planck Institute of Cognitive Neuroscience in Leipzig with a 3T scanner (Medspec 30/100, Bruker, Ettlingen, Germany) equipped with a standard birdcage head coil. Participants were supine on the scanner bed, and cushions were used to reduce head motion. Fourteen axial slices (19.2 cm FOV, 64×64 matrix, 5 mm thickness, 2 mm spacing), parallel to the AC-PC plane and covering the whole brain were acquired using a single shot, gradient recalled EPI sequence (TR 2 s, TE 30 ms, 90° flip angle) sensitive to BOLD contrast. One functional run with 504 volumes was administered, with each volume sampling all 14 slices. Prior to the functional runs, 14 anatomical MDEFT slices and 14 EPI-T1 slices were acquired. In a separate session, high-resolution whole brain images were acquired from each participant using a T1-weighted three-dimensional segmented MDEFT sequence. These images were linearly rotated and translated, but not resized, into the stereotactic space of Talairach and Tournoux [65].

2.5. Data analysis

2.5.1. Preprocessing

The functional MRI dataset was analyzed using the software package LIPSIA [38]. Firstly, the functional data were preprocessed. For that purpose, artifacts at scan-borders were removed and a slice-wise two-dimensional movement correction in the X- and Y-directions was applied (for details see Ref. [38]). A Gaussian spatial filter (FWHM 5.65 mm) was used for smoothing. The temporal offset between acquisition times of different slices acquired in one volume were corrected using a linear interpolation. After preprocessing, the functional and anatomical data were co-registered: firstly, the MDEFT and EPI-T1 slices geometrically aligned with the functional slices were co-registered with the high-resolution 3D

reference T1-data set of each participant. Rotational and translational parameters computed for this registration were stored in individual transformation matrices. Secondly, each transformation matrix was transformed into a standard brain size [65] by linear scaling. Finally, these normalized transformation matrices were applied to the individual functional MRI data. After anatomical co-registration, the functional data were spatially rescaled to a resolution of 3 mm³ using trilinear interpolation.

2.5.2. Statistics

Statistical analysis was based on a least squares estimation using the general linear model for serially autocorrelated observations [20]. A boxcar function with a response delay of 6 s was used to generate the design matrix. Low-frequency signal drifts were controlled by applying a temporal high-pass filter with a cut-off frequency of 0.0036 Hz to the functional data. Furthermore, design matrix and functional data were linearly smoothed with a 4 s FWHM Gaussian kernel. The degrees of freedom were adjusted to account for temporal autocorrelation due to smoothing and filtering [74]. Contrasts between different conditions were calculated using the *t*-statistics. Subsequently, *t*-values were transformed into *z*-scores. As the individual functional datasets were all aligned to the same stereotactic reference space, a group analysis of fMRI-data was performed using a voxelwise one-sample *t*-test [4]. All resulting SPMs were thresholded at $z > 3.09$ ($P < 0.001$), uncorrected. To account for multiple comparisons, we further performed a Bonferroni adjustment for an overall false-positive probability of 0.05, which was based on the total number of voxels in the brain.

To detect dual-task-related activation we interpreted our design as a 2×2-factorial design with the factors ‘auditory task’ and ‘visual task’, both incorporating the levels ‘task present’ or ‘task absent’. Both tasks absent constitute the resting baseline condition (BASE), either auditory or visual task present the single-task conditions (AUD or VIS)

and both tasks present the dual-task condition (DUAL). This enables to test for interaction following the critical interaction contrast ((DUAL–AUD)–(VIS–BASE)). If this contrast yields additional activation, then the summed effects of activation in both single tasks cannot explain it. In this case, additional neural computation must be assumed in the dual-task situation compared to both single-task situations.

3. Results

3.1. Behavioral data

As was expected, the increase of RT on task 2 with decreasing SOA ($F(2,20)=71.49$, $P < 0.001$) replicates the well-known effects of other studies [47] with the overlapping dual task paradigm (see also Fig. 2). This indicates that participants processed both tasks in overlapping fashion and that interference emerged between both tasks as illustrated in Fig. 1.

In addition, we analyzed dual-task costs by comparing performance in the dual-task conditions with that in the single-task conditions. This analysis revealed increased RT for the auditory dual-task condition (mean RT=776 ms) compared to the auditory single-task condition (596 ms), ($t(10)=10.37$, $P < 0.001$), and for the visual dual-task condition (754 ms) compared to the visual single-task condition (467 ms), ($t(10)=11.91$, $P < 0.001$). As can be seen in Fig. 2, error rates paralleled this pattern of results suggesting increased error rates in the dual-task condition (19.35%) compared to the error rate in both single-task conditions together (2.4%), ($t(10)=4.644$, $P < 0.001$).

3.2. Imaging data

3.2.1. Activation related to the single tasks

Activation related to the single tasks was detected by

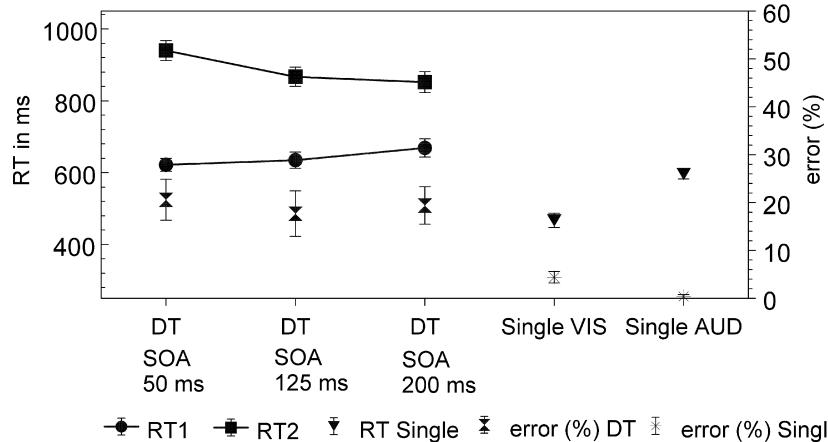


Fig. 2. Error rates and reaction times of participants in the dual-task condition (DT) and in the single-task conditions (VIS and AUD). RT, reaction time; SOA, stimulus onset asynchrony.

computing statistical contrasts between the task conditions (VIS or AUD) and the baseline (BASE), i.e. VIS–BASE and AUD–BASE (Table 1; Fig. 3, bottom rows). This analysis revealed for both tasks bilateral prefrontal activation, which extended along the superior frontal sulcus in anterior superior regions of the lateral PFC. Further activation was detected in the ascending and horizontal segments of the intraparietal sulcus (IPS) and in regions surrounding the precentral sulcus. Furthermore, commonly in both tasks activation was found in the medial superior frontal gyrus (SFG; supplementary motor area).

In addition to these regions, each task activated modality-specific cortical regions, which were related to the processing of the input information in the VIS and the AUD conditions. Thus, the VIS condition activated location-identification regions [71] in the middle temporal gyrus, while the AUD condition activated auditory cortices in the superior temporal sulci.

3.2.2. Activation related to the dual-task condition

To detect activation related to the performance of the dual-task compared to the single-task conditions, we conducted an interaction analysis and computed the interaction contrast ((DUAL–AUD)–(VIS–BASE)). The results of this analysis are presented in Fig. 3 and Table 2.

Confirming our hypothesis, the results revealed strong dual-task-related activation in the left lateral PFC. More specifically, this activation was located in regions along the left IFS and extended from anterior portions of this sulcus up to the precentral sulcus. Compared to the prefrontal activation in the single-task conditions it was located more ventrally and posterior, although some spatial overlap between lateral prefrontal foci in the dual- and the single-task conditions has to be noted (see Fig. 3). The same basic pattern was observed in the right lateral PFC, although here the extent and size (as measured by the SPMs) of the activation foci were much smaller than in the left hemisphere. Further prefrontal activation was detected in the left and right anterior insular cortex (AIC). The latter activation focus, however, did not survive after Bonferroni correction of the significance level (see Table 2).

Activation foci in medial prefrontal regions were separable in a smaller activation focus in the anterior cingulate cortex (ACC), not passing the Bonferroni correction of the significance level, and a larger activation focus within the pre-supplementary motor area (preSMA) [49,51].

In addition to the above-mentioned prefrontal regions, dual-task processing evoked bilateral activation in cortical regions in the postcentral gyrus, the middle occipital gyrus, the temporal gyrus, and in the precuneus (see Table 2).

Table 1
Talairach coordinates and Z values of activated regions in the single-task conditions. Brodmann's areas in parentheses

Brain region (Brodmann area)	Visual single task				Auditory single task			
	x	y	z	Z-score	x	y	z	Z-score
Frontal								
L middle frontal gyrus (9)	-29	41	30	9.96	-32	41	33	13.0
R middle frontal gyrus (9)	25	40	27	7.47	25	43	27	13.4
L precentral sulcus (6, 44)	-50	7	29	13.5	-50	7	29	15.0
					-32	-6	49	22.1
R precentral sulcus (6, 9)	49	3	38	12.0	31	9	28	13.7
R precentral sulcus (6)	28	-7	46	14.7				
Superior frontal gyrus, medial (6)	-5	2	47	18.7	-2	2	50	22.0
L central sulcus (4)	-35	-20	55	22.5				
R central sulcus (4)					34	-20	55	25.1
Parietal								
L intraparietal sulcus (7, 40)	-17	-70	54	14.8	-35	-46	49	18.1
	-44	-30	51	21.3				
R intraparietal sulcus (7, 40)	25	-52	50	12.5	34	-44	57	17.2
R precuneus (7)					10	-67	5	15.2
Other								
L superior temporal gyrus (41, 42)					-47	-25	7	19.9
R superior temporal gyrus (41, 42)					46	-22	9	22.6
L middle temporal gyrus (37)	-47	-58	11	9.21				
R middle temporal gyrus (39)	43	-64	12	10.6				
L middle occipital gyrus (18, 19)	-26	-88	14	15.2				
L calcarine sulcus (17)	-20	-91	1	17.3	-20	91	1	13.4
R calcarine sulcus (17)	16	-88	0	22.3	16	-88	0	17.7

Statistical significance according to Bonferroni adjustment: an asterisk denotes activation peaks, which proved nonsignificant after Bonferroni correction for multiple comparisons. Significance levels after Bonferroni correction: $P < 0.05$ corresponds to $z > 4.79$, $P < 0.01$ to $z > 5.11$, and $P < 0.0001$ to $z < 5.921$. For details of Bonferroni correction see Section 2.

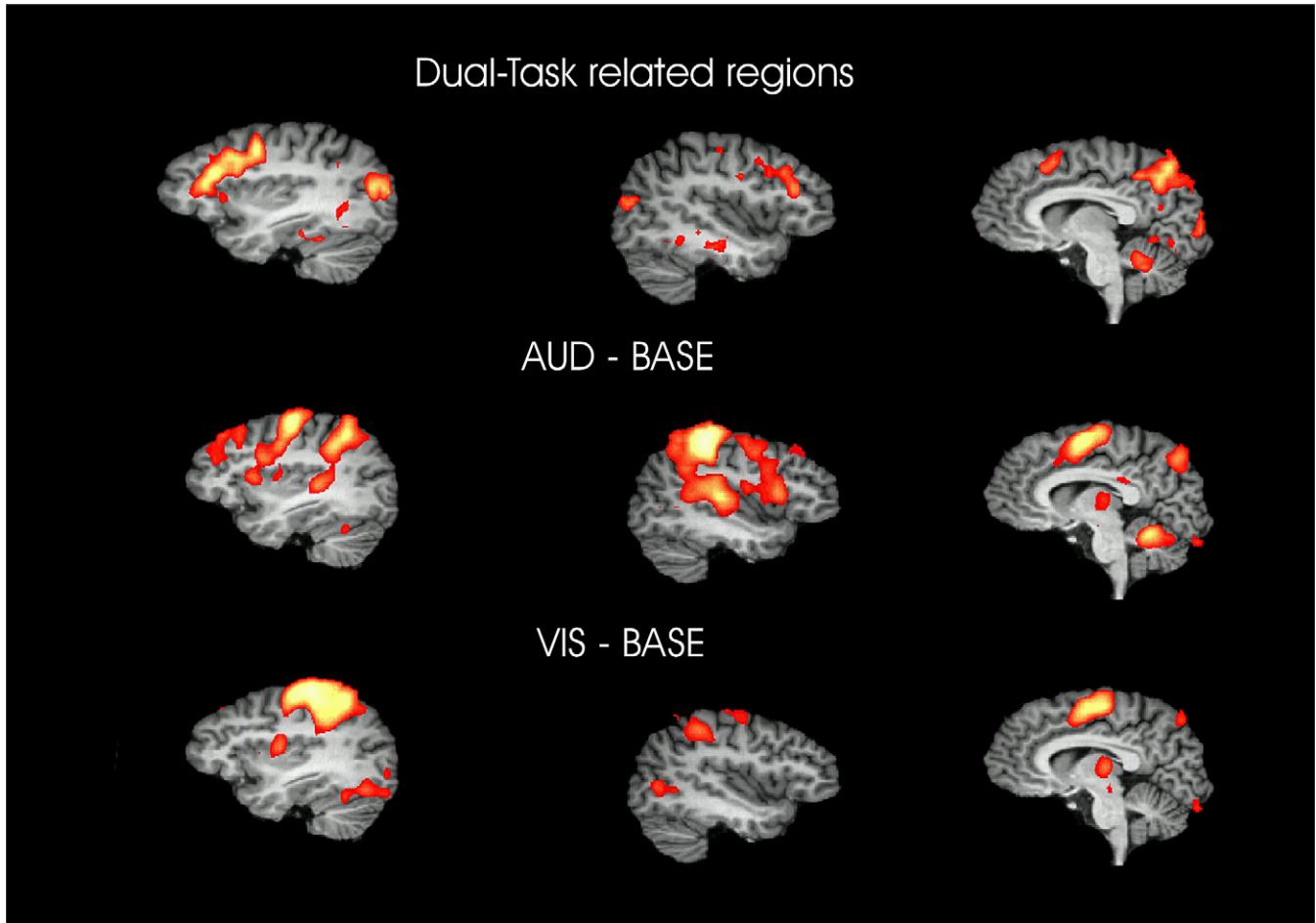


Fig. 3. Activation maps for the dual-task and for both single-task conditions. Activation in the DUAL condition was detected by computing the interaction contrast ((DUAL-AUD)-(VIS-BASE)). Activation in the single-task conditions was detected by comparing activation in the task conditions AUD, respectively VIS with BASE. For illustration purposes, a z -threshold of 4.1 was chosen for the DUAL condition and threshold of 7.1 for the single-task conditions. Sagittal views are presented with $x = -41$ for the left, $x = 31$ for the middle, and $x = -8$ for the right columns of images.

3.2.3. Region-of-interest (ROI) analysis

Finally, an ROI analysis was performed to analyze the activation changes in those dual-task-related areas that proved significant (after Bonferroni correction) with respect to the SPM-analysis mentioned above. As ROIs, we determined prefrontal voxels with peak z -values in the DUAL condition and the spatially directly surrounding voxels in a 3-D space.

The first aim of this analysis was to test for an overadditive signal change in the DUAL compared to both single-task conditions, as was the case for the SPM results. We again treated our design as a two-factorial one with the factors ‘auditory task’ and ‘visual task’, both incorporating the levels ‘task present’ and ‘task absent’ (for details see Section 2.5.2). This enabled us to test for interaction between the factors auditory task and visual task. If this statistical interaction term proves significant then there must be a non-proportional change of activation in the DUAL compared to both single-task conditions.

The analysis revealed significant interactions between

auditory task and visual task on the signal change in all tested prefrontal ROIs (all $P < 0.02$, see Table 3) with the exception of the left AIC ($P > 0.2$).

The second aim was to test whether the non-proportional signal change in the DUAL condition is indeed associated with an overadditive increase (and not a decrease) of the percent signal change in this condition relative to the percent signal changes in both single-task conditions. Furthermore, we tested whether the amounts of the signal changes associated with the comparison—DUAL versus both single-task conditions—differ between the separate prefrontal ROIs.

For that purpose, we first calculated the percent signal change in each task condition relative to the BASE condition. Next, the amount of overadditivity in the DUAL was calculated by subtracting the percent signal change of both single-task conditions from that in the DUAL condition, i.e. DUAL-VIS-AUD (see Fig. 4, panel A).

As can be seen in Fig. 4A, in all regions tested there were indeed non-proportional increases of the percent

Table 2

Talairach coordinates and Z values of the dual-task-related cortical regions. Brodmann's areas in parentheses

Brain region (Brodmann area)	Dual task			Z-score
	x	y	z	
Frontal				
L middle frontal gyrus, precentral sulcus (6, 9)	-41	8	34	9.46
L inferior frontal sulcus (9, 46)	-41	26	19	8.83
L superior frontal sulcus (6)	-20	2	50	10.2
R inferior frontal sulcus, middle frontal gyrus (9, 46)	31	24	22	7.23
R precentral sulcus/gyrus (6)	34	-2	28	5.73
R precentral gyrus (6)	34	-9	38	5.64
R superior frontal sulcus (6)	19	-1	45	6.45
L anterior insula (47)	-38	18	0	4.91
R anterior insula (47)	31	21	-2	*4.26
Anterior cingulate cortex (24)	-2	20	20	*3.51
Pre-supplementary motor area (32, 6, 8)	-8	19	41	5.79
Parietal				
L postcentral gyrus (7)	-23	-36	55	8.01
R postcentral gyrus (7)	19	-33	54	6.77
L precuneus (7 m)	-8	-61	52	7.37
R precuneus (7 m)	7	-58	51	6.40
Other				
L middle temporal gyrus (21, 37)	-50	-46	-2	8.36
R inferior temporal gyrus (37)	46	-62	-5	6.01
L parahippocampal gyrus (19, 30)	-29	-43	-3	7.73
R parahippocampal gyrus (19, 30)	22	-43	-3	6.56
L middle occipital gyrus (19)	-38	-82	27	8.12
R middle occipital gyrus (19)	34	-74	23	7.17
L lingual gyrus (18)	-14	-73	0	5.68

Statistical significance according to Bonferroni adjustment: an asterisk denotes activation peaks, which proved nonsignificant after Bonferroni correction for multiple comparisons. Significance levels after Bonferroni correction: $P<0.05$ corresponds to $z>4.79$, $P<0.01$ to $z>5.11$, and $P<0.0001$ to $z<5.921$. For details of Bonferroni correction see Section 2.

signal changes in the DUAL compared to both single-task conditions. Subsequent multiple *t*-tests revealed that the amount of the non-proportional increase was larger in the left IFS ROI than in the preSMA and in the left AIC ROIs ($t_{(10)}=2.3$ and 2.4, respectively, both $P<0.05$). Further-

more, it was larger than that in the right lateral PFC ($t_{(10)}=1.83$, $P<0.05$; one-sided).

Taken together, these findings reveal a major role of the left IFS compared to other prefrontal ROIs for dual-task processing.² Since the percent signal change parameter allows conclusions about the real amount of activation in the corresponding ROIs, the findings of the present ROI analysis complement and extend the findings about the functional neuroanatomy of dual-task processing as observed with SPMs.

Table 3
ROI analysis: results of the ANOVAs across the percent signal change values in selected prefrontal ROIs

Region of interest (ROI)	F-values (df=1,10)	P-values
L inferior frontal sulcus	11.66	0.007
R inferior frontal sulcus, middle frontal gyrus	74.26	0.000
Pre-supplementary motor area	7.55	0.018
L anterior insula	1.75	0.215

A two-factorial design with two factors—auditory task and visual task, both incorporating the levels task present and task absent—was used. Presented are the results for the interaction term between the factors auditory task and visual task. If this statistical interaction term proves significant then there is a non-proportional increase of activation in the DUAL condition compared to both single-task conditions (for details see Sections 2 and 3).

²It could be argued that the percent signal change in the left IFS ROI might have been overestimated due to a relative decrease of the amount of activation in the VIS compared to the BASE condition (Fig. 4, panel B), and that this would restrict the conclusion mentioned above. However, this seems not to be a reasonable argument because the choice of the BASE condition as a baseline against which the percent signal changes are computed is arbitrary. Therefore, the decrease of the percent signal change in the VIS condition is relative to the BASE condition. If we had chosen a different baseline with an even lower level of activation, we would not get a relative decrease of the percent signal change in the VIS condition against this new baseline. However, the relationship between the different conditions (DUAL, VIS, AUD) would remain the same, thus, resulting in the same amount of an overadditive increase in the percent signal change (DUAL vs. both single tasks).

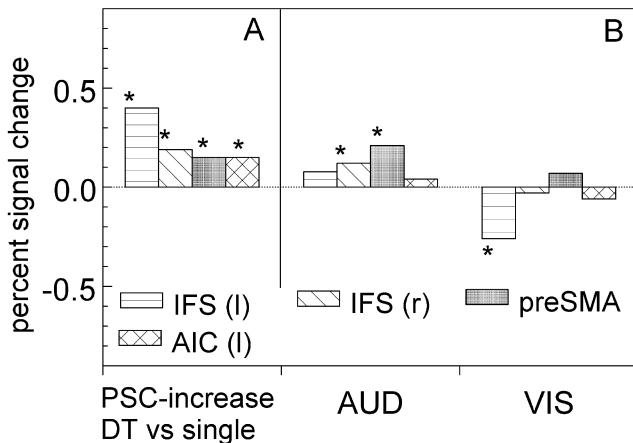


Fig. 4. Results of the ROI analysis. Panel A, increase of the percent signal change (PSC) in the DUAL relative to both single-task conditions. The numerical values for increase of the PSC were calculated according to the formula: PSC-increase/DT vs. single tasks=PSC (DUAL)–PSC (VIS)–PSC (AUD). PSCs in the conditions DUAL, VIS, and AUD were computed against the BASE condition. Presentation for dual-task-related prefrontal ROIs, which proved significant with respect to the overall SPM-analysis as well as survived subsequent Bonferroni-correction. *Denotes significant increase of the PSC in the DUAL relative to both single-task conditions. Panel B, percent signal change relative to BASE in prefrontal ROIs for the single task conditions AUD and VIS. IFS, inferior frontal sulcus; AIC, anterior insular cortex; preSMA, pre-supplementary motor area; l and r, left and right hemisphere, respectively. *Denotes a significant difference relative to BASE ($P < 0.05$).

4. Discussion

In the present study, we were interested in the functional neuroanatomy of interference, which emerges in an overlapping dual task consisting of two choice RT tasks. The results show that simultaneous performance of two choice RT tasks compared to its single component tasks leads to additional dual-task-related activation in a network of several cortical regions including the lateral and medial prefrontal, the temporal, parietal, and occipital cortices.

4.1. Overlapping dual tasks and differences in the site of activation

Importantly, the observed network is different from the findings of a recent fMRI study by Herath et al. [28]. That study indicated a region along the right IFG near the precentral sulcus to be related to interference in overlapping dual tasks. Although in our study activation was found in the right lateral PFC (e.g. in regions along the IFS) as well, this activation was located far more anteriorly (Talairach coordinates of the activation peak 31, 24, 22) than the right IFG activation in Ref. [28] (Talairach coordinates 46, 6, 26 and 52, 0, 28).

This discrepancy in findings is in accordance with the proposed differences between the processes involved in the present overlapping dual task and those in the Herath et al.

study. First of all, the specific task requirements in Ref. [28] precluded interference between competing response alternatives such that the participants performed the same rapid sequence of two right hand motor reactions on each dual-task trial. Consequently, the task required the rapid sequencing and timing of simple consecutive finger responses, which has recently been shown to activate regions in the vicinity of the precentral sulcus [3,54] close to the activation peaks observed in Ref. [28] (e.g. Talairach coordinates in Ref. [3] 54, 4, 24).

In contrast, participants in our study performed two choice RT tasks together, which required the selection of one among three alternative responses concurrently in two tasks. Because this was not the case in Ref. [28], the activation of the above mentioned network seems to be characteristic for overlapping dual tasks involving interference between competing response alternatives as compared to tasks lacking such interference.

4.2. Activation in regions along the inferior frontal sulcus

As predicted, in the present study the main activation focus was located in the lateral PFC. More precisely, this activation was located predominantly in cortical regions along the left IFS where it extended from anterior portions of this sulcus up to the precentral sulcus.

Increased activation of the IFS was recently shown in a number of neuroimaging studies, which investigated the functional neuroanatomy of tasks exhibiting increased demands on the management of interfering response alternatives. For example, reliable activation of the left IFS was found in task switching paradigms [18], in the Stroop-task [75], or in stimulus-response compatibility tasks [59]. Moreover, studies with neurological patients indicated increased difficulties of patients with left lateralized lesions in the lateral frontal cortex in the task-switching paradigm [43,53] or in the Stroop-task [50].

Based on these findings as well as on our findings we conclude that interference between competing response alternatives is associated with increased activation of the predominantly left IFS.

Compared to previous results, the findings of the present study, however, allow an even more elaborate understanding of the IFS function in interference processing.

In paradigms like the Stroop-task or the task-switching paradigm, interference usually occurs between two competing responses that are related to one and the same stimulus within one task. (For example in the Stroop-task, saying RED or GREEN to the red colored word ‘green’.) Moreover, the competing response alternatives are often related to the same motor effector, e.g. the speech muscles in the Stroop-task. Therefore, one cannot exclude that the observed IFS activation in these studies is specific to interference between competing motor programs of one

effector, which would suggest a rather reduced role of the left IFS in interference processing.

In contrast, interference in the present overlapping dual-task situation emerges between the processing streams of two independent tasks, which, moreover, require responses with two different motor effectors. Thus, in this respect, our results extend those of previous studies because they suggest that activation in regions surrounding the left IFS is not limited to interference between competing motor responses for the same stimulus. In contrast, it must be related to higher order mechanisms [10,40], which are required when interference between two independent tasks has to be managed.

A question arises about the possible nature of these mechanisms. According to recent models of overlapping dual-task performance, the processing stream in one of the two tasks of an overlapping task is interrupted while competing processing in the other task is underway. Most researchers assume that this interruption is located at the response selection stage of choice RT tasks [42,47,55], thus representing a case of central interference. Usually, this results in increasing RT2 with decreasing SOA as can be observed in our study as well as in a large body of other RT studies (for an overview, see Ref. [47]).

The interruption of one processing stream during the ongoing processing of another task requires a number of additional executive processes regulating the attentional demands between both tasks [14,44]. Specifically, the fast switching of attention between different processing streams [23,36], the fast preparation of competing task sets [5], as well as the preparation of the order of potentially interfering processes [14,44] just before or at a bottleneck is required if two tasks have to be coordinated with respect to an involved bottleneck. Because these processes are exclusively involved in the dual-task and not in the single-task situation, we conclude that the observed dual-task-related activation of the IFS is related to these processes.

This proposal is also supported by findings of another of our own studies [64]. In that study, a parametric manipulation [6,32,61] of the attentional demands in different overlapping dual-task conditions led to changing activation in those regions, which proved to be dual-task-related in the present study. It would be interesting for future studies to investigate whether different parametric manipulations of the different executive processing aspects, e.g. the switching between processing streams or the fast preparation of competing task sets, draw on the same or different subregions of the IFS as observed in the present study [19].

It could be argued, however, that behavioral evidence [42,47,55] suggesting central interference in the present paradigm is ambiguous because of findings indicating attenuation of central interference in overlapping dual tasks [58]. The latter study and some other studies highlight the role of a motor bottleneck instead of [44,58], or in addition to [14], a central bottleneck when participants respond with two hands on both tasks in an overlapping dual task.

Therefore, theoretically, it could be that activation of regions surrounding the IFS might be associated with processes managing motor interference just as well as with processes associated with central interference.

In the present study, we do not exclude the possibility of additional motor interference because both tasks required manual responses. However, a localization of processes associated with pure motor interference in the IFS instead of those associated with central interference seems unlikely because this assumption would contrast pre-existing knowledge about the corresponding cortical regions. Thus, in the case of pure motor interference other cortical regions than the IFS are expected to be activated, such as e.g. the precentral sulcus [28,56] or the preSMA [41,69]. Furthermore, such an assumption would strongly contrast with recent findings [10,40] pointing to a functional dissociation between lateral and medial prefrontal regions that will be discussed more extensively in the next section.

4.3. Activation in medial prefrontal regions

The presently observed activation in medial prefrontal regions was located within the preSMA [49,51]. A number of studies investigating the functional neuroanatomy in different interference paradigms indicated concomitant activation of the lateral PFC and the preSMA [10,40]. For example, activation in these regions had been shown in studies investigating response competition with the Stroop-paradigm [10,40,75] as well as with the Eriksen-flanker task [69]. Recent models of Carter and co-workers [10,40] suggest a functional dissociation of the lateral and the medial PFC in cognitive control during task processing. While the lateral PFC is suggested to be involved in higher-order control of the attentional demands of a task, medial prefrontal regions seem to be involved in local control of specific motor competition whenever alternative responses have to be performed.

In the present overlapping task, subjects had to respond with the fingers of both hands on two different tasks. As had been mentioned earlier, in this situation motor interference between competing effectors may emerge in addition to central interference [14]. Single cell and tracer studies with monkeys [41,66,67] indicated a prominent role of preSMA neurons in mechanisms of motor preparation and sequencing [41] as well as in situations where a currently activated motor program has to be discarded in order to activate a different motor program [60]. These characteristics qualify the preSMA in addition to the precentral sulcus [28] as an appropriate cortical area involved in local mechanisms of response competition in overlapping dual tasks.

Our data do not allow differentiating the functions of the IFS from that of the preSMA in the present overlapping task. However, the results fit quite well with the above-mentioned conception of Carter and co-workers [10,40] about different functions of the lateral and medial PFC in

situations requiring the management of interfering response alternatives.

4.4. Activation in other cortical areas

Activation in medial parietal, occipital, and temporal regions has been shown by different neuroimaging studies that investigated mechanisms of focusing visual attention. Thus, results of Corbetta et al. [11,12] indicate that requiring participants to focus visual attention on different task-relevant features of the stimulus material may increase activation in the middle temporal gyrus as well as in the parahippocampal gyrus and in the precuneus. Activation in these regions is also in accordance with findings from single cell studies with monkeys [26] as well as from lesion studies in monkeys [70] and humans [2] on the involvement of these areas in visual object and spatial processing [70]. We believe that in our study increased activation of these regions reflects an enhancement of the neural activity in visual association areas during the perception of visual stimuli when auditory information has to be processed simultaneously [73].

In sum, these findings indicate that a number of different cortical areas are involved at different levels of task control when subjects have to manage interference between different response alternatives in overlapping dual tasks.

4.5. Subcortical regions

A puzzling finding for the assumed role of cortical areas in interference management comes from studies that investigated the performance of commissurotomy patients in overlapping dual-task situations [30,48]. Commissurotomy patients suffer from a lack of cortical interhemispheric information transfer due to surgical transection of the transcallosal fibres. Pashler et al. [48] reported normal interference effects (i.e., increasing RT₂ with decreasing SOA between S₁ and S₂) when those patients performed two concurrent choice RT tasks, which are mapped separately to the different hemispheres. The authors concluded that interference in overlapping dual tasks is associated with subcortical mechanisms.

In our view, an exclusive attribution of interference in overlapping dual tasks to subcortical structures seems premature. The data with commissurotomy patients show that interference management does not rely on cortical information processing alone. There seem to be additional subcortical projections, which complement cortical processes involved in the management of interference in overlapping dual tasks. Such projections might be associated with subcortical motor coordination in commissurotomy patients as has recently been suggested [30,52].

An involvement of additional subcortical neuronal pathways would not contradict the findings of the present study. In contrast, our data, while indicating the in-

volvement of cortical areas, extend the results of the commissurotomy studies [30,48], which focused exclusively on subcortical neural structures as correlates of interference in overlapping dual tasks.

4.6. Relationship to other studies on the functional neuroanatomy of dual-task processing

The issue of dual-task-related activation in overlapping dual tasks is important against the background of previous neuroimaging research, which used other dual-task paradigms than the present overlapping dual tasks. These studies focused mainly on the localization of brain areas associated with increased working memory load during dual-task processing [8,16,35].

Taken together, these studies yielded rather contradictory evidence with respect to the question of whether additional cortical areas are associated with dual-task compared to single-task performance. Thus, some studies [17,36] have shown additional dual-task-related activation in lateral prefrontal and parietal areas, which is, in particular, consistent with the present findings. However, other studies [1,8,35] could not find any additional activation associated with dual-task processing.

Although these studies and the present one focused on different phenomena, the specific methodology of overlapping dual tasks employed in the present study may help to improve future investigations about the functional neuroanatomy of dual-task processing. This in turn, may help to get a more appropriate answer on the question of additional cortical areas associated with dual-task processing.

Previous studies used rather complex dual-task paradigms, which did not allow identification of the exact type of interference involved in the particular dual-task situation. For example, in Ref. [8] participants had to read sentences and, concurrently, to remember for recall some pieces of information from these sentences. In contrast to these paradigms, the component tasks in an overlapping dual-task paradigm are relatively simple and well-defined. This allows identification of the exact nature of dual-task interference, as opposed to the previous studies in which an additional influence of task complexity might have contaminated the neuroimaging results (e.g. Refs. [1,8,16,24]).

Moreover, the tasks in the overlapping dual-task paradigm are presented with a short SOA, which ensures the occurrence of interference between both component tasks. The occurrence of interference, however, seems to be an important precondition for the involvement of additional neural regions during dual-task processing [28,64]. Previous studies with other dual-task paradigms, due to the use of large time scales for the component tasks, often did not allow controlling for the occurrence of dual-task interference at all [1]. Therefore, the absence of dual-task-related activation in some of these studies has to be interpreted with caution.

The above-mentioned methodological characteristics make the overlapping dual-task paradigm an appropriate paradigm for studying the functional neuroanatomy of dual-task processing. By manipulating different types of interference in greater detail and localizing its neural correlates in the brain, future studies with the overlapping dual-task paradigm may further uncover the neural mechanisms involved in capacity-limited information processing.

5. Conclusion

When participants perform two choice RT tasks in close succession, i.e. in an overlapping dual task, severe dual-task costs emerge at least for the second of these tasks as indicated by increased reaction times or error rates. While this interference effect seems to represent a basic processing limitation of the human brain, little is known about the functional neuroanatomy of interference processing in overlapping dual tasks. In the present investigation, we showed that the processing of overlapping dual tasks is accompanied by increased fMRI activation in prefrontal, temporal, parietal, and occipital cortices. These data suggest that the performance of overlapping dual tasks requires an extensive and distributed network of processing centers. As a further main finding, a subsequent ROI analysis revealed that the main focus of the dual-task-related activation was located in regions surrounding the left inferior frontal sulcus. Based on this finding and on converging evidence from other neuroimaging studies, we argue that activation of the left inferior frontal sulcus reflects increased neural activity associated with the management of interference between competing response alternatives. It is assumed that interference management requires a number of executive processes regulating the attentional demands between two or several processing streams. These processes are additionally involved in dual-task compared to single-task conditions. Therefore, they are assumed to be associated with the observed increased activity of regions surrounding the left IFS.

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