available at www.sciencedirect.com www.elsevier.com/locate/brainres**BRAIN
RESEARCH****Research Report****The capacity constraint in the prefrontal and parietal regions for coordinating dual arithmetic tasks**Bo-Cheng Kuo^a, Yei-Yu Yeh^{a,*}, Der-Yow Chen^{a,b}, Keng Chen Liang^a, Jyh-Horng Chen^b^aDepartment of Psychology, National Taiwan University, Taipei, Taiwan^bInterdisciplinary MRI/MRS Laboratory, Department of Electrical Engineering, National Taiwan University, Taipei, Taiwan

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ABSTRACT

Using a dual-serial-arithmetic paradigm, we examined whether a capacity limitation constrains the neural activation that underlies dual-task performance. Six conditions were run in the experiment (the baseline, single-addition, single-subtraction, dual-addition, dual-subtraction, and the dual-operation condition). In the baseline condition, participants were asked to remember the initial pair of numbers and ignore subsequent stimuli. In the single-addition and single-subtraction conditions, participants had to calculate a running total over a series of stimuli. In the dual-addition and dual-subtraction conditions, they had to do two arithmetic tasks involving the same operand (e.g., + 2 and + 7, – 3 and – 5). Participants performed one addition and one subtraction task (e.g., + 2 and – 7, – 3 and + 5) in the dual-operation condition. The functional magnetic resonance imaging results showed strict left prefrontal and parietal regions in the single-addition condition and bilateral activation in the single-subtraction condition. Greater activation in the prefrontal and parietal regions was observed in both the dual-operation condition and the dual-addition condition in comparison to the single-addition condition. No greater activation was observed in either the dual-operation condition or dual-subtraction condition in comparison to the single-subtraction condition. These results suggest a constraint imposed by a limit in capacity for the neural activity subserving dual-task performance when one of the tasks places high resource demands on the executive network.

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1. Introduction

Coordinating two tasks requires executive processes such as task switching, response selection, and resource allocation (Baddeley, 1996). Two approaches have been adopted in imaging studies to uncover the neural correlates of dual-task coordination. One approach, based on a theory that emphasizes a central bottleneck in response selection (Pashler, 1994; Pashler and Johnston, 1998), manipulates the stimulus onset asynchrony (SOA) between the stimuli of the two tasks to investigate the neural correlates

related to resolving dual-task interference (Dux et al., 2006; Herath et al., 2001; Jiang, 2004; Schubert and Szameitat, 2003; Sigman and Dehaene, 2005, 2006; Stelzel et al., 2006; Szameitat et al., 2002, 2006). Another approach, the concurrent dual-task method, presents the stimuli of the two tasks simultaneously. As the SOA in stimulus presentation is zero in this context, the two tasks must compete for attentional resources. This approach has been used to uncover the neural mechanisms of dual-task coordination (Adcock et al., 2000; Bunge et al., 2000; Collette et al., 2005; D'Esposito et al., 1995; Erickson et al., 2005; Goldberg et al.,

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1998; Jaeggi et al., 2003; Just et al., 2001; Klingberg, 1998; Klingberg and Roland, 1997; see Collette and Van der Linden, 2002 for a review).

A resource model has been proposed to account for neural activation in dual-task coordination (Bunge et al., 2000). It suggests that dual-task performance is merely associated with stronger and more extensive activation of the same brain regions that are associated with the corresponding single tasks. However, there may be a limit on the brain activation that can support concurrent processing (Just et al., 2001). Previous image studies using the concurrent method have not provided conclusive evidence of the context under which capacity limitation constrains the neural activation that subserves dual-task performance.

Using the concurrent method, Goldberg et al. (1998) found less prefrontal activation when the Wisconsin Card Sorting Test (WCST) and an auditory verbal shadowing task were performed concurrently in contrast to the single WCST condition. This finding suggests an attenuation of prefrontal (PFC) activation when the task demand is high. Just et al. (2001) used two relatively independent tasks (a visual mental rotation task and an auditory sentence comprehension task) in a concurrent task paradigm. They found the activation volume in the dual-task condition was less than the sum of the activation volumes in the domain-specific visual and auditory areas subserving each single task. Their results also showed that the PFC activation volume in the dual-task condition was not greater than the PFC activation summed from the two single tasks. As the PFC activation was minimal in performing each single task, their results suggest that PFC activation does not increase in order to subserve dual-task performance even when each task does not place a high resource demand on the PFC.

Jaeggi et al. (2003) showed that dual-task performance does not necessarily lead to a reduction of neural activation. They asked participants to perform a visual n-back task, an auditory verbal n-back task, or both concurrently. They also manipulated the memory load in each task. Their results showed a lower neural activation subserving dual-task performance under the high memory load only when activation in the dual-task condition was analyzed with the summed activation of the corresponding single tasks. When the neural activation from the single tasks was used in the analysis, there was no attenuation in the neural activation subserving dual-task performance under a high load. The appropriate measure for reflecting a capacity constraint in the neural activation subserving dual-task performance remains a research question.

The purpose of the present study is to understand whether and under what conditions a capacity limitation constrains the neural mechanisms that subserve dual-task performance. Except for Jaeggi et al.'s (2003) study, previous imaging studies using the concurrent task method did not manipulate the resource demand in each task. Jaeggi et al. (2003) manipulated the memory load in each n-back task, but the load was always the same between the two tasks. It is unclear whether their results would generalize to dual-task conditions in which different processes are involved in the two tasks.

We designed a serial-arithmetic task (see Fig. 1 and the Experimental Procedure section for a detailed description) in which participants had to perform a series of arithmetic operations until the test probes were presented. Six conditions

Fig. 1 – An example of stimuli used in the six conditions.

were designed: baseline, single-addition, single-subtraction, dual-addition, dual-subtraction, and dual-operation. In all six, each block consisted of an initial pair of stimuli, three subsequent presentations of pairs of stimuli, and then a pair of test probes. In the baseline condition, participants were required to hold the first pair of numeric digits in working memory while they viewed the three subsequent pairs of stimuli. They then indicated whether the test probes matched the initial pair. In the other five conditions, they performed either one or two arithmetic operations during each of the three middle presentations, and then indicated whether the test probe matched their resulting calculations.

An arithmetic operation engages multiple executive processes including ordering arithmetic procedures, retrieval of arithmetic facts, maintaining and updating intermediate results for further operations, and response selection (Burbard et al., 1999; Chochon et al., 1999; Dehaene et al. 1999, 2003; Fürst and Hitch, 2000; Kong et al., 2005; Lee and Kang, 2002; Logie et al., 1994; see Ashcraft, 1992 for a review). In contrast to the baseline condition, the single-addition task and the single-subtraction task involve three units of multiple processes with each unit consisting of one arithmetic operation and also temporary storage of the results for the next operation. Thus, each single task should impose a resource demand on the prefrontal-parietal executive network.

Converging evidence from imaging studies has shown that a subtraction operation is more complex than an addition operation. A left hemispheric dominance in the prefrontal-parietal network has been observed for addition operations (Kong et al., 2005) to subserve executive processes and also the use of a verbal number code for phonological representations and verbal rehearsal. Subtraction tasks engage additional

visuospatial processes such as representing the numbers in analog codes and aligning them in a continuous manner on a number line (Burbard et al., 1999; Chochon et al., 1999; Dehaene et al., 1999; Kazui et al., 2000; Kong et al., 2005). The additional processes also engage executive processes such as ordering and comparing the stimuli on the number line. As a result, bilateral prefrontal and parietal regions are activated for subtraction tasks as the neural mechanisms of the visuospatial processing are predominantly in the right hemisphere (Burbard et al., 1999; Chochon et al., 1999).

The contrast between the single-addition task and the single-subtraction task reflects the demand imposed by three arithmetic operations. Given the difference in the amount of neural activation for one arithmetic operation, the resource demands that the single-subtraction task places on the prefrontal-parietal network should be much higher than the demands that the single-addition task imposes. With this difference, we can examine whether the capacity constraint in a dual-task condition depends on the resource demand imposed by a single task.

The use of a serial-arithmetic task also ensures that competition for limited resources is strong in the dual-task condition, as the two tasks place demands on a common visual modality, working memory maintenance, arithmetic operations, the updating process, and response selection. In contrast to each single-task condition, the dual-task conditions demand another arithmetic operation in each of the three intermediate stimulus presentations. All three dual-task conditions require a coordination of cognitive processes between the two tasks that is mediated by the executive network for planning, switching, and resource allocation. With these three dual conditions, we extend Jaeggi et al.'s (2003) study.

The question of interest is whether neural activation increases in a dual-task condition in contrast to the single-task conditions. If a biological constraint sets the maximum level of neural activation in the prefrontal-parietal executive network, it is likely that no greater activation in the prefrontal and parietal regions would be observed when contrasting a dual-task condition (dual-subtraction or dual-operation) with the single-subtraction condition because the subtraction task places high resource demands on the executive network. In contrast, greater prefrontal and parietal activation should be observed when contrasting a dual-task condition (dual-addition or dual-operation) with the single-addition condition as the single task's resource demands on the executive network do not approach the asymptote. Whether neural activation in the dual-task condition is greater than in the single-task condition depends on the level of neural activation evoked in the single task.

2. Results

2.1. Behavioral results

Table 1 shows the mean accuracy (percentage of correct responses) and reaction time (RT) of correct responses in each condition. A one-way repeated measure analysis of variance (ANOVA) was conducted with task condition as the single

Table 1 – Means and standard errors in accuracy (% correct) and reaction time (RT in ms)

	Accuracy	RT
Baseline	98.86 ± 2.41	865 ± 103
Single-addition	95.46 ± 8.04	896 ± 134
Single-subtraction	89.77 ± 10.42	885 ± 139
Dual-addition	75.00 ± 18.46	971 ± 150
Dual-subtraction	68.18 ± 18.74	925 ± 326
Dual-operation	65.34 ± 13.42	997 ± 181

Accuracy in all the conditions is above the chance level of 25% based on the probability of correct guessing each response in a two-alternative forced choice is 50%.

factor to compare performance among the five arithmetic conditions. The main effect of task condition was significant on accuracy [$F(4, 10) = 13.19, p < .0001$] and the post hoc analysis showed that performance in all three dual-task conditions was significantly ($p < .05$) worse than performance in each of the single-task conditions. There was no significant difference among the dual-task conditions; there was no significant difference between the two single-task conditions.

As the chance of correctly guessing a response to each test probe is 50%, the chance of a correct response to both probes is 25% for all the six conditions. Performance was well above the chance level, with a high percentage of correct responses in each single-task condition. There was a double-task cost, as the accuracy in each dual-task condition was lower than the mean expected value in accuracy on the assumption that the two tasks were independently performed.

The low accuracy in the dual-task conditions is of concern as it is possible that participants gave up on one task. To investigate this possibility, we examined whether there was a bias toward responding only to one task in the three dual-task conditions. The results showed that participants did not adopt this strategy as the accuracy was not significantly different [$t(10) = 0.09, p > .1$] between the left-matching blocks that required a motor response for the left task and the right-matching blocks that required a motor response for the right task (see the Experimental Procedure section).

The RTs may be less informative because of the instruction that emphasized accuracy and because there was a 2s blank interval for response preparation between the last arithmetic pair and the probes. The ANOVA result showed a null main effect of task condition [$F(4, 10) = 1.09, p = 0.37$]. However, planned comparisons showed a significant result between the single-addition condition and the dual-operation condition [$t(10) = 2.52, p < .05$] and between the single-subtraction and the dual-operation condition [$t(10) = 2.58, p < .05$]. There was no significant difference between the dual-addition and the dual-subtraction [$t(10) = 0.44, p > .5$], between the dual-addition and dual-operation [$t(10) = 0.42, p > .5$], and between the dual-subtraction and the dual-operation [$t(10) = 1.04, p > .1$]. The null difference in the contrasts involving the dual-subtraction condition may have arisen because there was a trend that the variance in this condition was larger than the variance in the other two dual-task conditions ($p < .1$). To some participants, the dual-subtraction task may have been more difficult than the dual-addition or the dual-operation task.

2.2. fMRI results

2.2.1. Brain regions in the single and dual arithmetic tasks

Only correct blocks were included in the analysis of imaging data. To show the brain regions activated for subserving the arithmetic task in the five conditions, the baseline condition was subtracted from each arithmetic condition. All five arithmetic conditions activated brain regions in the frontal, parietal, and occipital cortices of the left hemisphere including the middle frontal gyrus (MFG, Brodmann areas, BAs 6, 8, 9, and 46), inferior frontal gyrus (IFG, BA 44/45), superior parietal lobule (SPL, BA 7), precuneus (PCu, BAs 7 and 19), inferior parietal lobule/intraparietal sulcus (IPL/IPS, BA 40), and the inferior occipital gyrus (IOG, BA 18). The right cerebellum was also involved in arithmetic operations (Table 2, Fig. 2).

The single-subtraction, dual-subtraction, and dual-operation conditions additionally activated the right MFG (BAs 9 and 46), SPL (BA7) and angular gyrus (AG, BA 39). Activation in the fusiform gyrus (FFG, BA 19/37) was observed in the dual-subtraction and dual-operation conditions and activation in the thalamus was observed in the dual-operation condition. The single-subtraction and all three dual-task conditions showed

extended activation in the left IFG (BA 46), the left middle occipital gyrus (MOG, BA 18/19), and the bilateral lingual gyrus (LG, BA 17/18).

2.2.2. Neural activity associated with dual series of arithmetic operations

The whole-brain comparison results accord with previous findings, demonstrating the involvement of the same brain regions in both the single- and dual-task conditions (Adcock et al., 2000; Bunge et al., 2000). We first examined whether participants processed the two tasks independently. As the summed activation reflects the neural activation involved when the two tasks are performed as independent tasks (Just et al., 2001), we compared the sum of the activation from the single-addition and single-subtraction tasks to the activation in the dual-operation task condition. Activation in the dual-operation condition was not significantly greater than the summed activation. Instead, the summed activation was greater than the activation in the dual-operation condition in the prefrontal regions including the MFG (BAs 6, 9, and 46) and IFG (BA 45) and in the parietal regions including the IPL/IPS (BA 40) and the SPL (BA 7) of the left hemisphere. This finding suggests that the

Table 2 – Brain areas and their Talairach coordinates in which significantly activated clusters were detected for single-addition, single-subtraction, dual-addition, dual-subtraction, and dual-operation conditions

Brain regions	BA	Single-addition		Single-subtraction		Dual-addition		Dual-subtraction		Dual-operation	
		x, y, z	t	x, y, z	t	x, y, z	t	x, y, z	t	x, y, z	t
MFG	L 8	-51, 8, 40	10.29	-48, 6, 35	9.53	-48, 6, 38	9.23	-51, 8, 38	5.16	-51, 10, 38	8.24
	L 6	-28, -2, 46	7.39	-28, -4, 39	7.00	-32, 0, 44	7.57	-26, 2, 39	6.36	-26, -2, 46	5.51
	L 9	-48, 15, 27	7.73	-48, 11, 25	11.71	-48, 11, 25	8.28	-48, 17, 29	5.25	-32, 6, 33	7.66
	R 9			40, 15, 23	6.17			46, 11, 22	10.12	46, 11, 23	7.10
	L 46	-51, 30, 21	4.59	-48, 26, 24	9.50	-48, 30, 24	7.75	-48, 32, 22	7.20	-50, 30, 22	9.02
IFG	R 46			51, 34, 20	5.76						
	L 46			-48, 43, 5	7.06	-48, 43, 3	4.45	-32, 32, 15	5.88	-36, 31, 6	4.31
SPL	L 44/45	-38, 24, 17	5.85	-32, 24, 8	4.69	-32, 24, 8	4.35	-38, 22, 17	4.73	-42, 22, 19	6.45
	L 7	-26, -62, 49	7.93	-26, -66, 49	10.72	-24, -65, 51	9.50	-22, -65, 51	5.05	-24, -63, 51	9.59
Pcu	R 7			30, -60, 42	6.68			30, -60, 51	5.74	28, -58, 47	5.30
	L 7	-24, -74, 44	6.70	-24, -66, 38	7.87	-24, -64, 36	6.04	-12, -67, 53	4.34	-20, -60, 34	11.65
IPL	L 19	-28, -76, 35	4.39	-28, -70, 27	7.3	-28, -69, 27	5.68	-20, -57, 34	7.70	-30, -76, 30	9.36
	L 40	-42, -39, 41	7.49	-40, -48, 50	5.81	-42, -45, 41	5.53	-46, -37, 41	6.14	-44, -39, 42	6.22
AG	R 39			32, -57, 34	5.96			32, -59, 32	4.96	30, -60, 36	4.93
FFG	L 19/37							-44, -74, -11	5.89		
MOG	R 19/37									48, -61, -19	7.28
	L 18/19			-32, -79, 15	5.19	-32, -87, -1	7.04	-30, -88, 21	7.86	-32, -85, 17	8.51
IOG	L 18	-30, -90, -11	9.31	-26, -88, -7	6.21	-40, -84, -8	7.65	-34, -86, -9	7.15	-32, -84, -4	9.53
	R 18	32, -90, -6	7.83					38, -84, -1	5.27	32, -86, -9	5.48
LG	L 17									-16, -90, -7	5.37
	R 17									26, -92, -6	7.51
Thalamus	L 18/17					-18, -94, -9	5.00	-12, -86, -18	4.40	-4, -90, -9	5.99
	R 18/17					24, -94, -5	5.93	18, -95, -5	5.27	8, -90, -11	5.11
Cerebellum	L									0, -23, 7	6.11
Uvula	R	28, -73, -23	6.35	20, -73, -23	6.91	18, -73, -23	7.10	28, -71, -23	5.20	18, -73, -23	7.17
Nodule	R									2, -59, -24	5.56
Declive	R	4, -79, -21	6.11							8, -81, -21	6.44
	L							-2, -82, -18	6.66	-16, -83, -19	5.41

Note. BA: Brodmann area, t: t-value, L: left hemisphere, R: right hemisphere, MFG: middle frontal gyrus, IFG: inferior frontal gyrus, SPL: superior parietal lobule; PCu: precuneus, IPL: inferior parietal lobule, AG: angular gyrus, FFG: fusiform gyrus, MOG: middle occipital gyrus, IOG: inferior occipital gyrus, and LG: lingual gyrus.

Fig. 2 – Areas of significant activation associated with (a) the single addition task, (b) the single subtraction task, (c) the dual-addition task, (d) the dual-subtraction task, and (e) the dual-operation task.

processes of the two tasks are not completely independent. Participants did not perform the two tasks independently in parallel or in sequence.

To verify the prediction based on the hypothesis of a biological constraint in the executive network, we compared neural activation in the following four contrasts: dual-addition minus single-addition, dual-subtraction minus single-subtraction, dual-operation minus single-addition and the dual-operation minus single-subtraction condition. When contrasting a dual-task condition (either the dual-addition or dual-operation) to the single-addition condition, greater activation was observed in the prefrontal regions including the IFG (BAs 44/45 and 46) and MFG (BAs 9 and 46) and also the parietal regions including

the SPL and PCu (BA 7), and IPL/IPS (BA 40) of the left hemisphere (Fig. 3). In contrast, no significant activation was observed in the prefrontal and parietal regions when a dual-task condition was contrasted with the single-subtraction condition. The findings support a biological constraint (Just et al., 2001) in the prefrontal-parietal executive network when one task places high resource demands on the network.

2.2.3. Regions-of-interest (ROI) results

Because the random effect analysis is a strict and conservative test (Göbel et al., 2004), the ROI analysis approach was also adopted in this study. Fig. 4 shows the mean signal changes in the five ROIs that are activated in all five arithmetic conditions (the right SPL and the MFG, IFG, IPL/IPS, and the SPL of the left hemisphere). Excluding the dual-operation condition, we first conducted a 2 (task condition: single or dual) $\times$ 2 (arithmetic operation: addition or subtraction) repeated measures two-way ANOVA. This result showed a significant main effect of task condition in the MFG [$F(1, 10) = 5.11, p < .05$] and IFG [$F(1, 10) = 5.46, p < .05$] of the left prefrontal regions. A trend of difference in task condition was also observed in the left SPL [$F(1, 10) = 3.09, p = .11$]. Activation in a dual-task condition was significantly greater than in a single-task condition. The main effect of arithmetic calculation was observed in the left MFG (BA 46/9) [$F(1, 10) = 6.78, p < .05$] and in the parietal regions including left IPL/IPS [$F(1, 10) = 5.98, p < .05$], left SPL [$F(1, 10) = 6.72, p < .05$], and right SPL [$F(1, 10) = 13.83, p < .001$]. Consistent with previous findings, subtraction operations engaged greater and extended prefrontal and parietal activation than addition operations. The interaction effect was not significant in any ROI region ($ps > .1$).

Fig. 3 – Areas of significant activation in contrast to the single-addition condition associated with (a) the dual-addition condition and (b) the dual-operation condition.

Fig. 4 – Mean signal changes in each ROI for each arithmetic condition; Left MFG ($x=-50, y=30, z=22$): middle frontal gyrus, left IFG ($x=-50, y=11, z=18$): inferior frontal gyrus, left IPL/IPS ($x=-44, y=-39, z=42$): inferior parietal lobule/intraparietal sulcus, left SPL: superior parietal lobule ($x=-24, y=-63, z=51$), and right SPL ($x=28, y=-58, z=47$).

To better uncover how different tasks alter the level of neural activation for each individual participant, paired t-tests were adopted to contrast different task conditions in the five ROIs. The contrast between the single-subtraction task and the

single-addition task condition revealed a significant difference in the left MFG (BA 46/9) [$t(10)=2.46, p<.05$], IFG (BA 44) [$t(10)=2.35, p<.05$], and a marginal difference in the right SPL (BA 7) [$t(10)=2.00, p=.07$]. When comparing each dual-task condition

with a single-task condition, greater activation was observed in the former than in the latter only when the single-addition task was used in the contrast. Activation was significantly greater in the dual-addition than in the single-addition condition in the left MFG (BA 46/9) [$t(10)=2.40, p<.05$] and IFG (BA 44) [$t(10)=3.65, p<.01$]. Activation was also significantly greater in the dual-operation condition than in the single-addition condition in the left MFG (BA 46/9) [$t(10)=4.35, p<.001$], IFG (BA 44) [$t(10)=6.52, p<.001$], IPL/IPS (BA 40) [$t(10)=2.59, p<.05$], and the left SPL (BA 7) [$t(10)=5.84, p<.001$]. In contrast, no significant difference was found in these ROIs when comparing the dual-subtraction or the dual-operation condition to the single-subtraction condition ($ps>.1$).

3. Discussion

In this study, we investigated whether a capacity limitation constrains the level of neural activation engaged in subserving dual-task performance in comparison to the level evoked in a single-task condition. As the executive system is limited in capacity (Baddeley, 1996; Carpenter et al., 2000), we expected to observe a constraint in the prefrontal-parietal executive network. We adopted a serial-arithmetic task using the concurrent dual-task methodology to maximize the degree to which the two tasks competed for a common modality and executive processes. A go/no-go response mapping rule was also adopted to impose a demand on response selection and inhibition so that the two tasks had to compete for response selection (Menon et al., 2001; Wager et al., 2005). Replicating the previous results, the prefrontal and parietal regions were associated with performing mental arithmetic operations. The addition task evoked unilateral activation in the left hemisphere, and bilateral activation was involved in the subtraction task (Chochon et al., 1999).

The issue of interest was the neural activity related to the dual-task performance. The results extend what has been observed in previous dual-task studies in which the processing demands were divided between two modalities, two forms of materials, or both (Adcock et al., 2000; Jaeggi et al., 2003; Just et al., 2001). First, the neural correlates for dual-task performance were the same as the correlates for single-task performance. Second, whether greater activation is observed for dual-task performance in contrast to a single-task condition depends on the level of resource demand that the single task places on the prefrontal-parietal network. When the single addition task did not place high resource demands on the prefrontal-parietal network, greater activation was observed in the dual-addition and the dual-operation conditions than in the single-addition condition. When the single subtraction task did place high resource demands on the prefrontal-parietal network, no greater activation was found in the dual-subtraction and the dual-operation conditions.

3.1. Prefrontal and parietal activation for subserving arithmetic tasks

The single arithmetic task, as expected, involved a distributed executive network including the prefrontal and parietal regions (Burbaud et al., 1999; Chochon et al., 1999; Kong et al.,

2005; Rickard et al., 2000). These results support that working memory is essential for processing numbers and operands in calculation (Fürst and Hitch, 2000; Logie et al., 1994). With the involvement of executive processes such as reordering procedures, retrieval of arithmetic facts, storage and update of intermediate results for further operations, and the execution of mental calculations, activation increased in the left MFG. Activation in the left MFG is frequently correlated with working memory and attentional control (Curtis and D'Esposito, 2003; Milham et al., 2001, 2003) and with the manipulation of information (D'Esposito et al., 1999). MacDonald et al. (2000) also suggested that the left MFG provides top-down support for task-appropriate behaviors.

In addition to the left MFG, greater activation was observed in the left phonological area of the IFG for arithmetic operations as people often use verbal rehearsal strategies and linguistic representations to understand the quantities involved in arithmetic problems (Dehaene et al., 1999). The left parietal cortex was also activated in the arithmetic task. Previous studies have shown that the left parietal region is crucial for subserving processes related to the retrieval of arithmetic facts and the manipulation of quantity information. The left parietal cortex interconnects numeric representations with linguistic codes for understanding the relation between numerical quantities (Dehaene et al., 1999, 2003).

In contrast to the addition task, which requires verbal rehearsal strategies for retrieving arithmetic facts to support a semantic representation of numerical quantities, mental subtraction may engage visuospatial processes such as aligning digits properly on a mental number line and number comparison (Chochon et al., 1999; Dehaene et al., 2003; Kazui et al., 2000). By using a dual-task paradigm, Lee and Kang (2002) demonstrated that a visuospatial task impairs subtraction operations but does not affect multiplication operations. Our results support the involvement of visuospatial processing for the subtraction task as the whole-brain comparison analysis showed greater activation in the right MFG and right SPL when contrasting the conditions with subtraction operations (single-subtraction, dual-subtraction, and dual-operation) to the baseline condition. The ROI results also showed a trend of greater activation than the addition task in the right SPL. The right MFG is associated with visuospatial working memory and on-line organization of spatial information (Goldman-Rakic, 1998). The right parietal regions are also related to visuospatial working memory (Burbaud et al., 1999; Chochon et al., 1999; Dehaene et al., 2003).

Despite the greater and extended activation observed in the single-subtraction condition than in the single-addition condition, there was no significant difference between the two conditions in either accuracy or RT. It is likely that the greater neural activation reflects the greater mental effort required in the subtraction condition to reach the same performance level as in the addition condition. It is not unusual to observe inconsistent findings between behavioral measures and neural activation. Manipulating the working memory load by increasing the retention interval and also the task difficulty by degrading the stimulus in presentation, Barch et al. (1997) observed greater activation in the prefrontal regions with increasing memory load despite null behavioral results. After asking participants to switch between a color discrimination task and a letter

discrimination task, Erickson et al (2005) observed greater activation in the SPL subserving switching despite null results in the behavioral measures.

In sum, the imaging results replicate previous findings with unilateral activation in the left prefrontal and parietal regions associated with the addition task, and bilateral activation related to subtraction performance. The total level of neural activation is higher in the single-subtraction condition than in the single-addition condition.

3.2. Capacity limitation in the prefrontal–parietal network

As the executive system is limited in capacity (Baddeley, 1996; Carpenter et al., 2000), there should be a limitation in the prefrontal–parietal network that subserves dual-task coordination. Similar views of capacity limitation have been proposed in theoretical models such as a single-component model of working memory (Cowan, 1995, 2005), a model of attentional control (Pashler, 1994), and the two-process theory of human information processing (Schneider and Shiffrin, 1977). The limitation is thought to be in the focus of attention (Cowan, 1995), in the central bottleneck of response selection (Pashler, 1994), or in controlled processing (Schneider and Shiffrin, 1977). The limitation may reflect a biological constraint on the amount of cortical activation that can be evoked at any given time (Just et al., 2001). The results of this study support a biological constraint in the prefrontal–parietal network while performing two tasks.

When two arithmetic tasks are performed concurrently, the tasks compete for limited resources (Just et al., 2001; Kramer et al., 1985; Wickens et al., 1983) especially when these tasks entail activation in the same parts of the cortex (Klingberg, 1998; Klingberg and Roland, 1997). Even if the cognitive processes of the two tasks can be executed in parallel until the central bottleneck of response selection occurs (Pashler, 1994), concurrent dual tasks should interfere with each other in response selection as the SOA is zero in stimulus presentation between the two tasks. Yet, whether greater activation is observed in a dual-task condition than in a single-task condition depends on the resource demand that the single task imposes on the executive network.

As the addition task does not place high resource demands on the prefrontal and parietal cortices, greater activation is observed in the dual-addition condition or dual-operation condition as compared to the single-addition condition. As the subtraction task places high resource demands on the neural network, no greater activation is found when comparing the dual-subtraction condition or the dual-operation condition with the single-subtraction condition. Dual-task performance does not necessarily lead to an attenuation in neural activation (Jaeggi et al., 2003), but it does not increase neural activation beyond the level evoked by a single task when the single task is difficult and places high resource demands on the executive network because of the involvement of many controlled executive processes. There is a biological constraint (Just et al., 2001) on the amount of neural activation in the prefrontal–parietal executive network that can subserve dual-task performance.

As the null result in contrasting a dual-task condition to the single-subtraction condition can arise from multiple causes, other possibilities should be considered in interpreting the

results of this study. We consider three alternatives. The first possibility is related to sequential processing in a dual-task condition. Given that participants had sufficient time to make a calculation after each stimulus presentation, it is plausible that they sequentially processed the two tasks when the difficult subtraction task was performed with an addition task in the dual-operation condition or with another subtraction task in the dual-subtraction condition. With sequential processing, no coordination was required and hence no greater activation was observed in the dual-task condition when one of the tasks required subtraction. There is no doubt that a certain degree of sequential processing is involved in concurrent dual tasks. Yet, the dual-task cost in accuracy does not support complete sequential processing between the tasks. Moreover, sequential processing entails switching or shifting attention. Switching or shifting is also an executive function (Kondo et al., 2004; Sylvester et al., 2003). Previous imaging studies have shown greater activation in the prefrontal and parietal regions for the switching function (Sylvester et al., 2003) or for the shifting function (Kondo et al., 2004).

The second possibility is the engagement of identical processes between the single- and dual-task conditions so that no additional cognitive processes are engaged in a dual-task condition. According to Pashler's (1994) model, cognitive processes of two tasks can be executed in parallel until the bottleneck of response selection occurs. Given that the single-task condition in this study also required response selection, identical processes were involved in the single- and dual-task conditions. However, this possibility cannot fully account for the results as greater activation was observed when a single addition task was performed concurrently with another task. The null results occurred only when a single subtraction task was performed concurrently with another arithmetic task.

A third possibility for observing a biological constraint is that dual-task coordination under a capacity limitation does not increase the mean signal intensity of the brain network, but does increase the activation volume involved in subserving cognitive processes. Using two independent tasks with different input modalities and different cognitive processes, Just et al. (2001) found no significant difference in the PFC when contrasting the activation volume in the dual-task condition with the summed activation volume in the corresponding single tasks. However, the activation volume was low in each single task condition in their results. Future research should explore how the prefrontal–parietal executive network supports dual-task performance when one of the tasks has already engaged a high level of neural activation in the network.

One possible resolution to the inconsistent findings in the PFC between Just et al.'s (2001) study and the present study is the mental effort that participants devoted to dual-task coordination. In Just et al.'s (2001) study, the demand on the PFC was minimal in each single task and the two tasks were independent in their resource demand on modality and cognitive processes. In this context, the effort in dual-task coordination may not have been greater than the total effort of performing the two single tasks. The greater activation in the prefrontal–parietal regions with the dual-task condition in comparison to the single-addition task condition arose from the difference in the mental effort. As the subtraction task was more difficult, the mental effort in the single-task condition may have been as high

as in each of the dual-task conditions. No greater activation was observed when the task was performed with another arithmetic task. How mental effort is associated with dual-task performance remains unclear, as the dual-task cost in performance was similar for both the single-addition task and the single-subtraction task in contrast to the dual-operation task. Yet, neural activation in the dual-operation condition was greater than in the single-addition condition, but not the single-subtraction condition.

3.3. Conclusion

The aim of this study was to examine whether a capacity limitation constrains the level of neural activation subserving dual-task performance. Using a serial-arithmetic task, we adopted an approach different from previous studies by maximizing the degree to which the two tasks competed for common resources in input modality and executive processing. Supporting Bunge et al.'s (2000) model, the results showed that the same prefrontal-parietal network that subserves the single task also subserves dual-task performance. However, whether greater activation is observed in a dual-task condition depends on the resource demand imposed on the neural network by the single task. Supporting Just et al.'s (2001) suggestion of a biological constraint in neural activation at any given moment, the results revealed the existence of a biological constraint in the prefrontal-parietal executive network. Greater activation in the prefrontal and parietal regions was observed only when the single-addition task was performed with another arithmetic task. No greater activation was observed when the single-subtraction task was performed with another serial-arithmetic task. Our results support the hypothesis that a biological constraint imposed by capacity limitation operates on neural activity subserving dual-task performance.

4. Experimental procedure

4.1. Participants

Twelve right-handed undergraduate and graduate students (6 female and 6 male) aged 21 to 29 were recruited from National Taiwan University. All participants were healthy and without any neurological or psychiatric history. The local ethical committee formally approved the experiment and informed written consent was obtained from all participants prior to the study. We analyzed data from only eleven participants as one female participant showed head movement in the scanner greater than 1 mm.

4.2. Design and procedure

Six conditions were constructed for the experiment. Before the functional magnetic resonance imaging (fMRI) session, participants were required to practice the tasks until they felt confident with dual arithmetic tasks. In the scanning session, participants performed four runs (300 s for each run), with all six conditions in each run. Each block consisted of four consecutive numeric pairs in white and the last numeric test pair in yellow on a gray background.

The task demands differed among the six conditions (Fig. 1). In the *baseline* condition, participants were asked to hold the

first numeric pair and ignore the following three stimulus presentations. Participants then indicated whether the yellow test probes matched the initial pair. In the *single-addition* and *single-subtraction* conditions, participants performed either addition or subtraction on either the left or right member of each set of numeric pairs and held the first digit of the other side. When the yellow test pair occurred on screen, participants indicated whether the probe matched the calculated total on one side and whether the other probe matched the first digit of the other side. The subtraction task always began with a 2-digit number, and the addition task began with a single digit number. In the *dual-addition* and *dual-subtraction* conditions, identical operations were performed on both numbers in each pair (e.g., +2 and +4, −5 and −7). In the *dual-operation* condition, different arithmetic operations were performed on the numbers in each pair (e.g., +2 and −5, −2 and +5). When the yellow test pair occurred on screen, participants indicated whether the number on each side matched the calculated total. These six conditions were randomized within a run so that the task order did not contaminate the activation pattern.

Each block began with a fixation cross for 3 s, followed by five numeric pairs with each pair being presented for 1 s and an inter-stimulus interval of 2 s. Participants had 2 s to judge whether each probe of the test pair matched the correct answer. A go/no-go response mapping rule was adopted in the experiment as it requires response inhibition and selection (Menon et al., 2001; Wager et al., 2005). Participants pressed a button only when the probe matched the correct answer and did not respond when the probe mismatched the answer. Participants pressed the left button with the thumb of the left hand when the left probe matched the correct answer (the left-matching block), and pressed the right button with the thumb of the right hand when the right probe matched the correct answer (the right-matching block). The four response types (both match, both mismatch, the right probe matches, the left probe matches) occurred with equal frequency in every condition. Participants were asked to respond as accurately as possible without using strategies such as finger movements to perform calculations. They were also asked not to perform calculations on one arithmetic stream and give up or guess on the other.

4.3. MRI technique

This experiment was run on a Bruker MedSpec 3 T system (Bruker, Ettlingen, Germany) at National Taiwan University with a quadrature birdcage head coil. The stimuli were visually presented on a goggle display system (Resonance Technology Inc., CA, USA). Both eyes were corrected to normal visual acuity with lenses during the experiment. A single-shot T2*-weighted gradient echo echo-planar imaging (EPI) sequence (TR=3000 ms, TE=33 ms, flip angle=90°) was used for BOLD imaging. Functional images were obtained from 16 contiguous axial-oblique slices (thickness=5 mm and gap=1 mm) which were acquired in axial orientation parallel to the AC-PC line. During each run, 100 volumes were obtained with a total time of 300 s.

4.4. Imaging data analysis

The fMRI data were analyzed using the SPM99 software (Wellcome Department of Cognitive Neurology, London, UK) in

MATLAB 6.0 (MathWorks, Inc., Natick, MA, USA). The first four scans of the EPI series were excluded from further processing to minimize the transit effects of hemodynamic responses. The remaining functional images were corrected for each participant's motion with sinc interpolation. The realigned images were then normalized into the standard SPM/MNI template, and transformed into a standard stereotaxic space and resampled with a resolution of $2 \times 2 \times 2 \text{ mm}^3$. A Gaussian filter of 10-mm full width at half maximum (FWHM) was then applied to smooth the data spatially, to accommodate for anatomical variability across subjects, as well as to satisfy the assumptions of Gaussian field theory (Worsley et al., 1996). The box-car function convolved with the canonical hemodynamic response function was used to identify significant activated voxels. No global or grand-mean scaling was performed during analysis. The time series data at each voxel were then processed using a high-pass filter with a cut-off period of 216 s to remove low frequency drifts in the BOLD signals.

The subject-level statistical analyses were performed using the general linear model for blocked designs. The following contrasts of statistical parameter estimate images were computed for each individual participant. To confirm the involvement of a prefrontal-parietal network in arithmetic calculations, the baseline condition was subtracted from each of the five calculation conditions. To test for the possibility of independent processing between two tasks, we compared the dual-operation condition with the summed neural activation of single-addition and single-subtraction tasks (dual-operation–single-addition–single-subtraction + baseline). To reveal the constraints imposed by capacity limitation on the neural activity, the single-addition and single-subtraction tasks were subtracted from the dual-task conditions that involved the single task.

These estimates for contrasts were then entered into a standard SPM second-level analysis with the participant treated as a random effect using a one-sample t-test. The expected mean difference value for the t-tests was set to zero. A voxelwise intensity threshold ($p < 0.001$) and a spatial extent threshold (cluster size greater than 27 voxels) were combined to control for multiple comparisons (Forman et al., 1995; Poline et al., 1997). All significant activated areas were transformed into Talairach space (Talairach and Tournoux, 1988). Anatomical localizations were done with Talairach Daemon software (Research Imaging Center, Health Science center, San Antonio, TX).

4.5. Regions of interest analysis

ROI analyses were then conducted using the Russell Poldrack's SPM ROI Toolbox (<http://sourceforge.net/projects/spm-toolbox>) to test the prior hypothesis on capacity constraint. We selected five common brain regions in the prefrontal-parietal network including MFG (BA 46/9), IFG (BA 44), IPL/IPS (BA 40), SPL (BA 7) in the left hemisphere and right SPL that showed significant contrast effects when comparing the five arithmetic conditions with the baseline condition. We defined the size of each ROI as a sphere with its center at the peak of activation with a radius of 6 mm. For each participant, the adjusted raw data of the ROI was extracted for all task conditions. The mean BOLD signal changes of the five arithmetic conditions were then computed for each participant to evaluate the statistical significance of the difference in each ROI

in both a 2×2 repeated measures ANOVA and paired t-test analyses.

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