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Response-specific sources of dual-task interference in human pre-motor cortex

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Abstract It is difficult to perform two tasks at the same time. Such performance limitations are exemplified by the psychological refractory period (PRP): when participants make distinct motor responses to two stimuli presented in rapid succession, the response to the second stimulus is increasingly slowed as the time interval between the two stimuli is decreased. This impairment is thought to reflect a central limitation in selecting the appropriate response to each stimulus, but not in perceptually encoding the stimuli. In the present study, it was sought to determine which brain regions are specifically involved in response selection under dual-task conditions by contrasting fMRI brain activity measured from a response selection manipulation that increased dual-task costs, with brain activity measured from an equally demanding manipulation that affected perceptual visibility. While a number of parieto-frontal areas involved in response selection were activated by both dual-task manipulations, the dorsal pre-motor cortex, and to a lesser extent the inferior frontal cortex, were specifically engaged by the response selection manipulation. These results suggest that the pre-motor cortex is an important neural locus of response selection limitation under dual-task situations.

Keywords fMRI · Pre-motor cortex · PRP

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Introduction

The processing of sensory information from stimulus presentation to action has been proposed to proceed through a series of stages (Sternberg, 1969), such as stimulus perception, response selection and response execution. At least some of these stages appear to be severely limited in their information processing capacities: considerable evidence indeed suggests that the flow of information hits a 'bottleneck' at the response selection stage, where only one selection or decision for action may be executed at any instant (Pashler, 1994; Welford, 1952). This processing limitation has been extensively studied with the psychological refractory period (PRP) paradigm, in which subjects are instructed to make two different speeded motor responses to two distinct sensory stimuli presented in rapid succession. The typical outcome is increasingly slowed response time to the second stimulus as the interval between the first and second sensory stimuli is decreased. Various experimental manipulations indicate that it is the overlap in response selection of the two tasks, not in perceptual encoding of the two stimuli, which is the rate-limiting step underlying the PRP (De Jong, 1993; Luck, 1998; Pashler & Johnston, 1989; Pashler, 1998). As such, the PRP paradigm represents a simple, but powerful way to demonstrate how the engagement of the response selection stage for one task temporarily delays similar stage engagement for another task (Pashler, 1994; Welford, 1980).

Despite the central role of this bottleneck in human information processing, its neural substrates have been elusive. Event-related potential studies have helped pinpoint when, but not where, the bottleneck occurs along the information processing pathway (Luck, 1998; Osman & Moore, 1993). Although split-brain patient studies have hinted at a subcortical component to dual-task limitations (Ivry, Franz, Kingstone, & Johnston, 1998; Pashler et al., 1994), they have yielded conflicting results about a cortical contribution. The paucity of

evidence in favour of a cortical involvement in the PRP is somewhat surprising given the substantial roles the frontal and/or parietal cortex is thought to play in motor attention (Rushworth, Krams, & Passingham, 2001b), in response/movement selection and competition (Decary & Richer, 1995; Hazeltine, Poldrack, & Gabrieli, 2000; Passingham, 1993; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000; Rushworth, Nixon, Renowden, Wade, & Passingham, 1997; Schall, 2001; Jiang & Kanwisher, 2003a; Schumacher et al., 2003) and in executive processes in general (D'Esposito et al., 1995; Miller & Cohen, 2001). Recent fMRI studies using dual-task paradigms suggested that several (parieto-frontal) cortical areas were activated under dual-task conditions relative to single-task conditions (Dreher & Grafman, 2003; Herath, Klingberg, Young, Amunts, & Roland, 2001; Schubert & Szameitat, 2003; Szameitat, Schubert, Muller, & von Cramon, 2002), but these studies were not designed to directly test whether brain regions involved in response selection contribute to the bottleneck of information processing revealed by the PRP, as predicted by behavioral and electrophysiological studies (De Jong, 1993; Luck, 1998; Pashler & Johnston, 1989; Pashler, 1998).

Using the PRP paradigm, the present study aimed at determining whether brain regions implicated in response selection may be specifically involved in dual-task interference. The experimental strategy capitalized on the notion that the PRP is directly caused by the response selection/decision stage of Task 1 (De Jong, 1993; Karlin & Kestenbaum, 1968; Pashler, 1994; Van Selst & Jolicoeur, 1997): According to the response selection 'bottleneck' model of the PRP, response selection to Task 2 is postponed until response selection to Task 1 is completed (Fig. 1a) (De Jong, 1993; Pashler, 1994; Pashler & Johnston, 1989). Here the PRP was manipulated by varying the demands of response selection: increasing the number of stimulus-response choices increases the duration of response selection at Task 1 and prolongs the PRP (i.e. increased Task 2 RT; Fig. 1b) (Karlin & Kestenbaum, 1968; Van Selst & Jolicoeur, 1997). An increase in the number of stimulus-response choices should correspondingly lead to enhanced and/or prolonged activity in neural substrates mediating response selection, thereby allowing their localization with fMRI. Such a parametric design is advantageous over a typical subtraction approach to isolate neural substrates associated with response selection (Schumacher & D'Esposito, 2002).

The comparison of two conditions that differ in the magnitude of the PRP effect is only the first step towards isolating the brain regions associated with a response selection bottleneck. It is also necessary to demonstrate that this activation is specific to the response selection stage and not simply related to task demands (difficulty). Most theories of information processing postulate that the selection of a response is preceded by a stage of perceptual encoding (Pashler, 1994) and, critically, that manipulations of perceptual visibility do not affect the

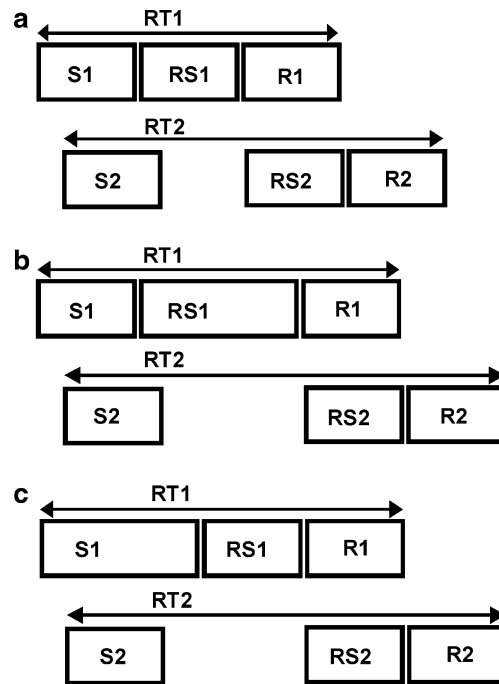


Fig. 1 Schematic of the effect of manipulating perceptual and response selection demands in dual-task conditions. (a–c) Cognitive models decompose sensori-motor tasks into stimulus encoding (S), response selection (RS) and response execution (R) stages of information processing. Evidence for the independence of the perceptual (S) and RS stages is reviewed in the text. Total duration of the 3 stages yields a task's reaction time (RT). **a** easy perceptual/response condition: the response selection stage to Task 2 does not begin until Task 1 response selection is completed. **b** effect of response selection difficulty manipulation: increasing RS1 duration leads to postponement of RS2 and increased RT2. **c** effect of perceptual difficulty manipulation: increased S1 duration postpones RS1, which leads to postponement of RS2 and increased RT2

duration of the response selection stage (Fig. 1c) (De Jong, 1993; Luck, 1998; Pashler & Johnston, 1989). Therefore, this experimental design also contained a manipulation of perceptual encoding demands. Regions specifically responsible for the capacity limits in response selection should be activated by the dual-task response selection manipulation, but not by the perceptual encoding manipulation, even when both manipulations are matched in difficulty.

Experiment 1: isolation of response selection areas

The principal aim of this study was to determine which response selection areas of the brain contribute to the PRP by comparing dual-task manipulations that affect the central 'bottleneck' stage of information processing with equally difficult dual-task manipulations known not to affect this central stage. In order to maximize the sensitivity of the dual-task fMRI experiment, an initial single-task fMRI experiment was carried out to localize brain regions engaged in response selection

(Experiment 1). These regions were isolated using a task that varied the number of stimulus-response alternatives (Fig. 2a): regions involved in response selection are expected to be activated more in a four-alternative discrimination (4AD) task than in a 2AD task. Comparison of 4AD and 2AD manipulations should therefore yield candidate brain regions involved in response selection. These regions of interest (ROIs) will subsequently be probed in a dual-task experiment (Experiment 2).

Methods

Participants

Nine right-handed volunteers (four females, age 20–32) with normal or corrected-to-normal vision gave informed consent for their participation in these experiments. The study was approved by the Vanderbilt University Institutional Review Board.

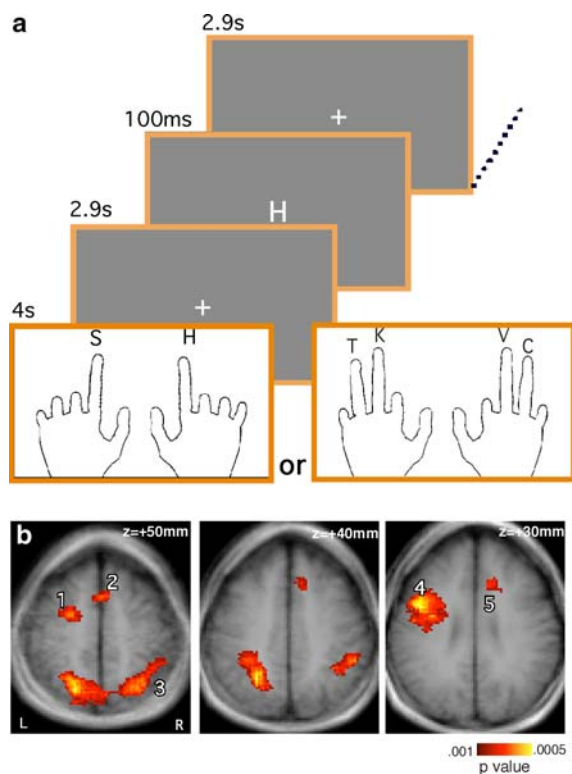


Fig. 2 Response selection manipulation of Experiment 1. **a** Trial design. Subjects were visually cued at the beginning of each block of trials about the letter-finger assignment (2AD or 4AD). **b** Statistical parametric maps of 4AD minus 2AD. Activation was observed in left pre-motor cortex (1; Talairach coordinates of the activation maximum: $x = -23$ mm, $y = -3$ mm, $z = +50$ mm), pre-SMA (2; $x = \pm 2$, $y = +11$, $z = +50$), left and right intra-parietal sulci (3; $x = -19/-24$, $y = -73/-63$, $z = +50/+41$), left inferior frontal gyrus (4; $x = -41$, $y = +3$, $z = +32$) and anterior cingulate (5; $x = +10/11$, $y = +20$, $z = +40/50$). 2AD-related activation in inferior parietal lobule, pre-cuneus and antero-medial dorsal frontal cortex (BA 8/9) is not shown

Stimuli and Apparatus

Imaging was performed on a 3T GE LX scanner (Milwaukee, WI). Stimuli were displayed on an LCD panel and back-projected onto a screen positioned at the front of the magnet. Subjects lay supine in the scanner and viewed the display through a mirror mounted above their eyes. Stimuli were presented with MATLAB software (Mathworks, Natick, Ma) running on a Macintosh Power PC G4, and synchronized with each fMRI volume acquisition. Stimuli consisted of single white letters (C, H, K, M, T or V) of about 0.5° high and 0.3° wide that were presented on a grey background.

Procedure

A trial consisted of target letter display for 100 ms, followed by 2.9 s of white fixation cross (0.4°) during which subjects made speeded responses. Trials were blocked, with each eight-trial block starting with a 4 s-long letter-finger assignment cueing panel. There were four 28 s-long blocks of each condition per fMRI run, and eight runs per subject, for a total of 256 trials per condition (experiment duration was approximately 1 h). For both the 2AD and 4AD conditions, each letter was associated with a specific finger (index, middle or ring finger of either hand), with distinct fingers used for the 2AD and 4AD conditions. For each subject, the letter-finger assignment was maintained throughout the experimental session. For half the subjects, the index fingers were assigned to the 2AD condition while the middle and ring fingers were assigned to the 4AD condition. For the other half, the ring fingers were assigned to the 2AD condition while the index and middle fingers were assigned to the 4AD condition. Thus, both the 2AD and 4AD conditions involved bi-manual responses (e.g. index finger of the two hands assigned to the two letters of the 2AD task). While the 4AD condition necessarily involved both inter-hand and intra-hand digits compared to only inter-hand digits in the 2AD condition, selecting between fingers of the same hand is as easy, if not easier, than selecting between fingers of different hands (S. Watter and G.D. Logan, submitted). The letters C, H, K, S, T, V were used, with the assignment of the letters to the 2AD and 4AD conditions counterbalanced across subjects. Subjects were instructed to remove the non-assigned fingers off the response buttons. Subjects practiced the task until they reached above 90% accuracy in each condition (typically within 10 min of practice).

fMRI data acquisition and analysis

Anatomical (T1-weighted) images were acquired using conventional parameters (Marois, Chun, & Gore, 2000). Functional (T2*) parameters were as follows: TR 2 s, TE 25 ms, FA 60° , 132 images/slice, with 14 axial slices

(7 mm thick, 0.5 mm skip) acquired parallel to the AC-PC line. fMRI analysis: Statistical parametric maps of blood oxygen level-dependent (BOLD) activation for each subject were created using a skew-corrected percent signal difference (Marois et al., 2000). The T1-weighted anatomical and Gaussian-filtered (half width to half maximum [HWHM] = 2.0 mm) BOLD images for each subject were transformed into standardized Talairach space (Talairach & Tournoux, 1988). The resulting maps from all subjects were superimposed to create group average maps. The probability that the mean percent signal change across subjects was different from zero was calculated using a *t*-test for each voxel. The composite maps for Experiment 1 were thresholded at a voxel-based *p* value < .001, corrected for a cluster size of 15 voxels and filter width of 1 voxel (Forman et al., 1995). ROIs were defined for Experiment 2 by drawing a 5×5 voxel grid centered on the activation peak, and included the contralateral homologue of the left inferior frontal gyrus (Fig. 5). If an activated site spanned more than one slice, the voxel grid was defined in the slice that contained the activation peak.

Results and discussion

The aim of this experiment was to isolate brain regions sensitive to response selection using a single-task fMRI experiment. These response-selection ROIs were isolated with a task that varied the number of stimulus-response alternatives: nine right-handed subjects performed a speeded 2AD or 4AD letter-finger discrimination task in separate blocks of trials (Fig. 2a). As expected, subjects were slower ($t_8 = 9.5, p < .0001$) in making decisions in the 4AD (mean = 644 ms ± 42 ms standard error of the mean) than 2AD condition (426 ms ± 32 ms). When subtracting the 2AD activation from the 4AD activation, several frontal cortex regions were isolated (Fig. 2b): the left medial frontal gyrus (BA6) corresponding to the dorsal pre-motor area (Boussaoud, 2001; Lee, Chang, & Roh, 1999; Picard & Strick, 2001; Wise & Murray, 2000); the mesial aspect of dorsal frontal gyrus (BA6) corresponding to the location of pre-supplementary motor area (pre-SMa) (Kurata, Tsuji, Naraki, Seino, & Abe, 2000; Lee et al., 1999; Picard & Strick, 2001); the anterior cingulate (BA32) (Picard & Strick, 2001); and the left inferior frontal gyrus (IFG) at the intersection of BA 44, 6, and 9. In addition to these frontal regions, the left and right intra-parietal sulci (IPS) were also engaged by the response manipulation (Schumacher & D'Esposito, 2002).

Subcortical activations were also observed in the basal ganglia with the present response selection manipulation. However, unlike several cortical ROIs (see later), these structures were not modulated (all p 's > .1) by either the perceptual or response manipulations of the dual-task experiment, and will therefore not be considered any further.

These results indicate that several frontal cortex regions previously associated with motor and/or executive functions (Passingham, 1993) were isolated by the present response selection manipulation: the dorsal pre-motor area (Boussaoud, 2001; Lee et al., 1999; Picard & Strick, 2001; Wise & Murray, 2000); the pre-SMa (Kurata et al., 2000; Lee et al., 1999; Picard & Strick, 2001); BA32 (Picard & Strick, 2001); and the left inferior frontal gyrus in lateral frontal cortex. The consistency of these results with previous studies of response selection confirms the validity of the present response selection manipulation. In addition, the left hemisphere bias for several of these activations is also consistent with neuropsychological and imaging studies of a left hemisphere dominance for higher motor functions and motor attention (Kimura, 1993; Rushworth et al., 2001b).

While the location of the activated cortical foci are consistent with the claim that they are associated with response selection, this experiment cannot discount the possibility that the blocked presentation of 2AD and 4AD trials may also have led to strategic, preparatory, or working memory differences between the two conditions that could have affected brain activations. These issues are solved in the second, event-related dual-task fMRI experiment.

Experiment 2: dual-task experiment

The second experiment tested which, if any, of the response selection ROIs isolated in Experiment 1 were modulated under speeded dual-task manipulations of response selection and perceptual visibility (Fig. 3a). Task 1 response selection manipulation consisted of the 2AD/4AD letter-finger task described earlier, while Task 1 perceptual visibility was manipulated by varying the contrast, size and extent of lateral masking of the target letter (Fig. 3b). Task 2 consisted of a two-choice speeded colour discrimination task involving a left/right thumb response according to the colour of a rectangular frame presented either 175 ms or 875 ms after stimulus onset of Task 1. The costs of carrying out Task 2 immediately after Task 1, that is the PRP, is revealed by the increased RT to Task 2 at short compared to long stimulus onset asynchrony (SOA) between Tasks 1 and 2 (Pashler, 1994). Importantly, this dual-task cost is expected to be larger in the 4AD than the 2AD condition (Karlin & Kestenbaum, 1968; Van Selst & Jolicoeur, 1997). This is because, carry-forward of the Task 1 manipulation is expected to have larger effects on RT2 at short SOA than at long SOA because at long SOA the response to Task 1 should be largely finished before the onset of the second stimulus. The perceptual manipulation is also expected to produce longer RTs for Task 2 in the hard compared to the easy perceptual identification condition, but by affecting a different stage of information processing than the response selection manipulation: degrading perceptual

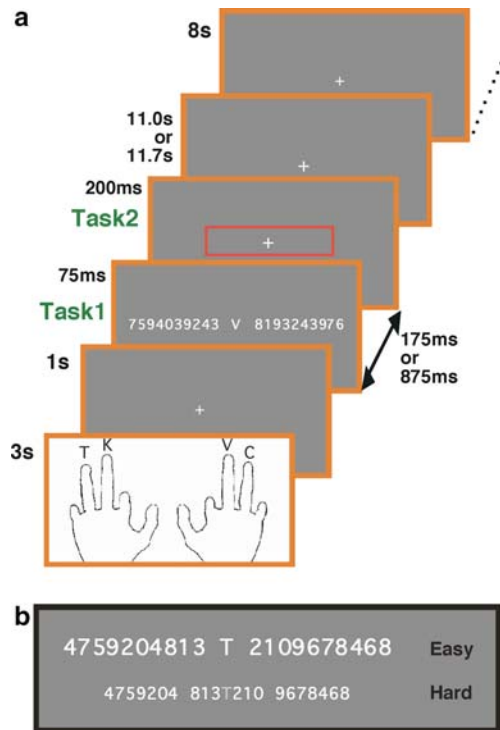


Fig. 3 Experimental design of the dual-task study (Experiment 2). (a) trial design. Task 1 consisted of a letter-finger response mapping, while Task 2 required subjects to make a colour-thumb response association. Stimulus 2 was presented 175 ms or 875 ms following Stimulus 1 onset. (b) stimulus displays for Task 1. In the easy perceptual identification manipulation, the high-contrast target letter was flanked distally by digits. In the hard identification condition, all characters were reduced in size and the low contrast target was flanked proximally by three of the digits (for illustration purposes, the target letter is displayed at a higher contrast than in the experiment)

encoding of the target letter increases the duration of the perceptual stage of Task 1, which postpones the onset of the response stage of Task 1 without affecting its duration (Fig. 1c) (Pashler, 1994; Van Selst, Ruthruff, & Johnston, 1999). As a result, the onset of Task 2 response stage is also delayed, thereby leading to comparable RT costs obtained with the response manipulation. Thus, although the perceptual and response manipulations should incur similar behavioural costs, only the response manipulation will affect the duration, and hence activity levels, of the response selection stage.

Methods

Participants

Fourteen right-handed volunteers with normal or corrected-to-normal vision gave informed consent for their participation in this experiment. The study was approved by the Vanderbilt University Institutional Review Board.

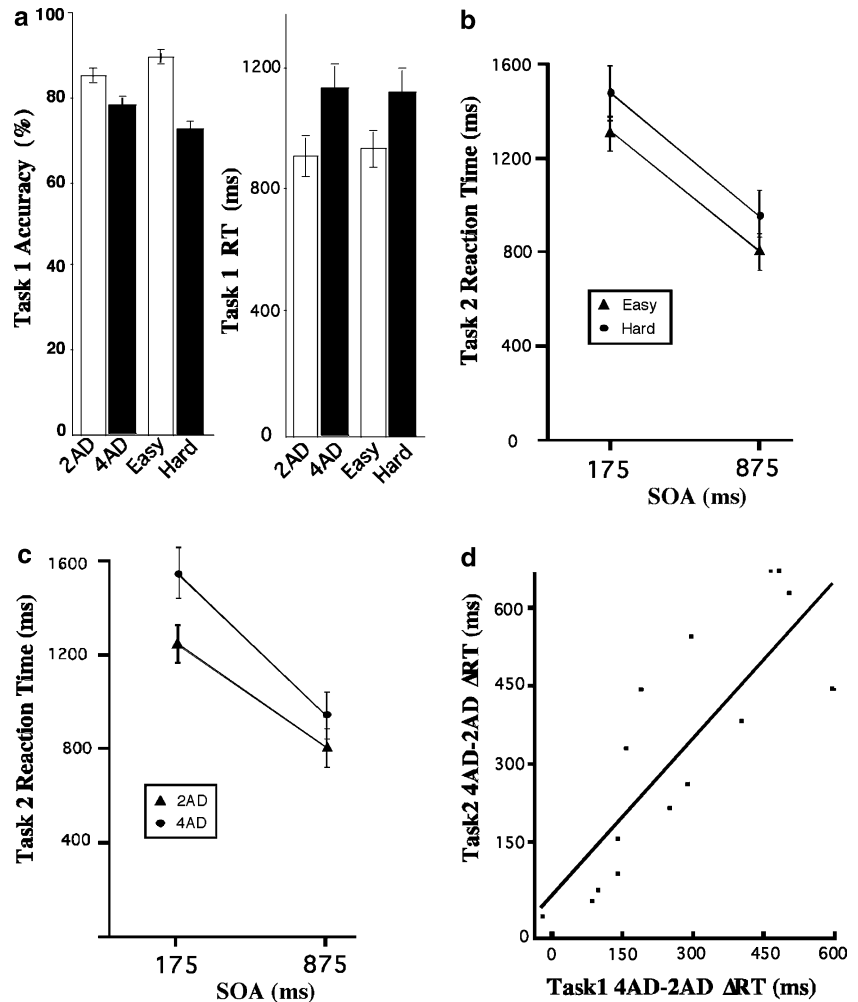
Stimuli and Apparatus

Stimuli for Task 1 were as described in Experiment 1, except that the target letters were flanked laterally by distractor digits in two possible arrangements: in the easy target identification condition, the target letter was flanked at a distance of 0.3° on either side by ten distractor digits. In the hard target identification condition, three of the ten digits immediately flanked the target letter to create lateral masking, and the contrast of the target and sizes of all alphanumeric characters were also reduced relative to the easy condition. The difficulty difference in target identification between these two conditions represents the *perceptual manipulation* of Task 1. The contrast of the target and sizes of the alphanumeric characters in the hard perceptual displays were adjusted between fMRI runs for each subject, in order to yield comparable reaction time differences between the perceptual and response manipulations. The *response selection manipulation* of Task 1 was as described in Experiment 1, consisting of the 2AD and 4AD manipulations. Finally, the perceptual and response manipulations were crossed, such that the Task 1 display of any given trial belonged to one of the four cells of a 2×2 matrix (i.e. easy perceptual–2AD, hard perceptual–2AD, easy perceptual–4AD, and hard perceptual–4AD). Task 2 stimuli consisted of a red or blue rectangular frame (width: 2.6° , height: 1.1° , thickness: 0.2°) presented at fixation.

Procedure

Participants performed two consecutive speeded response tasks on each trial in this fMRI experiment. A trial began with Task 1 stimulus presentation for 75 ms. After an SOA of either 175 ms or 875 ms, the Task 2 stimulus was shown for 200 ms, followed by a large (0.5°) fixation cross for 11.0 s or 11.7 s and then by a small (0.17°) cross for 8 s before the onset of the next trial (total trial duration: 20 s, see Fig. 3). The Task 1 response selection manipulation was mapped onto six fingers (index, middle and ring fingers of each hand), whereas the two rectangle colours of Task 2 were mapped to the two thumbs. The response manipulation (2AD versus 4AD) was blocked, with the subjects cued at the beginning of each block regarding the level of AD manipulation, while the presentation order of the perceptual identification displays (Hard versus easy) was pseudo-randomized within each block. SOA was also randomized within blocks. There were six trials per block, four blocks per fMRI run, and six runs per subject (experiment duration was approximately 1 h). Thus, 18 trials were acquired per experimental cell (two SOAs \times two response conditions \times two perceptual conditions). Subjects performed six runs of practice trials (48 trials/run) prior to scanning. Two additional practice runs were given in the scanner during the anatomical scans.

Fig. 4 Behavioural data for the dual-task study (Experiment 2). (a) the response (2AD/4AD) and perceptual (easy/hard) manipulations affected Task 1 accuracy and reaction times similarly. (b, c) all dual-task conditions produced longer Task 2 reaction times at the 175 ms SOA than at the 875 ms SOA (PRP effect). In addition, both the perceptual (b) and response (c) manipulations increased the RT2 time costs. (d) correlation of the RT differences between the 4AD and 2AD conditions to Task 1 and Task 2 for the 14 subjects. The latter data are for 175 ms SOA and correct Task 1 and Task 2 responses



fMRI data acquisition and analysis

fMRI parameters were as described in Experiment 1, except for the following modifications: 253 images/slice, eighteen 6 mm-thick axial slices with 1 mm gap.

For data analysis, the anatomical and Gaussian-filtered (FWHM = 4.0 mm) BOLD images for each subject were transformed into standardized Talairach space. Following slice timing correction, the activation time courses were extracted for each subject in each ROI, time-smoothed with a Gaussian filter (HWHM = 0.2 s), and normalized to each trial's onset (time 0 s = 0 percent signal change) to exclude potential preparatory/working memory confounds due to the blocked presentation of 2AD and 4AD trials. Only the correct trials were used for fMRI analysis. For each ROI, the time courses for each perceptual and response conditions were first isolated. Since the interest was not only in testing the separate effects of the perceptual and response manipulations in each ROI, but also in determining whether the effect of the response manipulation was significantly larger than the effect of the perceptual manipulation (as opposed to interactions between manipulations), *t*-tests were selected instead of

ANOVAs, although the latter analyses yielded similar main effects to the *t*-tests. The 2AD, 4AD, hard, and easy trials were pooled separately, and *t*-tests (one-tailed based on the a priori hypothesis derived from Experiment 1 of greater activation with increased response demands) were performed between the signal peaks of the 4AD and 2AD conditions, and between the signal peaks of the hard and easy conditions. Signal peaks used for statistical analysis corresponded to the time points between 4 and 8 s. To provide a measure of the sensitivity of the peak response analysis and generality of the results, an area under the curve (AUC) analysis (using the Trapezoid Rule of Integration) was also carried out. The AUC analysis yielded indistinguishable results from the peak analysis, and hence only data from the latter are reported in the *Results* section.

Results and discussion

Behavioral data in fMRI sessions

The behavioral results produced the expected results, confirming the adequacy of the manipulations. Both the

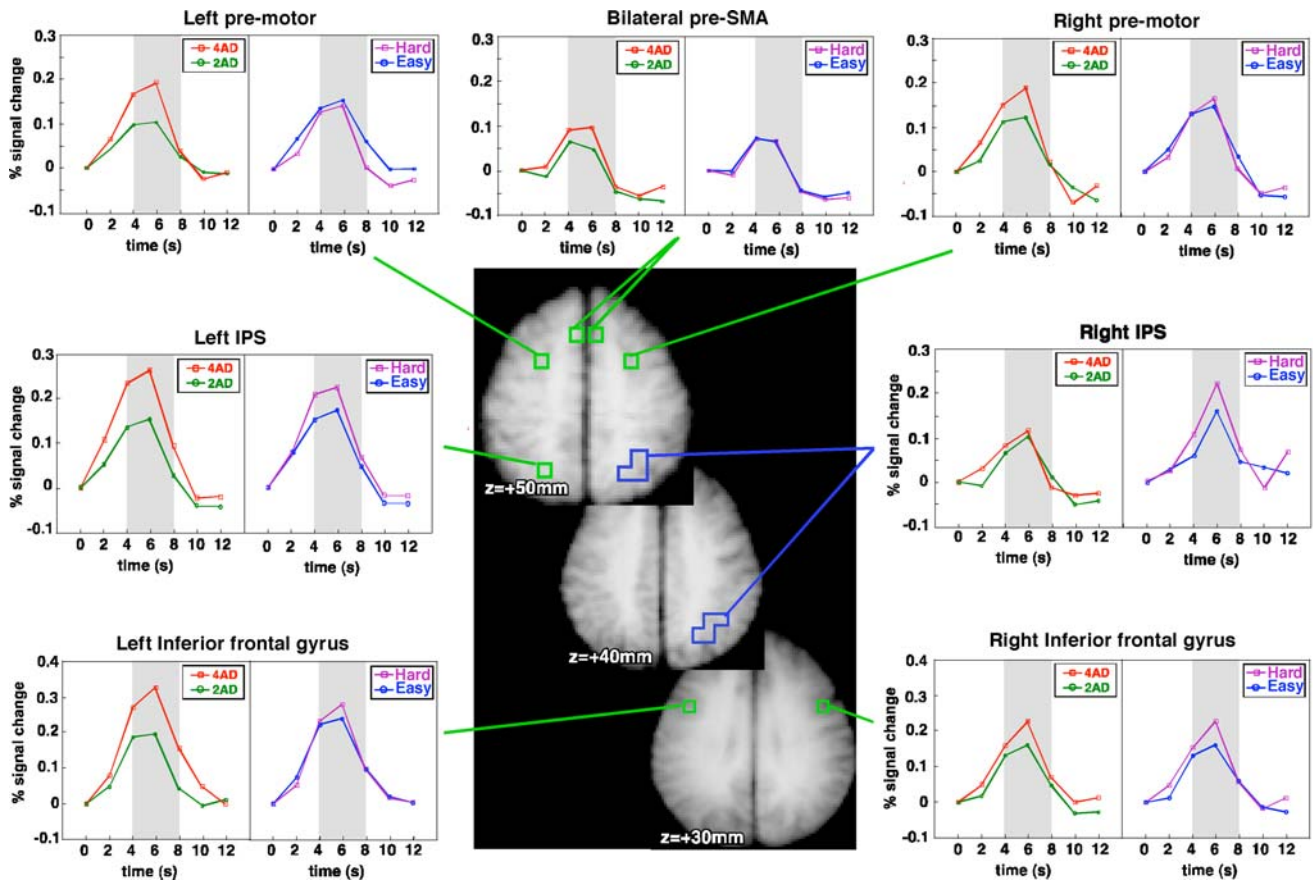


Fig. 5 Activation time courses for the response (red/green) and perceptual (purple/blue) manipulations in the dual-task experiment. The green ROIs were derived from Experiment 1, while the blue

(right IPS) ROI was selected from a previous perceptual manipulation study (Marois et al., 2000). Vertical gray band indicates the peak time points used for statistical analysis

response and perceptual manipulations yielded significant costs for Task 1 accuracy ($F[1,13]=9.9, p < .01, MS_e=0.19$, for response and $F[1,13]=140.5, p < .0001, MS_e=0.07$, for perceptual manipulations) and Task 1 RT ($F[1,13]=41.8, p < .0001, MS_e=502667$, for response and $F[1,13]=81.4, p < .0001, MS_e=132458$, for perceptual manipulations) (Fig. 4a). Similar reaction time costs were observed for Task 2 under both perceptual and response manipulations (Fig. 4b, c): subjects were slower with the 175 ms SOA than with the 875 ms SOA ($F[1,13]=182, MS_e=387518, p < .0001$ for response and $F[1,13]=192, MS_e=355043, p < .0001$ for perceptual manipulation), that is, they demonstrated a classic PRP effect. Importantly, this PRP effect was larger in the 4AD than the 2AD condition (AD \times SOA interaction: $F[1,13]=9.5, p < .01, MS_e=178234$, Fig. 4c), but not in the hard versus easy perceptual manipulation ($F[1,13]=0.1, p > .75, MS_e=178234$). However, the lack of a significant interaction between SOA and perceptual manipulation appeared to be simply due to the insufficient delay between the two SOAs for the PRP effect to fully dissipate, for when eight subjects performed an identical behavioral experiment with SOAs of 175 ms and 1275 ms, a significant contrast \times SOA interaction was observed ($F[1,7]=12.1, p < .05, MS_e=1115$). These

findings confirm that, just as with the response manipulation, the perceptual difficulty manipulation affected the magnitude of the PRP. Indeed, there were no significant differences ($F[1,13]=0.1, p > .75, MS_e=135881$) in Task 2 RT costs between the response and perceptual manipulations, suggesting that both manipulations were equally difficult. Finally, the 4AD–2AD RT differences in Task 2 were highly correlated with those in Task 1 (Pearson correlation: $r=.81, p < .0005$; Fig. 4d), suggesting that the RT costs in Task 2 were caused by lengthening of the response selection process in Task 1. Furthermore, Task 1 RT was not affected by the SOA (175 ms SOA: 1015 ms \pm 62 ms, 875 ms SOA: 1058 ms \pm 80 ms, $t_{13}=1.35, p > .2$). Taken together, these behavioural results are consistent with the postponement models of the PRP (De Jong, 1993; Pashler, 1994; Pashler & Johnston, 1989), wherein Task 2 response selection is delayed due to response selection processing of Task 1.

FMRI results

For each ROI, the data were analysed to detect two types of effects; first, whether the ROI was significantly

activated by either one or both of the perceptual and response manipulations and, second, whether the ROI was significantly more recruited by one manipulation than the other. A subset of the frontal cortex ROIs was engaged by the response manipulation (4AD versus 2Ad) but not by the perceptual manipulation (hard versus easy) (Fig. 5): the left ($t_{13}=2.5, p<.01$ for response versus $t_{13}=-.31, p>.75$ for perceptual) and right ($t_{13}=1.91, p<.05$ versus $t_{13}=.41, p>.65$) pre-motor cortex, and left IFG ($t_{13}=1.94, p<.05$ versus $t_{13}=.45, p>.65$). The pre-SMA showed a similar but non-significant trend (combined hemispheres, $t_{13}=1.03, p>.15$ versus $t_{13}=-0.1, p>.90$). The absence of significant perceptual manipulation activity in these ROIs does not appear to be due to a lack of sensitivity as there was little or no differences in activation between the high and low interference conditions (Fig. 5). To determine if the response manipulation recruited these ROIs significantly more than the perceptual manipulation, paired *t*-tests were performed between the response and perceptual effects (i.e. 4AD–2AD difference compared to high–low difference). The left dorsal pre-motor cortex was more activated in the response manipulation than the perceptual manipulation ($p<.05$), and both the right pre-motor and left IFG showed similar marginal effects ($p<.10$). In contrast, two other cortical regions were engaged by both the response and perceptual manipulations: the left and right IPS (left: $t_{13}=2.26, p<.05$ for response; $t_{13}=1.83, p<.05$ for perceptual) (right: $t_{13}=1.72, p<.05$ for response; $t_{13}=1.99, p<.05$ for perceptual) and to a lesser extent the right IFG ($t_{13}=1.31, p<.10$; $t_{13}=1.7, p<.06$). The anterior cingulate did not differentially activate with either manipulations (response left: $t_{13}=.77, p>.20$; response right: $t_{13}=1.52, p>.075$; perceptual left: $t_{13}=.57, p>.25$, perceptual right: $t_{13}=0.48, p>.30$).

While several ROIs were recruited by the response manipulation, none were solely or even preferentially engaged by the perceptual manipulation. Even a whole-brain voxel-wise analysis (thresholded at $p<.001$) failed to detect perceptual activation. Yet, most theories of information processing suggest that attentional bottlenecks not only occur at the response stage, but at the perceptual stage as well (Arnell & Duncan, 2002; Pashler, 1998). It has previously been shown that a region of the posterior parietal/occipital cortex, particularly in the right hemisphere, is activated by manipulations of perceptual demands (Marois et al., 2000) (Marois, Chun, & Gore, 2004). When the present data set were probed with this parietal ROI (which is lateral and ventral to the response selection ROI isolated in Experiment 1), the right hemisphere was engaged by the perceptual identification manipulation ($t_{13}=2.44, p<.05$), but not by the response manipulation ($t_{13}=0.53, p>.30$; Fig. 5), although the two manipulations were not significantly different from each other ($p>.10$).

It has been argued that increasing response selection demands can also increase the level of interference (competition) between Tasks 1 and Task 2 in a PRP

paradigm (Kantowitz, 1974). According to this view, the brain activations might reflect the engagement of areas involved in detecting and/or resolving response interference rather than stage postponement *per se*. Given that short SOAs between Tasks 1 and 2 lead to more task overlapping than long SOAs (Fig. 4), then this account predicts that greater task interference should occur at shorter SOAs. Since frontal cortex is activated when two tasks are executed simultaneously (Dreher & Grafman, 2003), and since its activity levels vary monotonically with task conflict (Durstun et al., 2003), then one might expect to observe greater frontal activity at short compared to long SOAs. However, none of the response-selection ROIs were more activated with the 175 ms SOA than with the 875 ms SOA (all *p*'s $>.1$), thus providing no support in favor of the response conflict account for these brain regions.

Voxel-wise analysis

The ROI approach demonstrated that specific regions of the frontal cortex are activated under dual-task conditions by a manipulation of response selection but not perceptual visibility. Do other brain areas besides these ROIs show similar activation pattern? To address this issue, the entire brain was examined with a voxel-wise approach. The results revealed no other brain regions, even at a liberal threshold of $p<.001$ (uncorrected) which were activated with the response selection manipulation. These results suggest that the modulation of the PRP most likely originates from the dorsal pre-motor cortex and left inferior frontal gyrus ROIs.

General Discussion

The PRP paradigm is widely viewed as revealing a capacity limit in selecting two responses at once (De Jong, 1993; Luck, 1998; Pashler & Johnston, 1989; Pashler, 1998). In addition, whereas modulating the number of response alternatives impinges on this central bottleneck of information processing (Karlin & Kestenbaum, 1968; Van Selst & Jolicoeur, 1997), varying the perceptual visibility of a stimulus does not (Pashler, 1994). By demonstrating that only a subset of brain regions involved in response selection remains unaffected by a perceptual visibility manipulation, this study refines to an unprecedented extent the candidate neural locus of response limitations under dual-task conditions.

Neural correlates of the capacity limits of response selection in dual-task conditions

The hypothesis that the capacity-limited process of response selection is associated with the dorsal pre-motor cortex is consistent with findings that this region

is involved in arbitrary sensori-motor associations (Kurata et al., 2000; Rushworth, Hadland, Paus, & Sipila, 2002; Wise & Murray, 2000) and that it impairs response selection when perturbed by magnetic stimulation (Rushworth et al., 2002). Two other frontal cortex regions, the left inferior frontal gyrus and pre-SMA, displayed similar activation trends to the dorsal pre-motor cortex (modulation by the response but not by the perceptual manipulation), suggesting that these other ROIs may also be important neural loci of the PRP bottleneck. The left IFG particularly merits further experimental scrutiny given that it has been hypothesized to play a supra-modal role in selecting among alternatives (Thompson-Schill et al., 1998) and that neighboring regions (BA 9 near 44) of the IFG are involved in executive control of attention (MacDonald, Cohen, Stenger, & Carter, 2000). It is possible that these different brain regions make somewhat distinct contributions to the PRP bottleneck. Since the lateral frontal cortex can be activated by a multitude of effector systems and tasks (Duncan & Owen, 2000; Thompson-Schill et al., 1998; Jiang & Kanwisher, 2003a), it may represent a purely amodal bottleneck of information processing. In contrast, since some areas of the macaque pre-motor cortex are somatotopically organized (Dum & Strick, 2002), it is conceivable that the human dorsal pre-motor cortex might be primarily involved in dual-task interference when both tasks involve manual responses. More research will be necessary to dissect the relative contributions of each of these brain regions to dual-task interference.

It should also be noted that manipulations of response selection are not the only ones demonstrating central processing limitations (Jolicoeur, 1999; Ruthruff, Miller, & Lachmann, 1995), and that this study was limited to a comparison between response selection and perceptual visibility. It is therefore possible that the dorsal pre-motor cortex or other frontal regions could be involved in other forms of selection or decision-making (De Jong, 1993; Gold & Shadlen, 2001; Jiang & Kanwisher, 2003b; Schall, 2001; Welford, 1952, 1980). Our study also does not rule out the possibility that processes other than response selection could also contribute to dual-task costs (Herath et al., 2001; Schubert & Szameitat, 2003; Szameitat et al., 2002).

Regardless of the precise number of cortical areas associated with the PRP or the range of cognitive operations that may feed into this processing bottleneck, our results provide substantial evidence that the PRP is a product of cortical processing. This conclusion resonates with a wealth of data implicating the cerebral cortex in response selection and competition (Decary & Richer, 1995; Hazeltine et al., 2000; Passingham, 1993; Rowe et al., 2000; Rushworth et al., 1997; Schall, 2001) and dual-task performance (Szameitat et al., 2002). To be sure, these results do not rule out the possibility of subcortical contributions as well (Ivry et al., 1998; Pashler et al., 1994). Indeed the data, together with the split-brain patient work (Ivry et al., 1998; Pashler et al.,

1994), is consistent with the view that there may be two structural bottlenecks to the PRP; a response *selection* bottleneck seated in the cerebral cortex, and a response *initiation/execution* bottleneck with a subcortical origin (De Jong, 1993; Ivry et al., 1998).

Implications for the cognitive models of the PRP

In addition to pointing to a potential neural locus for response selection limitations, the results also provide insights into the nature of this capacity-limited process. The fact that these brain activations were modulated by manipulations of the magnitude of the PRP, but not by manipulations of the SOA between Tasks 1 and 2, proffers key support for the postponement model of the PRP (De Jong, 1993; Pashler, 1994; Pashler & Johnston, 1989), and argues against models that describe the PRP as a result of the recruitment of brain regions to resolve simultaneous interference or conflict between tasks (Kantowitz, 1974; Herath et al., 2001). A conflict resolution account implies greater activation at shorter SOAs because there is more conflict (Durstun et al., 2003; Dreher & Grafman, 2003). In contrast, serial bottleneck accounts of the PRP do not predict differences in activation between 175 ms SOA and 875 ms SOA since the total duration of response selection (RS1 + RS2) is the same at both SOAs. Two fMRI studies of the PRP have observed greater right inferior frontal activation at short than at long SOAs (Herath et al., 2001; Jiang et al., 2004). However, while one study found a positive correlation between dual-task costs and magnitude of right inferior frontal activation (Herath et al., 2001), the other observed an opposite trend (Jiang et al., 2004). Furthermore, this brain region may be more involved in resolving interference in visuo-spatial attention than in resolving interference at response selection (Jiang, 2004). Thus, the interference resolution/monitoring account of the PRP does not find much support from neuroimaging studies. In addition, the present study does not provide any evidence of capacity sharing (Navon & Miller, 2002; Tombu & Jolicoeur, 2003), since reaction times to Task 1 were not affected by Task 1 – Task 2 SOAs. In contrast, the findings are highly consistent with the response selection postponement models of the PRP (De Jong, 1993; Pashler, 1994; Pashler & Johnston, 1989). Ultimately, however, evidence for postponement models will have to be supported by chronometric studies of dual-task interference that can directly visualize postponement of Task 2-specific brain activations.

Perceptual versus Response Processing Limitations

Several theories of information processing suggest that attentional capacity limits not only occur at the response selection or decision stage, but at perceptual stages of processing as well (Duncan, 1980; Pashler, 1989).

Although none of the response-selection ROIs were solely or even preferentially engaged by the perceptual manipulation, it was observed that a right parietal region previously isolated under similar perceptually challenging conditions (Marois et al., 2004) was recruited by the present perceptual task. Furthermore, these perceptual manipulations modulate the attentional blink (AB) (Marois et al., 2000), a transient deficit in the perception of the second of two visual targets that is thought to reveal perceptual processing limitations (Chun & Potter, 1995; Raymond, Shapiro, & Arnell, 1992). The location of this perception-related parietal ROI, ventral and lateral to the activation observed with the response manipulation (Fig. 5), is consistent with a comparative study of visual and motor attention (Rushworth, Paus, & Sipila, 2001a). Taken together, these neurobiological findings support the behavioural notion that response and perceptual processing limitations are at least partly distinct (Arnell & Duncan, 2002; Chun & Potter, 2001; Ruthruff & Pashler, 2001).

Of course, these conclusions rest on the assumption that the perceptual and response manipulations selectively affected perceptual and response-related stages of information processing. While there is little doubt that manipulations of stimulus visibility and response selection alternatives would largely affect distinct processing stages, it cannot be ruled out that each manipulation also impinged on the other processing stage. In particular, the response selection manipulation may have included a perceptual component as well, since twice as many visual stimuli were associated with the 4AD than the with the 2AD conditions. Conversely, it is conceivable that the perceptual manipulation included some post-perceptual component since the distractor digits may have added noise to the stimulus-response translation. However, given that the RT cost of the AD manipulation was about 250 ms (Fig. 4c), it seems improbable that a significant portion of that cost (or of the related brain activity) could be due to an increased difficulty in identifying a singly presented letter among a choice of four letters than among a choice of two letters. Likewise, if there is a post-perceptual component to the perceptual manipulation, it is likely to be minimal. First, manipulations of contrast and, in all likelihood, size should specifically affect target visibility (e.g., Jolicoeur et al., 2001). Likewise, the distractor interference manipulation should minimally affect post-perceptual stages of processing: All distractors were taken from a different stimulus class (digits) than the targets (letters), and hence should be associated with no or little response. Finally, it should be emphasized that these confounds, however minor they may be, work against finding perceptual- and response-specific brain activations. Thus, these confounds cannot account for the brain activations observed earlier, although they should be kept in mind for the discussion that follows.

In addition to largely reflecting distinct stages of information processing, perceptual and response processes may also be drawing on common central resources

(Arnell & Duncan, 2002; Jolicoeur, 1998; Jolicoeur, Dell'Acqua, & Crebolder, 2001; Ruthruff & Pashler, 2001). This is consistent with theoretical (Allport, 1987) and neurophysiological (Gold & Shadlen, 2001; Hernandez, Zainos, & Romo, 2002; Schall, 2001) work implying a tight relationship between the mechanisms involved in sensory representation and motor selection. Correspondingly, in the present study an overlapping set of parietal and lateral frontal cortex activations was observed with the perceptual and response manipulations. These results are consistent with a neuroimaging study demonstrating that manipulations of response selection compatibility and perceptual selection discriminability yielded similar fronto-parietal activations (Jiang & Kanwisher, 2003b). Although common activation of a brain area by two distinct cognitive operations does not necessarily guarantee that these operations share identical neural implementations, these findings at least suggest a close association between perceptual and response stages of information processing.

In conclusion, it can be proposed that a core of lateral frontal and anterior intra-parietal cortex regions, perhaps such as those associated with a wide variety of cognitive functions (Duncan & Owen, 2000), may represent shared neural substrates for limited-capacity perceptual and response information processing (Arnell & Duncan, 2002; Jolicoeur, 1998; Ruthruff & Pashler, 2001). Beyond this core, regions of the posterior parietal cortex, particularly in the latero-ventral area (Shapiro, Hillstrom, & Husain, 2002), may preferentially process perceptual information, while the pre-motor cortex may represent a key neural locus for our limited ability in selecting more than one response at a time.

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