Common Neural Mechanisms for Response Selection and Perceptual Processing

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Abstract

■ Behavioral evidence supports a dissociation between response selection (RS; stimulus-to-response [S–R] mapping) and perceptual discrimination (PD): The former may be subject to a central processing bottleneck, whereas the latter is not (Pashler, 1994). We previously (Jiang & Kanwisher, 2003) identified a set of frontal and parietal regions involved in RS as those that produce a stronger signal when subjects follow a difficult S–R mapping rule than an easy mapping rule. Here, we test whether any of these regions are selectively activated by RS and not perceptual processing, as predicted by the central bottleneck view. In Experiment 1, subjects indicated which of four parallel lines was unique in length; PD was indexed by a higher BOLD response when the discrimination was difficult versus easy. Stimuli and responses were closely matched across conditions. We found that all regions-of-interest (ROIs) engaged by RS were also engaged by perceptual processing, arguing against the existence of mechanisms exclusively involved in RS. In Experiments 2 and 3, we asked what processes might go on in these ROIs, such that they could be recruited by both RS and perceptual processing. Our data argue against an account of this common activation in terms of spatial processing or general task difficulty. Thus, PD may recruit the same central processes that are engaged by RS. ■

INTRODUCTION

Human cognitive abilities are astonishing: We remember events for decades, we acquire knowledge of the world and of ourselves, we recognize faces and objects in a glimpse, and we walk and talk and write and sing. Yet, our cognitive limitations are also striking. We can only keep track of about four visual objects at a time (Pylyshyn & Storm, 1988), and we sometimes fail to see objects that are right in front of us (Mack & Rock, 1998; Levin & Simons, 1997). Over and above our limitations in perceptual processing, behavioral studies have shown that we typically cannot compute more than a single stimulus-to-response (S–R) mapping (or "response selection" [RS]) at a time (Pashler, 1994). Thus, human information processing is limited both at the perceptual level, restricting the amount of information passing through the perceptual system, and at a RS level, limiting what can be acted upon (Allport, 1993). In this study, we investigate with fMRI the relationship between these two limitations in information processing.

Behavioral studies using dual-task paradigms have suggested that RS may represent a central bottleneck in human information processing (Pashler, 1994). This bottleneck has two key properties. First, it is a central limitation, occurring after perceptual processing but before motor execution. Any two RSs must be carried out sequentially, even when they are based on different input and output modalities. Thus, while we can see a shape and hear a tone at the same time, and we can press a key and say a word at the same time, we cannot simultaneously determine which key to press on the basis of the shape and determine which word to say on the basis of the tone. Exceptions to this rule are also observed under some conditions (Schumacher et al., 2001). Second, while RS is subject to this "central processing bottleneck," perceptual processing is not (Pashler, 1989). Perceptual processing for one task (e.g., visual search) can often, though not always (see Arnell & Duncan, 2002) concur with RS for another (Pashler, 1984, 1989). In an earlier paper, we tested the first property of RS (modality generality); here, we tackle the second property (dissociation from perceptual processing).

Jiang and Kanwisher (2003) identified a set of parietal and frontal regions involved in RS that produced a higher BOLD response in a visual–manual task when the S–R mapping rule was complex versus simple (Figure 1). We then showed that these regions were commonly active during RS for both visual and auditory inputs, and both manual and verbal outputs. Thus, these regions behaved in accordance with the modality generality of the RS mechanism found behaviorally.

In the present study, we tested the second prediction from the central processing bottleneck hypothesis

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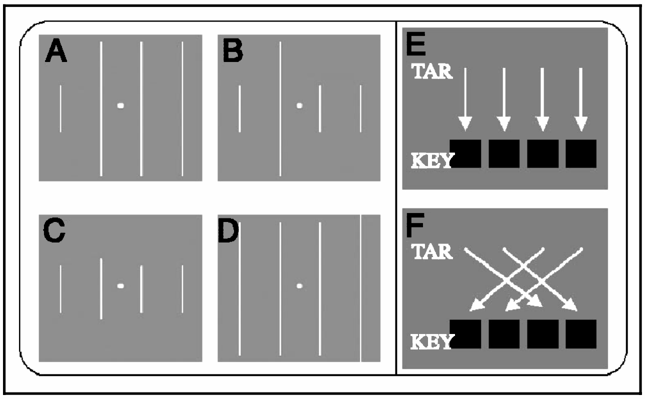


Figure 1. Sample displays (A–D) and instruction displays (E–F) used in the localizer scans and in Experiment 1. The target is the line in a unique length on each display. Perceptual discrimination was tested by contrasting coarse discrimination (A and B) against fine discrimination (C and D); a natural mapping rule (E) was used during instructions in both conditions. RS was tested on displays of coarse discrimination (A and B) only, by contrasting natural mapping (E) against unnatural mapping (F).

(Pashler, 1994): If a central bottleneck affects RS but not perceptual processing (Pashler, 1994), then to the extent that functionally distinct processes engage distinct brain regions (Kinsbourne, 1981), at least some of the brain regions involved in RS should not also be engaged by perceptual processing. However, if a central bottleneck affects both RS and perceptual processing (Arnell & Duncan, 2002; Dell'Acqua & Jolicoeur, 2000), then brain regions involved in the two tasks may be largely similar. We used a regions-of-interest (ROI) approach, first functionally identifying brain regions involved in RS in a localizer scan, and then asking whether these regions are engaged by perceptual processing.

RESULTS

Behavioral Data Collected During Scanning

Figure 1 shows the task used in Experiment 1. Table 1 shows mean RT and accuracy collected during scanning for all experiments. Increased difficulty in perceptual processing led to slower RT and poorer accuracy in both the length discrimination (Experiment 1) and the color-matching (Experiment 2) tasks. There was also a significant drop in performance during the more difficult condition in the word task (Experiment 3). These data confirmed that our manipulation of the difficulty of these tasks was successful.

Experiment 1: Length Discrimination Task

Whole-Brain Activation Map for Perceptual Processing

In the random effects analysis on the whole brain, the contrast of Fine versus Coarse length discrimination reveals activation in the parietal regions running along the intra-parietal sulcus (IPS), extending into the superior parietal lobule (SPL), in the superior frontal regions near the frontal eye fields (FEF) bilaterally, and in the bilateral dorsal and ventral lateral prefrontal cortex and the frontal operculum/insula. There was also significant activation in occipital–temporal regions.

We also scanned the same subjects in a RS task involving visual–manual mapping. Two conditions—compatible and incompatible response mapping—were tested. We created a statistical map for incompatible minus compatible mapping. To visualize the relationship between the two contrasts, we overlaid the activation map for visual RS (in red) and perceptual processing (in blue) and highlighted the common activations in green (Figure 2). This activation map reveals a striking degree of overlap. Activation in the parietal regions was similar for the two contrasts. Other overlapping regions include the FEF, the lateral prefrontal cortex, and the frontal operculum. The stunning degree of overlap suggests that many brain regions are commonly engaged in RS and perceptual processing and, thus, do not show the response profile expected of the RS bottleneck.

RS ROI Analysis: Do Any Brain Regions Act as RS Bottleneck?

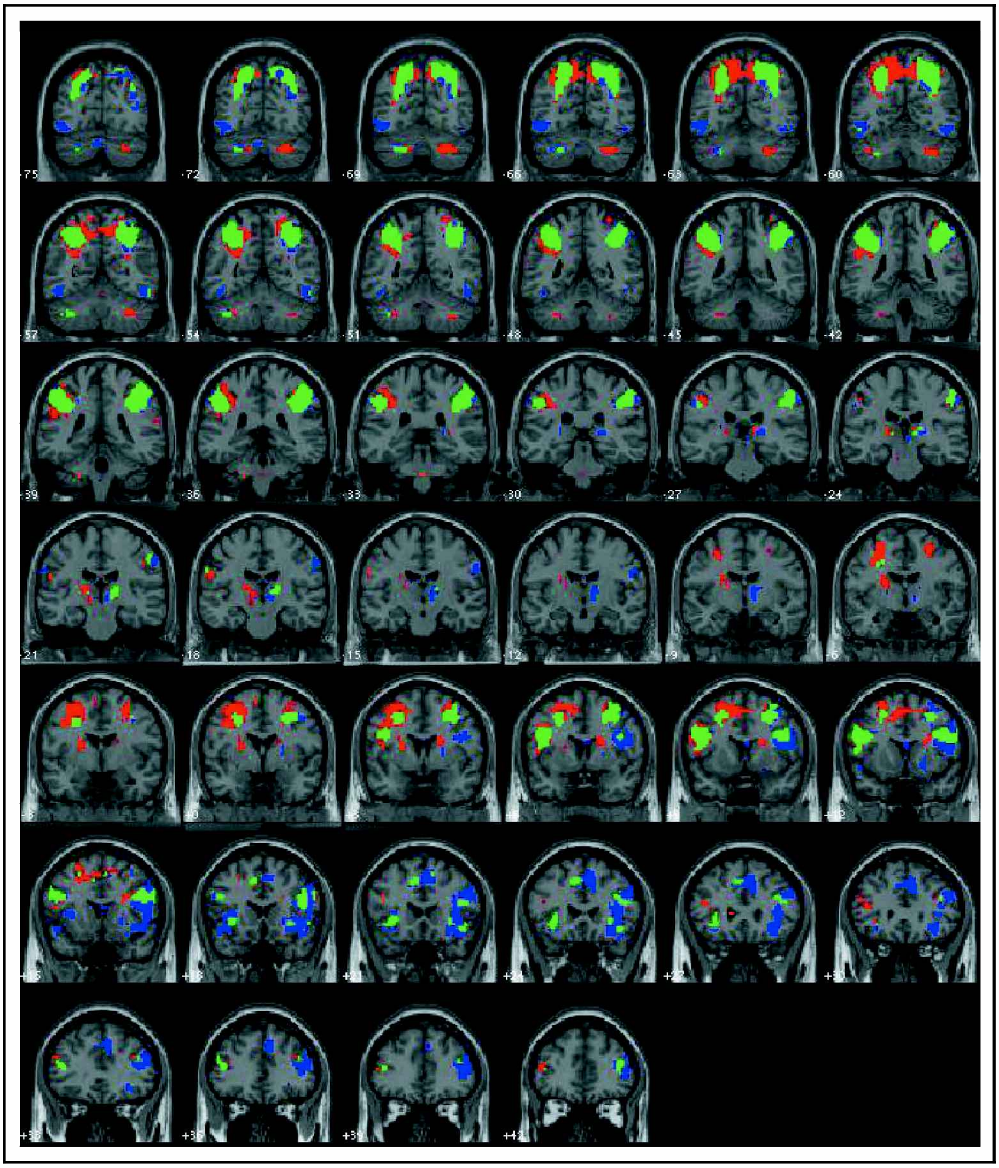
The ROI analysis permits us to ask in a more focused fashion and with correspondingly greater statistical power whether any of the regions involved in RS fail to show an activation for perceptual processing, as expected from the behavioral literature. To address this question,

Table 1. Behavioral Performance During Scanning

	Accuracy (%)				*RT (msec)*			
Experiment	*Difficult*	*Easy*	*SE*	*p*	*Difficult*	*Easy*	*SE*	*p*
1. Length discrimination	72	97	4	.0001	515	349	16	.0001
2. Color discrimination	69	98	4	.0001	518	404	24	.001
3. Word	84	97	3	.002	1283	813	30	.0001
Localizer scan[a]	94	95	2	*ns*	561	383	22	.0001

[a] Data were taken from Jiang and Kanwisher (2003).

Figure 2. Overlapping activation (in green) between visual RS (in red, unnatural mapping > natural mapping) and perceptual processing (in blue, fine discrimination > coarse discrimination) in a random effects analysis ($n = 14$; $p < .001$ uncorrected).



we measured the percent signal change (PSC) relative to fixation in the fine and coarse length discrimination tasks within the ROIs defined by their RS function. Our logic is that if any of these ROIs shows a significant effect of perceptual processing, that would argue against its role as the cortical locus of the RS bottleneck; whereas if an ROI shows no effect of perceptual processing, it is a candidate locus of the RS bottleneck.

The 13 ROIs were defined based on their activation during RS as reported in a previous study (Jiang & Kanwisher, 2003); these ROIs are: anterior and posterior IPS on the left and the right side (centered on: [−36 −54 43], [−30 −69 45], [42 −45 45], [30 −66 48]), right precuneus ([18 −66 60]), bilateral FEF ([−27 3 48], [33 3 48]), left inferior prefrontal cortex ([−48 9 21]), bilateral middle frontal gyrus ([−45 33 18], [36 44 27]), bilateral frontal operculum/insula ([−33 24 0], [48 21 −12]), and right cerebellum ([33 −72 −33]). Table 2 shows the PSC for each of these ROIs in each perceptual processing condition of Experiment 1.

Twelve of the 13 ROIs showed a highly significant activation for perceptual processing (fine > coarse length discrimination), and activation in the other ROI (right cerebellum) was not significant. The weakness of the cerebellar activation most likely reflects the fact that not everyone's cerebellum was covered to the same degree in the slice prescription. The magnitude of activation in the length discrimination task in all the ROIs was comparable to, or higher than, that for the RS task (Jiang & Kanwisher, 2003). In contrast to the behavioral evidence that RS relies on a mechanism distinct from that of perceptual processing, our data showed that all RS ROIs were also involved in perceptual processing.

The length discrimination task of Experiment 1 showed that none of the ROIs satisfied both conditions of a bottleneck for RS: (1) significant activation during RS; and (2) nonsignificant activation during perceptual processing. These results suggest that in terms of brain regions, there is either no localizable central bottleneck, or there is a central bottleneck but its function extends to perceptual processing. In the next two experiments, we sought to understand what processes are shared by both RS and perceptual processing that could explain the common activation.

Experiment 2: Nonspatial Color-Matching Task

Here, we tested whether the common activation of our ROIs by both RS and perceptual processing may reflect spatial processing, either in the form of finding a target among a spatial array of items (Experiment 1) or in the form of spatial remapping. In a previous study (Jiang & Kanwisher, 2003), we tested nonspatial RS by having subjects make an overt verbal report using either a compatible rule (say "same" if two sequential stimuli matched) or an incompatible rule (say "different" if they matched). The RS ROIs based on incompatible spatial mapping rules were also activated in the nonspatial verbal naming task, suggesting that cognitive tasks broader than spatial processing activate these ROIs.

In the current Experiment 2, we provide further evidence that the RS ROIs investigated here have a broader function than spatial processing. We tested subjects on a nonspatial perceptual task using sequential color matching. Subjects were asked to report whether two consecutively presented patches were identical or different in color. Discrimination difficulty was increased by making the two colors more similar on mismatch trials. If the RS ROIs perform specifically spatial function, they should not be activated in a comparison of difficult versus easy sequential color matching.

Whole-Brain Activation Map for Color Matching

Figure 3 shows the regions significantly activated by difficult versus easy color matching. To help visualize the similarities and differences in activation, we also overlaid the activation map for the visual–manual RS task of Experiment 1. A large amount of common activation can be seen (in green), in the bilateral IPS, middle frontal gyrus, frontal operculum/insula, and thalamus. In addition, the color-matching task activated the fusiform gyrus (see also Beauchamp et al., 1999 for a role of this region in color perception), pre-SMA (Rushworth, Hadland, Paus, & Sipila, 2001), and the anterior and inferior prefrontal cortex.

ROI Analysis: Are the RS ROIs Activated by Nonspatial Perceptual Discrimination (PD)?

To determine whether the RS ROIs are activated by nonspatial PD, we measured PSC relative to fixation in each ROI in the easy and difficult color-matching task (see Table 3). Among the 13 ROIs that showed RS

Table 2. PSC Relative to Fixation in the Coarse and Fine Length Discrimination Tasks (Experiment 1) in the ROIs Defined by Their RS Activity

	Left Hemisphere ROI		*Right Hemisphere ROI*	
	PD: Easy/Difficult	*RS: Easy/Difficult*	*PD: Easy/Difficult*	*RS: Easy/Difficult*
aIPS	0.15/0.46***	0.11/0.27**	0.10/0.55***	0.00/0.19***
pIPS	0.09/0.36**	0.00/0.20***	0.11/0.57***	0.03/0.23***
FEF	0.21/0.40***	0.17/0.35***	0.15/0.41***	0.13/0.27**
GFm	−0.08/0.22***	−0.03/0.09***	−0.03/0.20**	−0.13/−0.06$^{\#}$
Operculum	0.05/0.30**	−0.02/0.08*	0.05/0.45**	−0.09/−0.01, *ns*
Precuneus	N/A		0.00/0.43***	0.00/0.22*
GFi	0.12/0.45***	0.05/0.22***	N/A	
Cerebellum	N/A		0.17/0.25, *ns*	0.14/0.19, *ns*

N/A = not applicable; aIPS = anterior intra-parietal sulcus; pIPS = posterior intra-parietal sulcus; FEF = frontal eye field; GFm = middle frontal gyrus; GFi = inferior frontal gyrus; PD = perceptual discrimination; RS = response selection. PSCs were calculated from the raw data after preprocessing (motion correction, normalization, and smoothing).

$^{\#}p < .10$.

$^{*}p < .05$.

$^{**}p < .01$.

$^{***}p < .001$.

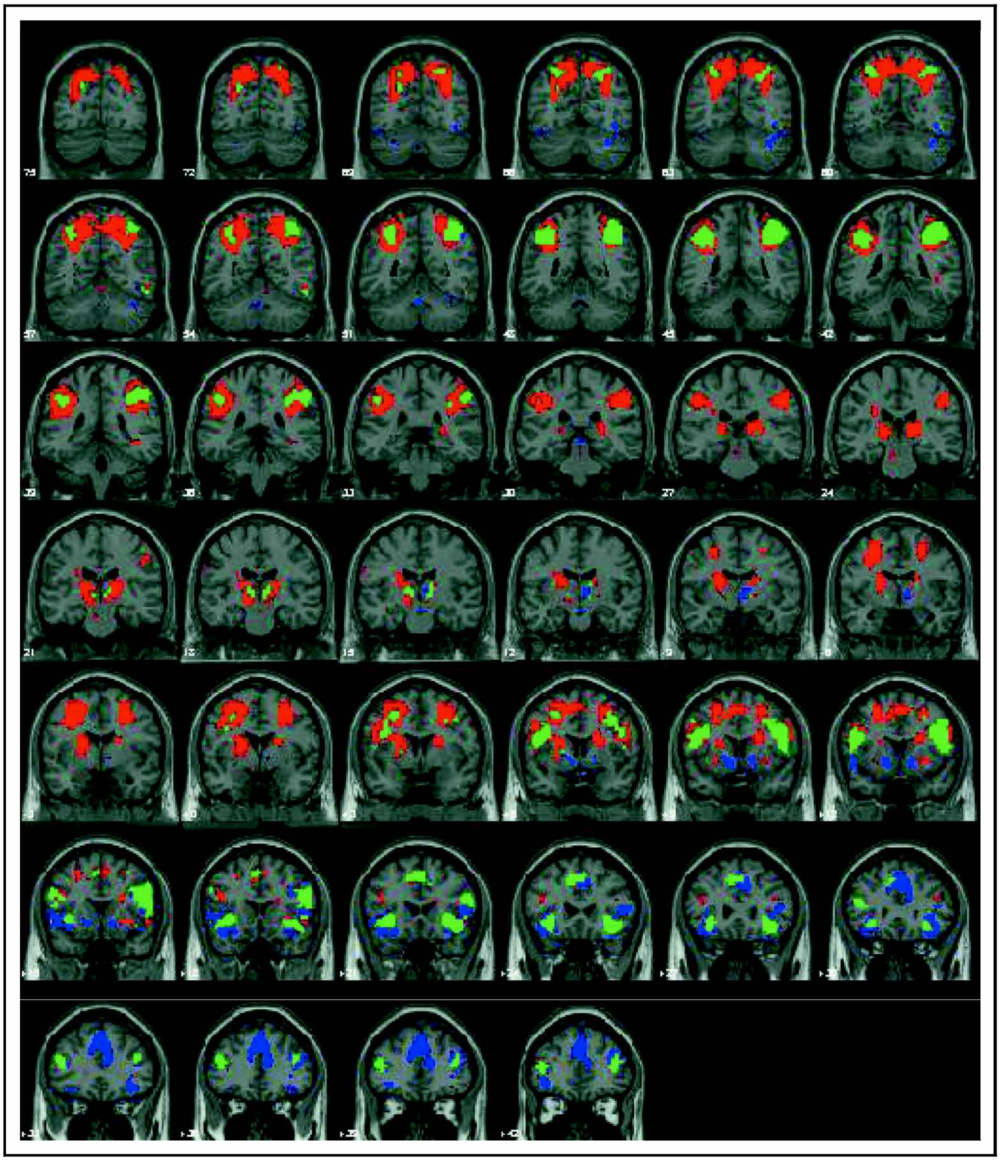


Figure 3. Whole-brain activation map of the color-matching task (in blue) overlaid on the activation map of the visual RS task (in red). Common regions of activation are shown in green. The two contrasts were generated from two different groups of 13 subjects ($p < .005$ uncorrected, random effects).

activity, 10 showed a significant effect for PD in the color task, including the anterior and posterior IPS, ventral and dorsal lateral prefrontal cortex, frontal operculum/insula, and right cerebellum. This reinforces the conclusion from Experiment 1 that these ROIs were not selective just for RS. Further, these ROIs were not just activated by spatial processing. Activation in two other ROIs—right FEF and precuneus—approached significance. Finally, the left FEF was not sensitive to the discriminability effect in color matching, suggesting that it may be involved in spatial processing. It is unlikely, however, that the left FEF is involved only in spatial processing, because it was significantly activated by nonspatial RS (Jiang & Kanwisher, 2003). Conversely, it is unlikely that the left FEF is insensitive to any nonspatial perceptual processing, because it was significantly activated when stimulus contrast was manipulated (Schumacher & D'Espisoto, 2000). Further studies are needed to fully characterize the function of the left FEF.

Experiment 3: Effort of Processing in a Word Task

The first two experiments showed that, first, all the ROIs involved in RS were also significantly involved in perceptual processing, and second, what drives this common activation is more general than spatial processing. It would be difficult to explain the common activation in terms of cognitive control required to maintain task set (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Miller & Cohen, 2001; Wagner, Maril, Bjork, & Schacter, 2001), because the instructions did not change between the easy and the difficult conditions of perceptual processing, yet, activation was different. In Experiment 3, we tested the hypothesis that the common activation across tasks reflect generic increases in mental effort. If so, then the ROIs should be activated by any difficult task.

In the word task, we presented English words visually to our subjects, who were required to decide in the easy, "Syllable" task whether the word contained one or more than one syllables, and in the difficult, "Verb + Noun" task, whether the word could be both verb and noun or either verb or noun but not both. The "Verb + Noun" task was considered more effortful than the "Syllable" task by subjective ratings and performance measures (RT and accuracy, see Table 1).

Whole-Brain Activation Map in the Word Task

Figure 4 shows the activation map for the difficult word task ("Verb + Noun" > "Syllables") in a random effects analysis. The activation was seen primarily in the lateral prefrontal cortex (ventral and dorsal lateral prefrontal cortex) and the frontal operculum/insula surrounding Broca's area, the SMA and pre-SMA, with a left-lateralized pattern. In addition, activation was also seen in the occipito-temporal gyrus ([−48 −45 −6]), near regions that have been shown to respond to visually presented words (Dehaene, Le Clec'H, Poline, Bihan, &, Cohen, 2002; Giraud & Price, 2001). To compare the difficulty effect in the word task and that in the RS task, we generated a whole-brain activation map for the visual RS task in the same subjects as the word task and overlaid the activation maps (see Figure 4). Some regions showed common activation for the two difficulty effects, in the thalamus/basal ganglia regions, and a subset of the left IPS, the left FEF, the left inferior prefrontal cortex, and the bilateral frontal operculum/insula.

To further visualize whether increased task difficulty had the same effect in the word task and the visual RS task, we created an activation map for the interaction between task and difficulty (see Figure 4). Here, we find that the parietal cortex, including the anterior and posterior right IPS, right precuneus, and most anterior segment of the left IPS, were more sensitive to the RS difficulty. In contrast, the left ventral lateral prefrontal cortex and the left operculum/insula were more sensitive to difficulty in the word task.

ROI Analysis: Are the RS ROIs Driven by Generic Effort?

Among the ROIs selected because they were activated by RS, the right parietal ROIs (right precuneus, right anterior and posterior IPS) failed to show any difference between the difficult word task (Verb + Noun) and the easy word task (Syllables). This stands in sharp contrast to the robust activation to perceptual processing and RS described earlier. Clearly, the right parietal regions do not respond to just any difficult task.

Table 4 shows the PSC in the word task and the visual RS task in the same group of subjects. Because difficulty was manipulated in both tasks, we were able to test the Task × Difficulty interaction effect. ANOVAs showed a significant interaction within all ROIs except the left FEF. The difficulty effect was larger for the word task than the RS task in bilateral middle frontal gyrus, frontal operculum/insula, left inferior frontal gyrus, and right cerebellum. The opposite pattern was seen in the right parietal ROIs.

The significant activation in several RS ROIs to the word task could reflect a role of these regions in

Table 3. PSC Relative to Fixation Within the Visual RS ROIs in the Color-Matching Task (Experiment 2)

	Left Hemisphere ROI		*Right Hemisphere ROI*	
	PD: Easy/Difficult	*RS: Easy/Difficult*	*PD: Easy/Difficult*	*RS: Easy/Difficult*
aIPS	0.00/0.15**	0.16/0.28**	0.08/0.29***	0.07/0.23**
pIPS	−0.14/−0.03*	0.06/0.22***	−0.06/0.12***	0.09/0.25***
FEF	0.16/0.18, *ns*	0.20/0.34***	0.15/0.21$^{\#}$	0.14/0.22***
GFm	−0.04/0.11**	−0.03/0.01, *ns*	0.04/0.15*	−0.06/−0.03, *ns*
Operculum	0.05/0.26***	−0.01/0.02, *ns*	0.07/0.43***	−0.03/0.03, *ns*
Precuneus	N/A		−0.24/−0.09$^{\#}$	0.06/0.25**
GFi	0.17/0.33**	0.06/0.16*	N/A	
Cerebellum	N/A		0.11/0.24**	0.22/0.31**

N/A = not applicable; aIPS = anterior intra-parietal sulcus; pIPS = posterior intra-parietal sulcus; FEF = frontal eye field; GFm = middle frontal gyrus; GFi = inferior frontal gyrus.

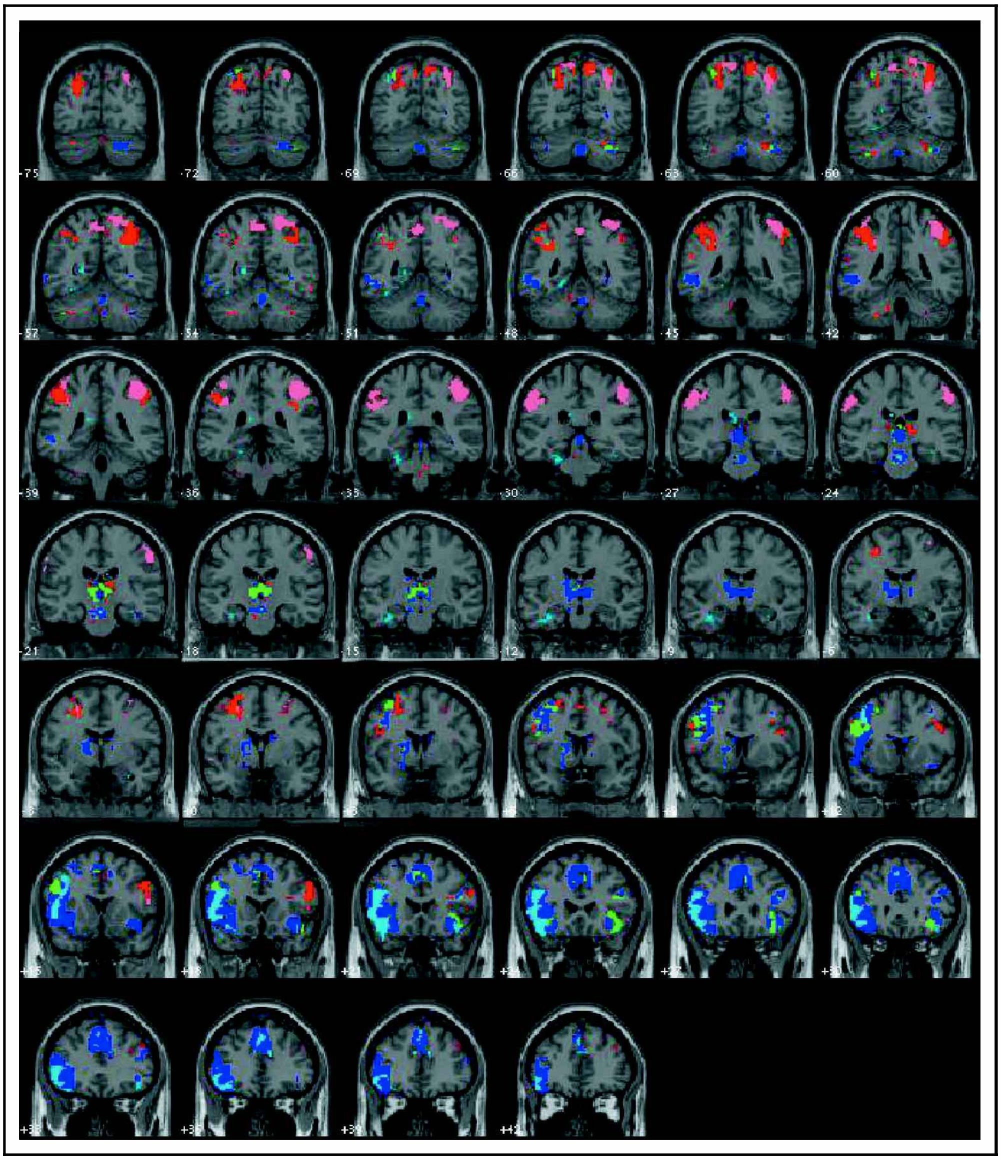
$^{\#}p < .10$.

$^{*}p < .05$.

$^{**}p < .01$.

$^{***}p < .001$.

Figure 4. Overlapping activation (in green) between the visual RS mapping difficulty (in red and pink) and the word difficulty (in blue and cyan) in 12 subjects ($p < .005$ uncorrected in a random effects analysis). Regions that showed significant interaction between task (RS vs. word) and difficulty were in pink (greater difficulty effect in the visual RS task than the word task) and in cyan (greater difficulty effect in the word than the visual RS task).



processing any difficult task. However, these activations could also reflect a more specific role in linguistic processing. For example, the left parietal, lateral prefrontal cortex, the frontal operculum/insula and the cerebellum were engaged in syntactic processing and in verbal working memory (Chein & Fiez, 2001; Poldrack et al., 1999; Jonides et al., 1998; Desmond, Gabrieli, Wagner, Ginier, & Glover, 1997; Smith & Jonides, 1997). These issues are discussed further in the Discussion.

Additional fMRI Results Across Experiments

Subtle Interaction Effects

So far, we have asked whether the regions activated by RS also showed main effects of perceptual processing. The answer is positive: Perceptual processing also recruits the ROIs defined by their RS activity, arguing against the hypothesis that these ROIs correspond to the cognitive central bottleneck. In a further analysis, we ask whether these ROIs are equally sensitive to RS and to perceptual processing. To simplify description, we will use the term ‘‘difficulty’’ to describe the difference between incompatible and compatible RS mapping, and between coarse and fine PD. We entered data from the ROI analysis into an ANOVA with two factors, process (RS or PD) and difficulty, and we performed this analysis on Experiments 1 (length discrimination) and 2 (color discrimination). In Experiment 1, we found a significant interaction between Process and Difficulty in the aIPS, pIPS, precuneus, GFm, and operculum. At all these ROIs, the perceptual processing-related activities were larger than the RS-related activities. This may be accounted for by the stronger task manipulation for perceptual processing, reflected by the accuracy data. In Experiment 2, we found significant interaction in the left FEF, the GFm, and frontal operculum. The left FEF was highly significant during visual RS but not during

Table 4. PSC Relative to Fixation Within the Visual RS ROIs in the Localizer Scans and the Word Task (Experiment 3)

	Left Hemisphere ROI				*Right Hemisphere ROI*			
	Visual RS		*Word Task*		*Visual RS*		*Word Task*	
	Natural	*Unnatural*	*Syllable*	*Verb + Noun*	*Natural*	*Unnatural*	*Syllable*	*Verb + Noun*
aIPS	0.10	0.24**	0.10	0.43**	0.10	0.31***	−0.02	0.02, *ns*
pIPS	0.12	0.28**	0.09	0.45***	0.12	0.28***	−0.14	−0.14, *ns*
FEF	0.23	0.39***	0.14	0.25**	0.18	0.35***	0.03	$0.10^{\#}$
GFm	−0.09	0.03*	0.15	0.73***	−0.07	−0.09, *ns*	−0.08	0.06*
Operculum	0.04	0.08, *ns*	0.12	0.45***	0.18	0.28, *ns*	0.12	0.45***
Precuneus	N/A				0.14	0.41**	−0.21	−0.20, *ns*
GFi	0.05	0.20**	0.30	0.72***	N/A			
Cerebellum	N/A				0.18	0.28**	0.12	0.45***

N/A = not applicable; aIPS = anterior intra-parietal sulcus; pIPS = posterior intra-parietal sulcus; FEF = frontal eye field; GFm = middle frontal gyrus; GFi = inferior frontal gyrus.

$^{\#}p < .10$.

$^{*}p < .05$.

$^{**}p < .01$.

$^{***}p < .001$.

color matching, but the GFm and frontal operulum showed the reverse. Thus, stronger task manipulation for PD than for RS can explain interaction effects found in Experiment 1 and the frontal ROIs in Experiment 2. The only exception was left FEF, which preferred RS to color discrimination (but not to length discrimination). As noted earlier, because of its sensitivity to manipulation of length discriminability and to stimulus contrast, the left FEF is not exclusively devoted to RS. In sum, although the interaction effects suggest that manipulations of RS and of PD activate several brain regions to different extents, they are primarily driven by the greater strength of the perceptual processing manipulation than the RS manipulation, and, hence, they do not support the existence of brain regions devoted to RS.

Negative Activation

During effortful cognitive tasks, some brain regions typically show reduced BOLD signal compared with a fixation baseline (Raichle et al., 2001; Shulman et al., 1997). Random effects analyses revealed that in the length discrimination task of Experiment 1 (but not the color task in Experiment 2), increased perceptual difficulty led to reduced BOLD in the following regions: the precuneus ([−3 −66 24]), posterior cingulate ([0 −45 36]), middle temporal gyrus ([−48 −63 24], [−54 −66 27], [51 3 −30], [54 −63 24], [27 −12 −27]), and superior frontal gyrus ([−12 51 25]], [−18 63 18]). Some of these regions, such as the medial frontal gyrus ([−12 51 −3]), middle temporal gyrus ([−54 −12 0]), and posterior cingulate cortex ([12 −54 21]), also showed decreased BOLD as the word task increased in difficulty. These were all regions that had previously been noted to show decreased BOLD signal during cognitive tasks (Gusnard & Raichle, 2001).

Activity in the Anterior Cingulate Cortex (ACC)

The ACC has been postulated to play an important role in monitoring cognitive conflict (Barch et al., 2001; Van Veen, Cohen, Botvinick, Stenger, & Carter, 2001; Botvinick, Nystrom, Fissell, Carter, & Cohen, 1999; Carter, Botvinick, & Cohen, 1999). In fact, Van Veen et al. proposed that the ACC monitors response conflict but not perceptual conflict. To test the activity in the ACC in

Table 5. PSC Relative to Fixation in the ACC Across Experiments

Experiment	*Easy*	*Difficult*	*Standard Error*	*p Level*
Visual RS (localizer)	−0.10	−0.05	0.05	Nonsignificant
1. Length Discrimination	−0.08	0.18	0.10	.02
2. Color Matching	−0.08	0.21	0.07	.001
3. Word	−0.06	0.28	0.05	.001

our study, here, we defined an anatomical ROI centered on the ACC ([0 33 30], Van Veen et al., 2001). It included a spherical volume of 33 voxels with a radius of 6 mm. Table 5 shows the PSC within the ACC in each of the experiments tested.

The ACC was significantly involved in all but the visual RS task. On one account, the lack of ACC activation in the visual RS task may be attributed to the blocked design, which involved constant response conflict within a block with correspondingly reduced necessity for conflict monitoring. However, the same logic would predict a lack of ACC activation for our other blocked design tasks, a prediction not borne out by the data. An alternative account is that the degree of conflict monitoring may be smaller in the visual RS task than our other tasks, because it was associated with a smaller performance decrement. Assuming that error rate is a good indicator of the amount of conflict involved in a task, the pattern of ACC activation seen in this study is consistent with the view that the ACC may be important for monitoring conflict (Botvinick et al., 1999; Carter et al., 1999). In any case, because the ACC was not involved in visual RS, the central cognitive bottleneck apparently does not reside here.

This conclusion may initially seem inconsistent with a study reported by Van Veen et al. (2001). These authors tested their theory that the ACC is involved in monitoring response conflict, using the flanker task in which a central target was flanked by three types of distractors: a letter identical to the target, a nonidentical letter from the same response category, or a letter from a different response category. Van Veen et al. found that the ACC was engaged in response interference (different response category—same category), but not in perceptual interference (same response category—identical letters). They argued that the ACC may be selectively involved in monitoring response conflict. However, in their study, perceptual conflict produced a much smaller behavioral cost; ACC may reflect the degree rather than the type of conflict. In a median RT split analysis, Van Veen et al. failed to find ACC activation for slow or fast trials for perceptual conflict. However, a median RT split analysis on response conflict showed no effect of RT on ACC either, supporting the idea that RT variance within a condition is better accounted for by random variation than degree of conflict. Thus, Van Veen et al.'s study does not provide strong evidence that response interference alone uniquely activates the ACC, and, hence, it does not contradict the conclusions that we reach here.

Activation in the Thalamus

The thalamus has been implicated as a possible locus of the central RS bottleneck. In a study on split-brain patients, Pashler et al. (1994) found that when two RSs were made, one with the left and the other with the right hemisphere, a severe dual-task interference was still observed in these patients. They proposed that the interference must have arisen from crosstalk in subcortical regions, perhaps in the thalamus. To find out whether thalamus is selectively involved in RS, here, we defined two functional ROIs centered on the most significant voxels (incompatible–compatible RS) in the left and the right thalamus ([−18 −21 9] and [18 21 12]). A spherical volume with a radius of 6 mm was defined surrounding the center of each ROI. Table 6 shows the PSC within the thalamus in all the tasks.

The left thalamus was significantly activated only in the word task, whereas the right thalamus was significantly activated in the length discrimination and the word task. In neither ROIs was the activation selective for visual RS. Thus, the thalamus does not correspond to the central processing bottleneck, although it may serve an important role in some cognitive processing (Huettel, Guzeldere, & McCarthy, 2001; Monchi, Petrides, Petre, Worsley, & Dagher, 2001).

Laterality Effects

So far, we have tested the 13 ROIs as regions unrelated to one another, yet, it is well known that homologous regions in the two hemispheres often have similar but

Table 6. PSC Relative to Fixation in the Thalamus across Experiments

ROI	*Experiment*	*Easy*	*Difficult*	*SE*	*p Level*
Left thalamus [−18 −21 9]	Visual SR (localizer)	0.00	0.01	0.03	*ns*
	1. Length discrimination	0.03	0.05	0.04	*ns*
	2. Color matching	−0.05	−0.01	0.02	*ns*
	3. Word	0.01	0.09	0.03	.017
Right thalamus [18 21 12]	Visual SR (localizer)	0.03	0.05	0.04	*ns*
	1. Length discrimination	−0.04	0.07	0.04	.008
	2. Color matching	−0.04	−0.02	0.02	*ns*
	3. Word	−0.08	0.05	0.05	.029

Table 7. PSC Relative to Fixation in Regions that Were Significantly Activated during Perceptual Processing but not RS

Experiment	*Coordinate*	*Location*	*Easy/Difficult RS*	*Easy/Difficult PD*
1. Length	[27 −78 30]	Occipital gyrus (area 19)	−0.13/−0.12, *ns*	−0.06/0.08*
	[−42 −72 −12]	Fusiform gyrus	−0.04/0.01*	0.08/0.22**
	[44 33 9]	GFi (area 46)	−0.15/−0.10, *ns*	−0.16/0.18***
2. Color	[39 −66 −9]	Occipital temporal G	−0.03/−0.02, *ns*	0.04/0.14***
	[−39 21 −12]	GFi (area 47)	−0.01/0.03, *ns*	0/0.24***
	[36 27 −9]	GFi (area 47)	−0.06/−0.03, *ns*	0.07/0.40***

RS: visual–manual response selection; PD = perceptual discrimination.

*$p < .05$.

**$p < .01$.

***$p < .001$.

nonidentical functions. To find any subtle functional differences between the left and the right ROIs, here, we tested the laterality effects in the five sets of bilateral ROIs. The visual RS task (localizer scan) produced largely symmetric activation in the two hemispheres. However, the length discrimination task of Experiment 1 produced a right-lateralized pattern, showing significant interaction between hemisphere and perceptual processing in all the ROIs. The effect of perceptual discriminability was significant on both left and right ROIs, but more so on the right. The right-lateralized perceptual processing effect is consistent with the observation that the right parietal regions are more important than their left counterparts in visual attention (Driver & Mattingly, 1998; Driver & Vuilleumier, 2001; Rafal, 1994). The right-lateralized effects may be related to orienting perceptual processing in space, because except for the frontal operculum/insular regions, the other ROIs did not show a right-lateralized pattern in the nonspatial color-matching task. Finally, the word difficulty task showed a left-lateralized pattern in the parietal cortex, the middle frontal gyrus, and the FEF, consistent with the generally accepted view that the left hemisphere may have a dominant role in language processing.

Unique Activation for Perceptual Processing

Although our ROI analysis addressed the question about whether there was a RS central bottleneck, by limiting analysis to RS regions, it does not answer whether there are any regions activated by perceptual processing but not RS. To find out, we performed a mapwise interaction test between difficulty and process (RS vs. perception) in Experiments 1 and 2. Across the length discrimination and the color-matching tasks, we observed at least two regions that showed unique perceptual effects (see Table 7). One lies in the occipital–temporal cortex. Its activation may be accounted for by increased attention to visual pattern or color as the PD became more difficult.

Another region lies in the anterior and ventral lateral prefrontal cortex. Such anterior activation is surprising for several reasons. First, it does not fit naturally with the view that the posterior attention network mediates visuospatial attention while the anterior attention network mediates response conflict and executive control (Casey et al., 2000; Posner & Petersen, 1990). Second, it does not fit with the characterization of the ventral lateral prefrontal as responsible for cognitive control of task set (Botvinick et al., 2001; De Fockert et al., 2001; Miller & Cohen, 2001; Wagner et al., 2001), because manipulation of PD does not alter the amount of cognitive control any more than the S–R incompatibility does. Whether the activation here was driven by the error trials only or by the greater generic difficulty of the perceptual task awaits further tests using event-related designs.

DISCUSSION

In this study, we asked whether any brain regions that are engaged in RS but not in perceptual processing, as predicted by the behavioral literature on the central processing bottleneck (Pashler, 1994), exist. In contrast to this prediction, we found in Experiment 1 that all of the ROIs that were engaged in RS were also activated by a perceptual length discrimination task. Our study thus poses a challenge to the notion of a cognitive bottleneck, the fMRI data, or both.

On the one hand, there may, in fact, be neural populations corresponding to the RS bottleneck that our fMRI data have failed to reveal. First, RS may rely on neural populations that are distinct from those involved in perceptual processing, but that are so closely intermingled that they cannot be resolved with fMRI. Second, even if RS is carried out by the same neural population as perceptual processing, it may nonetheless be functionally dissociable from perceptual processing. This may be accomplished by separating the two functions into distinct temporal stages or phases of processing within the same neural population (Singer, 1993). Testing these (and other) accounts will require the use of other techniques beyond fMRI.

On the other hand, the central bottleneck may not only be selective for RS, but it may also be engaged in difficult PD. In fact, recent behavioral studies have suggested that memory retrieval, short-term memory consolidation, change detection of visual patterns, mental imagery, and other forms of image manipulation may also tie up the central processing bottleneck (e.g., Arnell & Duncan, 2002; Dell'Acqua & Jolicoeur, 2000). Our fMRI data are consistent with these studies by showing that fronto-FEF–parietal regions may have a role more general than RS, but more specific than generic difficulty.

An important task for future behavioral, as well as neuroimaging studies is to enumerate the tasks that engage the central bottleneck. It is important to note, however, that as the list gets longer, the notion of a structural bottleneck loses some of its attraction. Indeed, some researchers argue that there may not be a central bottleneck after all, and the reported dual-task interference may be attributed to a strategic, rather than a structural, cognitive bottleneck. On this view, subjects may flexibly adjust its locus (and existence) depending on task priority, practice, or S–R compatibility (Meyer & Kieras, 1997; Schumacher et al., 2001). Thus, another interpretation of our fMRI data is that RS and perceptual processing do not rely on distinct functions after all. On this interpretation, the remaining challenge will be to characterize the actual processes that occur in common during both RS and perceptual processing.

Effects of Spatial Processing and Task Difficulty

The patterns of activation that we found for RS and for perceptual processing were strikingly similar (Figure 2). Experiments 2 and 3 asked what might be going on in the cortical regions that are activated during both tasks (i.e., the IPS, FEF, GFi/GFm, and frontal operculum/insula). Their function is apparently more general than spatial processing alone, because most of these regions show unambiguous activation in nonspatial tasks. For example, these ROIs were all involved in a nonspatial RS task, when subjects verbally reversed the response (e.g., say ''different'' when successive colors matched in color; Jiang & Kanwisher, 2003). In addition, with the possible exception of the left FEF, the ROIs were also implicated in a nonspatial color-matching task, when PD was made more difficult (Experiment 2 here). Even the left FEF may be involved in some nonspatial perceptual processing, because its activity has been shown to increase as stimulus contrast decreases (Schumacher & D'Espisoto, 2000). Thus, although some regions, such as the SPL, precuneus, and FEF, may be preferentially engaged in spatial processing (Berman et al., 1999; Labar et al., 1999; Culham et al., 1998), all the ROIs investigated here apparently play an important role in both spatial and nonspatial attention (Wojciulik & Kanwisher, 1999).

However, the function of the RS regions is less general than generic mental effort. An account of our ROI activations based on general task difficulty would predict that these regions are activated by any difficult task. However, the complete lack of activation in the right parietal cortex when the word task increased in difficulty (Experiment 3) argues against this account. Less clear is the interpretation of the other regions that showed a significant Task (visual RS vs. word task) × Difficulty interaction, but that were also significant in both tasks. If these regions responded only as a function of generic difficulty, then all regions should show the same activation profiles, which, in turn, should reflect the task difficulty measured behaviorally (e.g., the 470-msec RT cost in the word task might be expected to lead to stronger activations than the 166-msec cost in the RS task). However, our results show that some regions were more strongly activated by the word task (e.g., the left operculum/insula), while others were more strongly activated by RS (e.g., the right FEF). This double dissociation cannot be easily handled by a simple account based on generic effort.

Thus, the function of these fronto-FEF–parietal ROIs is apparently more general than spatial processing and is more specific than generic effort. Although an understanding of the precise functions of these regions must await future research, they may include RS, working memory, LTM encoding and retrieval, and executive control (Culham & Kanwisher, 2001; Duncan & Owen, 2000). The necessity to exert cognitive control may be a common theme across many of these tasks (De Fockert et al., 2001; Miller & Cohen, 2001; Wagner et al., 2001). However, as argued earlier, cognitive control, in the sense of maintaining task set, is unlikely to be strongly affected by the perceptual discriminability manipulation used in Experiments 1 and 2. An important task for future studies is to determine the essential process(es) that activate these brain regions.

Generalization of the Findings

Both RS and perceptual processing may be operationalized in various ways. Do our results generalize to other paradigms for testing RS and perceptual processing? The regions that we identified here for RS are based on a companion study that found the same regions to be activated in manipulations of S–R compatibility using both visual and auditory input modalities, and both spatial and nonspatial mapping paradigms (Jiang & Kanwisher, 2003). Other studies that manipulate RS using the Stroop task, the flanker task, the antisaccade task, and other response competition tasks have activated regions similar to those that we identified here (Banich et al., 2000; Connolly, Goodale, Desouza, Menon, & Vilis, 2000; Hazeltine, Poldrack, & Gabrieli, 2000; Leung, Skudlarski, Gatenby, Peterson, & Gore, 2000; Botvinick et al., 1999; Carter et al., 1999; Bush et al., 1998; Pardo, Pardo, Janer, & Raichle, 1990). Paradigms for testing perceptual processing have varied even more widely (Pashler, 1998). Many neuroimaging studies have demonstrated that the frontal-FEF–parietal network is involved in allocating attention to space (Corbetta & Shulman, 2002; Culham & Kanwisher, 2001), one of the most commonly tested forms of perceptual attention. Here, we have extended these findings to show that even nonspatial attention can also activate the same network (see also Coull, Frith, Buchel, & Nobre, 2000; Marois, Chun & Gore, 2000; Wojciulik & Kanwisher, 1999). Thus, our finding of activation in the fronto-FEF–parietal regions for perceptual processing and RS apparently generalizes to other paradigms for testing these functions.

Relation to Prior Studies

Although many studies have investigated RS or perceptual processing alone, only a few have tested whether RS selectively activates brain regions not engaged by perceptual processing. In two relevant studies, Marois, Larson, Chun, and Shima (2002) and Schumacher and D'Espisoto (2000) orthogonally varied perceptual difficulty (via stimulus contrast) and RS difficulty (via S–R compatibility or the number of response alternatives). Many of the findings of these studies are consistent with those that we report here. However, in important contrast to our findings, both studies reported some regions activated by RS but not perceptual processing. The failure of these studies to find an increased activation for perceptual processing in these regions may result from a lack of statistical or experimental power. Consistent with this interpretation, Schumacher and D'Esposito reported activations for perceptual processing in the premotor cortex not found by Marois et al., and Marois et al. reported perceptual activations in the parietal cortex not found by Schumacher and D'Esposito. Further, other studies have reported activations from spatial attention in regions these studies found to be selective for RS (Cabeza & Nyberg, 2000; Culham & Kanwisher, 2001). Note that even if only some, not all, perceptual processing manipulations activate each region implicated in RS, that is sufficient to undermine the claim that these regions are selective for RS. Thus, although we do not yet have a complete account of the discrepancies between our findings and those of Marois et al (2002) and Schumacher and D'Espisoto (2000), these studies do not provide evidence against our claim that brain regions involved in RS are also involved in perceptual processing. Our data thus challenge the notion of a localizable RS bottleneck.

METHODS

Subjects

Twenty-eight subjects between the age of 18 and 43 (Mean = 23.2, *SD* = 5.2) participated in these studies (13 women and 15 men). Fourteen subjects were tested in Experiment 1, 13 in Experiment 2, 12 in Experiment 3, and 17 in the localizer scans. Some subjects were scanned in multiple experiments.

Testing Procedure

Subjects received 5 min of practice in each task on the same day or the day before the scan. They were scanned on a Siemens 3.0 T head-only scanner. All scanning took place at the Athinoula A. Martinos Center for Biomedical Imaging in Charlestown, MA. The scanning procedure and parameters were similar to the one used in the companion paper (Jiang & Kanwisher, 2003). Twenty oblique axial slices 6 mm thick with 0 mm distance between slices were scanned. We used a T2*-weighted EPI sequence (TR = 2,000 msec, TE = 20 msec, flip angle = 90°, resolution = 3.13 × 3.13 × 6.00 mm) for the functional scans. For the localizer scan and Experiments 1 (length discrimination) and 2 (color matching), each scan lasted 6 min 4 sec. For Experiment 3 (word task), each scan lasted 5 min 44 sec. The first 8 sec of each scan was discarded.

Scan Composition

Each functional scan used a blocked design with three conditions: fixation (F), task A, and task B. The comparison between tasks A and B is our main contrast of interest. In all experiments, the two tasks were matched in low-level visual input and in motor output. Differences between tasks were introduced by instructions (Experiment 3 and the localizer scans) or by stimulus similarity within a trial (Experiments 1 and 2). In the localizer scan and the first two experiments, the scan was composed of a series of blocks in which task was counterbalanced in order (ABAB/BABA or ABBA/BAAB), and fixation blocks preceded each task and followed the last task. Each task block lasted 64 sec, and each fixation was 20 sec. The first four fixation blocks were each composed of a 15-sec fixation followed by a 5-sec instruction.

In the word task (Experiment 3), the scan was also composed of fixation and two tasks, in a similar structure as in the other experiments. Each task block lasted 60 sec, and the first four fixation blocks each lasted 20 sec, composed of a 16-sec fixation followed by a 4-sec instruction. The last fixation block was 16 sec.

Materials and Tasks

Stimuli were presented using the Psychtoolbox, implemented in MATLAB (Brainard, 1997).

Experiment 1: Length Discrimination

Each trial (2 sec) of the length discrimination task started with a visual display of 100 msec, followed by a 100-msec mask, and then a 1800-msec fixation display. Each display contained four vertical lines, three of which were identical and the other was unique in length, either shorter or longer. The lines were chosen from four possible lengths: 3.1°, 2.8°, 1.0°, or 0.8°. The four lines were evenly spaced on a 6.25° × 6.25° display (Figure 1A–D). The mask was made of 18 vertical and 18 horizontal lines (length = 6.25°) semiirregularly displaced.

The task was to identify the line with a unique length in each display and report its spatial position among the four lines by pressing one of four keys. Subjects comfortably rested their index, middle, ring, and little fingers of the right hand on keys 1, 2, 3, and 4. The target position was mapped onto the keys according to a compatible mapping rule for every block (Figure 1E), so the instructions preceding each block were the same. Tasks A (coarse discrimination) and B (fine discrimination) differed in how the lines were paired on a trial. In the coarse discrimination task, the shorter line(s) was either 1.0° or 0.8°, and the longer line(s) was either 3.1° or 2.8°. In the fine discrimination task, the two shortest lines (1.0° and 0.8°) were paired on a trial and the two longer lines (3.1° and 2.8°) were paired on a trial. Each subject performed two scans.

The Localizer Scan: Visual RS

The localizer scans were similar in procedure to the length discrimination task. This task has been described previously (Jiang & Kanwisher, 2003). Stimuli tested in this task were the same as those in the coarse discrimination of Experiment 1, in which the target length was obviously different from the distractors. What differed between tasks was the instructions preceding each block. The S–R mapping rule between the target position and the key position was either compatible (Figure 1E) or incompatible (Figure 1F).

Experiment 2: Color Matching

On each trial, two color patches (diameter = 0.93°) were presented at fixation; each was presented for 100 msec, and a 100-msec blank interval intervened between them. Subjects were asked to judge whether the colors were identical or different. The colors were chosen from two shades of green (RGB values [0 255 0] and [0 175 0]) and two shades of blue (RGB values [0 0 255] and [0 0 170]). The background was black. Half of the trials were match trials, the other half were mismatch trials. In the easy color-matching condition, when colors mismatched, one was chosen from one of the green colors and the other was chosen from one of the blue colors. In the difficult color-matching condition, when colors mismatched, the two colors were two shades of green, or two shades of blue. In each task block, each color was presented the same number of time in the easy and difficult color matching, but the pairing within a trial differed.

Subjects were instructed to push the left key with their right index finger if the colors matched and the right key using their right middle finger if they mismatched. The instructions preceding each block informed subjects whether the difference on mismatch trials would be small or large, so subjects could adopt an appropriate criterion to differentiate mismatch from match trials. Each subject performed two or four scans.

Experiment 3: Word Task

Ten different lists of 24 words (4–7 letters) were created. Each list contained equal number of one-syllable words (e.g., "flight," "pause") and multisyllable words (e.g., "locate," "copy"). Further, one- or multisyllable words contained equal number of one- or multicategory words: Multicategory words were both a verb and a noun (e.g., "pause," "copy") while one-category words were either a verb (e.g., "locate") or a noun (e.g., "flight"), but not both (half of these were verb only and half were noun only). In the "Syllable" task, subjects pushed the left key for one-syllable words and the right key for multisyllable words. In the "Verb + Noun" task, subjects pushed the left key for one-category words, and the right key for multicategory words.

In the 60 sec of each block, there were 24 trials, each lasting 2.5 sec. The word was presented at fixation for 200 msec (in helvetical font, point size 72), followed by a fixation period of 2.3 sec. The same word was judged twice, once in the Syllable task and once in the Verb + Noun task. Each scan (e.g., in either ABBA or BAAB order) tested two different lists, one list for the first two blocks and the other for the last two blocks. The block order ensured that half of the lists were tested in the Syllable task first and the other half in the Verb + Noun task first. All subjects practiced on two lists and were scanned on the other eight (or four) lists. Each subject performed two or four scans.

fMRI Data Analysis: Logic

Two different kinds of analyses were conducted on the data from each experiment. First, we created a whole-brain statistical map using a random effects analysis for the effect of interest (e.g., perceptual processing in the length task). The activation map was then overlaid on an activation map from the RS task from the localizer scans, so as to visualize the similarities and differences in activation between different contrasts.

Second, to test the specific question of our study—which brain regions underlie the RS bottleneck—we relied on the ROIs approach. Here, we defined ROIs based on their RS activity in a previous study (Jiang & Kanwisher, 2003) and calculated the PSC from fixation for perceptual processing. A significant perceptual processing effect in a particular ROI indicates that this ROI is sensitive to perceptual processing and therefore does not satisfy the criterion of a RS bottleneck. In contrast, an ROI that does not show an effect of perceptual processing would be a candidate region for the RS bottleneck.

fMRI Data Analysis Procedure

Activation Map

Data were analyzed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm/spm99.html). After preprocessing (see Jiang & Kanwisher, 2003), we analyzed each subject's data for the contrast of interest and conducted a random effects analysis ($p < .001$ uncorrected for the localizer scan and Experiment 1, and $p < .005$ uncorrected for Experiments 2 and 3).

We localized RS ROIs in a previous study (Jiang & Kanwisher, 2003). There, we split the four scans of the visual RS task into two sets of two scans each. One data set was used in the random effects group analysis, which functionally defined ROIs (incompatible > compatible mapping) at the group level. Each group ROI contained voxels that are significant at $p < .001$ level uncorrected for multiple comparisons and was centered on the local maximal. Each group ROI was within a spherical volume containing the significant voxels; the radius of the ROIs was between 6 and 12 mm, with the constraint that different ROIs did not overlap. Once these ROIs were defined, we measured the PSC within these ROIs in the other half of the data and confirmed that these ROIs were involved in RS.

In the current study, we selected the same ROIs as defined by the previous study. Most subjects in Experiment 1 ($N = 13$) and all subjects in Experiment 3 were tested in those localizer scans, allowing us to adjust the functional ROIs according to individual subjects' localizer activation. For these subjects, we adjusted the ROIs by taking only the voxels that fell within the group ROIs that were also active in that individual subject's localizer scans. The individually adjusted ROIs allowed anatomical variation across subjects to be expressed while ensuring that the voxels were still representative of the general population. For other subjects, the individual ROIs were the same as the group ROIs.

PSC relative to the fixation baseline was calculated for each task of interest (e.g., coarse and fine length discrimination) within each ROI for each subject. We then tested whether there was a significant effect of (say) perceptual processing within each ROI. A lack of activation for perceptual processing within the RS ROIs would mean that ROI was a candidate brain region for the RS bottleneck.

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The data reported in this experiment have been deposited in The fMRI Data Center (http://www.fmridc.org). The accession number is 2-2003-113RG.

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