

# Investigating the modality specificity of response selection using a temporal flanker task

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**Abstract** The neurocognitive architecture for response selection is uncertain. Some theorists suggest that it is mediated by an amodal central mechanism, whereas others propose a set of independent control mechanisms. In a functional neuroimaging experiment, we investigated the nature of response selection by examining how its underlying brain mechanisms are affected by stimulus modality. To do this, we used a modified flanker task, in which the target and flanker (distractor) stimuli differed in time rather than space, making it accessible for both visual and auditory stimuli. As in the traditional flanker task, larger reaction times were observed for incongruent than congruent trials (i.e., a congruency effect) for both modalities. Congruency affected brain activation for both modalities in prefrontal cortex, parietal cortex, and the putamen. Modality-dependent activation was found in additional prefrontal and parietal regions for the visual modality and in left inferior prefrontal cortex for the auditory modality. Modality-dependent activity specifically related to response congruency was also found in sensory cortical regions. These data suggest that modality affects the brain regions throughout the cortex mediating response selection even for conceptually identical stimuli and tasks. They are consistent with the hypothesis that (at least partially) independent brain networks mediate response selection and that input modality may be a powerful factor for organizing neural activity to support task performance.

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## Introduction

Response selection is the cognitive process, or collection of processes, that activate a response representation based on a particular stimulus representation and a set of stimulus–response (S–R) rules. How responses are selected based on stimulus inputs is controversial. Many theorists consider response selection a processing stage distinct from modality-specific stimulus encoding and response production stages (for reviews see Meyer & Kieras, 1997a; Pashler, 1994; Pashler & Johnston, 1998). Other theorists (e.g., Cohen & Feintuch, 2002; Magen & Cohen, 2010; Wickens & Liu, 1988; Wickens, Mountford, & Schreiner, 1981) emphasize the effect on response selection of input and output modalities (and the pairings between them). The current functional magnetic resonance imaging (fMRI) experiment investigates the effect of manipulating stimulus modality on response selection within an otherwise identical task. In this way we may isolate the effect of modality on the brain mechanisms underlying response selection.

According to the amodal view of response selection (e.g., Byrne & Anderson, 2001; Pashler, 1994; Pashler & Johnston, 1998), a unitary mechanism applies the abstract S–R rules and selects appropriate responses for all incoming task-relevant stimuli. Evidence for this hypothesis comes mainly from behavioral experiments, in which the effect on behavioral dependent variables (viz., reaction time, RT, and accuracy) of performing two tasks simultaneously (or nearly so) are measured. These experiments typically show that processing of the secondary task stimulus is delayed by processing of the primary task stimulus—even when the tasks do not share stimulus or response modalities (e.g., Pashler, 1990). Additional experimental manipulations have been used to suggest that a bottleneck in response selection processing (i.e., response selection

can only process one task stimulus at a time) causes this delay (e.g., McCann & Johnston, 1992). A bottleneck in response selection is consistent with the idea that there is only one central mechanism for this process because one process may not be able to select two distinct responses simultaneously.

The unitary response selection mechanism account has been challenged by evidence suggesting that the response selection delay in typical dual-task experiments is not due to competition for a unitary central mechanism. Rather the delays stem from strategic choices participants make to control their performance in dual-task situations (Hazeltine, Weinstein, & Ivry, 2008; Israel & Cohen, 2011; Meyer & Kieras, 1997a, b; Meyer et al., 1995; Schumacher et al., 1999, 2001). These delays can be overcome under the right conditions (Hazeltine, Ruthruff, & Remington, 2006; Hazeltine, Teague, & Ivry, 2002; Hazeltine et al., 2008; Israel & Cohen, 2011; Ruthruff, Van Selst, Johnston, & Remington, 2006; Schumacher et al., 1999; Schumacher & Schwarb, 2009; Schumacher et al., 2001). Moreover, Hazeltine et al. (2006) demonstrated that the pairings of the stimuli and responses can affect the magnitude of dual-task costs without affecting single-task RTs. Accounting for these data with a unitary mechanism requires that its duration depends on operations occurring within other processing stages, which undermines its elegance and predictive power.

If dual-task processing delays do not stem from competition for a unitary response selection mechanism, then it remains possible that multiple (perhaps modality specific) response selection mechanisms exist in the human information processing system. However the strategic response selection bottleneck interpretation of Meyer and Kieras has been criticized and alternate interpretations have been proposed (e.g., Ruthruff, Johnston, & Van Selst, 2001; Ruthruff, Johnston, Van Selst, Whitsell, & Remington, 2003; Ruthruff, Pashler, & Klaassen, 2001; Ruthruff, Van Selst et al., 2006). That these issues have persisted in the face of an extensive dual-task literature attempting to determine the nature of the bottleneck mechanism (e.g., Anderson, Taatgen, & Byrne, 2005; Byrne & Anderson, 2001; Hazeltine et al., 2002; Israel & Cohen, 2011; Ruthruff, Hazeltine, & Remington, 2006) suggests that behavioral dual-task procedures may not be sufficient, in and of themselves, to resolve the controversy about the nature of response selection.

### Functional neuroimaging investigations of response selection

To provide additional data to resolve this issue, functional neuroimaging has recently been used to investigate the

nature of response selection under dual-task conditions. A series of experiments by Dux, Ivanoff, Asplund, and Marois (2006) identified regions in posterior and superior medial prefrontal cortex as likely candidates for the neural substrate supporting an amodal central response selection mechanism. These two regions were activated with tasks using different stimulus and response modalities, their activation increased with response selection difficulty, and they showed evidence for a delay in the onset of activity with dual-task slowing. Several other studies have reported that inferior frontal sulcus also mediates dual-task processing (e.g., Schubert & Szameitat, 2003; Stelzel, Schumacher, Schubert, & D'Esposito, 2006; Szameitat, Schubert, Muller, & Von Cramon, 2002). Stelzel et al., for example, manipulated the stimulus and response pairings under single and dual-task conditions and found that inferior frontal sulcus was sensitive not only to dual-task processing (replicating Schubert & Szameitat, 2003; Szameitat et al., 2002) but also to modality pairings. That is, the dual-task visual–vocal and auditory–manual condition produced more activity in inferior frontal sulcus than the dual-task visual–manual and auditory–vocal condition. Given the behavioral findings of Hazeltine and Ruthruff (2006), these data suggest that modality and their pairings affect task processing.

Several fMRI studies have used an alternative approach to investigate the nature of response selection (Hazeltine, Bunge, Scanlon, & Gabrieli, 2003; Jiang & Kanwisher, 2003; Morimoto et al., 2008; Schumacher, Elston, & D'Esposito, 2003). Rather than manipulate whether performance takes place under single- or dual-task conditions, these studies manipulated response selection difficulty under single-task conditions. Using a variety of tasks and stimulus representations (i.e., color, verbal, spatial, nonspatial), these studies examined the extent of neural overlap between the representation types. If response selection is an amodal process, then the same brain network should be activated by response selection difficulty, regardless of the stimulus type. If, however, there are multiple response selection processes, then difficulty manipulations may activate distinct brain networks based on the stimulus material used. Although there are inconsistencies and alternate interpretations, the bulk of the evidence suggests that multiple networks for response selection may exist.

For example, Hazeltine et al. (2003) used visual color and visual letter stimuli in a standard flanker task (i.e., central target flanked by distractors; Eriksen & Eriksen, 1974). They found regions in frontal and parietal cortices sensitive to congruency in both tasks (consistent with an amodal response selection mechanism). However, they also found stimulus dependent regions. Specifically, bilateral regions in middle frontal gyrus, postcentral gyrus, and left inferior parietal lobule showed a significantly larger congruency effect for letter than color stimuli. Conversely, a region in

right inferior frontal gyrus showed a significantly larger congruency effect for color than letter stimuli. These material-dependent activations suggest at least partially distinct networks for response selection based on stimulus type.

One region that Hazeltine et al. (2003) found to be sensitive to congruency across tasks was in right middle/inferior frontal gyrus. However, a similar study reported material-dependent results in a very similar region using verbal and color stimuli in a flanker task (Morimoto et al., 2008). Specifically, Morimoto and colleagues found a region in inferior frontal gyrus sensitive to congruency for verbal distractors in the left hemisphere and color distractors in the right. It is currently unclear what to make of these discrepancies, but both Hazeltine and colleagues and Morimoto and colleagues report evidence consistent with material-dependent response selection mechanisms.

Yet, evidence exists that is inconsistent with this claim (Jiang & Kanwisher, 2003). These authors manipulated S–R compatibility across three experiments using a visuospatial–manual task, an auditory–manual task, and a visual nonspatial–vocal task. Although there were some regions of task-specific activity, most activity, including bilateral dorsal prefrontal and superior parietal cortices were affected by compatibility across all three tasks. This common activation appears to be compelling evidence for an amodal response selection mechanism because Jiang and Kanwisher manipulated both stimulus and response modality across their experiments and still identified a common brain network associated with response selection.

Unfortunately, the results from Jiang and Kanwisher (2003) may not resolve the issue. Schumacher et al. (2003) conducted two experiments manipulating response selection using spatial and nonspatial visual–manual tasks. In these experiments, the difficulty of response selection was parametrically manipulated. The authors reasoned that an effective way to isolate brain regions specifically associated with response selection would be to identify regions showing a monotonic increase in activity with response selection difficulty. There were many regions of overlap in comparisons between the easiest and hardest levels of each task (comparable to the Jiang and Kanwisher results), but some regions showing a monotonic increase with response selection difficulty were task specific. Right dorsal prefrontal, right superior parietal, bilateral premotor and precuneus cortices showed changes in activation that were specific to manipulations of response selection difficulty for the spatial response selection task, whereas left dorsal prefrontal, left inferior parietal, left middle temporal, and left extrastriate cortices showed changes that were specific to manipulations of response-selection difficulty for the nonspatial task. These results (*viz.*, that stimulus type affects the brain networks for response selection) are more consistent with Hazeltine et al. (2003) and Morimoto et al. (2008) than

with Jiang and Kanwisher (2003) and suggest that multiple response selection mechanisms may exist in the human brain.

Jiang and Kanwisher (2003) and Schumacher et al. (2003) manipulated spatial and nonspatial stimuli and reported conflicting results. One key difference between these studies is the pattern of activation in the dorsal prefrontal cortex. Jiang and Kanwisher found bilateral dorsal prefrontal activity for both spatial and nonspatial response selection. In contrast, Schumacher and colleagues found left dorsal prefrontal activity for nonspatial response selection and right dorsal prefrontal activity for spatial response selection. Schumacher and D’Esposito followed up this discrepancy in two additional experiments. Schumacher, Hendricks, and D’Esposito (2005) investigated the effects of practice on spatial response selection. They found that the right dorsal prefrontal, bilateral premotor, and right superior parietal cortices implicated in spatial response selection by Schumacher et al. (2003) remained active during the performance of a spatial response selection task even after extensive practice. Left dorsal prefrontal, however, was only active during the early stages of task performance. These data suggest that left and right dorsal prefrontal cortices mediate distinct processes for spatial task performance, with only the right hemisphere specifically related to spatial response selection.

Additional evidence also supports the association between left dorsal prefrontal cortex and nonspatial response selection (Nagel, Schumacher, Goebel, & D’Esposito, 2008). The relevant comparison in that study was between parametrically manipulated response selection difficulty conditions (by varying S–R numerosity) using a visual–vocal task with verbal stimuli (*viz.*, participants learned a set of unrelated cue–target paired associates and responded with the target word when the cue was presented). Results showed that left dorsal prefrontal cortex activity increased monotonically with verbal response selection difficulty, but that right dorsal prefrontal showed no change in activity. These results confirm the relationship between nonspatial response selection and left dorsal prefrontal cortex and further suggest a hemispheric dissociation between dorsal prefrontal cortex and stimulus material (*c.f.*, Morimoto et al., 2008).

Finally, a recent fMRI study attempted to identify amodal central mechanisms not by varying response selection difficulty, but by varying the task and modality pairings across participants. Extending the work of Stelzel et al. (2006), Ivanoff, Branning, and Marois (2009) searched for amodal response selection processes by manipulating the stimulus and response modality pairings. Under single-task conditions, they paired visual and auditory stimuli with manual and vocal responses between subjects and found at least two brain regions (*i.e.*, bilateral precentral gyrus and

right anterior insula) that showed similar activation across all task pairings. Consistent with the interpretation from Dux et al. (2006), these regions may mediate amodal central processes. However, Ivanoff and colleagues' approach did not necessarily isolate response selection processes (i.e., they did not manipulate response selection difficulty), therefore the effect of modality on response selection processes specifically remains to be answered completely.

### Present experiment

One limitation of the experiments reviewed thus far is that response selection was varied across different tasks and experiments. Therefore, it is possible that the brain activation differences reported may be due to task, participant, and/or statistical threshold (i.e., given the low power in many fMRI studies, a null result does not mean a region is not involved in a particular cognitive process) differences and not due to distinct brain networks for response selection. The present experiment attempts to overcome this limitation by manipulating response selection difficulty within the same task and having participants use both visual and auditory modalities. In this way, we may identify modality-specific regions for response selection unconfounded by ancillary differences in the experimental procedure.

To do this we used a temporal flanker task from Hazeltine, Lightman, Schwarb, and Schumacher (2011). In this task, participants were presented two stimuli sequentially and instructed to ignore the identity of the first stimulus (i.e., the flanker/distractor) and respond only to the second (i.e., the target). As in the standard flanker task, the flanker/distractor in the temporal flanker task can be congruent (i.e., mapped to the same response as the target) or incongruent (i.e., mapped to a different response than the target). Hazeltine et al. previously used this and similar tasks in a series of behavioral experiments to investigate the effect of stimulus and response modality on sequential modulations of the congruency effect. The results of those experiments suggest that control processes obey flexible boundaries defined by task constraints and are not completely determined by modality. Here we use this task to investigate the neural mechanisms for response selection within the same task across two modalities.

With the temporal flanker procedure, we can manipulate stimulus modality while holding the task demands nearly constant. That is, because the target and distractor are presented one after the other, it is possible to use both visual and auditory stimuli with the same S–R mappings. For example, letters can be presented in different modalities but with the same task instructions (e.g., “if second stimulus is the letter A, then press button with right index finger”). In this way, the visual and auditory stimuli are conceptually

related and critical features of the task (i.e., the S–R mappings) are shared across input modality.

Therefore, the temporal flanker task procedure provides a viable means for identifying modality-specific response selection mechanisms. If modality affects the brain networks that support response selection, then we may find modality-dependent effects of congruency on distinct regions of brain activity. Moreover, because the stimuli are conceptually related (i.e., the S–R mappings are identical) and the data come from the same participants, the changes in brain differences will likely be due to the change in modality across trials rather than differences between the tasks, procedures, or participants tested.

The current procedure offers a second advantage. Many previous studies have included only two levels of response selection difficulty and assumed that the difference between them reflects response selection, however, other differences in stimulus and/or response processing may be affected by these manipulations as well (c.f., Schumacher et al., 2003). With the current design, we can investigate this question directly. We used a 4–2 mapping in both the auditory and visual tasks so we can compare incongruent versus congruent trials under two conditions: (1) on congruent trials when both the target and distractor are identical (identical congruent) and (2) on congruent trials when the target and distractor are distinct (nonidentical congruent). Congruency effects comparing incongruent to identical congruent trials should identify all regions related to an increase in task difficulty. Congruency effects comparing incongruent to nonidentical congruent trials may identify those regions specifically related to response selection.

### Method

#### Participants

Sixteen volunteers (ages 20–41; 10 females, 6 males) participated in this experiment. All participants were recruited from the Georgia Institute of Technology community and gave their informed consent prior to participation.

#### Behavioral procedure

The experimental procedure was similar to the one used by Hazeltine et al. (2011). Participants performed a temporal flanker task, in which two letters (A, B, C, or D) were presented in sequence on each trial. Participants responded to the identity of the second letter, ignoring the first. Visual stimuli, instructions, and performance feedback were projected in white font onto a black screen that participants viewed through a mirror mounted on the radio-frequency (RF) coil while lying supine in the MRI scanner. The visual

letters were presented in 26 point Arial bold font, centered within a fixation square. All letter stimuli subtended roughly 0.5° visual angle. The fixation square subtended roughly 1.25° visual angle. Auditory stimuli were presented via MRI compatible air-conduction headphones. Auditory stimuli were WAV files of a male voice speaking the letters. Sound volume was adjusted so participants could hear the letters over the gradient noise of the scanner. Participants made manual responses with their right middle and index fingers by pressing keys on an MRI compatible response box. They pressed the button with their right index finger if the second letter presented was an A or B and with their right middle finger if the second letter was a C or D.

Each trial lasted approximately 3.5 s. It began with a fixation square appearing in the center of the display. The fixation square remained onscreen for the duration of the trial. After 190 ms a distractor letter stimulus appeared for 200 ms. After a 150 ms inter-stimulus interval, a second letter stimulus (*viz.*, the target) appeared for 200 ms. The second stimulus was followed by a 2,730 ms response period. This is an efficient fMRI experimental design because we varied the stimulus onset asynchrony of the trial types of interest without including long periods within experimental trials where no task was required of participants and the TR was not evenly divisible by the inter-stimulus interval, allowing us to accurately estimate the influence of each condition on the BOLD response (Henson, 2007).

The experiment included six trial types, which composed a 2 × 3 design, with one axis indicating the modality of the stimuli and the other indicating the congruency of the stimuli. On half of the trials, both letter stimuli were presented aurally, and on the other half of the trials both letter stimuli were presented visually. For each modality, half of the trials were incongruent (*i.e.*, the first and second letter stimuli mapped to different responses) and the other half were congruent (*i.e.*, the first and second letter stimuli mapped to the same response). To further specify the source of the congruency effects in the temporal flanker task, we used two types of congruent trials. On half of the congruent trials the distractor and target were identical (identical congruent). On the other half, the distractor mapped to the same response as the target letter but was not the same letter (nonidentical congruent). Identical congruent trials are typically used in flanker studies and can facilitate performance because the distractor reinforces the identity of the target stimulus and because the distractor indicates the same response as the target. Including non-identical congruent distractors allows these two sources of performance benefits to be distinguished, because the non-identical congruent distractors provide a different stimulus identity but activate the same response code. The typical finding in standard flanker tasks is that nonidentical congruent stimuli produce RTs that are shorter than neutral or

incongruent trials but longer than identical congruent trials (*e.g.*, Eriksen & Eriksen, 1974).

The fMRI session was divided into 10 separate runs. Each run was composed of blocks of temporal flanker trials (20 trials each) separated by 20 s fixation baseline blocks. The trials were organized such that across the session an equal number of each trial type (modality and congruency) randomly followed every other trial type. Each fMRI run began with an experimental block and alternated between experimental and fixation blocks. Runs 1–9 included three experimental and three fixation blocks. Run 10 included two experimental and two fixation blocks. Feedback about accuracy and RT were presented for each modality after each run.

Prior to the beginning of the fMRI runs, participants completed four blocks (order: visual, auditory, visual, auditory) of practice trials while in the MRI scanner. Each block consisted of 32 trials, half congruent and half incongruent (randomly ordered).

#### fMRI procedure and analysis

An echo planar sequence (TR = 2,000 ms, TE = 30 ms, flip angle = 90°) on a Siemens 3T Trio MR scanner with a standard RF coil was used to collect data. Foam padding was used to restrict head motion. Each volume contained 33 axial slices of 3.4 mm isotropic voxels. A high resolution structure scan (TR = 2250 ms, TE = 2.52 ms, flip angle = 9°, slice thickness = 1 mm) was collected prior to the first functional run.

Data reconstruction, processing and analyses for each participant were performed using SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>). After reconstruction, slice acquisition timing differences and head-motion artifacts were corrected and the data were smoothed with a 6 mm full-width half-maximum Gaussian kernel. Data were analyzed using modified general linear models, including motion parameters (Worsley & Friston, 1995). We created design matrices for each participant with the covariates of interest (each modality and congruency pairing). These covariates were convolved with an idealized hemodynamic response function. A high-pass filter removed frequencies below 0.0078 Hz. Contrast images were computed for each participant for the contrasts of interest as well as each condition versus baseline (*i.e.*, the fixation blocks). These images and each participant's structural image were normalized to the Montreal Neurological Institute reference brain.

#### Results

Trials with errors were removed from both the RT and brain activation analysis. All other trials were included.



Accuracy rates were above 97% in all conditions and there were no significant main effects or interactions on accuracy rates so the behavioral analyses will focus on mean RTs.

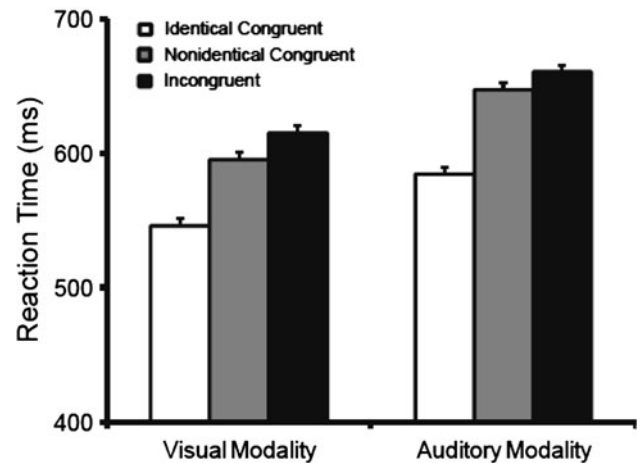
### Behavioral results

The mean RT data were analyzed with a  $2 \times 3$  within-subjects analysis of variance (ANOVA) with modality (auditory and visual) and trial type (incongruent, identical congruent, nonidentical congruent) as factors. There was a significant main effect of modality,  $F(1,15) = 30.16$ ,  $p < 0.001$ . Overall, auditory trials (631 ms) were slower than visual trials (586 ms). There was also a significant main effect of trial type,  $F(2,30) = 53.23$ ,  $p < 0.001$  and there was no interaction between modality and trial type  $F(2,30) = 0.84$ ,  $p = 0.44$ . As shown in Fig. 1 and consistent with the literature (e.g., Eriksen & Eriksen, 1974), participants were slowest on incongruent trials and fastest on identical congruent trials. Post hoc comparisons showed that, within each modality, all trial types were significantly different than all others except for auditory incongruent compared to nonidentical congruent,  $t < 1$ . In sum, the behavioral data indicate a robust congruency effect for the temporal flanker task. Moreover, the advantage observed for identical congruent trials appears to stem from both their physical similarity between the target and distractor and their co-activating the same response code.<sup>1</sup>

### Functional neuroimaging results

We focus first on the comparison between incongruent and identical congruent trials. This comparison is most similar to comparisons in the literature, which often do not control for differences in stimulus overlap between target and distractors in congruent and incongruent trials (e.g., Botvinick, Nytrom, Fissell, Carter, & Cohen, 1999; Coles, Gratton, Bashore, Eriksen, & Donchin, 1985; Eriksen & Schultz, 1979; Yeung, Botvinick, & Cohen, 2004). Moreover, as is typical, this comparison showed the largest difference in mean RTs, thus increasing the possibility for finding activation differences between these conditions. However,

<sup>1</sup> The RT data were also analyzed with two  $2 \times 2$  ANOVAs with modality (auditory and visual) and congruency as factors. The first ANOVA compared incongruent to identical congruent trials. The second ANOVA compared incongruent to nonidentical congruent. There were main effects of modality for both ANOVAs: 1)  $F(1,15) = 31.75$ ,  $p < 0.001$ ; 2)  $F(1,15) = 24.23$ ,  $p < 0.001$ . There were main effects of congruency for both ANOVAs: 1)  $F(1,15) = 81.64$ ,  $p < 0.001$ ; (2)  $F(1,15) = 5.26$ ,  $p < 0.05$ . The interaction was not significant for either ANOVA: 1)  $F(1,15) = 0.37$ ,  $p = 0.55$ ; 2)  $F(1,15) = 0.38$ ,  $p = 0.55$ . These analyses show that there were behavioral congruency effects both when there was stimulus repetition between the congruent distractors and targets and when there was not.



**Fig. 1** Mean reaction time and standard errors (based on the modality by congruency interaction) for the effect of congruency within each modality

because this comparison may include the effects of stimulus repetition as well as response congruency, the activation pattern in nonidentical congruent trials will also be presented where appropriate.

### Modality-specific activation

To identify modality-dependent congruency-related brain regions, we used the same analysis procedure used by Hazeltine et al. Hazeltine et al. (2003) in their study of color- and verbal-dependent response selection. Specifically, modality-dependent congruency activation was defined as those regions with larger differences between incongruent and identical congruent trials for one modality than the other. The following contrast was used to identify visual-dependent regions: (visual incongruent–identical congruent) > (auditory incongruent–identical congruent),  $p < 0.05$  uncorrected, 10 voxel extent threshold, masked to include only regions active at  $p < 0.001$  uncorrected in the (visual incongruent–identical congruent) contrast. Similarly, the following contrast was used to identify auditory-dependent regions: (auditory incongruent–identical congruent) > (visual incongruent–identical congruent),  $p < 0.05$  uncorrected, 10 voxel extent threshold, masked to include only regions active at  $p < 0.001$  uncorrected in the (auditory incongruent–identical congruent) contrast. Thus, a region was classified as a modality-dependent region if it showed a larger increase in congruency-related activity for one modality over the other (i.e., a modality by congruency interaction).

### Visual-specific activation

Many regions throughout the cortex showed greater congruency-related activity for the visual modality than the

**Table 1** Modality-dependent brain regions

	BA	<i>x</i>	<i>y</i>	<i>z</i>	Cluster size	<i>t</i> -value	Visual congruency effect	Auditory congruency effect	
Visual dependent activation									
Cingulate gyrus		24	−3	−1	49	10	3.89	0.55	−0.04
Precentral gyrus	L	6	−51	−1	37	23	3.78	0.55	0.31
	L	6	−18	−10	64	40	4.74	0.40	0.07
Supplementary motor area		6	−3	−4	40	23	4.8	0.43	0.13
		6	−3	−16	61	13	2.82	0.54	0.09
Inferior temporal gyrus	R	19/37	48	−67	−5	20	9.08	0.52	−0.09
	L	37	−45	−58	−11	34	5.73	0.47	−0.04
Postcentral gyrus	L	2/3	−45	−34	52	107	3.52	0.53	0.15
Fusiform gyrus	L	37	−39	−49	−20	22	7.61	0.42	0.00
	L	19	−33	−64	−11	21	7.75	0.46	−0.17
	L	19/37	−30	−55	−14	10	5.93	0.54	−0.02
	R	19/37	39	−55	−20	63	7.87	0.53	−0.09
Superior parietal lobule	L	7/40	−30	−52	58	61	4.83	0.57	0.03
Inferior parietal lobule	L	40/28	−36	−52	55	35	2.96	0.54	0.12
Lingual gyrus	L	19	−27	−52	−2	31	3.82	0.43	−0.10
	R	19	24	−64	4	19	3.62	0.35	−0.07
Middle occipital gyrus	L	19	−24	−70	22	19	4.18	0.52	−0.05
	L	18/19	−39	−85	−5	92	6.3	0.46	−0.05
	R	18/19	39	−85	10	48	7.78	0.41	−0.07
Superior occipital gyrus	L	18/19	−24	−76	31	25	5.24	0.40	−0.01
Inferior occipital gyrus	L	19	−42	−82	−5	93	6.82	0.47	−0.06
	R	19	36	−91	−5	83	8.22	0.47	−0.06
Putamen	L		−30	−4	−5	12	4.85	0.32	0.00
Thalamus	L		−15	−19	−2	11	4.07	0.25	−0.06
Cerebellum	R		9	−58	−11	22	2.95	0.37	−0.05
	L		−18	−67	−17	29	3.62	0.48	−0.05
Auditory-dependent activation									
Inferior frontal gyrus	L	47	−31	27	−2	30	2.7	0.08	0.33

The congruency effect lists the  $\beta$ -values for the incongruent versus identical congruent comparison for each modality

BA Brodmann area, *x*, *y*, *z* MNI coordinates, *L* left, *R* right

auditory (Table 1; Fig. 2). Nonidentical congruent trials showed intermediate activity between incongruent and identical congruent in all of these regions. Only one region showed significantly ( $p < 0.001$ , 10 voxel extent threshold) more activity in the visual incongruent relative to visual nonidentical congruent condition (viz., right insula [39,17,−2]).

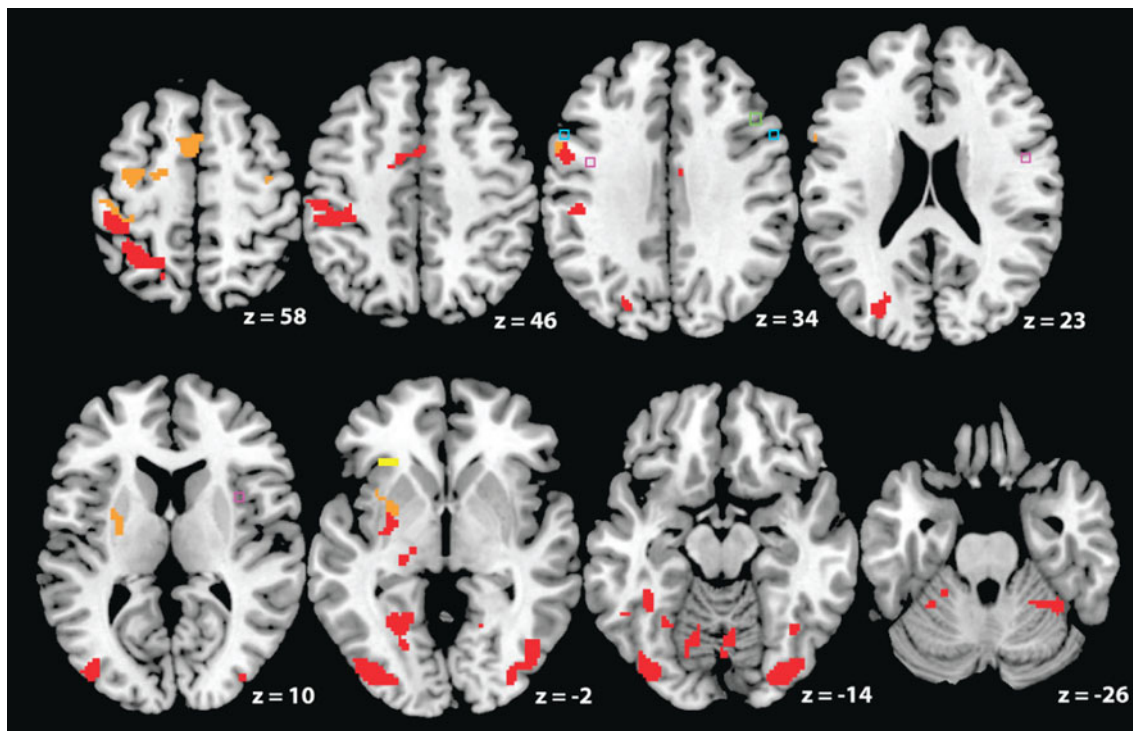
#### Auditory-specific activation

There was only one cluster of activity, in left inferior frontal gyrus, showing greater congruency-related activity in the auditory than the visual modality (Table 1; Fig. 2). Nonidentical congruent trials showed intermediate activity, between incongruent and identical congruent in this region,

but there were no significant differences between auditory incongruent and auditory nonidentical congruent.

#### Incongruent versus nonidentical congruent activation

As stated previously the incongruent versus identical congruent contrast confounds the effect of stimulus repetitions, which occur on the congruent trials only, with the effect of response-selection difficulty. The behavioral differences between incongruent and nonidentical congruent were very small (viz., 19 ms for the visual and 13 ms for the auditory task). Nevertheless, we may be able to leverage the differences between modalities to identify congruency-related differences in this contrast. To investigate this, we compared the incongruent condition to the nonidentical congruent



**Fig. 2** Congruency-related activity is shown on a normalized structural brain template. Activity shown in *red* shows greater congruency-related activity for visual than auditory stimuli. Activity shown in *yellow* shows greater congruency-related activity for auditory than

visual stimuli. Activity shown in *orange* shows congruency-related activity in both stimulus modalities. The *squares* represent the approximate locations of ROIs based on Hazeltine et al. (2003) (*green*), Morimoto et al. (2008) (*blue*), and Ivanoff et al. (2009) (*purple*)

**Table 2** Incongruent–nonidentical congruent regions

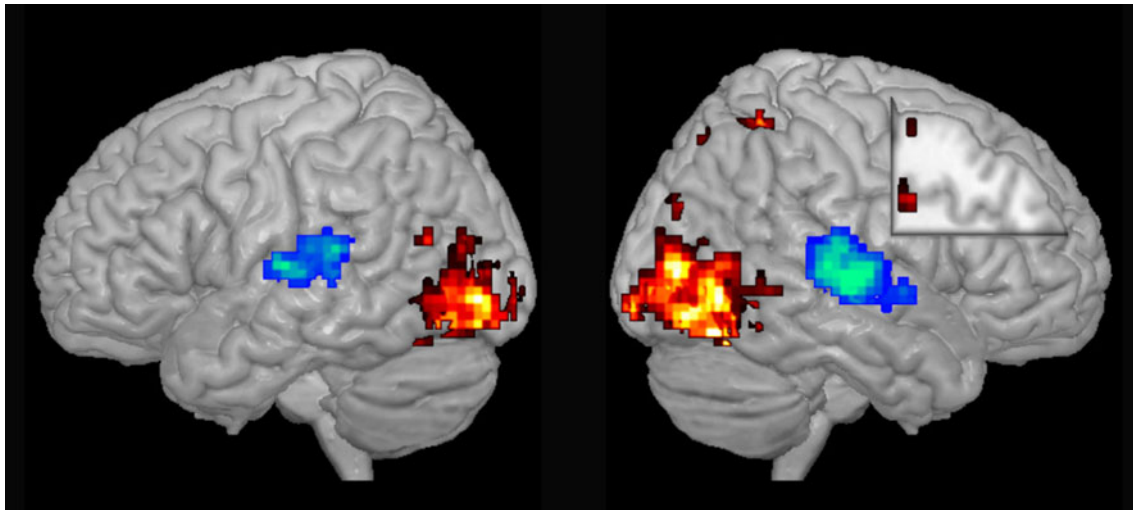
		BA	x	y	z	Cluster size	t-value
Visual congruency > auditory congruency							
Middle frontal gyrus	R	6	30	2	58	14	5.27
Precentral gyrus	R	6/44	36	2	31	10	4.79
Fusiform gyrus	L	37	-36	-55	-11	182	8.81
Fusiform gyrus	R	37	42	-55	-17	193	9.22
Inferior occipital gyrus	L	37	-45	-58	-11	142	8.45
	R	19	36	-79	-2	174	8.34
Inferior temporal gyrus	R	37	48	-67	-5	157	8.96
Superior parietal lobule	R	7	18	-73	52	51	4.55
Middle occipital gyrus	L	19	-42	-85	-5	178	8.08
Auditory congruency > visual congruency							
Superior temporal gyrus	L	22/42	-60	-16	7	172	7.3
	R	21/22/42	60	-19	4	260	10.31
Middle temporal gyrus	L	21	-54	-31	10	27	7.12
Superior temporal gyrus	L	48	-36	-34	22	30	6.44

BA Brodmann area, x, y, z MNI coordinates, L left, R right

condition in one modality to the same contrast in the other [i.e., (visual incongruent–nonidentical congruent) versus (auditory incongruent–nonidentical congruent); 10 voxel extent threshold]. As shown in Table 2 and Fig. 3, after controlling for stimulus repetition and isolating the response

selection differences between the conditions, significant congruency effects were found for the visual modality in premotor and parietal cortices as well as secondary visual cortical regions. For the auditory modality, significant activity was found only in primary and secondary auditory cortex.





**Fig. 3** Incongruent–nonidentical congruent modality-related activity from Table 2 superimposed on a spatially normalized brain, with frontal section removed at [36,–6,18]. Visual congruent regions

( $p < 0.001$ ) are shown in warm colors and auditory congruent regions ( $p < 0.001$ ) are shown in cool colors

**Table 3** Modality-independent brain regions

	BA	x	y	z	Cluster size	t-value	Auditory			Visual			
							Incongruent	Nonidentical congruent	Identical congruent	Incongruent	Nonidentical congruent	Identical congruent	
Supplementary motor area	6/32	–3	8	55	31	6.05	1.85	1.91	1.42	1.76	1.51	1.24	
Precentral gyrus	L	6	–57	5	34	12	5.73	1.97	1.99	1.61	2.02	1.87	1.60
	L	6	–36	–10	58	35	5.25	2.41	2.54	2.15	2.43	2.19	1.89
	R	6	36	–13	61	10	5.14	0.66	0.71	0.51	0.81	0.74	0.46
Superior frontal gyrus	L	6	–18	–7	55	14	6.33	2.04	2.16	1.79	1.98	1.87	1.48
Postcentral gyrus	L	3	–45	–25	55	12	4.64	2.86	2.91	2.68	2.91	2.82	2.50
Supramarginal gyrus	L	40	–51	–31	25	17	6.15	0.87	1.03	0.71	0.57	0.50	0.25
Putamen	L		–27	–1	4	29	4.68	0.50	0.44	0.25	0.52	0.41	0.21

The  $\beta$ -values for each trial type versus baseline is included for both modalities

BA Brodmann area, x, y, z MNI coordinates, L left, R right

### Modality-independent activation

Hazeltine et al. (2003) used a conjunction analysis of significant activity ( $p < 0.00001$  in the congruency contrasts in each modality) to identify regions of common activity across modality. This threshold did not produce any significant voxels in the present experiment. However, this may not mean that there were no common areas of activation across modality. A less strict measure of activation overlap is used to identify regions that show a congruency effect that does not interact with modality. To identify such regions, we used the contrast between incongruent and identical congruent (collapsed across modality,  $p < 0.001$  uncorrected, 10 extent threshold) to identify congruency-related regions, then we masked this contrast with the regions identified as modality dependent (i.e., those regions identified in the previous analysis). Thus, these are the

regions mediating response selection but not significantly affected by modality. These regions are shown in Table 3 and Fig. 2.

### Region-of-interest analysis of prefrontal cortex

The analyses described thus far did not identify many prefrontal regions. Yet, many studies have implicated prefrontal cortex for response selection (e.g., Hazeltine et al., 2003; Jiang & Kanwisher, 2003; MacDonald, Cohen, Stenger, & Carter, 2000; Merriam et al., 2001; Morimoto et al., 2008; Nagel et al., 2008; Schumacher, Cole, & D'Esposito, 2007; Schumacher & D'Esposito, 2002; Schumacher et al., 2003, 2005; Schwarb & Schumacher, 2009). To investigate the potential effect of modality on prefrontal regions for response selection, we investigated the present data with a series of region-of-interest (ROI)

analyses, using an  $\alpha$ -level of 0.05 for each of these planned comparisons. Hazeltine et al. (2003) identified a region in right middle/inferior frontal gyrus related to congruency for both the color and verbal stimuli used in their experiment. We created a spherical ROI (radius = 4 mm) centered on their peak activation coordinate (MNI coordinates: 44, 22, 32; shown in Fig. 2). We then extracted the activation ( $\beta$ -values) from each modality and trial type from each participant and submitted them to a  $2 \times 2$  ANOVA<sup>2</sup> with modality (auditory and visual) and congruency (incongruent and identical congruent) as factors. There were no significant main effects or interactions: modality,  $F(1,15) = 0.86$ ,  $p = 0.37$ ; congruency  $F(1,15) = 2.41$ ,  $p = 0.14$ ; interaction,  $F(1,15) = 1.20$ ,  $p = 0.29$ . However, there was a trend for increased activity for incongruent relative to identical congruent in both modalities ( $\beta$ -values: 0.31 for auditory and 0.07 for visual).

We conducted a similar ROI analysis on the modality-specific inferior frontal regions identified by Morimoto et al. (2008). As described previously, they found that stimulus material (verbal and color) affected the laterality of the congruency effect in inferior frontal gyrus (MNI coordinates:  $\pm 55, 15, 31$ ; shown in Fig. 2). After extracting brain activation data from these ROIs, we analyzed them with a  $2 \times 2 \times 2$  ANOVA with hemisphere (left and right), modality (auditory and visual) and congruency (incongruent and identical congruent) as factors. There was a significant main effect of hemisphere,  $F(1,15) = 24.88$ ,  $p < 0.001$ , with significantly more activity in the left (average  $\beta$ -value = 1.46) than the right (average  $\beta$ -value =  $-0.76$ ) hemisphere. The effect of modality was not significant,  $F(1,15) = 0.02$ ,  $p = 0.90$ . The effect of congruency approached significance,  $F(1,15) = 3.12$ ,  $p < 0.10$ , with incongruent trials producing more activity (average  $\beta$ -value = 0.48) than identical congruent trials (average  $\beta$ -value = 0.23). The interaction between hemisphere and congruency was not significant,  $F(1,15) = 1.22$ ,  $p = 0.29$ . This suggests that, although there was more activity in the left than right hemisphere (perhaps because responses were made with the right hand), congruency modulated this overall activity in a similar way in both hemispheres.

The Hazeltine et al. (2003) and Morimoto et al. (2008) experiments used visual stimuli in a standard spatial flanker task. To more thoroughly investigate the role of left inferior and middle frontal gyri in the temporal flanker task, we conducted an additional ROI analysis. Specifically, within each of these anatomical regions, we identified all voxels showing a congruency effect (incongruent vs. identical congruent,  $p < 0.05$ , uncorrected). A relatively low statistical

threshold was used for this analysis to identify all voxels potentially related to congruency within the left prefrontal cortex. As such, the extent of the activity spanned both gyri. Therefore, it is not depicted in Fig. 2 and there is no site of peak activity. We then submitted the activation ( $\beta$ -values) in each ROI to the same ANOVA described by Hazeltine and colleagues (viz.,  $2 \times 2$  ANOVA with modality and congruency as factors). There was a significant main effect of congruency in both ROIs (inferior frontal gyrus:  $F(1,15) = 15.89$ ,  $p < 0.005$ ; middle frontal gyrus:  $F(1,15) = 11.27$ ,  $p < 0.005$ ). This main effect is not surprising, given that the voxels were chosen based on this contrast. The main effect of modality was significant in the inferior frontal gyrus ( $F(1,15) = 5.83$ ,  $p < 0.05$ ) and approached significance in middle frontal gyrus ( $F(1,15) = 3.15$ ,  $p < 0.10$ ). Auditory stimuli produced more activity than visual stimuli in both ROIs. Critically, there was no interaction between modality and congruency in either ROI (inferior frontal gyrus:  $F(1,15) = 0.01$ ,  $p = 0.93$ ; middle frontal gyrus:  $F(1,15) = 1.56$ ,  $p = 0.23$ ); the effect of congruency was similar for both modalities.

Lastly, Ivanoff et al. (2009) identified three regions as potential candidates for amodal central processing (bilateral precentral gyrus, left  $[-40, -2, 39]$ , right  $[48, 1, 25]$ ; right anterior insula  $[37, 8, 9]$ , shown in Fig. 2). We created spherical ROIs based on the extent of activity in each region reported by Ivanoff and colleagues (5 mm for left precentral and 3 mm for right precentral and anterior insula). Each of these ROIs was activated across two tasks with different stimulus–response modality pairings. Neither task produced significant activity in right precentral gyrus ( $t < 1$  in both cases). Both tasks produced significant activity in both of the other regions (left precentral gyrus: visual task,  $t(15) = 2.21$ ,  $p < 0.05$ ; auditory,  $t(15) = 2.41$ ,  $p < 0.05$ ; right anterior insula,  $t(15) = 6.25$ ,  $p < 0.0001$ ; auditory task,  $t(15) = 6.26$ ,  $p < 0.0001$ ). We submitted the activation ( $\beta$ -values) from each of these ROIs to the same ANOVA described for Hazeltine et al. (2003, viz.,  $2 \times 2$  ANOVA with modality and congruency as factors). There were no significant main effects or interactions in either region (left precentral gyrus: modality,  $F(1,15) = 0.33$ ,  $p = 0.58$ , trial type  $F(1,15) = 1.35$ ,  $p = 0.28$ , interaction  $F(1,15) = 0.07$ ,  $p = 0.94$ ; right anterior insula: modality,  $F(1,15) = 0.63$ ,  $p = 0.44$ , trial type  $F(1,15) = 2.22$ ,  $p = 0.13$  interaction  $F(1,15) = 0.56$ ,  $p = 0.58$ ).

## Discussion

The present experiment manipulated response congruency across visual and auditory modalities within the same task (i.e., using conceptually identical stimuli and S–R mappings). We found modality-dependent activity across

<sup>2</sup> ANOVAs were also conducted on all ROI data with the nonidentical congruent condition replacing the identical congruent condition. Results from these analyses were consistent with the reported analyses.

the cortex—suggesting the existence of modality-specific processes associated with response selection mechanisms. Congruency-dependent activity for visual stimuli was found in medial prefrontal, premotor, parietal, temporal, occipital cortices, and the putamen. Congruency-dependent activity for auditory stimuli was found in left inferior frontal gyrus.

Congruency-related activity common to both modalities was found in left prefrontal, medial prefrontal, premotor, parietal cortices and the putamen. These common areas of activity are similar to the frontal-parietal network identified for response selection in the literature (e.g., Hazeltine et al., 2003; Jiang & Kanwisher, 2003; MacDonald et al., 2000; Merriam et al., 2001; Morimoto et al., 2008; Nagel et al., 2008; Schumacher et al., 2007; Schumacher & D'Esposito, 2002; Schumacher et al., 2003, 2005; Schwarb & Schumacher, 2009).

Many more regions showed congruency-dependent activity for the visual than the auditory modality. This is not because the task was more difficult for visual than auditory stimuli. The congruency effects were very similar across modalities (69 ms for visual and 76 ms for auditory). It is also not the case that the auditory stimuli always produced less congruency-related activation in the brain. Indeed, left prefrontal cortex activity was significantly greater for auditory than visual stimuli. It is not clear what to make of this discrepancy. Hazeltine et al. (2003) also found disparate amounts of activity between their stimulus types—with verbal stimuli producing more congruency-related activity than color stimuli, even though the congruency effect was larger for the color stimuli in that experiment. In Hazeltine et al. experiment, all of the stimuli were visual and greater activation was observed for letter than colors, whereas in the present experiment all of the stimuli were verbal and greater activation was observed for the visual stimuli than for the auditory stimuli. Thus, it may be that visual-verbal stimuli paired with manual responses are a particularly effective means of activating the task-related neural systems, possibly because the stimulus–response translation spans a range of processes involving visual, verbal, and spatial information. It may also be that gradient noise provided sufficient interference with the auditory task so that regions involved in auditory conflict were active on every trial.

Many of the congruency-dependent visual regions are in similar brain regions as activity common to both modalities (e.g., left premotor, left supplementary motor area, left putamen). It may be that the common brain network for response selection was recruited more heavily, in conjunction with visual-specific regions in parietal, temporal and occipital cortices, to mediate response selection for visual stimuli.

The auditory stimuli produced only one area of modality-dependent activity—left inferior frontal cortex.

Again, this lack of modality-dependent activity is not due to a lack of a behavioral effect. The left inferior frontal activity is near Broca's area (Dronkers, 1996), an area associated with language production. Thus, similar to the visual modality, the common brain network for response selection may work in conjunction with auditory/speech-related regions to mediate congruency for auditory stimuli.

All of these congruency-related significant differences occurred between the incongruent and identical congruent conditions. Thus, it is impossible from these data to associate the activation differences found here specifically with response selection. However, many of the regions activated have previously been implicated in response selection, and the nonidentical congruent condition produced intermediate activity in these regions. Thus, it is likely that some of these activation differences reflect response selection differences and not stimulus processing differences between the incongruent and congruent trials. Moreover, comparing the incongruent and nonidentical congruent trials produced an interesting and surprising result: Most of the congruency-related activity was in primary and secondary sensory cortical regions. Importantly, the targets and distractors were different letters for both modalities and conditions; the only difference between the incongruent and nonidentical congruent trials within a modality was the congruency of the response mapping between the two letters. Nonetheless, this difference led to modality-specific activity in sensory cortex. This suggests that response selection affects early sensory regions. Prefrontal and parietal regions were also affected by visual more than the auditory congruency. This is consistent with previous studies concluding that these regions mediate modality-specific processes associated with response selection. However, given the small behavioral effect, the lack of modality-specific activation in other brain regions does not preclude their existence. This is a question for future research.

#### Relationship to previous research

The present data are consistent with existing literature suggesting that response selection is modality- and material-dependent, and therefore multiple response selection mechanisms may exist in the human brain (e.g., Hazeltine et al., 2003; Jiang & Kanwisher, 2003; MacDonald et al., 2000; Merriam et al., 2001; Morimoto et al., 2008; Nagel et al., 2008; Schumacher et al., 2007; Schumacher & D'Esposito, 2002; Schumacher et al., 2003, 2005; Schwarb & Schumacher, 2009). In addition, they hint at a resolution for the discrepant results in inferior frontal gyrus reported by Hazeltine et al. (2003) and Morimoto et al. (2008). Recall, that Hazeltine et al. reported a modality-independent congruency effect in right inferior frontal gyrus using color and letter

flanker stimuli. Using a similar flanker task, Morimoto et al. reported a larger congruency effect for letters in left inferior frontal cortex and for colors in right inferior frontal cortex. Here, using auditory and visual letter stimuli, we report a congruency effect using letter stimuli in both left and right inferior frontal gyrus and no interaction between them. Therefore, both regions appear to mediate congruency for letter stimuli consistent with Hazeltine et al. However, the overall activity was much greater in the left than right hemisphere. Thus, it is possible that this region plays a larger role in verbal response selection than for other materials. This is consistent with Morimoto et al., who proposed that tasks using verbal material may rely more on left prefrontal cortex and tasks using nonverbal material may rely more on right prefrontal cortex (see also, Nagel et al., 2008; Schumacher et al. 2003, 2005, 2007). Together, these findings emphasize that the neural regions supporting the central operations associated with response selection appear to depend on stimulus and response modalities, as well as the particular types of information conveyed along those modalities.

The current data do not support the conclusions of Ivanoff et al. (2009). Based on the finding that bilateral precentral gyrus and right anterior insula showed activity across tasks of different stimulus and response modalities and pairings (viz., visual, auditory, manual and vocal), they hypothesized that these regions mediate amodal response selection. Both of our tasks failed to produce any task-related activity in right precentral gyrus. The other two regions (i.e., left precentral gyrus and right anterior insula) showed significant task-related activity but did not show a congruency effect—even between incongruent and identical congruent. These results raise doubts about the role these regions play in response selection—amodal or otherwise. However, right anterior insula did show a congruency effect for the visual incongruent versus nonidentical congruent contrast. More research is necessary to explain the divergent results in this area. Nevertheless, the present results do not support a role for amodal response selection in these areas.

Several recent experiments have investigated the specificity of cognitive control by analyzing how so-called sequential effects (viz., the modulation in the congruency effect on a particular trial based on the congruency of the previous trial) are affected by changes in task or modality (for a review see, Egner, 2008). In fact, the effect of modality on sequential effects in temporal flanker task used here was investigated by Hazeltine et al. (2011). Briefly, in Experiment 1, which is most similar to the present one, we found that the congruency effect of a particular trial was affected by the congruency of a previous trial only when the stimuli on the two trials were presented in

the same modality. When stimuli changed from one modality to the other, no sequential modulation was observed. The sequential effects in the present study are not as straightforward. There were significant sequential modulation effects for visual stimuli—both when the previous trial was visual and when it was auditory ( $p < 0.05$  in both cases). However, there were no sequential modulation effects for the auditory stimuli—neither when the previous trial was visual nor when it was auditory ( $p > 0.2$  in both cases). We suspect that performing the auditory task in the presence of the gradient noise may have affected how participants allocated control in this experiment. More research is necessary to understand how the MR context affects cognitive processing, but the lack of a sequential effect on auditory temporal flanker trials suggests that the current data are not an ideal test for the effect of modality on the control processes mediating sequential modulations. Therefore, we focused our current analyses on the within trial congruency effects, which were robust across modalities.

## Conclusion

The present data are consistent with the large body of literature implicating material-specific regions associated with response selection. The present data add to this literature by showing that stimulus modality also affects the brain network for response selection. Distinct regions mediate response selection for the same conceptual stimuli and during the performance of the same task depending on stimulus modality. These data also show that the modality effects on response selection extend to sensory cortical regions.

The present experiment did not vary stimulus–response modality pairings. Thus, it is possible the current effects relate to differences between modality pairings rather than modality (c.f., Hazeltine & Ruthruff, 2006; Stelzel et al., 2006). However, recent research suggests that the effect of modality pairings may require varying the response pairings within an experiment (Lukas, Philipp, & Koch, 2010) and/or dual-task procedures (Stephan & Koch, 2010). Therefore, stimulus–response modality pairings may not play a major role in the current single-task experiment with a fixed response modality. Additionally, the present design did not vary stimulus modality within a trial (e.g., visual distractor paired with auditory target). This is a potentially useful extension for future research to identify how the brain mediates cross modal congruency between stimuli. Yet, even without this condition, the current data highlight the specificity of processes associated with response selection.



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