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Made you look! Consciously perceived, irrelevant instructional cues can hijack the attentional network

Katherine Sledge Moore, **Clare B. Porter**, and **Daniel H. Weissman**
Department of Psychology, University of Michigan, Ann Arbor, MI

Abstract

Functional neuroimaging studies of endogenous cued attention suggest that a fronto-parietal attentional network keeps track of current task objectives in working memory and enhances activity in posterior sensory regions that underlie the perceptual processing of behaviorally relevant stimuli. Relatively little is known, however, about whether consciously perceived, irrelevant instructional cues can hijack the attentional network, leading to an enhancement of the perceptual processing of irrelevant stimuli. Using a cross-modal attentional cueing task in combination with functional magnetic resonance imaging, we found that such irrelevant cues can indeed hijack the attentional network, as indexed by increased activity in (a) frontal regions that control attention and (b) sensory cortices that underlie the perceptual processing of task-irrelevant stimuli. Furthermore, we found that in left ventrolateral (but not dorsolateral) prefrontal regions, the magnitude of this increased activity varies with whether an irrelevant instructional cue is presented simultaneously with (versus after) a relevant instructional cue. These findings show that consciously perceived, irrelevant instructional cues can activate inappropriate task objectives in working memory, resulting in a hijacking of the attentional network. Moreover, they reveal different time courses of hijacking effects in ventrolateral and dorsolateral prefrontal regions, consistent with models in which these regions make distinct contributions to cognitive control.

Keywords

fMRI; attention; visual; auditory

Introduction

The ability to voluntarily and flexibly orient attention toward behaviorally relevant stimuli is a fundamental aspect of human cognition. Some models posit that this ability is enabled by a fronto-parietal attentional network (Corbetta et al., 2000; Corbetta and Shulman, 2002; Hills, 2006; Mesulam, 2004), in which lateral prefrontal regions of the brain keep track of current task objectives in working memory (Banich et al., 2000; Milham et al., 2003; Miller and Cohen, 2001) and communicate those objectives to parietal regions that allocate attention to behaviorally relevant stimuli (Corbetta et al., 1998; Hopfinger et al., 2000). The attentional network is also thought to bias activity in sensory regions of the brain to favor the perceptual processing of upcoming relevant stimuli (Kanwisher and Wojciulik, 2000; Kastner et al.,

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Address correspondence to: Katherine Moore (E-mail: mooreks@umich.edu) or Daniel Weissman (E-mail: danweiss@umich.edu), Department of Psychology, 1012 East Hall, 530 Church St, Ann Arbor, MI 48104.

1998; Kastner et al., 1999). Consistent with this model, cueing humans to attend to an upcoming behaviorally relevant feature of the task environment (e.g., a specific color or spatial location) leads to a relative enhancement of activity in frontal and parietal regions of the attentional network as well as in sensory regions that underlie the perceptual processing of the behaviorally relevant feature (Hopfinger et al., 2000; Kastner et al., 1999; Shulman et al., 1999).

While often beneficial, the cognitive flexibility that allows us to voluntarily direct our attention can have costs. One such cost is attentional capture, a phenomenon in which attention is drawn to irrelevant stimuli that share critical features (e.g., color) with target stimuli as defined by task objectives (Downing, 2000; Folk et al., 2002; Folk et al., 1992) or that, for other reasons, stand out in the environment (Theeuwes, 1994; Yantis and Hillstrom, 1994). Presenting irrelevant stimuli that capture attention greatly impairs the identification of target stimuli that are presented soon afterwards (Folk et al., 2002). As an everyday example, while searching for a friend in a red shirt at a crowded sporting event, the appearance of a stranger wearing a red shirt may capture one's attention and interfere with one's ability to locate the friend.

A second cost that derives from this cognitive flexibility is that representations of previously relevant task objectives sometimes remain activated in working memory even when they are no longer relevant, resulting in increased attention to irrelevant stimuli and in slower and/or less accurate performance (Yeung et al., 2006). Drawing again from everyday experience, if the goal of playing offense remains activated in a basketball player's working memory for too long after the other team steals the ball, then the player may be unable to quickly switch to playing defense in order to prevent the other team from scoring. Disruptions of attention associated with the activation of irrelevant task objectives in working memory are also prominent after brain damage to the lateral prefrontal cortex (Berger and Posner, 2000) and in numerous clinical syndromes, such as drug addiction (Ventura et al., 2005), and attention deficit and hyperactivity disorder (Casey et al., 1997; Max et al., 2005). For these reasons, there has been growing interest in understanding under what circumstances irrelevant task objectives become activated in working memory.

The authors of two recent studies used variants of attentional cueing tasks, in combination with functional magnetic resonance imaging (fMRI), to directly investigate some of the conditions under which irrelevant task objectives become activated in working memory, and the behavioral and neural consequences of experimentally inducing such activation (Brass and von Cramon, 2004b; Lau and Passingham, 2007). In both studies, a relevant instructional cue directed participants to perform one of two possible tasks on an upcoming target stimulus, while an irrelevant instructional cue signaled either the same task (congruent cues) or a different task (incongruent cues). Brass and von Cramon (2004b) reported increased error rates to identify targets that followed incongruent (versus congruent) cues (i.e., a behavioral cue congruency effect). However, they observed no difference in brain activation for incongruent and congruent cues (i.e., a neural cue congruency effect). Thus, this initial study revealed a behavioral deficit associated with activating irrelevant task objectives in working memory, but shed no light on the neural underpinnings of that deficit.

Lau & Passingham (2007) also manipulated cue congruency to investigate the behavioral and neural consequences of activating irrelevant task objectives in working memory. Similar to Brass and von Cramon (2004b), they reported slower and less accurate behavioral performance for targets that followed incongruent (versus congruent) cues. However, they also observed significantly greater activation for incongruent than for congruent cues in the mid-dorsolateral prefrontal cortex (DLPFC), a neural structure that is thought to play a key role in maintaining task objectives in working memory (Banich et al., 2000; Hopfinger et al., 2000; Milham et al., 2003; Miller and Cohen, 2001). One interpretation of this neural cue congruency effect is that incongruent cues led to the activation of both relevant and irrelevant task objectives in working memory while congruent cues led to the activation of only relevant task objectives (Lau and Passingham, 2007). Consistent with this interpretation, activity in posterior cortical regions underlying performance of the irrelevant task was greater for incongruent than for congruent cues. These findings suggest that activating irrelevant task objectives in working memory impairs behavioral performance by hijacking the attentional network into enhancing the processing of currently irrelevant task representations, including representations of irrelevant stimuli.

Of importance, such hijacking differs from various distracter interference effects that are more traditionally reported in the selective attention literature. For example, while hijacking leads to the activation of an irrelevant task goal in working memory, contingent attentional capture results in a shift of spatial attention toward irrelevant stimuli whose features match a relevant task goal (Folk et al., 1992; Serences et al., 2005). Similarly, distracters in selective attention tasks (e.g., the Stroop and flanker tasks) often impair performance because they activate competing responses that are associated with a relevant task goal (MacLeod, 1991). Thus, hijacking effects differ from various other types of distracter effects because they stem from the activation of an irrelevant goal in working memory, rather than from the activation of a relevant goal.

A key finding in Lau and Passingham's (2007) study was that cue congruency effects in the dorsolateral prefrontal cortex were observed only when irrelevant instructional cues were not consciously perceived. This finding concurs with evidence indicating greater distraction from irrelevant stimuli that are unconsciously (versus consciously) perceived, an effect that may occur because unconsciously perceived stimuli sometimes fail to be inhibited by attentional control mechanisms (Tsushima et al., 2006). However, it conflicts with a vast literature indicating that consciously perceived, irrelevant stimuli robustly interfere with the performance of selective attention tasks by activating irrelevant semantic and response representations in working memory (MacLeod, 1991). From the perspective of this latter literature, it is perplexing that both Brass and von Cramon (2004b) and Lau and Passingham (2007) did not observe neural evidence indicating that consciously perceived irrelevant stimuli can activate irrelevant task objectives in working memory.

One possible explanation is that the simple shapes that served as irrelevant instructional stimuli in these studies (e.g., squares and diamonds) were not strongly associated with irrelevant task objectives. The degree to which a stimulus is strongly and automatically associated with an irrelevant semantic or response representation often predicts the amount of interference that it will evoke when it serves as a distracter in a selective attention task (Dunbar and MacLeod, 1984; MacLeod and Dunbar, 1988). For example, due to our extensive language training, words automatically activate irrelevant semantic and response representations in working memory which, in turn, interfere with the performance of selective attention tasks (MacLeod, 1991). Given these considerations, effects of consciously perceived cue congruency on brain activity should be most clearly visible when irrelevant instructional cues are strongly associated with irrelevant task objectives.

In which brain regions might one expect manipulations of consciously perceived cue congruency to influence activity? First, one might expect to observe cue congruency effects in posterior sensory regions whose nature is similar to the effects reported by Lau and Passingham (2007). More specifically, for congruent cues one should expect a relative enhancement of activity in task-relevant sensory regions, consistent with the existing literature on endogenous cued orienting of attention (Kanwisher and Wojciulik, 2000; Kastner et al., 1998; Kastner et al., 1999). For incongruent cues, however, one should expect a reduction of this enhancement, or possibly even a reversal, in which there is an enhancement of activity in task-irrelevant sensory regions (Lau & Passingham, 2007). In short, the nature of cue congruency effects in the sensory cortices should reveal whether consciously perceived, irrelevant instructional cues can hijack the attentional network.

Second, one might expect to observe larger effects of cue congruency on brain activity when a relevant and an irrelevant instructional cue are presented simultaneously than when they are presented sequentially (i.e., when the irrelevant cue is presented nearly a second after the relevant cue) in the left ventrolateral prefrontal cortex (VLPFC). The left VLPFC is thought to retrieve task sets or stimulus-response mappings from memory (Brass and von Cramon, 2004a; Bunge, 2004). Overall, the demands imposed on such retrieval processes should be greater when an irrelevant cue signals a different (versus the same) task than a relevant cue (Brass and von Cramon, 2004b; Lau and Passingham, 2007; Mattler, 2005). However, since cue-triggered retrieval of a task set from memory is usually completed in well under a second (Monsell and Mizon, 2006), any increase in the demands on task-set retrieval processes that is imposed by varying cue congruency should be maximal when a relevant and an irrelevant cue are presented simultaneously and minimal when they are presented sequentially (i.e., when the irrelevant cue is presented almost a second after the relevant cue). Drawing once again from everyday life, it is often much more difficult to retrieve from memory the mental set that is appropriate for performing a particular cognitive task (e.g., playing chess) when a distracter (e.g., a commercial on TV) simultaneously activates a competing, irrelevant task set in working memory (e.g., watching a movie) than when a distracter activates a competing task set only after the relevant task set has been retrieved.

Third, in contrast to the left VLPFC, one might expect to observe relatively similar cue congruency effects in a simultaneous and a sequential presentation condition in dorsolateral prefrontal cortex (DLPFC) regions that help to maintain task sets in working memory (Banich et al., 2000; Miller and Cohen, 2001) and in dorsal anterior cingulate cortex (ACC) regions that detect or resolve conflict between relevant and irrelevant task sets (Luks et al., 2002; Orr and Weissman, in press). In both presentation conditions, it may be harder to maintain information about the relevant task set after an irrelevant instructional cue activates a competing task set in working memory (i.e., incongruent cues) than after it activates the relevant task set (i.e., congruent cues). Similarly, in both presentation conditions incongruent cues should impose greater demands than congruent cues on processes that detect and/or resolve conflict between the relevant and the irrelevant task sets. Thus, cue congruency effects in the DLPFC and the dorsal ACC may not vary as a function of the relative timing with which a relevant and an irrelevant instructional cue are presented.

Fourth, one might expect to observe cue congruency effects in superior and/or inferior parietal regions that manage and allocate attentional resources. As we stated earlier, lateral prefrontal regions that keep track of current task objectives in working memory (Banich et al., 2000; Milham et al., 2003; Miller and Cohen, 2001) are thought to communicate with parietal regions that allocate attentional resources to behaviorally-relevant stimuli (Corbetta et al., 1998; Hopfinger et al., 2000). Thus, if irrelevant instructional cues influence activity in lateral prefrontal regions underlying working memory, they might also influence activity in parietal regions that allocate attentional resources.

With the considerations above in mind, we used a cross-modal attentional cueing task (Fig 1) in combination with fMRI to investigate whether consciously perceived, irrelevant instruction words can hijack the attentional network, and whether the extent of any such hijacking depends on the relative timing with which the relevant and the irrelevant instruction words are presented. In each trial, a relevant visual cue (“Look” or “Hear”) instructed participants to attend to and identify either the visual letter (“X” or “O”) or the auditory letter (“X” or “O”) within a possibly upcoming, multisensory letter pair. Accompanying the relevant visual instruction word was an irrelevant auditory word (“Look” or “Hear”) that signaled either the same task as the visual instruction word (congruent cues) or the opposite task (incongruent cues). The irrelevant auditory instruction word was presented either at the same time as the relevant visual word (simultaneous condition) or 850 ms later (sequential condition). In cue-plus-target trials, a multisensory letter pair was presented 1.875 seconds after the relevant visual cue word. Participants were asked to identify the target letter (“X” or “O”) that appeared in the cued sensory modality while ignoring the distracter letter in the other modality. The distracter letter was either the same as the target letter in the cued modality (congruent target-distracter pairs) or different (incongruent target-distracter pairs). In cue-only trials, the cue was not followed by a target. These trials allowed us to isolate the neural correlates of attentional control processes that were specific to our cue stimuli (Corbetta et al., 2000). We note that the simultaneous condition used here was also used in a different study from our laboratory (Orr & Weissman, in press), but that only the present study, which involved different participants, included both the simultaneous and the sequential presentation conditions.

The view that consciously perceived, irrelevant instruction words can activate irrelevant task objectives in working memory leads to four predictions. First, it predicts that the typical pattern of biasing activity in the sensory cortices for an audiovisual cued attention task (i.e., a relative enhancement of activity for “Look” versus “Hear” cue-only trials in the visual cortex, and the opposite effect in the auditory cortex) (Weissman et al., 2004) should be observed more strongly for congruent than for incongruent cue-only trials. Second, it predicts larger effects of cue congruency in the simultaneous than in the sequential condition in left VLPFC regions that retrieve task sets from memory to guide subsequent performance (Bunge, 2004). Third, it predicts cue congruency effects in DLPFC regions that maintain task sets in working memory (Lau & Passingham, 2007) and in dorsal ACC regions that detect and/or resolve conflict between relevant and irrelevant task sets (Luks et al., 2002; Orr and Weissman, in press) and that the magnitude of these effects will not vary across the simultaneous and the sequential conditions. And fourth, it predicts cue congruency effects in parietal regions that allocate attentional resources to behaviorally-relevant stimuli (Corbetta et al., 1998; Hopfinger et al., 2000).

Materials and Methods

Participants

Twenty University of Michigan students (10 female) between the ages of 18 and 30 participated in the study. All participants were right-handed, had normal or corrected to normal vision, and had no history of neurological disorders. Each received $20 per hour for participating, and the experiment lasted approximately 2 hours. Participants gave informed consent before the experiment in accordance with the University of Michigan Medical School Institutional Review Board.

Data acquisition

A Dell PC running Presentation software (Neurobehavioral Systems, Albany, CA) presented the experimental stimuli and recorded participants' responses. Visual stimuli were projected onto a screen at the back of the magnet's bore and were viewed through a mirror. Auditory stimuli were delivered through MR-compatible headphones. Headphone volume was adjusted for each participant separately, such that the auditory stimuli could be heard clearly over the background noise produced by the MR scanner. Participants' responses in the scanner were registered by an MR-compatible response box.

All MRI images were collected on a 3T Signa whole-body scanner equipped with a standard head coil. The blood oxygenation level-dependent (BOLD) signal was measured using a reverse spiral imaging sequence (repetition time (TR), 1250ms; echo time (TE), 30ms; field of view (FOV) 22cm; flip angle, 70°; 27 contiguous 4.5-mm-thick slices; in-plane resolution 3.44 × 3.44 mm). Anatomical images were collected in the same axial orientation as the functional images, but with a T1-weighted gradient-echo (GRE) sequence (TR, 250 ms; TE, 5.4ms; flip angle, 90°; in-plane resolution 0.86 × 086 mm). Every participant completed six runs of the experimental task, each of which consisted of 96 trials over a period of 8 minutes and 10 seconds. During each functional run, 389 brain volumes were collected. The first six images from each run contained no trials and were discarded prior to analysis.

Task

Participants were instructed to maintain fixation on a small white dot (0.15° × 0.17°) presented at the center of the screen throughout each run. At the start of every trial, a relevant visual cue word (“LOOK”, 3.12° × 0.86°; or “HEAR” 3.12° × 0.86°) appeared on the screen for 350 ms (Fig 1, top). The visual cue word instructed participants either to maintain attention in the visual modality (i.e., “LOOK”) or to switch attention to the auditory modality (i.e., “HEAR”). An irrelevant (binaural) auditory word was also presented, either at the same time as the visual cue word (simultaneous condition) or 850 ms after the onset of the visual cue word (sequential condition). The irrelevant auditory word signaled either the same task as the relevant visual word (congruent cues; 50% of trials) or the opposite task (incongruent cues; 50% of trials). In cue-plus-target trials (66%), a briefly-presented multisensory letter pair (duration, 350 ms) appeared 1875 ms after cue onset (Fig 1, bottom). Each letter within this audiovisual letter pair was either an “X” or an “O” (in the visual modality, the “X” subtended 1.10° × 1.36° of visual angle and the “O” subtended 1.18° × 1.38° of visual angle). The distracter letter in the uncued modality was equally likely to be the same letter as the target (congruent target-distracter pairs; Fig 1, bottom left) or a different letter (incongruent target-distracter pairs; Fig 1, bottom right). In cue-only trials (33%), the cue was not followed by a multisensory letter pair, which allowed us to isolate brain activity that was specific to our cue stimuli (Corbetta et al., 2000).

Participants were instructed to indicate whether the letter in the cued modality was an “X” or an “O” by pressing one of two response buttons as quickly and as accurately as possible, using either the index or the middle finger of their right hand. If a response was not detected within 1875 ms after target onset, an error was recorded. Decision-response mappings were counterbalanced across participants. In all trials, the fixation dot changed color from white to red 1875 ms after cue onset. Because this change was coincident with target presentation in cue-plus-target trials, in cue-only trials it signaled to participants that no target would occur and, hence, that they could cease attending (Corbetta et al., 2000). At the end of each trial (i.e., 3750 ms after trial onset), the fixation dot reverted to white.

Design

For each participant, we interleaved three runs of the sequential condition with three runs of the simultaneous condition. Half of the participants started with the sequential condition (i.e., sequential, simultaneous, sequential, simultaneous, sequential, simultaneous) while the other half started with the simultaneous condition. Prior to entering the scanner, participants completed a training session in which they briefly practiced the sequential and simultaneous task conditions. Participants were required to achieve 90% accuracy over a 32-trial block for each task condition before performing the task in the scanner. Every participant achieved this criterion on the first attempt.

In each run, there were 12 trial types (four cue-only and eight cue-plus-target), each of which was presented eight times in a randomized order. Thus, there were a total of 96 trials per run. The four cue-only trial types consisted of the four possible combinations of Cued Modality (Look, Hear) and Cue Congruency (congruent, incongruent). The eight cue-plus-target trial types consisted of the eight possible combinations of Cued Modality, (Look, Hear), Cue

Congruency (congruent, incongruent), and Target Congruency (congruent, incongruent). To optimize regression estimates of the BOLD responses that were produced by each of our 12 trial types, the inter-trial interval (ITI) was varied between zero and five TRs using a nearly exponential distribution that favored short ITIs (Miezen et al., 2000).

Data analysis

The behavioral data were analyzed using SPSS (SPSS, 2006). Next, the functional images were corrected for asynchronous slice acquisition, head movement, normalized to Montreal Neurological Institute (MNI) space (voxel size: 3.75 × 3.75 × 4.5 mm), and spatially smoothed with a three-dimensional Gaussian filter (8 mm full-width half-max) using SPM2 (Friston, 1995). Due to head movements greater than 3 mm, two participants were excluded from further analyses, leaving a total of 18 participants.

The time series for each functional run was modeled using a finite impulse response model. This model empirically derives the stimulus-locked BOLD response across time to each trial type in an event-related design without assuming a canonical hemodynamic response shape, and has been validated in prior studies (Ollinger et al., 2001a; Ollinger et al., 2001b). We estimated 14 TRs (17.5 s) of the BOLD response for each trial type, yielding 168 regressors (12 trial types × 14 TRs) in the design matrix. We also included six motion regressors (i.e., SPM2 estimates of translation along and rotation around the x, y, and z axes) and two regressors for the linear trend and the *y*-intercept term. For every participant, parameter estimates for each trial type were converted to units of percent signal change from baseline (i.e., the *y*-intercept term) in each run and then averaged across runs of the same type (i.e., sequential or simultaneous).

Voxelwise analyses

We performed two random effects, one-sample t-tests. The first t-test localized voxels in which the cue congruency effect (i.e., greater peak activity for incongruent than for congruent cue-only trials) was significantly larger in the simultaneous condition than in the sequential condition. Peak activity was defined as the maximum fMRI signal between 3.75 and 6.25 seconds after stimulus onset. The second t-test localized voxels that showed significantly greater peak activity for incongruent than for congruent cue-only trials, averaging across the simultaneous and the sequential conditions. Each of these directional t-tests was thresholded at $t(17) = 3.63$, $p < 0.001$ (one-tailed).

Region of interest analyses

Regions of interest (ROIs) in the left DLPFC, the right DLPFC, and the dorsal ACC were centered on coordinates that were localized in a prior study of cross-modal attention, which used the same multisensory target stimuli (Weissman et al., 2004). All other ROIs were defined functionally, based on average activity for all cue-only or all cue-plus-target trials. We first performed a one-way repeated-measures analysis of variance (ANOVA) across time (14 TRs) on the average stimulus-locked response to all types of cue-only trials. After the resulting F-map was height and extent thresholded ($p < 0.01$; five contiguous voxels), we defined ROIs in the right VLPFC and in the left middle/posterior VLPFC. Because we did not identify ROIs in either the superior parietal lobe (SPL) or the inferior parietal lobe (IPL) in the cue-only map, we next constructed an analogous F-map (height and extent thresholded to $p < 0.01$; five contiguous voxels) based on the average stimulus-locked BOLD response across time (14 TRs) to cue-plus-target trials. Using this map, we defined ROIs in the right SPL, the left SPL, and the left IPL (no right IPL region was identified). We also defined two ROIs in the sensory cortices: the top-activating region of visual (occipital) cortex and the top-activating region of auditory (temporal) cortex. The relatively liberal thresholds that were used to define our ROIs did not bias the outcome of our subsequent analyses because all subsequent ROI-level contrasts were orthogonal to the contrasts that we used to create the ROIs. Each ROI consisted of a 27-voxel cube centered on a local maximum (see Table 1).

Parameter estimates for each trial type were averaged across all voxels in each ROI. Random effects analyses were then performed to contrast peak activity for different trial types. As in the voxelwise analyses, peak activity in cue-only trials was defined as the maximum fMRI signal between 3.75 and 6.25 seconds after cue onset. To allow for both task- and participant-related variability, peak activity was estimated separately for each trial type and participant.

Results

Behavior

Mean reaction time and mean accuracy were analyzed in separate repeated-measures analyses of variance (ANOVAs) with four within-participants factors: Condition (simultaneous, sequential), Cued Modality (visual, auditory), Cue Congruency (congruent, incongruent), and Target Congruency (congruent, incongruent). Two significant main effects replicated our findings from a prior study (Weissman et al., 2004). First, participants were both faster (864 ms vs. 939 ms, $F(1,17) = 59.01$, $p < 0.0001$) and more accurate (97.8% vs. 96.5%, $F(1,17) = 11.79$, $p < 0.003$) when responding to congruent (versus incongruent) target-distracter pairs. Second, participants were both faster (865 ms vs. 938 ms, $F(1,17) = 44.18$, $p < 0.0001$) and more accurate (98.1% vs. 96.2%, $F(1,17) = 8.789$, $p < 0.009$) when responding to targets in the visual (versus the auditory) modality.

We also observed a significant interaction between Target Congruency (congruent, incongruent) and Cued Modality for accuracy, $F(1,17) = 5.85$, $p < 0.027$. Accuracy for congruent targets was always numerically higher than accuracy for incongruent targets, but this difference was significantly larger when participants were cued to “Hear” (97.3% vs. 95.1%; $F(1,17) = 17.47$, $p < 0.001$) than when they were cued to “Look” (98.4% vs. 97.7%; $F(1,17) = 1.93$, $p > 0.18$). No other behavioral effects were significant.

FMRI

Sensory Regions—Our first prediction was that the typical pattern of biasing activity in the sensory cortices for an audiovisual cued attention task (Weissman et al., 2004) would be observed more strongly in congruent than in incongruent cue-only trials. Specifically, for congruent cues we predicted an interaction between Cued Modality (visual, auditory) and Brain Region (visual cortex ROI, auditory cortex ROI) indicating a relative enhancement of activity in the visual cortex for “Look” versus “Hear” cue-only trials, and a relative enhancement of activity in the auditory cortex for “Hear” versus “Look” cue-only trials. For incongruent cues, however, we predicted that this pattern would be significantly less pronounced, or possibly even reversed, consistent with a hijacking of the attentional network (Lau & Passingham, 2007). We tested these predictions in the regions of visual and auditory cortex that were most highly activated by our stimuli (Fig 2a; see *Materials and Methods*).

Consistent with our first prediction, we observed a significant three-way interaction among Cue Congruency (congruent, incongruent), Cued Modality (visual, auditory) and Brain Region (visual cortex ROI, auditory cortex ROI), $F(1,17) = 9.36$, $p < 0.0071$ (Fig 2b). For congruent cues we observed a significant two-way interaction between Cued Modality and Brain Region, $F(1,17) = 5.18$, $p < 0.036$. As expected, this interaction reflected a relative enhancement of activity in the visual cortex for “Look” versus “Hear” cue-only trials, and a relative enhancement of activity in the auditory cortex for “Hear” versus “Look” cue-only trials (Fig 2b, left). Neither of the simple effects associated with this interaction was significant (both $p > 0.06$, one-tailed). However, the nature of the significant interaction clearly indicates a relative shift of activity toward the sensory cortex corresponding to the cued modality. For incongruent cues, we also observed a significant interaction between Cued Modality and Brain Region, F (1,17) = 7.15, p < 0.016. As expected, this interaction reflected a relative enhancement of activity in the visual cortex for "Hear" versus "Look" cue-only trials, and a relative enhancement of activity in the auditory cortex for "Look" versus "Hear" cue-only trials (Fig 2b, right). Neither of the simple effects associated with this interaction was significant (both p > 0.12, two-tailed). However, the nature of the significant interaction clearly indicates a relative shift of activity toward the task-irrelevant sensory cortex signaled by the irrelevant auditory word. These findings support our hypothesis that consciously perceived, irrelevant instruction words that signal a competing task set can hijack the attentional network, leading it to enhance the perceptual processing of irrelevant stimuli.

We also investigated whether the magnitude of the cue congruency effects above varied in the simultaneous and sequential conditions. The four-way interaction among Condition (simultaneous, sequential), Cued Modality (visual, auditory), Cue Congruency (congruent, incongruent), and Brain Region (visual ROI, auditory ROI) did not achieve significance, F (1,17) < 1. Therefore, cue congruency effects in the sensory cortices did not differ for the simultaneous and the sequential conditions.

Finally, we investigated whether merely presenting the irrelevant auditory word simultaneously with (as compared to 850 ms after) the relevant visual cue might distract participants in a relatively general way, causing them to orient less attention to the cued sensory modality. To test this prediction, we defined an overall measure of positive biasing activity, which was the average of positive biasing activity in the visual cortex (i.e., activity for "Look" cue-only trials minus activity for "Hear" cue-only trials) and positive biasing activity in the auditory cortex (i.e., activity for "Hear" cue-only trials minus activity for "Look" cue-only trials). As expected, we found significantly less positive biasing activity in the simultaneous condition than in the sequential condition, F(1,17) = 5.29, p < 0.034 (Fig 2c). Thus, independent of cue congruency, presenting the irrelevant auditory word simultaneously with (versus after) the visual cue interfered with orienting attention to the cued sensory modality.

Frontal Regions—Our next two predictions concerned activity in frontal regions. Our second prediction was that left VLPFC regions that retrieve task sets from memory would show a cue congruency effect that was significantly larger in the simultaneous than in the sequential condition. Our third prediction was that activity in DLPFC regions involved in maintaining task sets in working memory and activity in dorsal ACC regions that detect or resolve conflict between relevant and irrelevant task sets would be greater for incongruent than for congruent cue-only trials, and that the magnitude of these effects would not differ for the simultaneous and the sequential conditions.

Voxelwise Analyses

To test our second prediction about the left VLPFC, we performed a voxelwise t-test to locate brain regions in which the cue congruency effect was significantly larger in the simultaneous than in the sequential condition. This analysis revealed no significant activations, t(17) = 3.63, p < 0.001 and 8 contiguous voxels.

To test our third prediction about the DLPFC and the dorsal ACC, we performed a voxelwise, random-effects t-test to localize brain regions that showed greater activation for incongruent cue-only than for congruent cue-only trials, averaging across the simultaneous and the sequential conditions, t(17) = 3.63, p < 0.001 and 8 contiguous voxels. This analysis revealed two activations in the left posterior superior temporal gyrus (center of mass coordinates in MNI space: x = -57, y = -42, z = 8, Brodmann Area (BA) 22, cluster size, 10 voxels; center of mass: x = -65, y = -53, z = 10, BA 22, cluster size, 8 voxels) and one activation in the culmen (i.e., anterior vermis) of the cerebellum (center of mass: x = 9, y = -42, z = -10; cluster size, 8 voxels). No other activations were observed.

ROI Analyses

As noted above, our voxelwise analyses did not reveal significant activations in either frontal or parietal regions. Thus, we functionally defined ROIs in bilateral regions of the middle/posterior VLPFC, the left superior parietal lobe (SPL), the right SPL, and the left inferior parietal lobe (IPL) and defined ROIs in bilateral regions of the DLPFC and the dorsal ACC using coordinates from one of our prior studies (Weissman et al., 2004) (see *Materials and Methods*, Table 1, and Fig. 3a).

Consistent with our second prediction, in the left middle/posterior VLPFC (Fig. 3b, top left) we observed a significant interaction between Cue Congruency (congruent, incongruent) and Condition (simultaneous, sequential), $F(1,17) = 9.24$, $p < 0.008$. As hypothesized, this interaction occurred because there was significantly greater peak activity in incongruent than in congruent cue-only trials in the simultaneous condition, $t(17) = 2.80$, $p < 0.0062$, but not in the sequential condition, $t(17) = 1$. In the right VLPFC (Fig. 3b, top right), which may play a role in inhibiting irrelevant task sets (Brass and von Cramon, 2004a), we observed significantly greater peak activity in incongruent than in congruent cue-only trials, $t(1,17) = 3.08$, $p < 0.004$ (averaged across the simultaneous and the sequential conditions), but there was no significant interaction between Cue Congruency and Condition, $F(1,17) = 1.22$, $p > 0.28$. Thus, as predicted, cue congruency effects in the left VLPFC were significantly larger in the simultaneous than in the sequential condition, in line with models suggesting a role for this region in retrieving task sets from memory.

Consistent with our third prediction, we observed significantly greater peak activity in incongruent than in congruent cue-only trials in bilateral regions of the DLPFC (left DLPFC: $t(17) = 1.88$, $p < 0.04$; Fig. 3b, bottom left; right DLPFC: $t(17) = 1.87$, $p < 0.04$; Fig. 3b, bottom middle). Moreover, the size of the cue congruency effect did not vary significantly across the simultaneous and the sequential conditions (left DLPFC: $F(1,17) = 2.28$, $p > 0.149$; right DLPFC: $F(1,17) < 1$). Also as predicted, we observed the same pattern in the dorsal anterior cingulate cortex (Fig. 3b, bottom right). Specifically, we observed significantly greater peak activity in incongruent than in congruent cue-only trials, $t(17) = 1.75$, $p < 0.05$ (averaged across the simultaneous and the sequential conditions), and the size of this effect did not vary significantly across the simultaneous and the sequential conditions, $F(1,17) < 1$. These findings are consistent with a role for the DLPFC in maintaining task sets in working memory and with a role for the dorsal ACC in detecting or resolving conflict between relevant and irrelevant task sets.

Parietal Regions—Our fourth prediction was that cue congruency effects would be observed in superior and inferior parietal regions that allocate attentional resources to behaviorally relevant stimuli (Corbetta et al., 1998; Hopfinger et al., 2000). However, ROI analyses in parietal regions revealed neither an overall cue congruency effect (i.e., averaged across the simultaneous and the sequential conditions) nor an interaction between Cue Congruency (congruent, incongruent) and Condition (simultaneous, sequential). Exploratory analyses, which should be interpreted with caution, revealed significant effects of Cue Congruency in the simultaneous condition (left SPL: $t(17) = 1.827$, $p < 0.043$; right SPL: $t(17) = 1.880$, $p < 0.039$; left IPL, $t(17) = 2.078$, $p < 0.027$), but not in the sequential condition (left SPL, $t(17) < 1$; right SPL, $t(17) <1$; left IPL, $t(17) < 1$).

Discussion

We often become distracted from performing a primary task (e.g., reading) when an irrelevant stimulus (e.g., a television commercial) activates representations of an irrelevant task in working memory (e.g., watching a movie). Consistent with such everyday experiences, current models of selective attention posit that a major source of distraction during task performance stems from the activation of irrelevant task objectives in working memory (MacLeod, 1991; Wagner et al., 2001). In line with such models, we found that consciously perceived, irrelevant instructional cues that were strongly associated with an irrelevant task hijacked the attentional network, as indexed by heightened activity in (a) frontal regions that control attention and (b) sensory cortices that underlie the perceptual processing of irrelevant stimuli. Moreover, we found that effects of irrelevant instructional cues on activity in the left middle/posterior VLPFC varied with whether a relevant and an irrelevant instructional cue were presented simultaneously or sequentially. These findings have important implications for our understanding of the functional neuroanatomy of selective attention in both neurologically-intact (Ventura et al., 2005) and clinical (Casey et al., 1997; Max et al., 2005; Vaidya et al., 2005) populations.

Consistent with our first prediction, we observed strong evidence in the sensory cortices that consciously perceived, irrelevant instructional stimuli can hijack the attentional network. Cueing participants to attend for a possibly upcoming target that is defined by its spatial location (Hopfinger et al., 2000; Woldorff et al., 2004), color (Giesbrecht et al., 2003), or sensory modality (Weissman et al., 2004) often leads to a relative enhancement of activity in sensory regions that process the attended attribute, even before the target is presented (Corbetta & Shulman, 2002). In line with such findings, we observed a relative enhancement of activity in the sensory cortex corresponding to the cued modality for congruent cues, in which the relevant visual cue and the irrelevant auditory word signaled the same task (e.g., “Hear”). However, for incongruent cues, in which the irrelevant auditory word (e.g., “Look”) signaled the opposite sensory modality as the relevant visual cue (e.g., “Hear”), we observed a relative enhancement of activity in the sensory cortex corresponding to the modality that was signaled by the irrelevant auditory word. Since the irrelevant auditory words were played at the same volume as the auditory targets that participants successfully identified, our findings show that consciously perceived, irrelevant instructional stimuli can hijack the attentional network.

Other results in the sensory cortices indicated that merely presenting the irrelevant auditory word simultaneously with (versus after) the visual cue interfered with attention-orienting processes in a relatively general way that did not depend on cue congruency. Specifically, regardless of cue congruency, there was significantly less positive biasing activity in the sensory cortices (i.e., greater activity for “Look” than for “Hear” cue-only trials in the visual cortex and greater activity for “Hear” than for “Look” cue-only trials in the auditory cortex) in the simultaneous than in the sequential presentation condition. This finding fits nicely with prior work indicating that presenting any sort of task-related information at an irrelevant stimulus dimension can be distracting (Milham et al., 2002).

In line with our second prediction, in the left middle/posterior VLPFC we observed a significantly larger cue congruency effect when the irrelevant auditory word was presented simultaneously with (versus after) the relevant visual cue. This result is highly consistent with models in which the left middle/posterior VLPFC participates in retrieving from memory either (a) task sets or (b) stimulus-response mappings that are associated with task sets (Brass and von Cramon, 2004a; Bunge, 2004). Given that a task set can be retrieved in well under a second (Monsell and Mizon, 2006), such retrieval processes likely operate relatively early in the cue-target interval. Moreover, demands on such processes are likely greater when a simultaneously presented irrelevant instructional cue signals a competing (versus the same) task set as a relevant cue. In light of the hijacking effects that we observed in the sensory cortices, the larger cue congruency effect in the simultaneous (versus sequential) condition might also index the retrieval of both the relevant and the irrelevant task set into working memory (Lau & Passingham, 2007). Future studies might therefore be aimed at determining whether cue congruency effects in the left middle/posterior VLPFC reflect processes that work harder to retrieve a relevant task set under conditions of distraction or, alternatively, processes that erroneously retrieve an irrelevant task set.

Our results in the left middle/posterior VLPFC may also be accounted for by models in which this region selects relevant semantic information in the context of competing semantic distracters (Badre et al., 2005; Badre and Wagner, 2007). Indeed, such models readily account for our finding that cue congruency effects were larger in the simultaneous condition, in which the relevant task representation needed to be selected in the context of a competing task representation, than in the sequential condition, in which the relevant task representation could be selected before the irrelevant task representation was retrieved. Also consistent with such models, the specific region of left VLPFC that we have identified is highly proximal to a region of the left middle/posterior VLPFC that has previously been linked to semantic selection (Badre et al., 2005). Future studies will be needed to determine whether cue congruency effects in the left middle/posterior VLPFC reflect processes that retrieve task sets from memory (Bunge, 2004) or processes that operate on such task sets after they are retrieved in order to select relevant task sets among competing ones (Badre et al., 2005; Badre and Wagner, 2007).

Consistent with our third prediction, we also observed cue congruency effects in bilateral regions of the DLPFC, the dorsal ACC, and the right VLPFC, and the magnitude of these effects did not significantly differ in the simultaneous and the sequential conditions. Cue congruency effects in the DLPFC may reflect increased demands on processes that maintain relevant representations in working memory after an irrelevant stimulus activates competing representations (Sakai and Passingham, 2002; Sreenivasan and Jha, 2007). Given the hijacking effects that we observed in the sensory cortices, cue congruency effects in the DLPFC may also index the maintenance of both a relevant and an irrelevant task set in incongruent cue-only trials (Lau & Passingham, 2007). Cue congruency effects in the dorsal ACC may reflect processes that detect or resolve conflict between relevant and irrelevant task sets (Luks et al., 2002; Orr and Weissman, in press). Finally, cue congruency effects in the right VLPFC may reflect increased demands on processes that inhibit irrelevant task sets that become activated in working memory during the processing of incongruent cues (Brass and von Cramon, 2004a). Future studies will be necessary to distinguish among these and other possible interpretations of the cue congruency effects that we have observed. Nonetheless, our findings are important because they provide some initial insight into which frontal regions are hijacked by consciously perceived, irrelevant instructional cues. Moreover, they both replicate and extend our findings from a prior experiment with different participants, the design of which included only a simultaneous presentation condition (Orr and Weissman, in press), by demonstrating that cue congruency effects in the DLPFC and the dorsal ACC do not vary with whether relevant and irrelevant task cues are presented simultaneously or sequentially.

In line with our fourth prediction, we also observed cue congruency effects in bilateral regions of the superior parietal lobe and in the left inferior parietal lobe. More specifically, exploratory analyses in these regions revealed greater activity for incongruent than for congruent cue-only trials in the simultaneous (but not the sequential) condition. Parietal regions are thought to allocate attention to behaviorally relevant stimuli (Corbetta et al., 1998; Hopfinger et al., 2000). Thus, cue congruency effects in parietal regions may index the effect of activating irrelevant task objectives in frontal regions on processes that orient attention.

Finally, we observed cue congruency effects in the left posterior superior temporal gyrus and in the anterior vermis (i.e., culmen) of the cerebellum. Activity in the left posterior superior temporal gyrus (BA 22) is thought to increase with demands on phonological processes (Graves et al., 2008; Rumsey et al., 1997). To the extent that participants sub-vocalized the visual cue word, demands on phonological processes were likely greater in incongruent than in congruent cue-only trials. Indeed, only in incongruent cue-only trials did the irrelevant auditory word activate phonological representations that conflicted with those needed to sub-vocalize the relevant visual word. Activity in the anterior vermis is thought to underlie processes related to response preparation and response inhibition (Desmond et al., 1997; Simmonds et al., 2008). We speculate that incongruent cue-only trials imposed greater demands than congruent cue-only trials on inhibitory processes that prevented participants from subvocalizing the irrelevant auditory word. In sum, we observed cue congruency effects in left posterior superior temporal and anterior vermis regions which underlie, respectively, phonological and motor processes that were likely recruited by our verbal cue stimuli.

Our finding that consciously perceived, irrelevant instructional cues can hijack the attentional network stands in stark contrast to the findings from two previous fMRI studies (Brass and von Cramon, 2004b; Lau and Passingham, 2007). In these studies, hijacking occurred only when the irrelevant instructional cues that signaled an irrelevant task were presented below the threshold of conscious perception. Notably, the simple geometric forms (e.g., squares and diamonds) that served as irrelevant instructional cues in these prior studies were not strongly associated with the irrelevant task objectives they were meant to activate in working memory. It is well known, however, that consciously perceived distracters in selective attention tasks produce the greatest interference when they are strongly associated with irrelevant semantic and response representations (MacLeod, 1991). For example, irrelevant words in the Stroop task are thought to produce especially large interference effects because words have been automatically associated with their meanings and vocal responses through extensive language training. The present finding that consciously perceived auditory words (“Look” and “Hear”) can hijack the attentional network is thus highly consistent with the existing literature on selective attention

Our data indicating that cue congruency effects in the left VLPFC were more pronounced in the simultaneous than in the sequential presentation condition is also generally consistent with the literature on selective attention. A predominant finding in this literature is that interfrence from irrelevant stimuli is greater when those stimuli are presented simultaneously with (versus after) target stimuli (for a review, see MacLeod, 1991). Such data clearly indicate that temporal overlap in the processing of relevant and irrelevant stimuli plays an important role in determining the efficiency of selective attention when only a single task set is activated. Here, we have shown that temporal overlap in the processing of relevant and irrelevant stimuli can also influence whether irrelevant stimuli can activate irrelevant task sets in working memory. Thus, our findings further underscore the importance of temporal factors in determining the efficiency of selective attention.

A limitation of the present study is that we did not observe significant effects of cue congruency on behavioral measures of performance. The lack of such behavioral effects makes it difficult to determine whether frontal and parietal regions whose activity is influenced by cue congruency participate in “protecting” a relevant task set from distraction (Jha et al., 2004; Sakai and Passingham, 2002) or, alternatively, in orienting attention to irrelevant stimuli (Lau & Passingham, 2007). Given that behavioral performance following incongruent (versus congruent) cues is impaired for only about 300 ms (Mattler, 2005), the absence of behavioral cue congruency effects in the present study (which featured a 1.875 second cue-target interval) is unsurprising. Due to the relatively short temporal duration of behavioral cue congruency effects, brain imaging techniques that offer higher temporal resolution than fMRI, such as, for example, magnetoencephalography (MEG), may be especially useful for dissociating brain regions that “protect” a relevant task set under conditions of distraction from brain regions that orient attention to irrelevant stimuli.

The present work may also be relevant to our understanding of attentional impairments in various clinical syndromes, such as drug addiction and attention-deficit and hyperactivity disorder. Patients with these syndromes are often highly distracted by consciously perceived stimuli that activate irrelevant task objectives in working memory (Casey et al., 1997), and in some cases this heightened distraction has been linked to activity in the fronto-parietal attentional network (Arnsten, 2006; Bonson et al., 2002; Garavan et al., 2000). For example, drug stimuli can trigger craving and relapse in addicts who are trying to quit (Hollander and Carelli, 2007). Although the precise manner in which the attentional network is hijacked may differ across various syndromes, our findings may provide some general insight into the neural and psychological mechanisms that are involved.

In conclusion, we have found that irrelevant instructional cues can hijack the attentional network even when they are consciously perceived. Moreover, we have found that the relative timing with which relevant and irrelevant instructional cues are presented influences the extent of this hijacking in certain regions of the attentional network. Future studies will be important for advancing our understanding of how irrelevant task objectives become activated in working memory and for revealing the behavioral and neural consequences of activating such representations in both neurologically-intact and clinical populations.

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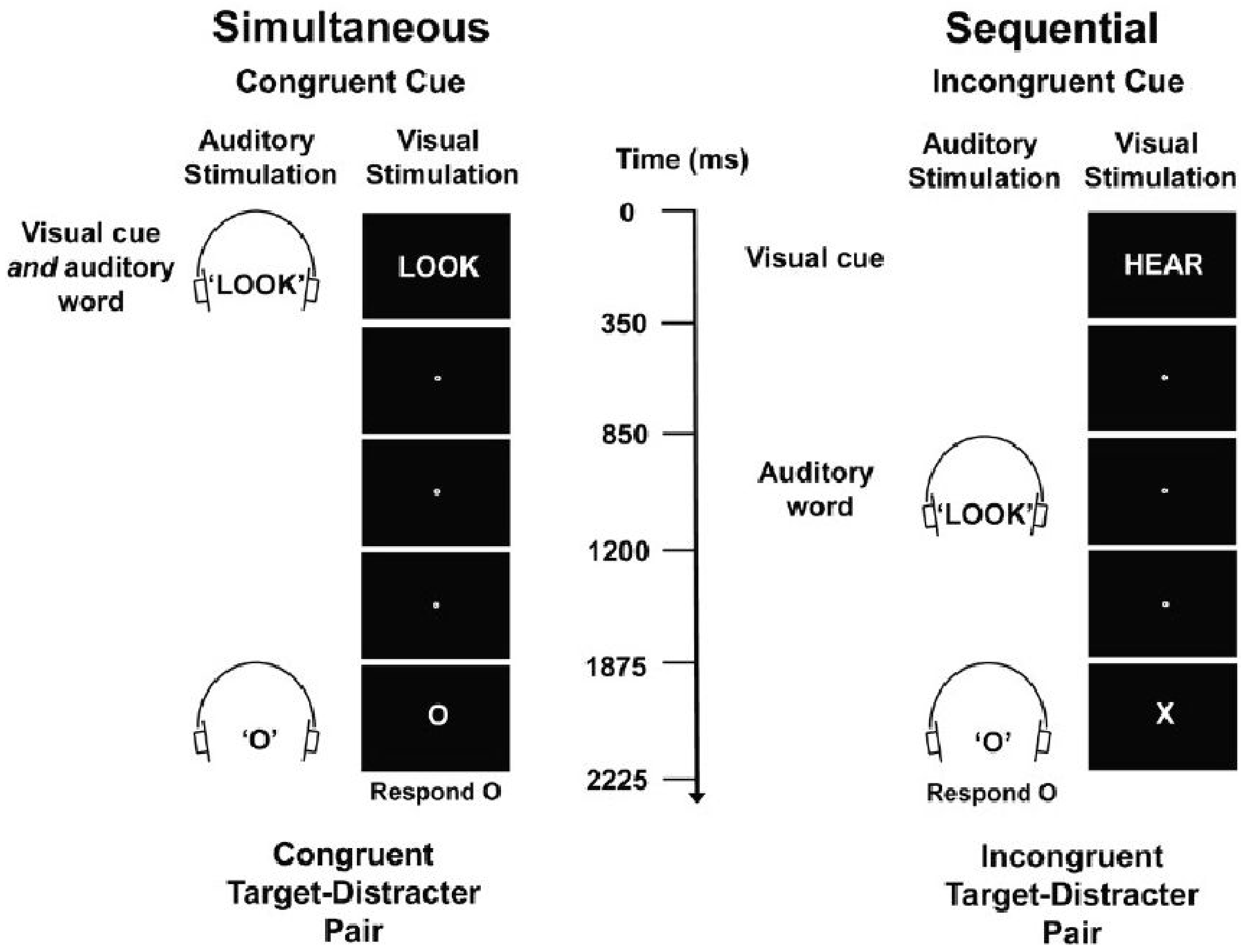

Figure 1.

Experimental task. In each trial, a visual cue ('LOOK' or 'HEAR') instructed participants to attend to and identify either the visual letter ('X' or 'O') or the auditory letter ('X' or 'O') of a possibly upcoming audiovisual letter pair. An irrelevant auditory word signaled either the same task as the visual cue or the opposite task. In the simultaneous condition, the irrelevant auditory word was presented at the same time as the visual cue. In the sequential condition, the irrelevant auditory word was presented 850 ms after the visual cue. In cue-plus-target trials, an audiovisual target-distracter letter pair was presented 1.875 seconds following the onset of the relevant visual cue. The distracter letter was presented in the opposite modality as the target letter and was equally likely to be the same letter as the target (congruent target-distracter pairs) or a different letter (incongruent target-distracter pairs). In cue-only trials (33%, not shown), the relevant visual cue was not followed by a target-distracter letter pair.

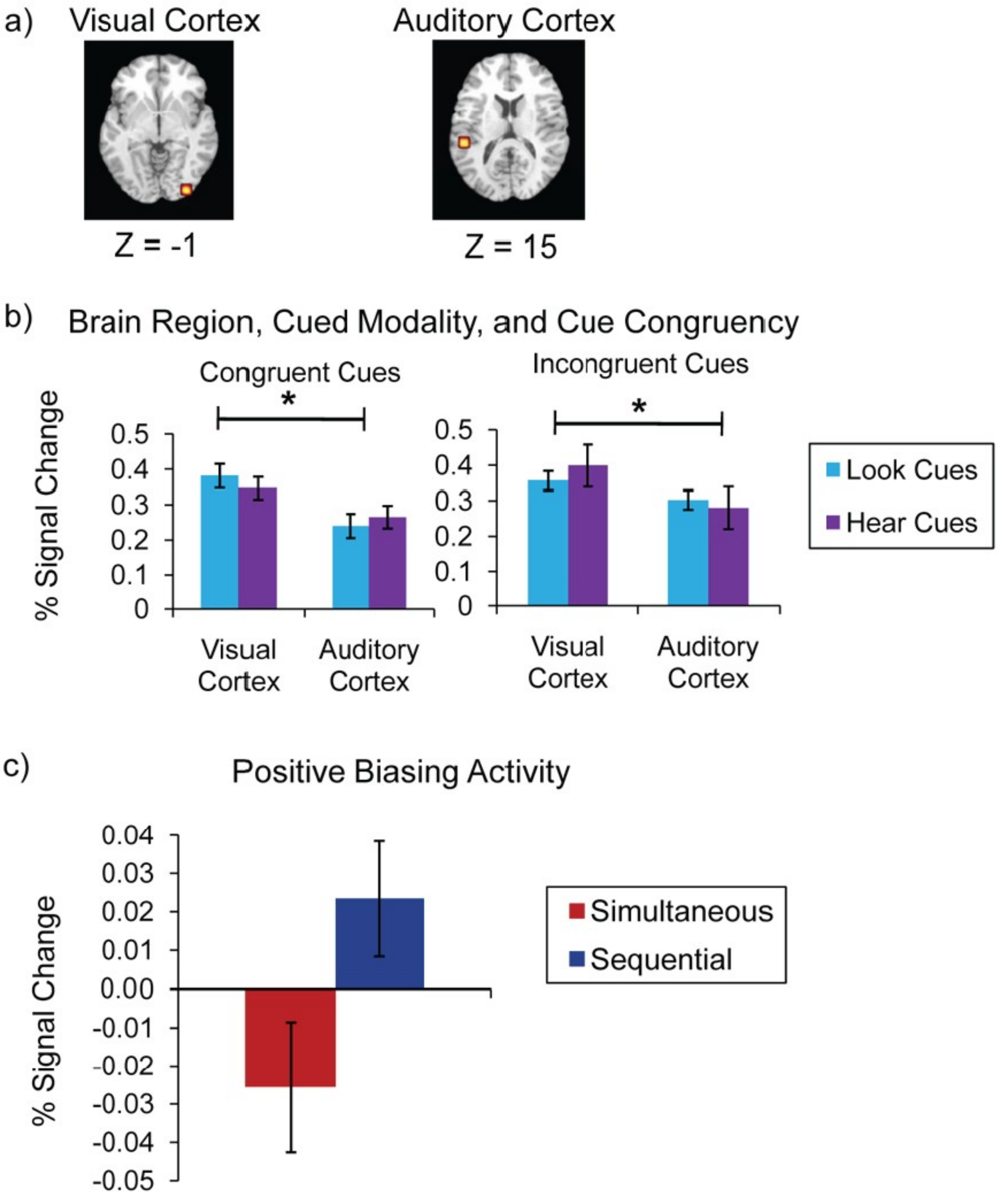

Figure 2.

Peak activity in cue-only trials in visual and auditory cortex regions of interest. **(a)** Axial slices of visual and auditory cortex regions of interest overlaid on an MNI-normalized anatomical brain. In this and subsequent figures, z coordinates refer to MNI space. **(b)** Peak activity in cue-only trials as a function of Brain Region (visual cortex, auditory cortex), Cued Modality (visual, auditory) and Cue Congruency (congruent cues, incongruent cues) averaged across the simultaneous and the sequential conditions. Asterisks indicate significant simple effects or interactions. Notice that the pattern of biasing activity that is typical for an audiovisual cued attention task (i.e., greater activity for “Look” than for “Hear” cues in the visual cortex and greater activity for “Hear” than for “Look” cues in the auditory cortex) was observed for congruent cues while the reverse pattern was observed for incongruent cues. **(c)** Positive biasing activity in the visual cortex (i.e., activity for “Look” cue-only trials minus activity for “Hear” cue-only trials) averaged with positive biasing activity in the auditory cortex (i.e., activity for “Hear” cue-only trials minus activity for “Look” cue-only trials), plotted separately for the simultaneous and the sequential conditions. Notice that there was significantly more positive biasing activity in the sequential condition than in the simultaneous condition.

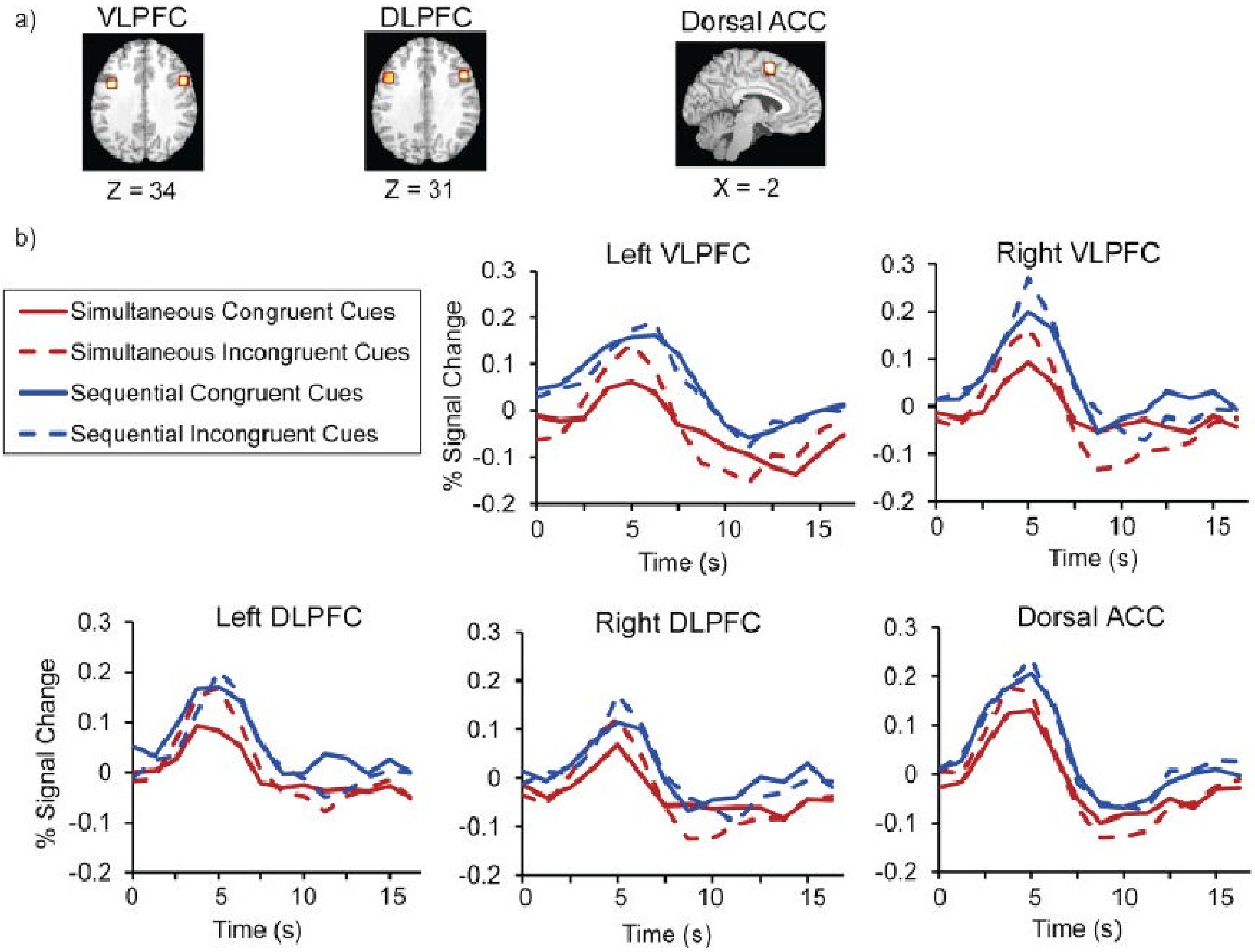

Figure 3.

Activity in cue-only trials plotted in frontal and parietal regions of interest. **(a)** Axial slices showing regions of interest on the MNI-normalized brain. These regions include the left VLPFC, the right VLPFC, the left DLPFC, the right DLPFC, and the dorsal ACC. **(b)** Activity in cue-only trials plotted as a function of Condition (sequential, simultaneous) and cue congruency (congruent, incongruent) in each region of interest. In the left VLPFC (but not in the other regions), cue congruency effects were significantly larger in the simultaneous condition than in the sequential condition.

Table 1

Regions of interest in the present study.

Region of Interest	**Brodmann Area**	**MNI Coordinates**		
		x	**y**	**z**
Left dorsolateral prefrontal cortex	9	-48	15	31
Right dorsolateral prefrontal cortex	9	48	19	31
Left ventrolateral prefrontal cortex	9/44	-41	8	32
Right ventrolateral prefrontal cortex	9/44	53	12	36
Dorsal anterior cingulate cortex	32	-2	6	52
Right superior parietal lobe	7	34	-68	45
Left superior parietal lobe	7	-15	-75	54
Left inferior parietal lobe	7	-34	-60	45
Right middle occipital gyrus	17/18	34	-90	-5
Left superior temporal gyrus	42	-53	-34	14