

Incongruent Abstract Stimulus–Response Bindings Result in Response Interference: fMRI and EEG Evidence from Visual Object Classification Priming

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Abstract

■ Stimulus repetition often leads to facilitated processing, resulting in neural decreases (repetition suppression) and faster RTs (repetition priming). Such repetition-related effects have been attributed to the facilitation of repeated cognitive processes and/or the retrieval of previously encoded stimulus–response (S-R) bindings. Although previous research has dissociated these two forms of learning, their interaction in the brain is not fully understood. Utilizing the spatial and temporal resolutions of fMRI and EEG, respectively, we examined a long-lag classification priming paradigm that required response repetitions or reversals at multiple levels of response representation. We found a repetition effect in occipital/temporal cortex (fMRI) that was time-locked to

stimulus onset (EEG) and robust to switches in response, together with a repetition effect in inferior pFC (fMRI) that was time-locked to response onset (EEG) and sensitive to switches in response. The response-sensitive effect occurred even when changing from object names (words) to object pictures between repetitions, suggesting that S-R bindings can code abstract representations of stimuli. Most importantly, we found evidence for interference effects when incongruent S-R bindings were retrieved, with increased neural activity in inferior pFC, demonstrating that retrieval of S-R bindings can result in facilitation or interference, depending on the congruency of response between repetitions. ■

INTRODUCTION

Repeated exposure to a stimulus often results in facilitated processing. Behaviorally, this facilitation can manifest as faster RTs or improved accuracy in the context of an indirect memory task (Richardson-Klavehn & Bjork, 1988). Such repetition priming often co-occurs with neural decreases, as measured by fMRI, in cortical regions engaged during initial stimulus processing, a phenomenon known as repetition suppression (RS; Grill-Spector, Henson, & Martin, 2006). Possibly analogous effects have also been shown in EEG, with modulations of ERPs between 200 and 600 msec poststimulus as a function of repetition of visual objects (Guillaume et al., 2009; Henson, Rylands, Ross, Vuilleumeir, & Rugg, 2004; Henson et al., 2003; Schendan & Kutas, 2003).

One cause of such behavioral and neural repetition effects is believed to be the retrieval of stimulus–response (S-R) bindings (Hommel, 1998; Logan, 1990). According to this account, whenever a response is produced to a stimulus in a given task, the co-occurrence of the stimulus and response entails the formation of a direct S-R binding. Subsequent encounters with that stimulus can then cue retrieval of these S-R bindings. Such S-R accounts have been studied within the context of task switching (Koch & Allport,

2006; Waszak, Hommel, & Allport, 2003; Allport & Wylie, 1999), short-lag subliminal priming (Kiesel, Kunde, & Hoffmann, 2006, 2007; Klauer, Eder, Greenwald, & Abrams, 2007; Kunde, Kiesel, & Hoffmann, 2003; Abrams, Klinger, & Greenwald, 2002; Damian, 2001), and negative priming (Frings, Rothermund, & Wentura, 2007; Rothermund, Wentura, & De Houwer, 2005; MacDonald & Joordens, 2000), as well as the long-lag semantic classification paradigms used in this study (e.g., Schnyer et al., 2007; Dennis & Schmidt, 2003).

One way in which such S-R retrieval might result in priming and RS is by obviating the need to repeat the neural computations that were required to generate a response on its initial presentation. In support of this “bypassing” account, Dobbins, Schnyer, Verfaellie, and Schacter (2004) used fMRI to show that RS in ventral temporal and prefrontal regions was reduced when a response was switched between presentations of a visual object compared with when the response was repeated. They attributed the reduction in RS to a need to re-engage the cortical regions associated with the neural computations required by the task, now that the previous response was no longer appropriate.

Such a bypassing account challenged the prevailing assumption that behavioral and neural repetition effects result from the facilitation of specific component processes (CPs) engaged during initial and subsequent presentation of a stimulus (Henson, 2003; Schacter & Buckner, 1998).

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Here RS is thought to reflect the “facilitation” of processes that are localized within specific cortical regions, rather than the bypassing of these processes. For example, RS in ventral temporal regions is often thought to reflect the facilitation of perceptual processes (Henson, 2003; Henson, Shallice, Gorno-Tempini, & Dolan, 2002; Blaxton, 1999), whereas RS in prefrontal regions is thought to reflect the facilitation of conceptual processes (Wagner, Koutstaal, Maril, Schacter, & Buckner, 2000; Wagner, Desmond, Domb, Glover, & Gabrieli, 1997).

More recent research, however, has suggested that both the retrieval of S-R bindings and the facilitation of CPs can contribute to behavioral and neural repetition effects. For example, although Horner and Henson (2008) found RS in inferior prefrontal regions that was sensitive to switches in response between presentations, as in Dobbins et al. (2004), the RS they found in a fusiform region was resilient to such response switches, unlike in Dobbins et al. (see also Race, Shanker, & Wagner, 2009; Wig, Buckner, & Schacter, 2009). They therefore proposed that the inferior prefrontal RS effect reflected the retrieval of S-R bindings, whereas the fusiform RS effect reflected the facilitation of (perceptual) CPs, rather than a bypassing of such processes.

If S-R retrieval and CP facilitation co-occur in the brain, how do they interact to generate an appropriate behavioral response? Logan (1990) proposed that the CP and S-R retrieval routes operate independently. According to his “instance theory,” each time a stimulus is encountered, an “algorithmic” (CP) route tries to generate the appropriate response (and for the first encounter, only this algorithmic route can do so). In parallel, however, any instances (S-R bindings) that have been encoded from previous co-occurrences of that stimulus and a response are also retrieved, such that the actual response is determined by a “race” between the algorithmic route and multiple potential instances. Assuming that each co-occurrence of a stimulus and response produces a new instance and that the algorithmic route is not itself affected by repetition (unlike CP theories), this theory can elegantly explain the power law reduction in both the mean and variance of RTs as a function of the number of repetitions.

It is less clear what happens when a switch in response is required between initial and subsequent stimulus presentations. One possibility is the race continues regardless, which would result solely in an increase in errors whenever incorrect S-R bindings win the race. Presuming priming analyses are restricted to correct responses, no priming should be seen as RTs for correct trials would be determined by the algorithmic route only. Another possibility is that retrieved S-R bindings are effectively ignored when it is known a priori that a retrieved S-R binding would be inappropriate (e.g., when the task is changed). However, this would also result in no RT priming given RTs will be solely determined by the algorithmic route. In both of these possibilities, faster RTs for repeated versus novel stimuli could still potentially occur if the algorithmic route

could also be facilitated by repetition (as in CP theories), but neither would be able to explain the increase in RT that is sometimes found for repeated versus novel stimuli when a response is reversed (see Horner & Henson, 2011). This “negative priming” would seem to imply some form of interaction (interference) between the CP and S-R routes, where conflicting evidence from both routes must be resolved to produce the task-appropriate response. Critically, such interference is hard to reconcile with either Logan’s (1990) instance theory or the “bypassing” account of S-R retrieval (Dobbins et al., 2004).

Although behavioral evidence for an interaction between CP and S-R routes has recently been presented (Horner & Henson, 2011), neural evidence has to date been absent. This is because it is vital to compare neural activity when the response is reversed at all levels of response representation (see Horner & Henson, 2009), which was not achieved by previous comparisons of “same” versus “reversed” task instructions (as in Horner & Henson, 2008; Dobbins et al., 2004). Here we used a “changing referent” paradigm (Denkinger & Koutstaal, 2009), which overcomes this limitation (see below and Horner & Henson, 2011, for further discussion). In this case, fMRI might show a shift from RS to repetition enhancement (RE) in some brain regions when CP and S-R routes interfere with each other. A further advantage of neural measures is to spatially or temporally dissociate effects of S-R retrieval from effects of CP facilitation. For example, behavioral priming is the end result of both CP and S-R contributions, whereas EEG offers the temporal resolution to potentially dissociate initial CP effects, which are likely to be time-locked to stimulus onset, from S-R effects, which are likely to be time-locked to response onset.

A further issue not previously addressed in the neuroimaging literature is the level at which stimuli are represented within S-R bindings. For example, some have used behavioral priming to argue that stimuli are coded at a highly specific perceptual level (see Schnyer et al., 2007), whereas others have argued for a more abstract level (see Denkinger & Koutstaal, 2009). Although behavioral evidence has recently been provided for simultaneous coding of both specific and abstract stimulus representations (Horner & Henson, 2011), the neural correlates of more abstract types of S-R retrieval are unknown.

To address the above issues of (1) interference following a response reversal and (2) the level of stimulus representation in S-R bindings, we used a study–test visual object classification design. During the study phases, participants saw pictures of common objects (pictures) and object names (words) and classified the objects according to whether they were “bigger than a shoebox” in real life. During subsequent test phases, the objects were repeated along with novel objects, all as pictures. Thus, the picture stimuli at test had either been seen as pictures at study (the within-format condition), words at study (the across-format condition) or were experimentally novel (the novel condition). Importantly, the referent for the size comparison was

changed from study to test, such that participants were required to classify whether the objects were “bigger than a wheelie bin” (a large trashcan) or “bigger than a pencil case.” This change in referent was such that one half of the repeated stimuli required the same response between presentations (the congruent condition), and the other half required a reversal in response between presentations (the incongruent condition; see Figure 1). By similarly splitting the novel stimuli at test according to their correct classification had they been presented at study, repetition effects could be defined as the difference between repeated versus novel stimuli within congruent and incongruent conditions (thereby controlling for proximity to the referents).

This resulted in a 2×2 factorial design on repetition effects, with factors format-match and congruency. Within this design, we were interested in the main effect of Congruency (on repetition effects), which would provide general evidence for S-R contributions and, more specifically, whether significant repetition effects occurred within congruent and incongruent conditions, yet with opposite sign. For example, a change in the fMRI response of a brain region from RS to RE across congruent and incongruent conditions would support a change from facilitation to interference because of S-R retrieval. We were also interested in the main effect of format-match, which would indicate perceptual CP contributions. Finally, we were interested in the interaction between format-match and congruency, which would suggest specific representations of stimuli within S-R bindings, and whether there was also a residual

congruency effect within the across-format condition, which would suggest (additional) abstract representations of stimuli within S-R bindings.

METHODS

Participants

Participants were recruited from the MRC Cognition and Brain Sciences Unit volunteer panel and from the student population of Cambridge University; all participants had normal or corrected-to-normal vision and were right-handed (self-report). Experiments were of the type approved by a local research ethics committee (LREC Reference 05/Q0108/401).

Eighteen participants (10 men) gave informed consent to participate in the fMRI experiment, with a mean age across participants of 25.9 years ($SD = 4.3$ years). A further 18 participants (eight men) took part in the EEG experiment, with a mean age of 23.5 years ($SD = 4.0$ years). No participant took part in both the fMRI and EEG experiment.

Materials

Stimuli were 384 colored images of everyday objects (and their name equivalents), previously used in Horner and Henson (2009). There were split evenly between the wheelie bin and pencil case referent so that, of the 192 stimuli per referent, 48 were bigger than a shoebox and bigger than a wheelie bin (or pencil case), 96 were bigger than a shoebox

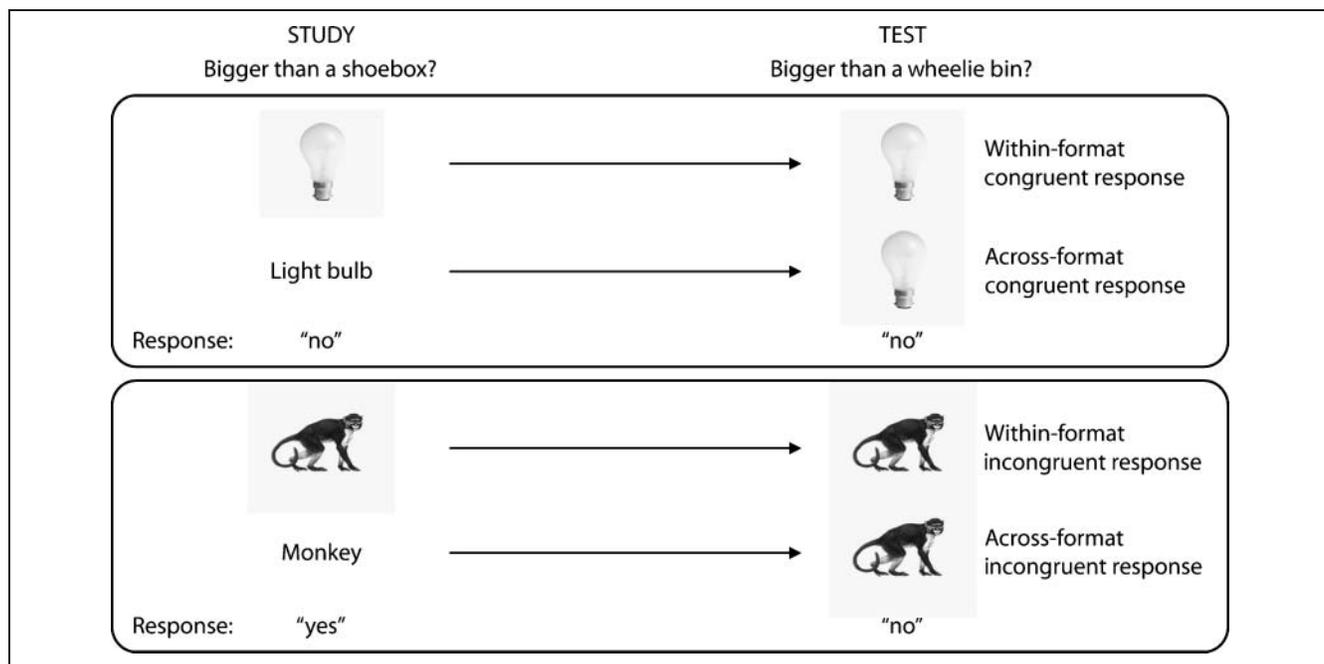


Figure 1. General design of fMRI and EEG experiment. Picture and word stimuli were presented at study, and participants asked to classify stimuli according to whether they are “bigger than a shoebox.” At test, all such “primed” stimuli were repeated as pictures, intermixed with novel picture stimuli. Participants either classified pictures according to whether they are “bigger than a wheelie bin” or “bigger than a pencil case.” Thus, half the repeated stimuli received a congruent response and half received an incongruent response.

and smaller than a wheelie bin (or smaller than a shoebox and bigger than a pencil case), and 48 were smaller than a shoebox and smaller than a wheelie bin (or pencil case). Therefore, per referent, 96 stimuli were congruent and 96 were incongruent. These 96 stimuli were then randomly assigned to one of three groups relating to whether they were presented as a picture at study (within-format condition), a word at study (across-format condition) or were experimentally novel (novel condition). This resulted in 64 stimuli per condition collapsing across the two referent changes (a manipulation that was not of theoretical interest). This resulted in a 3×2 design with factors format-match (within-format, across-format, and novel conditions) and congruency (congruent and incongruent conditions). The assignment of stimuli to the three study context factors was rotated across participants. Note that stimuli in the incongruent condition are, on average, closer in size to the referent than stimuli in the congruent condition. This is because a stimulus that is, for example, smaller than a wheelie bin but constrained to be bigger than a shoebox (in the incongruent condition) is likely to be closer in size to the wheelie bin than a stimulus that is constrained to be smaller (or bigger) than both (in the congruent condition). We controlled for this potential confound by using the congruent and incongruent novel conditions as separate baselines for defining repetition effects (see Horner & Henson, 2011, for more details, and analysis of proportional as well as additive priming).

Procedure

The experiment consisted of four study–test blocks (two relating to the wheelie bin referent change and two to the pencil case referent change), with each block lasting approximately 15 min. During each study phase, 64 stimuli were shown three times each resulting in 192 trials. Thirty-two stimuli were presented as pictures (within-format), and 32 stimuli were presented as words (across-format). Each set of 32 stimuli consisted of equal numbers of congruent and incongruent items. Participants performed the “bigger than a shoebox” task, deciding whether each object (depicted as either a picture or a word) was bigger than an average sized shoebox in real life. During each test phase, the 64 stimuli from the study phase (within-format and across-format) were randomly intermixed with 32 novel stimuli (novel). All items at test were presented as pictures. Participants either performed the “bigger than a wheelie bin” or “bigger than a pencil case” task. The wheelie bin and pencil case tasks at test were counterbalanced across participants in an ABBA/BAAB manner.

For the fMRI experiment, each trial sequence began with a centrally placed fixation cross presented for 500 msec, followed by a stimulus for 1000 msec, followed by a blank screen for 1500 msec. For the EEG experiment, following the 1000-msec stimulus presentation, a fixation cross was presented for 500 msec. This was followed by a centrally placed circle, presented for a varied time of 750–1250 msec,

with a mean of 1000 msec. Thus, the mean trial length was 3000 msec for both experiments, and the trial sequence only differed following stimulus offset. Images subtended approximately 6° of visual angle. Words were presented in black on a white background with the same pixel dimensions as the object picture stimuli. Participants were able to respond at any point up to the start of a new trial (i.e., the presentation of another fixation cross). All participants responded using a “yes” or “no” key with their right or left index finger, respectively.

Behavioral Analyses

Trials in which RTs were less than 400 msec or two or more standard deviations above or below a participant’s mean for a given block (i.e., a separate study or test phase) were excluded. Given the variability in size judgments across participants, due in part to the subjective nature of the task, accuracy was on the basis of the modal response across participants for a given stimulus. For the RT analyses, trials were further excluded if stimuli were given an incorrect response during previous presentation (i.e., at study or test). Repetition priming was then calculated as the difference in mean RTs between novel and repeated stimuli. All statistical tests had alpha set at .05, and a Greenhouse–Geisser correction was applied to all *F* values with more than one degree of freedom in the numerator. *t* tests were two-tailed, except where stated otherwise.

fMRI Experiment

fMRI Acquisition

Thirty-two T2*-weighted transverse slices (64×64 , 3 mm \times 3 mm pixels, echo time = 30 msec, flip angle = 78°) per volume were taken using EPI on a 3-T TIM Trio system (Siemens, Erlangen, Germany). Slices were 3-mm thick with a 0.75-mm gap, tilted up approximately 30° at the front to minimize eye ghosting, and acquired in descending order. Eight sessions were acquired, equating to the four study–test cycles. Two hundred ninety-eight volumes were acquired during each study phase, 154 were acquired during each test phase, with a repetition time of 2000 msec. The first five volumes of each session were discarded to allow for equilibrium effects. A T1-weighted structural volume was also acquired for each participant with 1 mm \times 1 mm \times 1 mm voxels using MPRAGE and GRAPPA parallel imaging (flip angle = 9° , echo time = 2.00 s, acceleration factor = 2).

fMRI Analyses

Data were analyzed using SPM5 (www.fil.ion.ucl.ac.uk/spm5.html). Preprocessing of image volumes included spatial realignment to correct for movement, followed by slice-timing correction. Each image was then spatially

normalized to Talairach space, using the linear and non-linear normalization parameters estimated from warping each participant's segmented structural image to a T1-weighted average template image from the Montreal Neurological Institute (MNI). These resampled images (voxel size = $3 \times 3 \times 3$ mm) were smoothed spatially by an 8-mm FWHM Gaussian kernel (final smoothness, approximately $11 \times 11 \times 11$ mm).

The statistical analysis was performed in a two-stage approximation to a mixed effects model. In the first stage, neural activity was modeled by a delta function at stimulus onset. The BOLD response was modeled by a convolution of these delta functions by a canonical hemodynamic response function. The resulting time courses were down-sampled at the midpoint of each scan to form regressors in a general linear model.

For each test session, seven regressors were modeled—the six experimental conditions (3×2 ; Format-match \times Congruency) plus an additional regressor for discarded trials (using the behavioral exclusion criteria). To account for (linear) residual artifacts after realignment, the model also included six further regressors representing the movement parameters estimated during realignment. Voxel-wise parameter estimates for these regressors were obtained by restricted maximum-likelihood (ReML) estimation, using a temporal high-pass filter (cutoff at 128 sec) to remove low-frequency drifts, and modeling temporal autocorrelation across scans with an AR(1) process.

Images from four repetition contrasts (within-format congruent–novel congruent; within-format incongruent–novel incongruent; across-format congruent–novel congruent; across-format incongruent–novel incongruent) collapsed across the four test phases, comprised the data for a second-stage model, which treated participants as a random effect. In addition to the 18 participant effects, this model had four condition effects, corresponding to a 2×2 (Format-match \times Congruency) repeated measures ANOVA. Within this model, SPMs were created of the F statistic for the various ANOVA effects of interest, using a single pooled error estimate for all contrasts, whose nonsphericity was estimated using ReML as described in Friston et al. (2002). The SPMs were thresholded for voxels whose statistic exceeded a peak threshold corresponding to $p < .05$ family-wise error-corrected across the whole space using random field theory. Stereotactic coordinates of the maxima within the thresholded SPMs correspond to the MNI template.

EEG Experiment

EEG Acquisition

EEG was recorded in a magnetically shielded room from 70 electrodes placed within an elastic cap (EasyCap GmbH, Herrching-Breitbrunn, Germany) according to the extended 10–10 system, using a nose electrode as the recording reference and also bipolar electrodes to

measure the vertical and horizontal EOG. All data were sampled at 1 kHz with a band-pass filter from 0.03 to 330 Hz. Although simultaneous magneto-encephalographic data were recorded with a VectorView system (Elekta-Neuromag, Helsinki, Finland), these data are not reported here.

ERP Analyses

Analyses were conducted using SPM5 (www.fil.ion.ucl.ac.uk/spm) as well as using custom-made scripts within MATLAB (The Mathworks, Inc., Natick, MA). The continuous EEG data from each test session were down-sampled to 100 Hz and band-pass filtered between 1 and 40 Hz in both forward and backward directions using a fifth-order Butterworth digital filter. These data were epoched in two ways: (1) from -100 to 800 msec relative to stimulus onset (and baseline-corrected from -100 to 0 msec) and (2) from -300 to 200 msec relative to response onset (and baseline-corrected from -300 to -200 msec). Epochs in which the signal from any channel, including EOG, exceeded $150 \mu\text{V}$ were removed (median number of trials = 8, range = $0-84$). Channels were removed if the proportion of rejected trials within a channel exceeded 20% of the total number of trials (median number of channels removed = 1, range = $0-3$). The data were then averaged across trials within each condition and rereferenced to the average across the left and right mastoid for comparison with previous EEG studies of visual object repetition effects (e.g., Race, Badre, & Wagner, 2010).

Space \times Time SPM Analyses

Given we had few a priori predictions regarding when (within an epoch) and where (over sensors) repetition effects would be present, particularly for the response-locked analysis, we adopted a mass univariate approach in which F tests were performed at every point in a 3-D image of channel space and time (Henson, Mouchlianitis, Matthews, & Kouider, 2008). The 2-D channel space was created by a spherical projection of the standardized Easycap channel locations onto a plane, followed by a linear interpolation to a 32×32 pixel grid. The time dimension consisted of the 91 (stimulus-locked analysis) or 51 (response-locked analysis) 10 msec samples in each epoch. As with the fMRI analysis, each contrast was performed within a general linear model using a pooled error over the four repetition contrasts, with nonsphericity across conditions estimated using ReML and peaks in the resulting SPMs corrected for multiple comparisons across the whole scalp-time space using random field theory.

General Analysis Approach

We adopted the same analysis approach for both the fMRI and EEG experiments. Searching across the whole-brain (fMRI) or the entire Scalp \times Time volume (EEG), we

report any voxel that survived correction for (1) the main effect (F test) of format-match, (2) the main effect of congruency, or (3) the Format-match \times Congruency interaction. Note that the contrast images in the 2×2 ANOVAs for both fMRI and EEG are repetition contrasts from the first-level analysis. As such, the main effects will reveal voxels that show a significant modulation of the repetition effect by either format-match or congruency.

RESULTS

Behavioral Results

A mean of 6% ($SD = 2\%$) of trials with outlying RTs were removed before accuracy analyses. A further 9% ($SD = 5\%$) of trials were removed because of errors at test, whereas a further 17% ($SD = 8\%$) of test trials were removed from analysis because of errors at study (these error rates are reported in more detail in Horner & Henson, 2011). This resulted in an average of 19 trials removed per condition. Here, we focus on the RT data for the remaining “correct” trials to relate behavioral repetition effects to the fMRI and EEG repetition effects (which were conditional on correct trials).

Mean RTs for novel stimuli in the fMRI study were 752 msec ($SD = 100$ msec) and 810 msec ($SD = 117$ msec) for the congruent and incongruent conditions, respectively, as would be expected given the incongruent stimuli were closer in size to the referent than congruent stimuli. RT priming from the fMRI experiment is shown in Figure 2A. A 2×2 ANOVA on priming (novel–repeated RTs) revealed main effects of Format-match, $F(1, 17) = 40.60, p < .001$, with greater positive priming in the within-format than across-format condition, and of Congruency, $F(1, 17) = 19.31, p < .001$, with greater positive priming in the congruent than incongruent condition. Any interaction between these two factors failed to reach significance, $F(1,$

17) < 1 . The Congruency effect was present in both the within-format, $t(17) = 4.84, p < .001$, and across-format, $t(17) = 3.41, p < .01$, conditions. Interestingly, a significant negative priming effect was seen in the across-format incongruent condition (error bars on Figure 2A are 95% confidence intervals).

Mean RTs for novel stimuli in the EEG study were 749 msec ($SD = 81$ msec) and 802 msec ($SD = 101$ msec) for the congruent and incongruent conditions, respectively. RT priming from the EEG experiment is shown in Figure 2B. The 2×2 ANOVA revealed main effects of Format-match, $F(1, 17) = 53.95, p < .001$, and Congruency, $F(1, 17) = 22.32, p < .001$. As with the fMRI study, greater priming for congruent than incongruent trials was present in both the within-format, $t(17) = 5.87, p < .001$, and the across-format, $t(17) = 2.65, p < .05$, conditions, and negative priming was seen in the incongruent across-format condition (see error bars in Figure 2B). Unlike the fMRI experiment, however, the Format-match \times Congruency interaction was significant, $F(1, 17) = 10.21, p < .01$, with a greater congruency effect in the within-format (79 msec) than across-format (38 msec) condition (see Horner & Henson, 2011, for full analysis across experiments).

In summary, the finding of a significant congruency effect in the across-format condition suggests that stimuli in S-R bindings are coded at an abstract level, although the additional finding that this Congruency effect was greater still in the within-format condition, at least in the EEG experiment, suggests that S-R bindings also include a more specific representation of stimuli (see Horner & Henson, 2011, for further discussion). The greater overall priming in the within-format than across-format condition (collapsed across congruency) also suggests an additional perceptual CP contribution to priming, occurring only when a stimulus is repeated in the same visual format between study and test. Most important for present purposes, whereas positive RT priming was found in congruent conditions, demonstrating

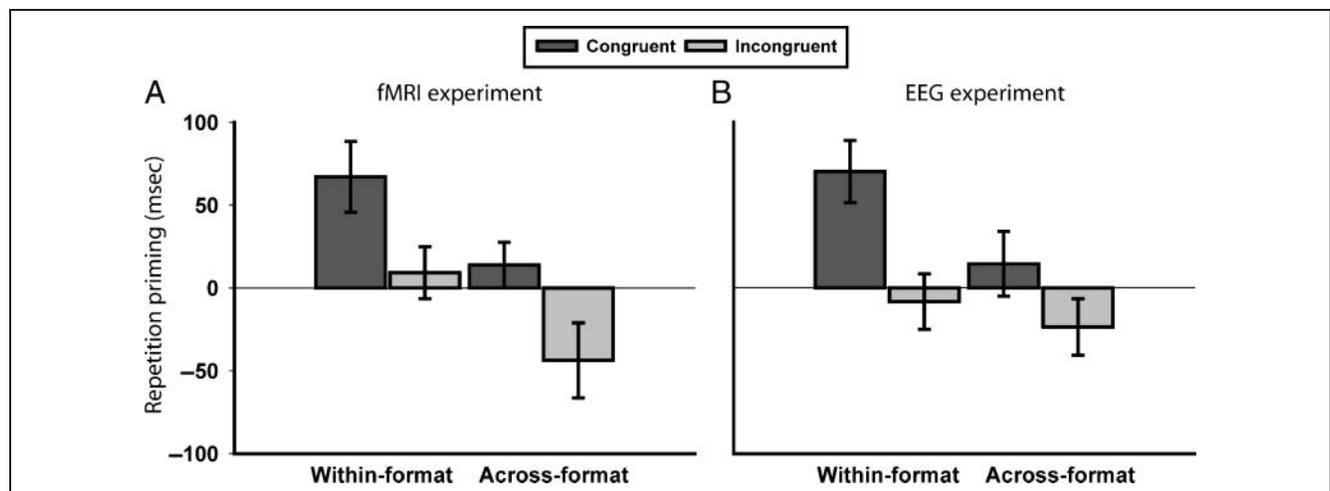


Figure 2. Mean priming effect (novel–repeated) in the fMRI (A) and the EEG (B) experiment across format-match and congruency. Error bars represent 95% confidence intervals (two-tailed).

that S-R bindings can facilitate RTs, significant negative priming was found in the across-format incongruent condition, suggesting that S-R bindings can also interfere with response selection when the responses retrieved from such bindings are incongruent with that required by the changed referent (e.g., with responses generated by a CP route). The lack of such negative priming in the within-format incongruent condition can be explained by the interfering effects of S-R retrieval being cancelled by the facilitatory effects of perceptual CP facilitation. We now turn to the neural correlates of these repetition effects.

fMRI Results

Analogous to the above 2×2 behavioral ANOVA, we focused on three F tests—the main effects of Format-match and of Congruency and their interaction—performed on BOLD repetition effects in every voxel. We report all maxima that survived a family-wise error correction of $p < .05$. The results for the main effect of format-match are shown in Table 1 and Figure 3 and included bilateral clusters in ventral occipito-temporal regions, peaking in the right and left fusiform gyrus. The main effect of Congruency included maxima in the right inferior frontal gyrus, pars triangularis, as well as further clusters in the right middle frontal gyrus and insula. The Format-match \times Congruency interaction failed to reveal any significant maxima.

Given our a priori interest in repetition effects in the fusiform gyrus and inferior frontal gyrus (see Introduction), we present the data from these ROIs in Figure 3. Data for each ROI were taken from the peak voxel in each cluster. As can be seen in Figure 3C, the right fusiform region showed robust RS in the within-format conditions, but no reliable repetition effects in the across-format conditions. Moreover, the repetition effects seemed largely unaffected by congruency. This contrasts with the right inferior frontal ROI shown in Figure 3D, where the effect of Congruency seemed largely unaffected by Format-match. Furthermore, this region showed RS in the congruent conditions, but RE in the incongruent conditions. Although the above contrasts failed to reveal any left frontal regions that survived correction, a similar pattern of RS and RE across congruency was seen in a homologous left inferior frontal region.

Thus, the two ROIs showed selective effects of either format-match or congruency, the summation of which might explain the two main effects on behavioral priming in the same experiment. Most importantly, the inferior frontal ROI showed clear evidence of a switch from RS to RE, consistent with a switch in the effects of S-R retrieval from facilitation to interference.

EEG Results

Stimulus-locked ERPs

As with the fMRI analysis, we first searched for a main effect of Format-match in the stimulus-locked ERP analysis

(Table 1). This revealed a cluster over parietal sensors between 400 and 500 msec, peaking at electrode PO3 (see Figure 4A and Table 1), as well as a smaller cluster over right frontal electrodes between 450 and 500 msec peaking at electrode FT10. The main effect of Congruency revealed a significant cluster over left temporal electrodes between 550 and 600 msec peaking at electrode T9 (although this is more difficult to interpret, because it encroaches on the mean RT for the within-format repeated trials, so could be related more to differences in motor preparation). Finally, the Format-match \times Congruency interaction failed to reveal any significant voxels.

Figure 5 shows the repetition effects for the PO3 electrode, where the main effect of format-match was maximal. In the within-format condition, repeated trials were more positive-going than novel trials during the rising-flank of a P600-like component from approximately 400 to 600 msec (Figure 5C). No such effect was significant in the across-format condition (Figure 5D), such that the overall pattern of mean deflection over the 400–500 msec window (Figure 5B) resembled the fusiform repetition effects in the fMRI data. Although there was no evidence of a modulation of these ERP repetition effects by congruency (i.e., no format-match by congruency interaction that survived correction), it should be noted that the repetition-related divergence, in the PO3 ERP at least, did appear larger and more prolonged in the within-format congruent condition than the within-format incongruent condition.

Response-locked ERPs

For the response-locked analyses, no maxima survived correction for the main effects of format-match or of congruency. However, the Format-match \times Congruency interaction revealed a significant cluster over right frontal electrodes from 200 to 100 msec before response onset, which peaked at electrodes AF8 and F4 (Figure 4B and Table 1). The ERPs for AF8 are shown in Figure 6, where the repetition effects were again restricted to the within-format conditions but showed opposite polarities for the congruent and incongruent conditions. Thus, the right frontal response-locked effect was sensitive to response congruency, like the inferior frontal ROI in the fMRI data, but only in the within-format condition. This interaction resembled that found in the behavioral priming of the EEG experiment—with a greater congruency effect in the within- than across-format conditions—and when combined with the main effect of format-match in the parietal stimulus-locked data, the results would resemble the complete pattern of behavioral priming (cf. Figures 5B and 6B with Figure 2B). The EEG correlates of the residual effect of Congruency on behavioral priming in the across-format condition remain unclear. Most importantly, like with the fMRI frontal ROI, the frontal response-locked ERP results provide evidence for a reliable repetition effect in the incongruent condition (at least when within-format) that was of opposite sign to that in the congruent condition,

Table 1. Clusters and Their Peaks Showing a Main Effect of Format-match, Congruency, or a Format-match \times Congruency Interaction ($p < .05$ Family-wise Error Whole-brain Corrected)

<i>Region/Topography</i>	<i>Voxels</i>	<i>MNI Coordinates</i>			<i>Z Score</i>
		<i>x</i>	<i>y</i>	<i>z</i>	
<i>fMRI</i>					
Format-match					
Right fusiform gyrus	366	+39	-54	-15	6.87
Left fusiform gyrus	103	-45	-60	-9	5.62
Left inferior temporal gyrus	37	-36	-78	-9	5.72
Congruency					
Right insula	32	+27	+24	0	5.79
Anterior cingulate cortex	3	-9	+18	+42	4.80
Right middle frontal gyrus	1	+39	+54	+15	4.70
Right inferior frontal gyrus	1	+39	+33	+15	4.59
Right inferior frontal gyrus	1	+42	+30	+12	4.60
Format-match \times Congruency					
No voxels survived correction					
<hr/>					
		<i>SPM Coordinates</i>			
		<i>x</i>	<i>y</i>	<i>Time</i>	
<i>EEG</i>					
Stimulus-locked analyses					
Format-match					
Left parietal	54	-18	-24	+460	4.81
Right frontal	3	+48	+12	+490	4.61
Congruency					
Left temporal	24	-36	-12	+540	4.86
Format-match \times Congruency					
No voxels survived correction					
Response-locked analyses					
Format-match					
No voxels survived correction					
Congruency					
No voxels survived correction					
Format-match \times Congruency					
Right frontal	12	+24	+6	-150	4.44
Right frontal	22	+30	+18	-150	4.28

Time in EEG stimulus-locked analyses is relative to stimulus onset and in response-locked analyses is relative to response onset.

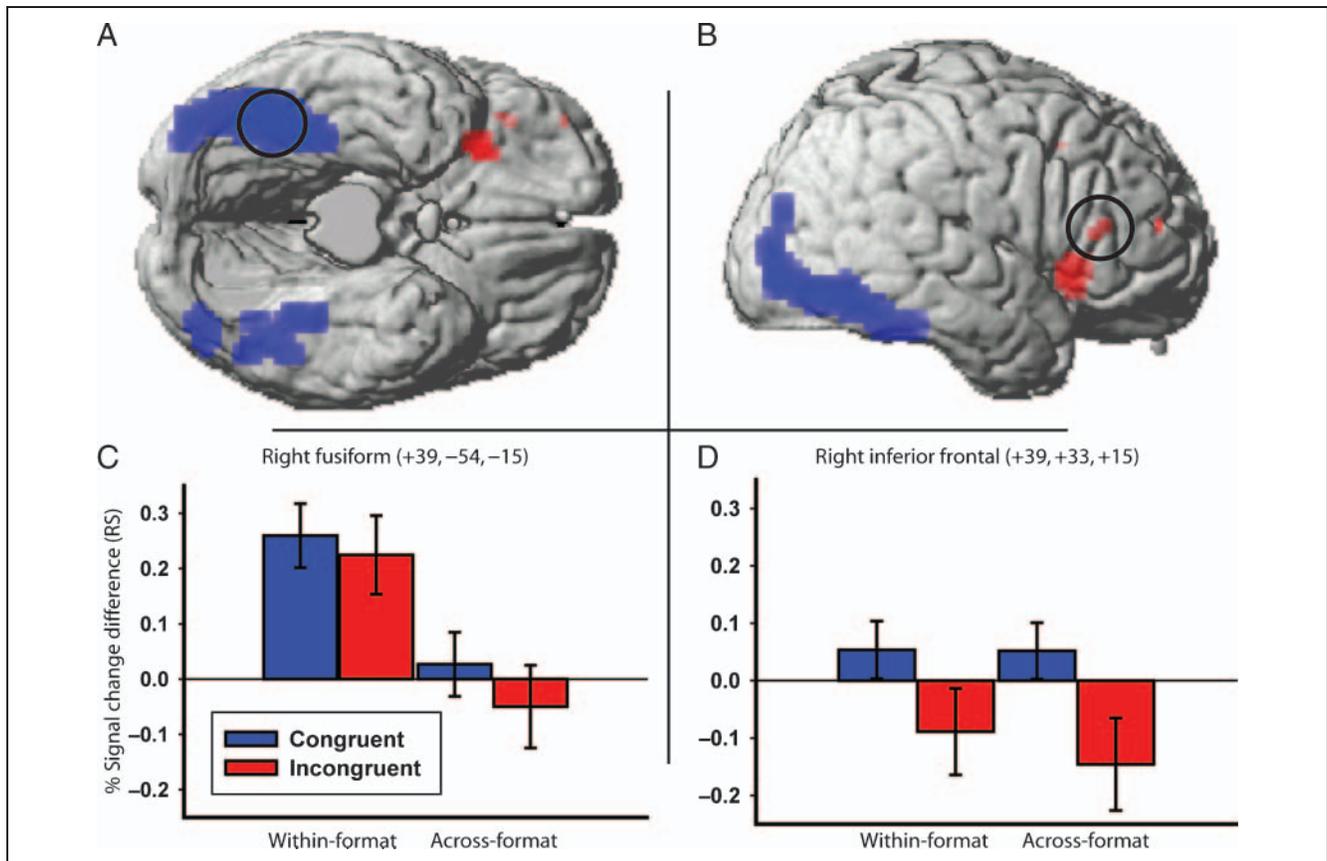


Figure 3. (A, B) The main effect of Format-match (blue) and the main effect of Congruency (red), F test, $p < .05$ family-wise error corrected: (A) view of ventral surface of temporal and frontal lobes highlighting the right fusiform ROI and (B) view of lateral surface of right hemisphere highlighting the right inferior frontal ROI. (C) RS effect (novel–repeated) in right fusiform ROI across format-match and congruency. (D) RS effect in right inferior frontal ROI. Error bars represent 95% confidence intervals (two-tailed). Note that the blue and red colors on the rendered brain (A, B) do not represent RS and RE, but the two main effects of Format-match and Congruency, respectively.

consistent again with the difference between interference and facilitation.

EOG Analyses

Analyses were also conducted on the vertical and horizontal EOG channels to check whether eye movements were the cause of any of the above ERP effects. The same two-way ANOVAs were conducted for the VEOG and HEOG in each of the above two time windows. For the stimulus-locked analysis from 400 to 500 msec, a significant Format-match \times Congruency interaction was present for the VEOG, $F(1, 17) = 4.93, p < .05$. Given this interaction was not seen in the parietal 400–500 msec effect, this interaction is unlikely to have contributed to our results. The VEOG also showed a Format-match \times Congruency interaction between 200 and 100 msec before response onset, $F(1, 17) = 7.59, p < .05$. This interaction, however, would not seem able to explain the full frontal response-locked effect, given it did not show a repetition effect in the within-format incongruent condition (as was seen in AF8). No further main effects or interactions were seen in either VEOG or HEOG in either time window, $F_s < 1.72, p_s >$

.21. Thus, eye movement artifacts would not seem able to explain the full pattern of data seen in the above ERP effects.

DISCUSSION

This study found both fMRI and EEG evidence for a dissociation between S-R and CP contributions to repetition-related neural changes. In the fMRI study, a repetition effect in the right inferior frontal gyrus was sensitive to response reversal, whereas a repetition effect in the right fusiform gyrus was insensitive to response reversals. In the EEG data, a repetition-related ERP effect from 200 to 100 msec before response onset over right frontal electrodes was sensitive to response reversals, whereas a repetition effect between 400 and 500 msec poststimulus onset over parietal electrodes was insensitive to response reversals. Thus, the present data support recent research, suggesting S-R and CP contributions to repetition-related changes in neural activity can be spatially (Race et al., 2009; Horner & Henson, 2008) and temporally (Race et al., 2010) dissociated.

Extending such research, we have presented several novel results. First, in the fMRI and behavioral data, we

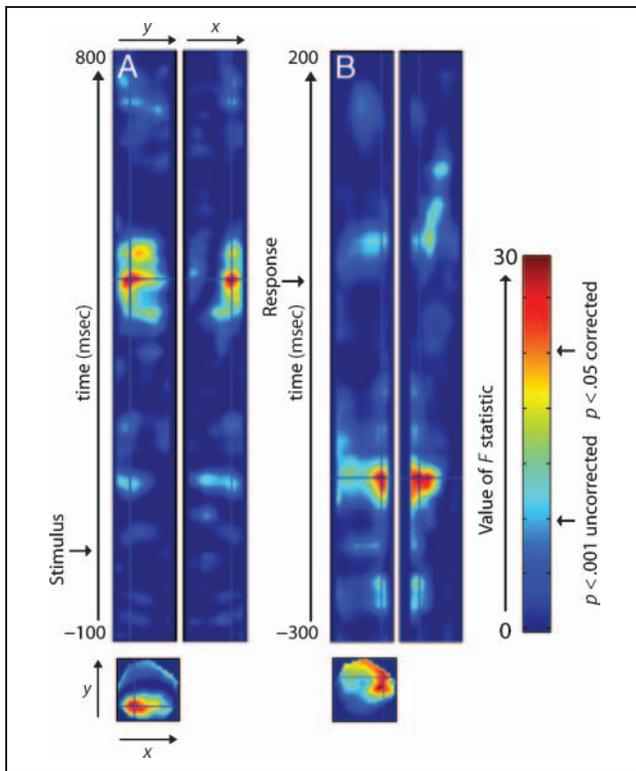


Figure 4. Unthresholded space-time SPMs for the F tests of the main effect of format-match on repetition in the stimulus-locked analysis with crosshair located on the parietal maximum at 480 msec poststimulus (A) and the Format-match \times Congruency interaction in the response-locked analysis with crosshair located on the right frontal maximum at 150 msec before response onset (B). The three images in each panel represent orthogonal planes ($y-t$, $x-t$, $x-y$) through the 3-D image at the location of the cross hair. Color maps show F values with approximate thresholds for $p < .001$ uncorrected and $p < .05$ corrected.

saw S-R effects when switching from a word stimulus at study to a picture stimulus at test. Thus, the present data suggest that stimuli within S-R bindings can be coded at a representational level that abstracts away from the specific visual form of the initial stimulus. Second, we saw evidence for S-R interference effects in the fMRI and EEG data. In the fMRI, response reversals resulted in increased activation for repeated versus novel stimuli (i.e., RE) in the right inferior pFC. In the EEG, a repetition-related ERP effect was seen 200–100 msec before response onset over right frontal electrodes that was positive going in the congruent condition and negative going in the incongruent condition. Thus, in both the fMRI and EEG data, we saw a reversal of the repetition effect across congruency. These are the first data to provide evidence for a reversal in the direction of a repetition effect within the same cortical region (fMRI) and the same time point (EEG) and suggest that the retrieval of an incongruent S-R binding at test results in interference, most plausibly to response selection processes in pFC that occur just before behavioral response onset. Such interference effects may slow RTs (i.e., decreasing repetition priming), even pro-

ducing negative priming when there is minimal CP contribution (as in our across-format condition).

How Does S-R Retrieval Result in Neural and Behavioral Changes?

In the Introduction, we outlined how previous research had failed to provide a compelling account of how the retrieval of S-R bindings affects neural activity and behavior. One suggestion has been that retrieval of S-R bindings “race” independently of (i.e., in parallel with) a CP route (Logan, 1990), such that when retrieval of an S-R binding “wins,” there is an effective “by-passing,” or curtailment, of activity in regions supporting the CP route (Dobbins et al., 2004). But what happens when a retrieved S-R binding is incongruent with the correct response required by the task?

One possibility is that a change in task (or change of referent in the present paradigm) means that S-R bindings are effectively ignored, and the system reverts back to the CP route. Assuming that CPs can be facilitated by stimulus repetition (cf. Logan, 1990), this would predict equivalent repetition effects for incongruent and congruent responses (i.e., positive priming and RS). The current effects of congruency clearly do not support such a conception. A related possibility is that only incongruent S-R bindings are ignored, such that congruent S-R bindings could still increase priming, but this raises the question of how the brain knows which S-R bindings to ignore (if the CP route has not yet completed). This issue is particularly problematic in the present experiment, where response repeat and response switch trials were randomly intermixed during the test phase. Another possibility is that S-R bindings are always retrieved and utilized, regardless of whether the retrieved response is correct or incorrect. This would result in repetition effects in the congruent and incongruent condition in the same direction (i.e., positive priming and RS), with a possibly reduced effect for incongruent responses, a pattern not consistent with the current results.

A more likely account is that the S-R and CP routes interact, rather than racing independently (Horner & Henson, 2009). Our neuroimaging data cannot tell us the precise nature of such interaction (other than it is response-locked, from our ERP data). For example, the increased fMRI response we saw in right inferior pFC for incongruent trials could reflect competition, interference, or even inhibition of incongruent responses (e.g., Aron, 2007). Nonetheless, we speculate that the interaction between S-R and CP routes is mediated by opponent-coding mechanisms (e.g., Kusunoki, Sigala, Nili, Gaffan, & Duncan, 2010; Machens, Romo, & Brody, 2005), whereby competitive groups of cells within pFC code opposing behavioral responses (e.g., bigger vs. smaller). Within this framework, we assume that a response decision is reached by a process of evidence accumulation, arriving from the CP and S-R routes, until some criterion is reached (as in diffusion models of decision processes; Ratcliff, 1978). In situations where the evidence from both routes is congruent, criterion will be reached more rapidly,

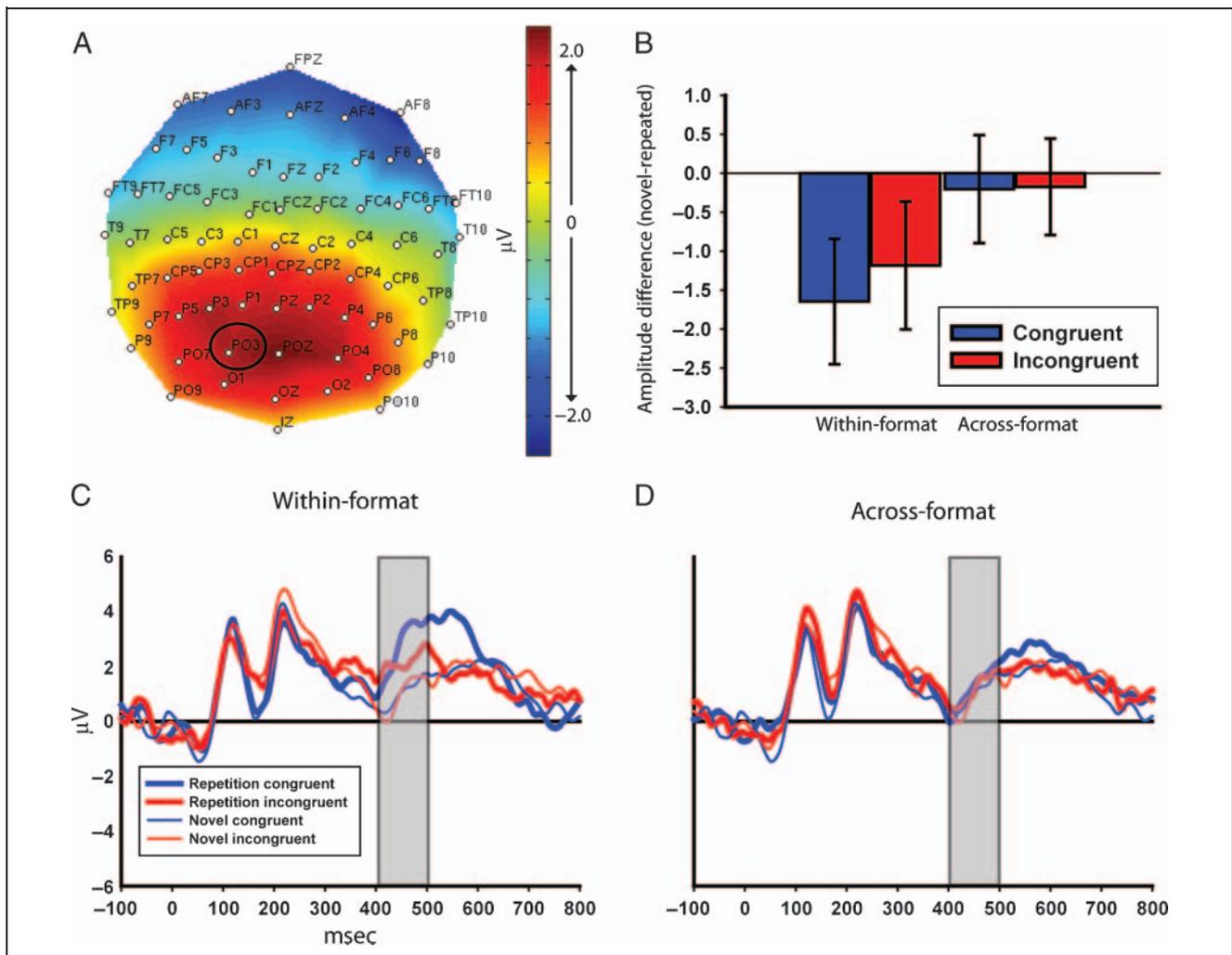


Figure 5. Stimulus-locked repetition effect. (A) Scalp topography of the main effect of Format-match on repetition effects from 400 to 500 msec, with peak electrode (PO3) circled. (B) Mean amplitude difference between repeated and novel trials from 400 to 500 msec across format-match and congruency for PO3. Error bars in B represent 95% confidence intervals (two-tailed). ERPs for within-format (C) and across-format (D) repeated and novel trials separately for PO3 (with 400–500 msec time window shaded in gray).

resulting in speeded RTs and less neural activity (akin to the “facilitation” model of RS; see Grill-Spector et al., 2006). Importantly, in situations where the evidence from the two routes is incongruent, opponent coding mechanisms will result in greater competition between response codes, that is, greater time to resolve the conflicting evidence, resulting in slower RTs and increased neural activity. In the fMRI data, we saw precisely this shift from RS to RE in a right inferior prefrontal region for congruent relative to incongruent conditions (in both within- and across-format conditions). We also saw this shift in the ERP data (though in the polarity of the potential difference, which cannot be related directly to increases or decreases in neural activity) over right frontal electrodes, though only in the within-format condition. That this effect of congruency was locked to the response onset is consistent with the ERP effect (and the fMRI prefrontal effect) relating to such decision processes.

The location of the fMRI congruency effects in posterior inferior pFC is consistent with more general theories of

hierarchical organization of cognitive control in pFC (Badre & D’Esposito, 2007, 2009; Fuster, 2001). More specifically, the fact that our referent change entailed a switch in all levels of response—the motor action, the yes/no decision, and the semantic classification (Horner & Henson, 2009)—is consistent with the results of Race et al. (2009), who showed that RS in posterior pFC regions was sensitive to switches in actions/decisions, whereas RS in a more anterior pFC regions was sensitive only to switches in classifications (and tasks).

The reason why the shift in ERP polarity across congruent and incongruent conditions was only present in the within-format condition, but not across-format condition, remains unclear. It is unlike the fMRI data in the right prefrontal region, which showed a shift from RS to RE in both within- and across-format conditions. Nonetheless, the ERP pattern resembles the behavioral priming data for the EEG study where we saw a decreased congruency effect in the across-format than within-format condition.

This was in contrast to the fMRI study where the behavioral congruency effects were equivalent in the within- and across-format conditions. This possibly suggests that there was a strategic difference in the two groups relating to how they used S-R bindings in the within- versus across-format conditions. For example, the EEG group may have placed a greater emphasis on specific rather than abstract stimulus representations relative to the fMRI group (see below).

S-R Bindings Code Abstract Stimulus Representations

In the fMRI data, congruency effects (in right pFC) were seen both when a picture of an object was primed with the same picture and when a picture of an object was primed by the object's written name. This latter condition was designed to assess whether stimuli within S-R bindings are coded at a representational level that abstracts

away from the specific visual characteristics of the prime. These fMRI data therefore fit with recent behavioral evidence (Horner & Henson, 2011), suggesting that stimuli can be coded in S-R bindings at a relatively abstract level (e.g., the object identity). However, as noted above, the congruency effects in the EEG data were only reliable when a picture of an object was primed with the same picture, suggesting more specific representations of stimuli within S-R bindings (e.g., a visual image). One possibility, consistent with the behavioral evidence of Horner and Henson (2011), is that S-R bindings can simultaneously code multiple representations of stimuli at various levels of abstraction in analogous fashion to how they appear able to simultaneously code multiple representations of responses (Horner & Henson, 2009).

Nonetheless, the present divergence between fMRI and EEG data (and between the precise pattern of behavioral priming across fMRI and EEG groups) raises another

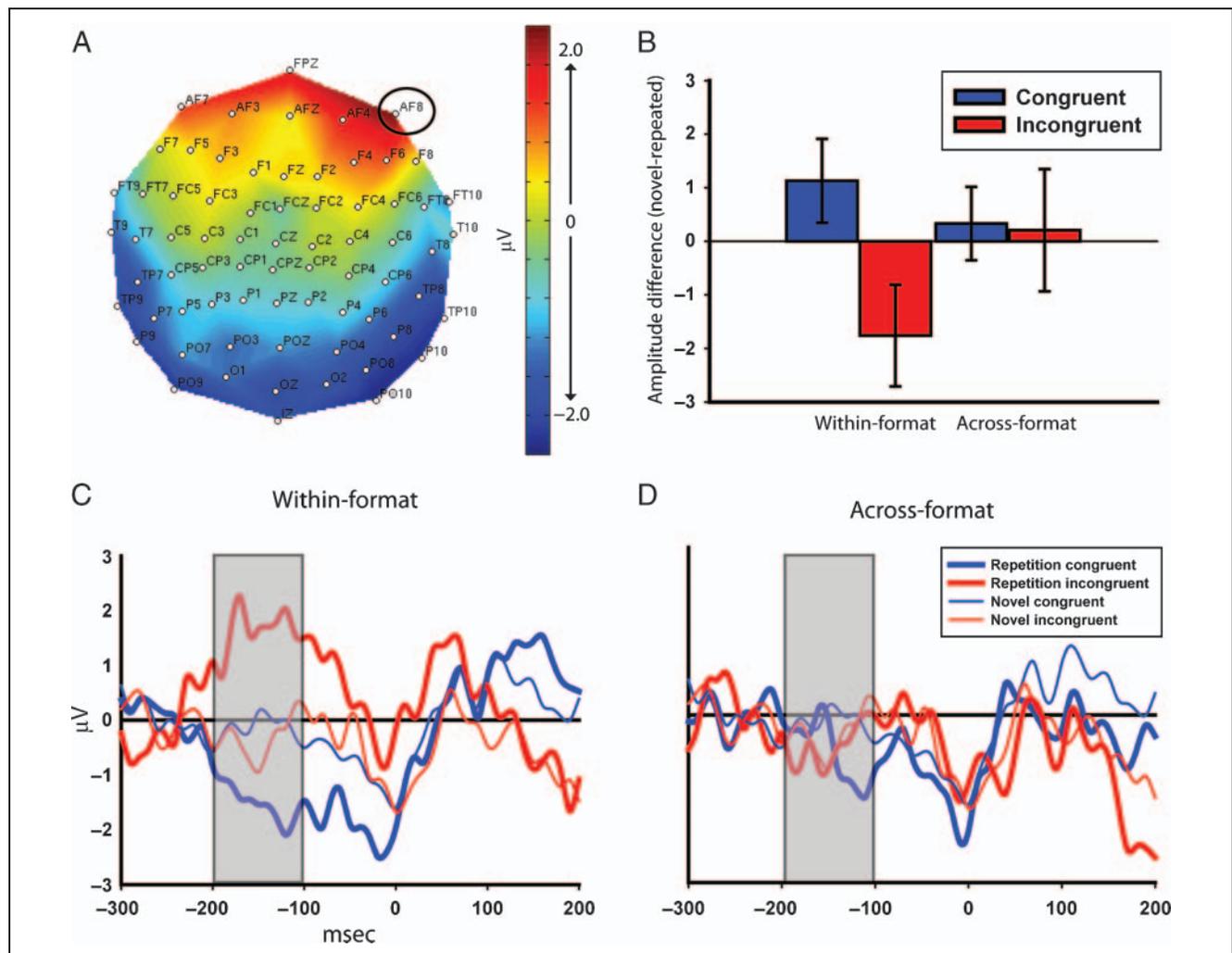


Figure 6. Response-locked repetition effect. (A) Scalp topography of the Format-match \times Congruency interaction from 200 to 100 msec before response onset with peak channel (AF8) circled. (B) Amplitude difference between repeated and novel trials across format-match and congruency for peak channel. ERPs for within-format (C) and across-format (D) repeated versus novel trials for peak channel with 200–100 msec time window shaded in gray. Error bars in B represent 95% confidence intervals (two-tailed).

possibility: that a single level of stimulus representation is coded in S-R bindings, but that this can differ across individuals, perhaps as a function of the experimental context or instructions. Thus, the majority of participants in the EEG experiment may have only encoded a relatively superficial representation of stimuli in S-R bindings (e.g., a visual image), which would explain the lack of ERP effect in the across-format condition (though note the across-format congruency effect was still present in the behavioral data). In the fMRI experiment, on the other hand, participants may have been more likely to encode solely at an abstract level of stimulus representation. This would explain the finding of equivalent congruency effects in the within- and across-format conditions for both the behavioral and BOLD results. Of course, the nature of the stimulus representation in S-R bindings might also vary across objects. These only remain hypotheses at present and would clearly benefit from further experimental investigation.

Finally, although not providing definitive evidence in the current study, it is plausible that the cortical regions seen in the fMRI study are the generators of the EEG effects. In particular, there was a close correspondence between the right inferior frontal region seen in the fMRI study and the right frontal effect seen in the EEG study. Source localization analyses would be more informative in this regard; however, we have not conducted these analyses in this study because of the poor spatial resolution of EEG. Further work utilizing the improved spatial resolution of simultaneous EEG and magnetoencephalography recordings would be better suited to resolving this outstanding issue.

Conclusion

Using the spatial and temporal resolutions of fMRI and EEG respectively, we presented clear evidence for a spatio-temporal dissociation between CP and S-R contributions to repetition-related neural changes. Importantly, S-R effects in an inferior prefrontal region were seen despite switching from a word to a picture stimulus between repetitions, suggesting stimuli within S-R bindings can be coded at abstract levels of representation. Moreover, when a response was reversed between repetitions, we saw evidence for interference effects in the behavioral data, the fMRI data in the right prefrontal ROI, and the response-locked ERP data over right frontal channels. On the basis of these results, we propose that the retrieval of S-R bindings at multiple levels of stimulus and response acts to facilitate or interfere with response selection processes dependent on the congruency of response between initial and repeated presentations.

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