The Neural Underpinnings of Event-file Management: Evidence for Stimulus-induced Activation of and Competition among Stimulus–Response Bindings

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Abstract

■ The present fMRI study tested the assumption that a single pairing of a stimulus and a logically unrelated response is sufficient for binding the corresponding stimulus and response codes into an event representation (event file) that is automatically retrieved upon processing of at least one of its components. In particular, we investigated whether repeating a face or a house stimulus and/or a left or a right manual response induces the automatic retrieval of the response or stimulus that it previously accompanied. ROI analyses of fusiform face area, parahippocampal place area, and right and left motor cortex revealed that repeating one component of a previously encountered stimulus-response episode leads to the suppression of cortical areas processing the other components, suggesting that these components were indeed automatically retrieved and conflicted with ongoing processing. The particular pattern obtained is consistent with predictions from diffusion models of decision making, which suggest a crucial role of local competition in response selection. ■

INTRODUCTION

The primate brain represents external events in a distributed fashion. This is true for perceived events, as evident from the parallel coding of the shape, color, orientation, and other visual features in dedicated neural maps in the visual cortex (e.g., DeYoe & Van Essen, 1988). And it is true for intentionally produced events, as evident from the distributed representation of action characteristics, such as the direction, distance, and force of intentional actions, in dedicated frontal areas (see Hommel & Elsner, 2009). The observation that cortical representations are distributed raises the question how the brain organizes and integrates the different sorts of neural activity representing a given event—an issue that has become to be known as the binding problem (Treisman, 1996).

Considering the binding problem has sparked interest in fast-acting, event-to-event integration phenomena and mechanisms. A particularly influential phenomenon has been demonstrated by Kahneman, Treisman, and Gibbs (1992) in visual perception. Human subjects were presented with an actually task-irrelevant preview display (S1) and a subsequent visual target stimulus (S2), such as a letter in a randomly chosen location. Responses to the target were facilitated when the eventual target letter already appeared

as part of the preview display, but performance was particularly good if the location of this letter was repeated as well. This suggests that letter shape was integrated with the corresponding location code. Repeating the letter may have reactivated this shape-location binding, which might have sped up feature processing or binding processes. Other studies have confirmed the demonstration of particularly good performance with the repetition of complete feature conjunctions (for a review, see Hommel, 2004). However, complete feature repetitions (e.g., same letter shape and same location of the letter) commonly do not yield better performance than "complete" alternations (e.g., different letter shape and different location of the letter; Hommel, 1998), suggesting that it is partial repetitions (e.g., different letter shape and same location of the letter or same letter shape and different location of the letter) that are the culprit. Repeating one feature may tend to reactivate all feature bindings that include this feature, which create feature conflict in all cases where some but not all features are repeated (Hommel, 2004; Hommel, Müsseler, Aschersleben, & Prinz, 2001).

A recent fMRI study by Keizer, Nieuwenhuis, et al. (2008) has looked into the neural consequences of feature binding. Subjects were presented with preview displays (S1) and targets (S2) that both consisted of two blended pictures showing a face and a house. Either the face or the house moved in one of two possible directions, and subjects were to respond to the direction of S2 irrespective of which object moved. Of particular interest were the

conditions where S1 showed a moving house and S2 a moving face: If the direction of motion in these two displays was the same (i.e., if the motion feature was repeated), the parahippocampal place area (PPA) was activated more than if the motion differed. Repeating the motion feature thus induced the retrieval of the previous binding that included this motion, which under these circumstances also included a house. In other words, repeating a feature reactivates the neural code of this feature, which spreads activation to the codes it is still bound to.

Although the binding of visual features has attracted by far the most attention and research activities, integration phenomena have also been obtained for nonvisual features. For instance, repeating auditory features like pitch or loudness have been shown to induce the retrieval of previous auditory (e.g., pitch-loudness), audiovisual, and audiotactile bindings (Zmigrod & Hommel, 2009; Zmigrod, Spapé, & Hommel, 2009). Other studies have provided evidence for the integration of stimulus and response features. For instance, complete repetitions or alternations of visual features and precued responses carried out in their presence have been observed to yield better performance than partial repetitions, that is, stimulus-feature repetitions paired with response alternations or stimulus-feature alternations paired with response repetitions (Hommel, 1998). Along the same lines, repeating stimuli that were just paired with a particular response induce the tendency to repeat the response as well (Hommel, 2007). All these observations suggest that even arbitrary single pairings of stimulus features and responses lead to the spontaneous binding of their corresponding neural codes into what Hommel (1998) called "event files" and that these files are reactivated whenever one or more of their ingredients are reactivated through stimulus and/or response repetitions.

Aim of the Study

The aim of the present study was twofold. First, we wanted to study the neural underpinnings of event files by applying the general logic underlying the fMRI investigation of Keizer, Nieuwenhuis, et al. (2008). As in other studies of stimulus-response binding, we presented subjects with two stimulus-response combinations in a row, S1/R1 and S2/R2. R1 consisted of a left or right keypress and S1 of a picture of a house or a face. The visual stimuli were chosen to activate discriminable cortical areas, namely, the PPA and the fusiform face area (FFA), respectively. R1 was precued in each trial so that S1 and R1 were uncorrelated and logically independent of each other. The precued R1 was to be carried out as soon as any S1 would appear, that is, irrespective of whether S1 was a face or a house. Nevertheless, on the basis of previous findings, we expected that perceiving S1 and executing R1 in close temporal succession would lead to a binding between the neural representations of their features. After subjects had carried out R1, they were presented with S2, another face or house. This second target stimulus required a particular response, a left keypress in response to a house and a right keypress in response to a face. The question was whether performance on R2 would be affected by the stimulus and/or response repetition (or alternation), that is, by whether S1 and S2 or R1 and R2 were the same.

Behaviorally, we expected the often-observed interaction between stimulus and response repetition, with better performance if stimulus and response repeat or alternate as compared with partial repetitions of only the stimulus or only the response (e.g., Keizer, Colzato, & Hommel, 2008; Hommel, 1998). With respect to neuroimaging, the predictions are more complicated to derive than that in the study of Keizer, Nieuwenhuis, et al. (2008) on visual integration. Consider Figure 1, a graphic of our theoretical assumptions, and assume that S2 consists of the picture of a house that requires a left-hand keypress as R2. Figure 1A shows an alternation of stimulus and response. The combination of face and right-hand keypress is assumed to induce a binding between the neural codes representing the face and the keypress, as indicated by the oval. However, given that neither the stimulus nor the response are repeated, the

Figure 1. Schematic drawing of event files (indicated by the oval) in context of (A) complete alternation of stimulus and response, (B) response repetition, and (C) stimulus repetition (dotted oval indicates effects of stimulus and response repetition; L = left-hand response; R = right-hand response).
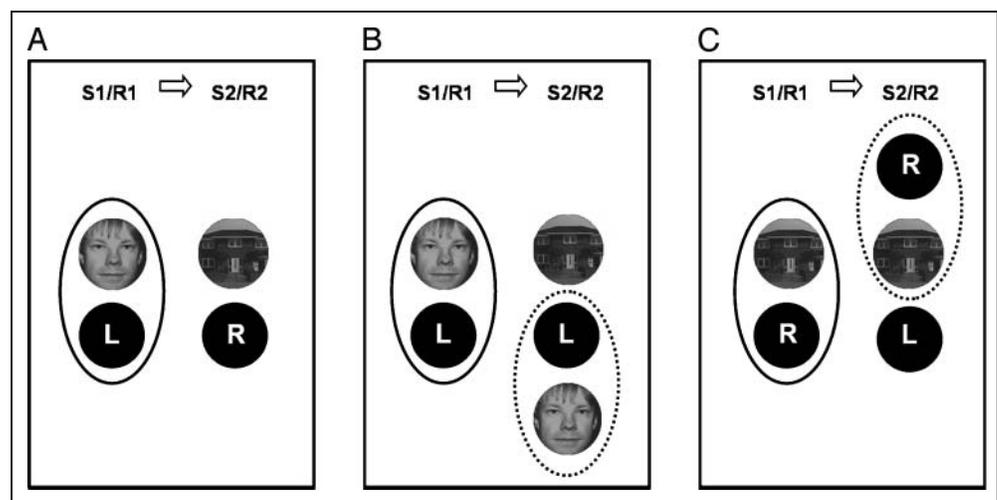
binding is not reactivated through the processing of S2 and R2. Things are different if the response is repeated, as assumed in Figure 1B. Here, the combination of house and left-hand keypress is preceded by the combination of face and left-hand keypress, which again is assumed to induce a corresponding binding. Reactivating the left-hand keypress response in the course of processing S2 and R2 reactivates the just-created binding, which brings into play the thereby reactivated face code. This is likely to induce stimulus uncertainty and code conflict, resulting in performance costs, such as delayed RT and/or more errors.[1] The same holds true when the stimulus is repeated as in Figure 1C. The combination of house and a right-hand response that is followed by a house that affords a left-hand response creates conflict because the repetition of the house stimulus reactivates the associated right-hand response. What this scenario means for the prediction of neuroimaging results depends on another theoretical issue constituting the second aim of our study.

Intentional and automatic activations of stimulus and response codes are likely to affect decision making. Models of human decision making fall into two categories or families (Bogacz, 2007). Models of both families assume that stimulus evidence in favor of members of the current response set is accumulated over time and that the response with the strongest evidence in its favor is being selected according to particular criteria and thresholds. However, models differ with respect to the way they consider criteria and thresholds to affect the decision process. *Race models* assume that the evidence counters involved are independent, as indicated in Figure 2A. Given that the two possible responses in our design are mapped onto faces and houses, we can consider two evidence counters that accumulate face- and house-related (stimulus and/or response) evidence, respectively. Now let us assume that stimuli and responses alternate, as in the scenario shown in Figure 1A. The presentation of S2 (the picture of a house) leads to a continuous increase of the activation of the "house counter" and the neural networks underlying it, until a particular threshold is reached (T1 in our example) and the associated response is executed. Now consider a repetition of the stimulus, as indicated in Figure 1B. If we assume that the activation of responses covaries with their evidence counters, processing the house picture will continuously increase the representation of the left-hand response. This response is still bound to the face (as a consequence of having processed the respective S1/R1 combination) so that activating the response will reactivate all members of the binding including the face code. If decision making requires some minimal lead of the most-activated evidence counter to its strongest competitor, as most models assume, this implies an increase of the effective threshold (as indicated by threshold T2) in Figure 2. More time and evidence is needed to reach that higher threshold, which explains RT costs.[2]

According to this independent-counter or race model, one would expect brain activation profiles that follow the
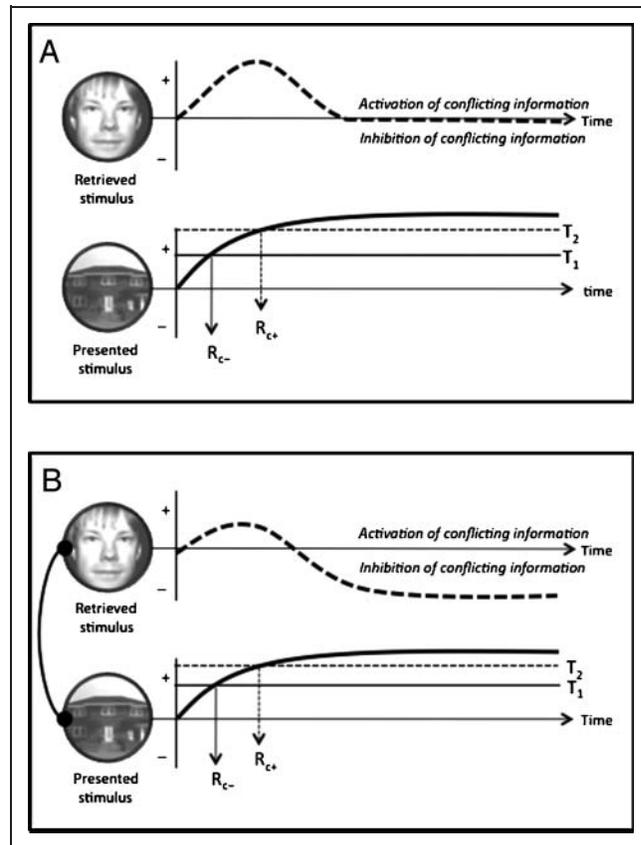
Figure 2. Schematic drawing of the predictions of (A) race models in which information for the face and house counter is accumulated independently and (B) diffusion models in which both counters are linked by means of inhibitory connections. In the example, the house represents the currently presented, relevant stimulus, and the face represents the supposedly retrieved stimulus. Subjects are assumed to respond if the activation of the relevant stimulus counter reaches a certain functional threshold, which depends on the degree to which activation of the relevant stimulus counter exceeds the activation of the counter of the competing, irrelevant stimulus code. That is, the functional response threshold is lower in the absence of conflict (T_1) than that in the presence of conflict (T_2). Accordingly, responses are faster in the absence of conflict (R_{c-}) than that in the presence of conflict (R_{c+}). Note that, according to race models, activation of the irrelevant stimulus counter increases and decreases to baseline whereas, and according to diffusion models, activation of the irrelevant counter first increases and is then suppressed below baseline.

logic of Keizer, Nieuwenhuis, et al. (2008). That is, repeating the response should lead to a higher activation of the brain area that codes for the stimulus that accompanied this response in the previous part of the trial. With respect to our scenarios in Figure 1, we would expect the combination of stimulus alternation and response repetition (Figure 1B) to induce a stronger activation of the FFA as compared with the corresponding "complete" alternation trial (Figure 1A). Along the same lines, combining stimulus alternation (house as S1 and face as S2) with a repetition of the right response should induce a stronger activation of the PPA because repeating the response should reactivate the binding of the right hand and the house picture created upon S1/R1 processing. The same binding logic can

be applied to predicting the effect of stimulus repetition. Assume that S2 and R2 consist of the picture of a house and a left-hand keypress, as before, and further assume that R1 is a right-hand keypress, as in Figure 1A and C. If S1 and S2 are different (as in Figure 1A), there is no code overlap between the combinations of S1 and R1 on the one hand and of S2 and R2 on the other, and thus no code conflict. If the stimulus is repeated (see Figure 1C), however, reactivating the stimulus code will reactivate the just-created binding and thus bring into play the other response—with time-costly response conflict as a result. In terms of activation, stimulus repetition should induce a higher activation of brain areas coding for the previous and now competing response. For our scenario, this would mean that areas related to the right-hand response should be activated more strongly if the stimulus is repeated (as in Figure 1C) than if it alternates (Figure 1A).

However, other decision-making models (characterized as "diffusion models" by Ratcliff & McKoon, 2008; Bogacz, 2007; Bogacz, Brown, Moehlis, Holmes, & Cohen, 2006) assume that evidence counters are not independent but linked by means of inhibitory connections, as indicated in Figure 2B. The idea is that more strongly activated counters do not only have a stronger impact on the eventual response but that they also inhibit possible competitors more strongly, the more so the stronger the competitors are. Not only do diffusion models allow for more dynamic and efficient decision making, as the currently strongest competitor can actively increase the difference in activation with other competitors, they also seem to be more biologically plausible (Bogacz, 2007). Directly linking competing counters may affect the temporal dynamics of the relevant counter (the house counter in our scenario) by allowing for faster increases of activation (which we did not consider in Figure 2B for the sake of convenience). More important for our purposes, however, the interdependency between the counters is likely to dramatically change the situation for competing counters, such as the face counter in our scenario. As the relevant counter collects more information in its favor, it inhibits competitors with increasing force so that their activation diminishes and eventually gives way to a subbaseline state of inhibition (as indicated by the negative activation of the face counter in Figure 2B). If this is what happens in the cases of response repetition (Figure 1B) and stimulus repetition (Figure 1C) we have discussed, the predictions for brain activation patterns would change. As BOLD responses integrate activation across a whole trial, the overall activation for competing irrelevant codes would be expected to turn negative. So, where race models predicted surplus activity that theoretically corresponds to the area under the activation function for the irrelevant face counter in Figure 2A, diffusion models would predict negative activation (or inhibition) that corresponds to the area under the face-counter function sketched in Figure 2B.[3] This means that response repetition should lead to reduced activation (as compared with response alternation) in the area coding for S1, whereas stimulus repetition should lead to reduced activation (as compared with stimulus alternation) in the area coding for R1.

One interesting feature of models of the diffusion "family" (Bogacz, 2007) is that the role that they allow local competition (between alternative and thus competing codes or between retrieved event-file features and task-relevant features as in our case) to play in decision making does not require any further external inhibitory process or system to prevent incorrect responses. This stands in sharp contrast to influential cognitive control models assuming central inhibition and/or conflict modules in lateral and/or medial frontal cortex or anterior cingulate cortex (Botvinick, Cohen, & Carter, 2004; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004; Ridderinkhof, van den Wildenberg, Segalowitz, & Carter, 2004; Botvinick, Braver, Barch, Carter, & Cohen, 2001). To investigate this issue, we also sought for evidence for or against the assumption of any central "inhibitor" that might be involved in resolving code conflict.

To summarize, we were interested to test predictions regarding two theoretical issues. First, we predicted that the spontaneous binding of S1 and R1 would lead to specific BOLD responses during the processing of S2 and R2: Repeating the response (R2 = R1) should induce systematic activation changes in brain areas that are coding for the type of stimulus presented as S1 (FFA or PPA for faces and houses, respectively), and repeating the stimulus (S2 = S1) should induce systematic changes in brain areas coding for R1. Second, we were interested to see whether we could characterize the decision-making mechanism responsible for the handling of stimulus-response bindings (event files) by testing whether stimulus- and response-repetition effects would induce positive or negative changes in brain activation. Positive changes (i.e., increases of activation as compared with nonrepetitions) would be expected from a race model of decision making, whereas negative changes (i.e., reduced activations as compared with nonrepetitions) would be predicted from diffusion models.

METHODS

Participants

We recruited 21 healthy volunteers (17 women and 4 men; age = 19–30 years, mean = 23 years) from whom we obtained written consent before the scanning session. The study was approved by the local ethical committee. All subjects had normal or corrected-to-normal vision and reported to be right-handed. No subject had a history of neurological, major medical, or psychiatric disorder.

Behavioral Task

The experimental task required two responses in each trial. First a 500-msec response cue signaled R1: Centrally presented rows of three left- or right-pointing arrows instructed participants to prepare for a button press with

the left or right hand, respectively (Figure 3). After a blank screen of 2000- to 5000-msec duration (varied randomly in steps of 500 msec), a picture of a face or a house was presented for 1000 msec (S1). This stimulus acted as a go signal for the response (R1) that was prepared according to the cue; the identity of this visual stimulus was instructed to be of no importance whatsoever. After another blank screen of 2000- to 5000-msec duration, another visual stimulus (face or house) was presented on the screen for 1000 msec (S2). To this second target stimulus, participants had to respond with the left hand if it depicted a house and with the right hand if it depicted a face. We used eight grayscale front-view photographs of male (four) and female (four) faces and eight grayscale photographs of houses (Keizer, Colzato, et al., 2008). All images were adjusted to assure the same average luminance. The intertrial interval consisted of a variable oversampling interval between 2000 and 5000 msec to obtain an interpolated temporal resolution of 500 msec. The experiment was divided into three runs between which we stopped and restarted the scanner; each run started and ended with a blank screen of 30 sec. The experiment consisted of 280 trials divided into three blocks of about 20 minutes each.

For the sake of clarity, we will in the following characterize the experimental conditions by means of a four-character code. The first two characters indicate the identity of S1 and R1, whereas the second two characters indicate S2 and R2. The lowercase letters "h" and "f" are used to indicate house and face stimuli, respectively, whereas the uppercase letters "L" and "R" indicate left- and right-hand responses.

According to this coding, condition fLfR, say, would imply a stimulus repetition and a response alternation.

Scanning Procedure

Images were collected with a 3-T Philips Achieva MRI scanner system (Philips Medical Systems, Best, the Netherlands). First, high-resolution anatomical images were acquired using a three-dimensional T1-weighted sequence (voxel size = $0.88 \times 0.88 \times 1.2 \text{ mm}^3$). Whole-brain functional images were collected using a T2*-weighted SENSE parallel EPI sequence sensitive to BOLD contrast (repetition time = 2211 msec, echo time = 30 msec, image matrix = 80×80, field of view = 220 mm, flip angle = 80°, voxel size = $2.75 \times 2.75 \times 2.75 \text{ mm}^3$, 38 axial slices) for the last nine subjects the TR was changed to 2200 msec because of an update of the scanner software.

fMRI Data Preprocessing and Main Analysis

The fMRI data were analyzed using SPM5 software (Wellcome Department of Cognitive Neurology, London, UK). The first four volumes of all EPI series were excluded from the analysis to allow the magnetization to approach a dynamic equilibrium. Data processing started with slice time correction and realignment of the EPI data sets. A mean image for all EPI volumes was created, to which individual volumes were spatially realigned by means of rigid body transformations. The high resolution structural image was coregistered with the mean image of the EPI series.

Figure 3. Schematic drawing of the experimental trial sequence and the contrasts of interest (red squares) for (A) effects of response repetition and (B) effects of stimulus repetition.
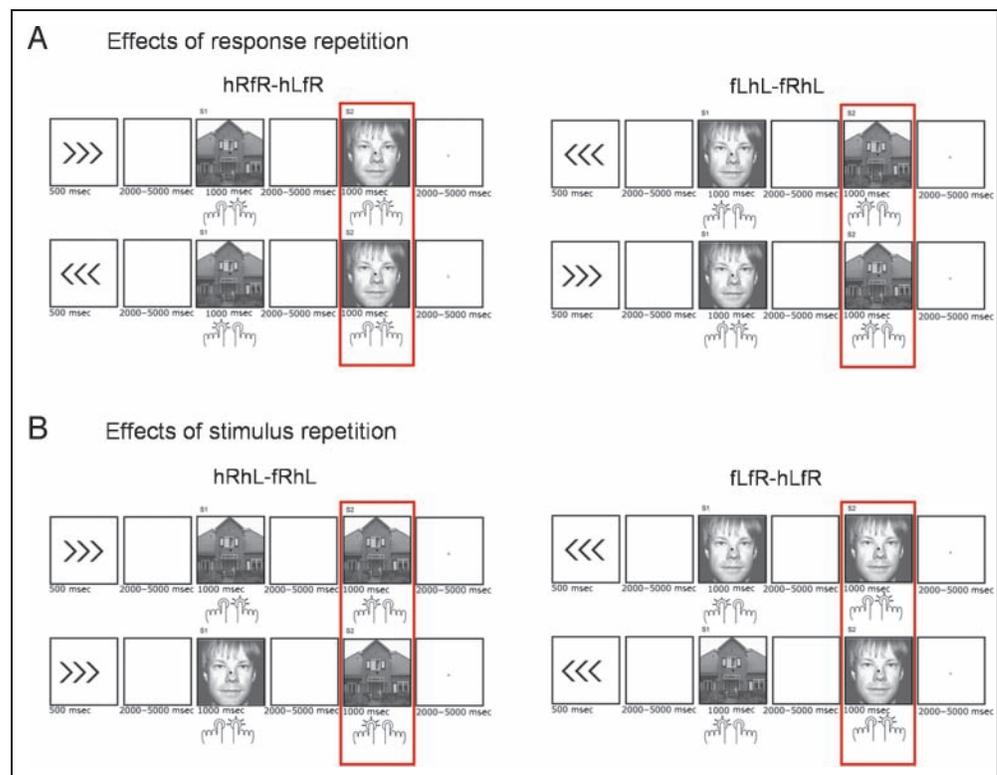
Then the structural image was normalized to the Montreal Neurological Institute template, and the normalization parameters were applied to the EPI images to ensure an anatomically informed normalization. During normalization, the anatomy image volumes were regridded to $1 \times 1 \times 1$ mm^3. A commonly applied spatial filter of 8-mm FWHM was used on EPI scans. Low-frequency drifts in the time domain were removed by modeling the time series for each voxel by a set of discrete cosine functions to which a cutoff of 128 sec was applied. The subject-level statistical analyses were performed using the general linear model. For the analysis, we modeled the onset of the right and left arrow (the two R1 precues) separately, the four conditions with an onset on S1 (fL, fR, hL, and hR), the eight conditions with an onset on S2 (response alternation: fLfR and hRhL; stimulus alternation: hRfR and fLhL; stimulus and response alternation: hLfR and fRhL; and complete repetition: fRfR and hLhL), and the errors on S1 and on S2 separately.

Vectors containing the event onsets were convolved with the canonical hemodynamic response function to form the main regressors in the design matrix (the regression model). Temporal derivatives of the regressors and regressors accounting for variance associated with head motion were also entered into the model. The statistical parameter estimates were computed separately for each voxel for all columns in the design matrix. Contrast images were constructed for each individual to compare the relevant parameter estimates for the regressors containing the canonical hemodynamic response function. Then group-level random effects analysis was performed. The resulting statistical values were thresholded with a level of significance of $p < .05$ (uncorrected) to allow for possible overlap in a conjunction analysis of the contrasts (hRfR–hLfR, fLhL–fRhL, hRhL–fRhL, and fLfR–hLfR).

Percent Signal Change Analysis

For the signal change analysis, we defined ROIs consisting of the peak voxels of each participant and a surrounding sphere with a radius of 6 mm. The statistical values of each subjects contrast were thresholded at $p < .001$. Two ROIs were defined in bilateral FFA resulting from the whole-brain contrast of faces S1 > houses S1 of each participant (Figure 4). The FFA ROIs were selected on the basis of coordinates reported by previous studies (Haxby et al., 1999; Kanwisher, McDermott, & Chun, 1997); the average coordinates for left FFA were $-42\ -53\ -20$ ($SD = 4$) and for right FFA $42\ -55\ -21$ ($SD = 5$). Furthermore, we defined ROIs in bilateral PPA resulting from the whole-brain contrast of the house S1 > face S1 of each subject (Figure 4). The PPA ROIs were also selected on the basis of previous reports (Epstein, Harris, Stanley, & Kanwisher, 1999; Epstein & Kanwisher, 1998); the average coordinates for left PPA were $-25\ -51\ -9$ ($SD = 4$) and for right PPA $27\ -49\ -11$ ($SD = 6$). In addition, we obtained ROIs in right-hand motor cortex by means of the whole-brain contrast of left response S1 > right response S1 and in left-hand motor cortex
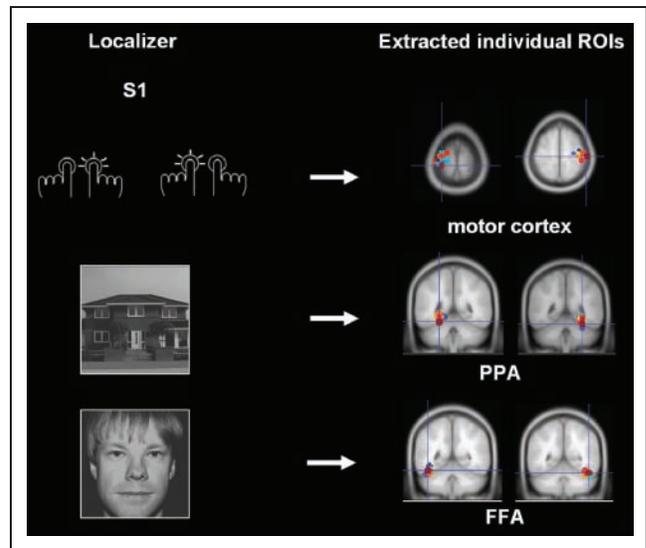
Figure 4. The localizer and the extracted individual ROIs in bilateral motor cortex, PPA, and FFA.

with the reverse contrast of each participant (left motor: $-39\ -22\ 67$, $SD = 7$; right motor: $42\ -21\ 63$, $SD = 7$). For each subject, region, and condition, the mean percent signal change over a time window of 4–6 sec after stimulus onset was calculated.

Two types of binding-related effects were tested. One type of effect was the impact of response repetition versus alternation on the activation of the previously bound stimulus. The effect of repeating the left response was tested by subtracting the conditions with complete alternation (fRhL) from the condition where the (left) response was repeated (fLhL). This contrast was expected to be associated with changes in the FFA. The effect of repeating the right response was tested by subtracting the conditions with complete alternation (hLfR) from the condition where the (right) response was repeated (hRfR). This contrast was expected to be associated with changes in the PPA. These data were analyzed by means of a $2 \times 2 \times 2$ repeated measures ANOVA with the factors ROI (FFA vs. PPA), hemisphere (left vs. right), and S1 (face vs. house).

The other type of effect of interest was the impact of stimulus repetition versus alternation on the activation of the previously bound response. The effect of repeating the house stimulus was tested by subtracting the conditions with complete alternation (fRhL) from the condition where the house stimulus was repeated (hRhL). This contrast was expected to be associated with changes in the motor area coding for the right response (Figure 3). Analogously, the effect of repeating the face stimulus was tested by subtracting the conditions with complete alternation (hLfR) from the condition where the face stimulus was repeated (fLfR). This contrast was expected to be associated with changes in the motor area coding for the left response. These data were analyzed by means of a 2×2 repeated measures ANOVA with the factors hemisphere (left vs. right) and R1 (left vs. right response).

RESULTS

Behavioral Data

RTs and error rates were analyzed by means of repeated measures ANOVAs with the factors response repetition (vs. alternation) and picture repetition (vs. alternation). The RTs (Table 1) revealed a significant main effect of picture repetition, $F(1, 20) = 52.32$, $p < .001$. Most importantly, there was a significant interaction of picture and response repetition, $F(1, 20) = 61.78$, $p < .001$, indicating faster RTs when both features were repeated or alternated. The error rates also showed a significant interaction of picture and response repetition, $F(1, 20) = 30.93$, $p < .001$.

fMRI Data

First we analyzed the effects of response repetition on repetition-induced signal changes (during S2/R2 processing) in the areas coding for the previous S1 (FFA and PPA). The ANOVA revealed a significant interaction of ROI and S1, $F(1, 20) = 14.53$, $p < .01$, and no main effect of hemisphere, $F(1, 20) = 0.06$, $p = .81$. As Figure 5A shows, repeating a response reduced the activation in the area that codes for the stimulus that accompanied that response in the previous part of the trial, that is, for the previous S1. This suggests that repeating a response reactivates the neural codes of the stimulus that this response was previously bound to, which again leads to the suppression of these codes in the course of selecting the currently relevant stimulus and response (S2 and R2). The fact that the signal change is negative (i.e., that response repetition led to the suppression of the previous stimulus rather than to stronger activation) suggests that decisions between conflicting codes were made according to the logic of a diffusion model of decision making rather than a race model, which would have predicted an increase of activation.

Next we analyzed the effects of stimulus repetition on repetition-induced signal changes in motor areas. The corresponding ANOVA revealed no main effect of hemisphere, $F(1, 20) = 0.38$, $p = .54$, but a marginally significant interaction between hemisphere and R1, $F(1, 20) = 3.58$, $p = .07$, that followed the predicted pattern. As Figure 5B shows, repeating a stimulus reduced the activation in the motor areas coding for the previous R1.

In search of a possible "central inhibitor," we computed a conjunction on four leniently thresholded contrasts ($p < .05$, uncorrected) for which we observed suppression of reactivated event-file features (house suppression: hRfR–hLfR; face suppression: fLhL–fRhL; right response suppression: hRhL–fRhL; and left response suppression: fLfR–hLfR). In line with the notion of local competition, we did not find any overlap in frontal brain areas that could be substrate of a central inhibitor.
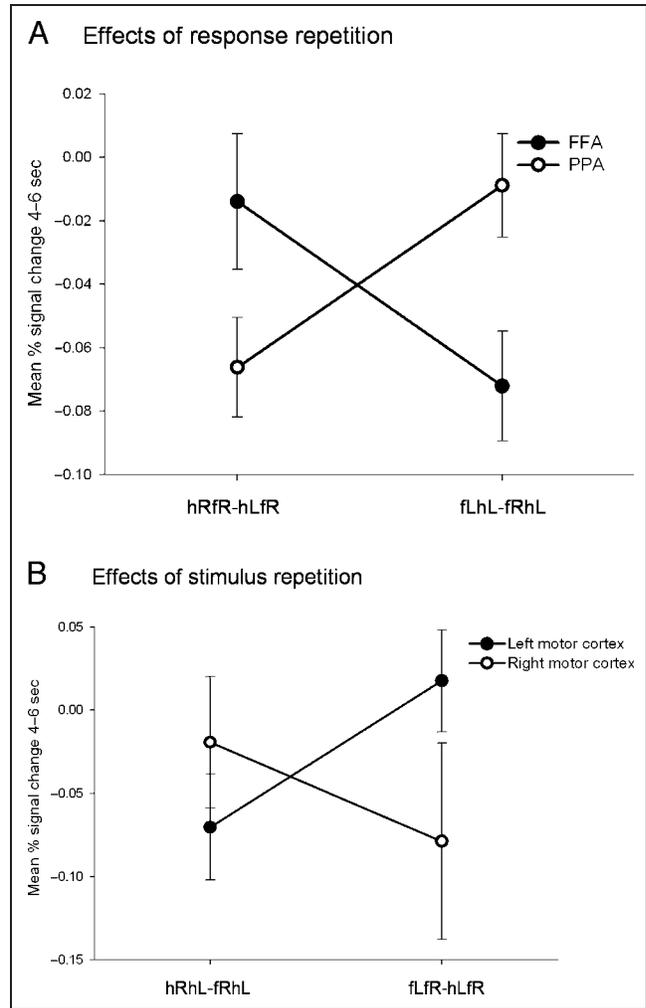
Figure 5. (A) Effects of response repetition. Percent signal changes of ROIs in bilateral PPA (sphere with radius 6 mm around individual peak voxel of the contrast house S1 > face S1) and bilateral FFA (sphere with radius 6 mm around individual peak voxel of the contrast S1 face > S1 house) for the contrast reflecting the effect of right response repetition (hRfR–hLfR) and the effect of left response repetition (fLhL–fRhL). Error bars depict *SEM*. (B) Effects of stimulus repetition. Percent signal changes of ROIs in right and left motor cortex (sphere with radius 6 mm around individual peak voxel of the contrast left response S1 > right response S1 and the reverse contrast) for the contrast reflecting the effect of house stimulus repetition (hRhL–fRhL) and the effect of face stimulus repetition (fLfR–hLfR). Error bars depict *SEM*.

Table 1. Mean RTs (in msec) and Mean Error Rates, with *SD* in Parentheses

	Complete Repetition	*Picture Alternation*	*Response Alternation*	*Complete Alternation*
RT	526 (63)	587 (69)	552 (72)	545 (59)
Errors	0.035 (0.038)	0.083 (0.056)	0.069 (0.046)	0.043 (0.037)

DISCUSSION

The present study was designed to address two theoretical questions. First, we asked whether repeating a response or a stimulus would induce the retrieval of the stimulus or response that it previously accompanied. If it would, this would support the claim that the co-occurrence of stimulus features and responses is sufficient to trigger the creation of event files, that is, of episodic traces that bind stimulus and response information (Hommel, 1998, 2004; cf. Logan, 1988). And indeed repeating at least one component of these event files seems sufficient to retrieve the whole file in a pattern-completion fashion so that all components become reactivated.

Our second question was whether the repetition-induced signal change would be of a positive or a negative sign, that is, whether repetition of one component would lead to an increase in activation or the suppression of other components. Although the effect of stimulus repetition only approached significance level, both response-repetition and stimulus-repetition effects go in the same direction, suggesting that repetition leads to the suppression of no longer valid components of the reactivated event file. As we have argued, this pattern is consistent with the assumption of diffusion models of decision making that competing codes inhibit each other, which eventually leads to a winner-takes-all pattern.

At first glance, the current observations seem at odds with the findings reported by Keizer, Nieuwenhuis, et al. (2008). As mentioned already, these authors demonstrated an increase, instead of a decrease, of brain activity in PPA during S2 when S1 displayed a moving house and S2 a moving face, and the motion feature was repeated. One might argue that this fits better with the logic of a race model than that of diffusion models. However, in our view, the crucial difference is that the design by Keizer, Nieuwenhuis, et al. did not involve any kind of stimulus or response conflict: Participants did not respond to S1 and responded to the *motion* of S2 so that responses were not bound at all and any reactivation of the motion-associated house feature could not conflict with current task performance. In contrast, our task involved responses to S1 and a forced-choice response to the *identity* of the S2 picture so that both reactivated responses and/or stimuli could directly compete with the relevant S2 and/or R2 codes. Accordingly, we consider the present study but not the study of Keizer, Nieuwenhuis, et al., a fair test of race and diffusion models, and conclude that the reactivation of event files in the presence of response conflict follows the predictions from diffusion models but not from race models. In the absence of response conflict, however, race models may very well do a good job.

Surely, the retrieval and the competition processes we have described so far are not the only processes contributing to both BOLD signals and RTs and the relation between them. For instance, complete repetitions are likely to be a special case in that subjects seem to shortcut response

selection and respond in a kind of "if everything stays the same I can do the same" mode (already reported by Bertelson, 1965). Likewise, complete alternation of features makes it possible to "reject" alternative codes at different feature maps faster if they are bound to each other, a principle that has been proposed by Duncan (1996; see Dutzi & Hommel, 2009). Moreover, there is evidence that repeating a stimulus or a response (feature) as such can lead to the reduced activation of the corresponding neural codes (for an overview, see Henson & Rugg, 2003), possibly by focusing or "sharpening" the cortical representation (Wiggs & Martin, 1998). This kind of process might very well have contributed to the suppression-like effects we have obtained. However, the theoretical crux of our findings consists in the demonstration that suppression was *contingent* on the repetition or alternation of the accompanying response or stimulus (feature), respectively, which we think goes beyond the previously reported suppression effects and the theoretical considerations offered to account for them.

Our current findings go beyond previous demonstrations of conflict as shown in classical Stroop or Simon task paradigms. The conflict present in a Stroop task, in which participants need to name the color of a word although the semantic refers to a different color and stems from automatic reading of printed words that has been established during lifetime (MacLeod, 1991; Stroop, 1935). Similarly, the Simon effect, namely, reduced reaction times when responding with the left hand to stimuli on the left side of the screen even if stimulus location is task irrelevant, is based on stimulus-response compatibility processes that are highly overlearned or even innate (Simon, 1969). In contrast to these long-term associations, the bindings we explored here are purely episodic short-term (i.e., trial-to-trial) effects that are effective instantaneously (Hommel, 2004).

The result pattern we obtained suggests that retrieved event-file features and task-relevant features compete at a local level, whereas we were unable to identify any contribution from central inhibiting systems. This is in line with predictions of diffusion models (Bogacz, 2007) but inconsistent with cognitive control models that assume a central inhibitor (Botvinick et al., 2001, 2004). Although the absence of an effect admittedly constitutes an only weak argument against central inhibition, our study does suggest that local inhibition may be sufficient to explain effective control: Repeating one feature of an event file can lead to the direct, apparently local suppression of retrieved features that conflict with task performance.

Notes

1. One might consider another potential problem with partial repetitions. If S2 and R2 are related by instructed stimulus-response rules, a partial repetition implies that S2 or R2 is preceded by a combination that violates these rules (e.g., if faces require a right-hand keypress, the combination of a face and a left-hand keypress implies a rule violation). However, previous studies suggest that this factor does not play a role. For instance, R1 RTs are not affected by rule violations (Hommel, 1998), and interactions between stimulus and response repetitions can be observed in free-choice tasks, where no stimulus-response rules are applied (Hommel, 2007).

2. Logically, it is possible that the activation of all competitors increases continuously so that no decision could ever be made. However, race models have several ways to account for the fact that people do reach decisions even if these are somewhat delayed. For instance, task-irrelevant information may be weighted less strongly and/or decay very quickly, as we have assumed in Figure 2. That is, race models do not necessarily deny that the activations of evidence counters change dynamically and that different counters may follow different dynamics, but they assume that the activation of one given counter is independent of the activation of the others.

3. Note, however, that the functions drawn in Figure 2 are not literal derivations from existing models but only serve to illustrate qualitative differences between the predictions from race and diffusion models.

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