Cerebral Cortex, April 2020;30: 2267–2280

doi: 10.1093/cercor/bhz238
Advance Access Publication Date: 7 November 2019
Original Article

ORIGINAL ARTICLE

Temporal Characteristics of Priming of Attention Shifts Are Mirrored by BOLD Response Patterns in the Frontoparietal Attention Network

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Abstract

Priming of attention shifts involves the reduction in search RTs that occurs when target location or target features repeat. We used functional magnetic resonance imaging to investigate the neural basis of such attentional priming, specifically focusing on its temporal characteristics over trial sequences. We first replicated earlier findings by showing that repetition of target color and of target location from the immediately preceding trial both result in reduced blood oxygen level-dependent (BOLD) signals in a cortical network that encompasses occipital, parietal, and frontal cortices: lag-1 repetition suppression. While such lag-1 suppression can have a number of explanations, behaviorally, the influence of attentional priming extends further, with the influence of past search trials gradually decaying across multiple subsequent trials. Our results reveal that the same regions within the frontoparietal network that show lag-1 suppression, also show longer term BOLD reductions that diminish over the course of several trial presentations, keeping pace with the decaying behavioral influence of past target properties across trials. This distinct parallel between the across-trial patterns of cortical BOLD and search RT reductions, provides strong evidence that these cortical areas play a key role in attentional priming.

Key words: attention priming, frontal cortex, parietal cortex, selective attention, visual search

Introduction

Our visual system allows us to attend and ignore objects in our environment. A large body of research has investigated this process using the visual search paradigm. One important finding is that search performance typically improves when an observer searches for the same target across consecutive trials, showing that the encoding of stimulus features becomes more efficient with experience (Maljkovic and Nakayama 1994; Kristjánsson and Campana 2010; Brascamp et al. 2011). Specifically, RTs are shorter and accuracy higher when target and distractor features repeat across trials, relative to when target and distractor features change, or reverse their roles (Wang et al. 2005; Kristjánsson and Driver 2008; Lamy et al. 2008; see Kristjánsson and Ásgeirsson 2019 for a recent review).

Attentional control has been proposed to reflect neural responses in a frontoparietal attention network that includes the frontal eye fields (FEF) and intraparietal sulcus (IPS). This network has been widely associated with spatial attention (see Scolari et al. 2015 for an overview) and also encodes feature-specific information (Bichot and Schall 2002; Liu et al. 2011) that drives feature-based attention. Direct evidence that these regions are also involved specifically in attentional priming during visual search comes from functional magnetic resonance imaging (fMRI) studies showing reduced blood oxygen level-dependent (BOLD) response associated with repetition of target color or location, as compared to role reversals of target and distractor features (Kristjánsson et al. 2007; Rorden et al. 2011; Becker et al. 2014). Such BOLD repetition suppression matches what is observed in other forms of priming (Henson & Rugg, 2003; Dobbins et al. 2004).

While, in such previous neuroimaging studies of attentional priming, researchers have focused on immediate priming effects, the temporal characteristics of attentional priming are far richer. The strength of attention priming during search is, for instance, negatively correlated with the lag of the repetition of search items' features: the facilitating effect of a given search trial decays approximately exponentially with the number of intervening trials and independently of the particular search display shown during these intervening trials (Maljkovic and Nakayama 1994; Maljkovic and Martini 2005; Martini 2010). Other neuroimaging studies, which investigated the effect of lag on repetition suppression in the BOLD signal in paradigms unrelated to visual search, have found that the strength of BOLD priming effects decreases over time, to scale with the decaying behavioral effects of priming (Henson et al. 2004; Brozinsky et al. 2005; Woodward et al. 2006). This correspondence across time scales has been taken as evidence that the priming effects at different lags reflect a single underlying mechanism in the case of the priming phenomena studied there (Henson et al. 2004).

With regard to visual attention priming, it is currently not clear to what extent the lag-1 effects in the BOLD response generalize to longer lags. For instance, the behavioral effects may be composed of multiple priming effects at the neural level that decay at different rates (Martini 2010). Such a potential mix of underlying mechanisms is difficult to identify from behavioral performance alone. In this study, we, therefore, aim to identify patterns in the BOLD signal that trace the lag-1 behavioral priming effect, as well as ones that trace longer-lasting behavioral priming effects as they gradually decay across consecutive trials. In this way, we can discriminate between 2 alternative hypotheses. First, the same cortical areas that have been identified in previous work on lag-1 priming may show longer-term BOLD reductions that mirror the more extended behavioral effects, providing stronger evidence than currently available that these areas are functionally involved in the attentional bias that produces attentional priming. Alternatively, the BOLD correlates of longer-term attentional priming may differ from the BOLD correlates of lag-1 priming identified previously, as would be expected if those latter correlates reflect additional cognitive components that are unique to the first trial following a target–distractor role reversal.

Materials and Methods

fMRI Stimuli, Tasks, and Procedure

Six male experienced psychophysics observers, all members of the Psychology Department at Utrecht University, each participated in 2 or more scanning sessions on separate days. For each participant, we collected 12 or more scans of 100 search trials each. Each scan lasted around 7 min and participants were allowed to take a short break in the scanner after each scan. A single session lasted around 1 h.

The main experiment involved a visual search task adapted from Maljkovic and Nakayama (1994). On each trial, 4 diamonds with a diameter of 2.4° of visual angle (VA) were presented 4° away from fixation at fixed positions in each quadrant of the display (Fig. 1*a*). Each diamond was blue or yellow (see below how we determined luminance per observer) displayed on a gray background (50 cd/m^2). On each trial, 3 diamonds were presented in one color, and one diamond was presented in the other color (the target). Observers were asked to search for the odd-colored diamond, while maintaining fixation on a small double ring at the center of the display. Each diamond had a notch in one corner and the notch positions were randomized across trials. On a given trial, each diamond had its notch at a different corner, so that the target item's notch corner was unique to that item. Observers were asked to respond by pressing the button corresponding to that corner on a response box, with their right hand. A response could be given after the onset of the search display until the onset of the next display. Each search display appeared for 200 ms, and the fixation stimulus was on screen for the entire experiment. Because we did not measure eye movements during the experiment, short stimulus presentation was chosen to encourage fixation at the center of the screen (Kristjánsson et al. 2007). Interstimulus intervals ranged linearly from 2.5 to 5.5 s, such that the average interval lasted 4 s. The duration of each interval was then randomly determined on each trial. Each experiment run lasted 420 s.

Target color and target location were drawn randomly on each trial, with the limitation that each target color and each target location occurred equally often. To select our trial sequences for the experiment, we analyzed candidate sequences by transforming each randomly created sequence of target colors and locations into a set of 6 design matrix columns of 1's and 0's to define repetitions at each of the 6 lags for color and location separately, given that priming of visual search affects RTs up to, approximately, that number of lags (Maljkovic and Nakayama 1994; Martini 2010). Specifically, in each sequence, 0 stood for a trial where there was no repetition at the lag in question and 1 stood for a repetition.

The random assignment of target color and of target location in each candidate sequence ensured that there were no systematic correlations between these sequences because, say, the target color on an immediately preceding trial was not systematically predicted by the target color 2 trials back. Even random sequences, however, although in the limit uncorrelated, can lead to incidental nonzero correlations, both positive and negative. To increase our statistical power, we therefore selected the color and location sequences for our experiment using a procedure that further minimized correlations between repetitions at various lags. Specifically, we generated many random candidate trial sequences and calculated for each the degree of correlation between the 6 repetition sequences described above. We did so iteratively until 1000 unique trial sequences were created for both location and color, for which no 2 vectors produced a higher absolute correlation coefficient than 0.1. Next, sequences for both target color and target location were ordered by the mean absolute correlation coefficient across lags. We then selected the sequences with the lowest mean absolute correlation coefficients to include in experiment runs,

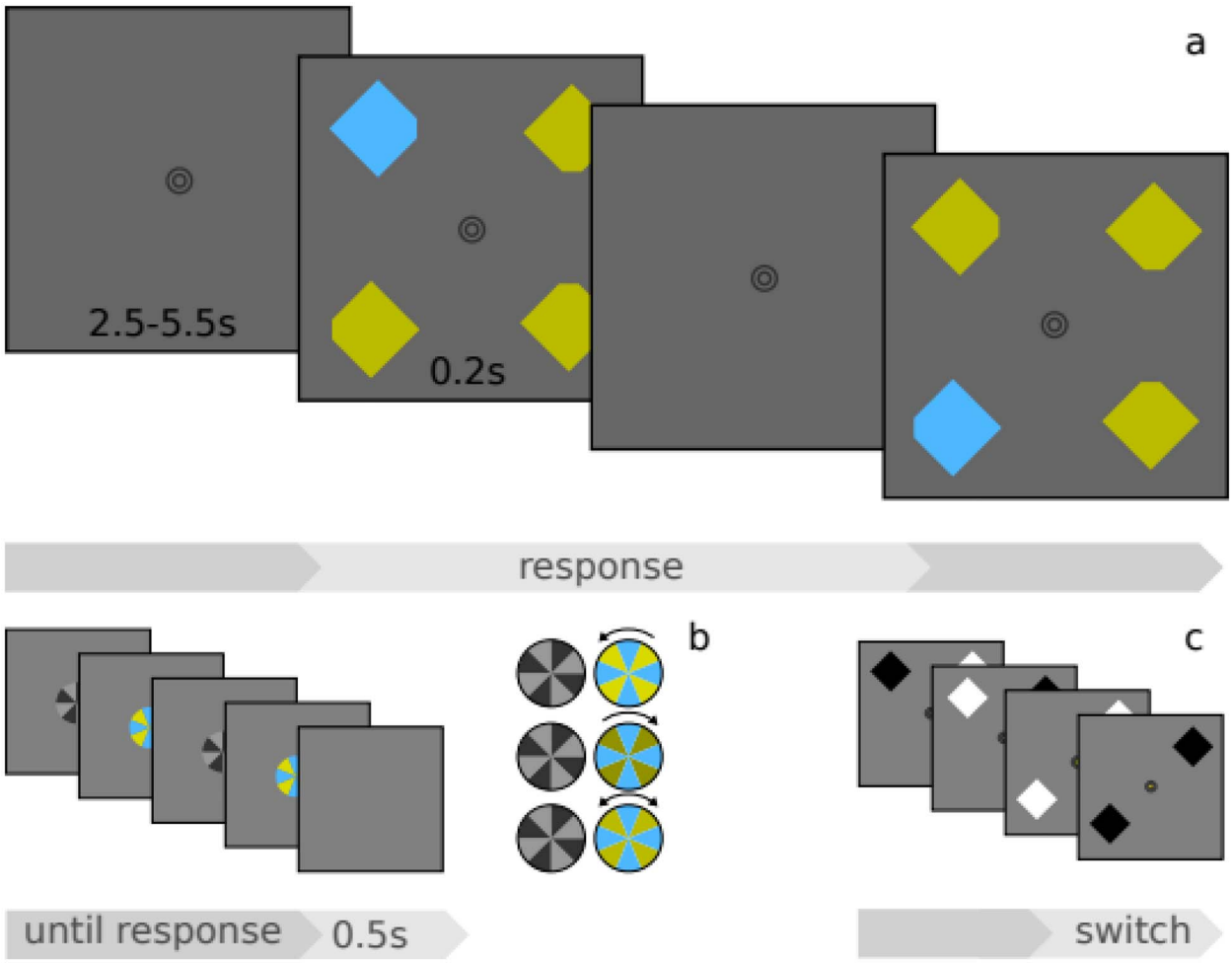

Figure 1. (*a*) A schematic view of the main experiment. Four diamonds were presented at 4 fixed positions on the display. The odd-colored diamond was designated as a target and was identified by reporting the notch' position. (*b*), left The task used to determine luminance values for yellow diamonds per observer. (*b*), right: Depending on the luminance of the yellow wedges, the circle was perceived as rotating clockwise or counterclockwise. (*c*) The task used to map the cortical locations of the visual search display elements. Black and white alternating stimuli appeared at the 4 stimulus positions corresponding to the main experiment. Observers reported a color change of the fixation stimulus at the center of the screen. See text for more details on all measurements.

using each sequence only once. The resulting mean absolute correlation coefficients for used target sequences were 0.02 (standard deviation [SD] = 0.01) for color and 0.01 (SD = 0.01) for location. To reiterate, this procedure does not reduce the across-sequence average correlation coefficient between lags relative to randomly drawing sequences without a further selection process (this average is 0 in either case), but it does reduce the across-sequence average "absolute" correlation coefficient or, in other words, the probability that any 2 sequences have correlation coefficients that differ much from 0.

Before the actual experiment, the luminance of the yellow diamonds was matched perceptually for each observer with the luminance of the blue diamonds (which was 100 cd/m^2) using a 1-up, 1-down, double staircase procedure. Specifically, we conducted a short task inside the scanner prior to each scan session, similar to the minimum motion design of Anstis and Cavanagh (1983). Observers were asked to indicate the rotation direction of a segmented circle (Fig. 1*b*). The circle was divided into alternating dark gray (500 cd/m^2) and light gray (800 cd/m^2) segments on odd frames and blue and yellow segments on even frames. On every frame, the circle rotated 22.5°, so that, depending on the luminance contrast of the yellow and blue segments the circle would be perceived as rotating clockwise or counterclockwise. After each response, the yellow luminance was altered toward a value that would render rotation direction more ambiguous due to equiluminance of yellow and blue. The luminance values at the start of the 2 staircases were 500 and 300 cd/m^2, and the initial step size was 50 cd/m^2 up and down and was set to 10 cd/m^2 after 6 reversals. After another 6 reversals, the staircase terminated. The 4 final reversal values of both staircases were averaged to determine the final luminance of yellow diamonds.

Following this luminance calibration, each session continued with a separate task to localize stimulus-related activations in the cortex. We presented diamond stimuli with the same size and positions as the ones used in the search task, but without notches. All 4 diamonds were presented on and off in parallel but at different rhythms, according to the following constraints. Stimulus-on durations were 5, 7, 9, or 11 s, and each duration occurred an equal amount of times, in random order independently at each location. Stimulus-off durations ranged linearly from 4 to 12 s and also occurred randomly. During

stimulus-on periods, the diamond was further manipulated to maximize BOLD responses: it flickered at 1 Hz and, when visible, its color alternated between black and white at a rate of 4 Hz. Observers were instructed to maintain fixation at the screen center. To verify fixation, the color of a central fixation dot toggled between blue and yellow and observers were asked to report each change by pressing a button.

fMRI Data Acquisition

For 4 observers, T1-weighted anatomical MRI data were acquired on a Philips Achieva 3T scanner at a resolution of $0.75 \times 0.75 \times 0.8$ mm. For the remaining 2 observers, T1-weighted MRI data were acquired on a Philips 7T scanner using a 32-channel head coil at a resolution of $0.5 \times 0.5 \times 0.8$ mm. For all observers, T2∗-weighted images were acquired on a Philips 7T scanner using a 32-channel head coil at a resolution of $1.77 \times 1.77 \times 1.75$ mm, with a field of view of $227 \times 227 \times 71.75$ mm. We scanned 41 slices in interleaved order, meaning that first odd slices and then even slices were scanned. Scans covered the visual cortex and extended into the frontal cortex to include the FEF. Time repetition was 2.1 s, time echo was 25 ms, and the flip angle was 70°. Functional runs were 205 frames for the main experiment and 188 frames for the localizer experiment.

Behavioral Analysis

To filter out potential slow learning effects irrelevant to our research question, RT data collected during scanning were detrended for each scan by subtracting the linear slope. We also excluded RTs shorter than 200 ms or longer than 2 s from further analysis. To facilitate analysis at the across-observer level, RTs were normalized within each observer by subtracting the mean RT for each scan and then dividing by the SD. One goal of the behavioral analysis was to ensure that our paradigm induced reliable attention priming. Moreover, because we aimed to identify BOLD correlates of behavioral priming effects, including the ones at higher lags, it was particularly important that we accurately characterized the behavioral time course of priming. To this end, we used multiple regression to calculate, for each participant individually, the RT effect of repetition (both for color and for location) separately for each lag (see Fig. 2). In other words, we calculated the degree to which RT was affected by a color or location match relative to the trial a certain lag prior. We first defined separate regressors to model repetition for each lag individually, where 0 in a regressor indicates a trial where the target feature (color or location) does not match the feature a given lag earlier, and 1 indicates a match (i.e., the same procedure as used to create vectors for selecting our target sequences; see above). We constructed a total of 24 such regressors, modeling trials with repetition at lag 1 to 12 for both color and location. After obtaining a parameter estimate (betas) for each regressor by entering all regressors into a multiple regression analysis on normalized RTs, we then fitted an exponential function to the 12 parameter estimates for color repetition and also to the 12 parameter estimates for location repetition. The resulting curves (see Fig. 2 and Results for details) are estimates of the decay of priming for each observer (cf. Maljkovic and Martini 2005), and the parameters of these curves could later be used to create a model of the observer's priming state throughout an experiment run, which served as the input to our fMRI analysis.

fMRI-Data Analysis

Preprocessing and the main analysis of fMRI-data were done using FMRIB Software Library (FSL) (Woolrich et al. 2004) and Python. We used NiPype (Gorgolewski et al. 2011) to set up our workflow in Python. Data were first corrected for interleaved slice timing using the "slicetimer" function in FSL. Next, we performed motion correction using FSL's "mcflirt" tool. Subsequently, the functional scans, using "flirt," were registered to a low-resolution anatomical scan that was collected at the beginning of each session and was in the same space as the functional scan. The functional scans were then further preprocessed using FSL's "fslmaths" tool. First, the scans were smoothed spatially by convolving them with a Gaussian kernel (with full width half max of 5 mm). We then high-pass filtered the scans in the temporal domain with a sigma of 60 s. Parametric analyses were done using the "film_gls" function in FSL. For within-observer across-scan analysis, we used the fixed effects "flameo" routine in each observer's native space. For across-observer analyses, we used the mixed effects "flameo" routine, set to 2 runs, after transforming the data to Montreal Neurological Institute (MNI) space using "flirt" for linear and "fnirt" for nonlinear transformations.

To improve statistical power, we limited the number of voxels included in our analyses, by creating a mask by selecting voxels that showed significant activity in response to the onset of a search display (see Fig. 3). This contrast was then intersected with a dilated mask of the cortex that was derived, using FMRIB's Automated Segmentation Tool (FAST), from the standardized whole brain image available in FSL. We then corrected for multiple comparisons given the number of voxels that were included in this mask using the false-discovery rate (FDR) (Genovese et al. 2002), thresholding images at a z-score corresponding to a selected q-value of 0.1. To verify earlier findings (Kristjánsson 2007) and to increase statistical power, we also looked at regions of interest (ROIs) based on peak BOLD response reductions to lag-1 repetition from the former study. We created spheres with a radius of 8 voxels around the peak coordinates, which we again intersected with the aforementioned cortical mask and significant voxels in the stimulus onset contrast. We determined a threshold for significant voxels corrected for the FDR within each of these ROIs.

To create design matrix regressors for lag-1 priming effects, we simply put a 1 for each trial that constituted a repetition, either in target color or in target location depending on the analysis, and a 0 otherwise. To accurately model the more gradual progression of priming that follows the first lag, we created regressors based on the per-observer exponential patterns in RT quantified above. Specifically, we first formulated a differential equation that allowed us to step chronologically through all trials in a scan and iteratively compute the states of priming of each individual color of each individual location on each trial. In other words, the equation integrated, for each observer and primed feature (1 of 2 colors and 1 of 4 locations), the exponential curve calculated above:

$$y_{n+1} = | x - (x - y_n) | * e^{-xt},$$

where t is a time constant determined on the basis of the behavioral data, y_n is the priming state on the current trial, and $y_n + 1$ is the priming state on the next trial. For each observer, we performed this calculation for each location and each color

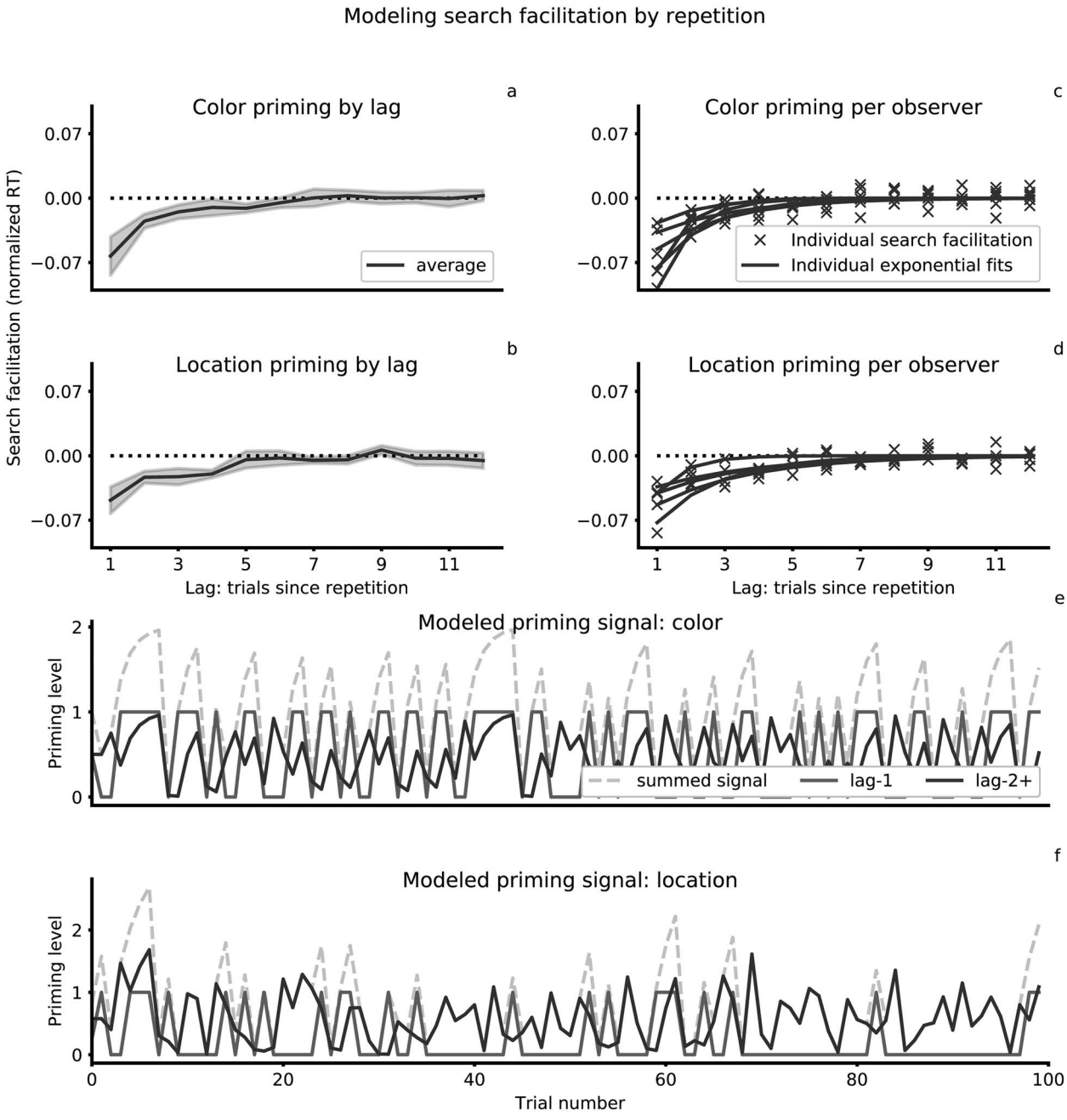

Figure 2. Search facilitation as a function of the number of trials between repetitions of the target color in the upper panels (*a* and *c*) and target location in the lower panels (*b* and *d*). The left panels (*a* and *b*) depict the average and 90% confidence intervals across observers of parameter estimates as a function of number of trials between repeated features. Right panels (*c* and *d*) present parameter estimates of all individual observers and the fitted exponential curves per observer. (*e* and *f*) The modeled course of priming at each trial onset, of a single observer throughout an experiment run, given the parameters of that observer's fitted curves in (*c*) and (*d*). The lighter solid curve represents priming due to lag-1 repetition only. The darker solid curve represents the modeled course of priming due to repetitions across all lags except lag-1 (i.e., lag-2+). The dashed gray line shows the sum of both factors. The lag-1 and lag-2+ priming levels at each trial onset, for both color and location, were included in the statistical model to analyze the fMRI-data, in addition to 4 regressors that modeled the onset of search displays for each target location.

separately, with *x* corresponding to the state of the feature during the trial in question: 1 if the target had that color or location on that trial or 0 if it did not. After having, in this fashion, calculated ongoing time courses of the priming states of all colors and locations separately, we then used these time courses to assemble a regressor that quantified priming toward the current target color, as well as one that quantified priming toward its location, by selecting values from the appropriate time courses, based on the current target color and location. Finally, we created regressors that covered only priming effects beyond lag-1 by appropriately scaling the full priming regressors obtained in this way and then subtracting out the lag-1 regressors described earlier. In other words, we ended up, for each observer and for both color and location, with one regressor that covered only

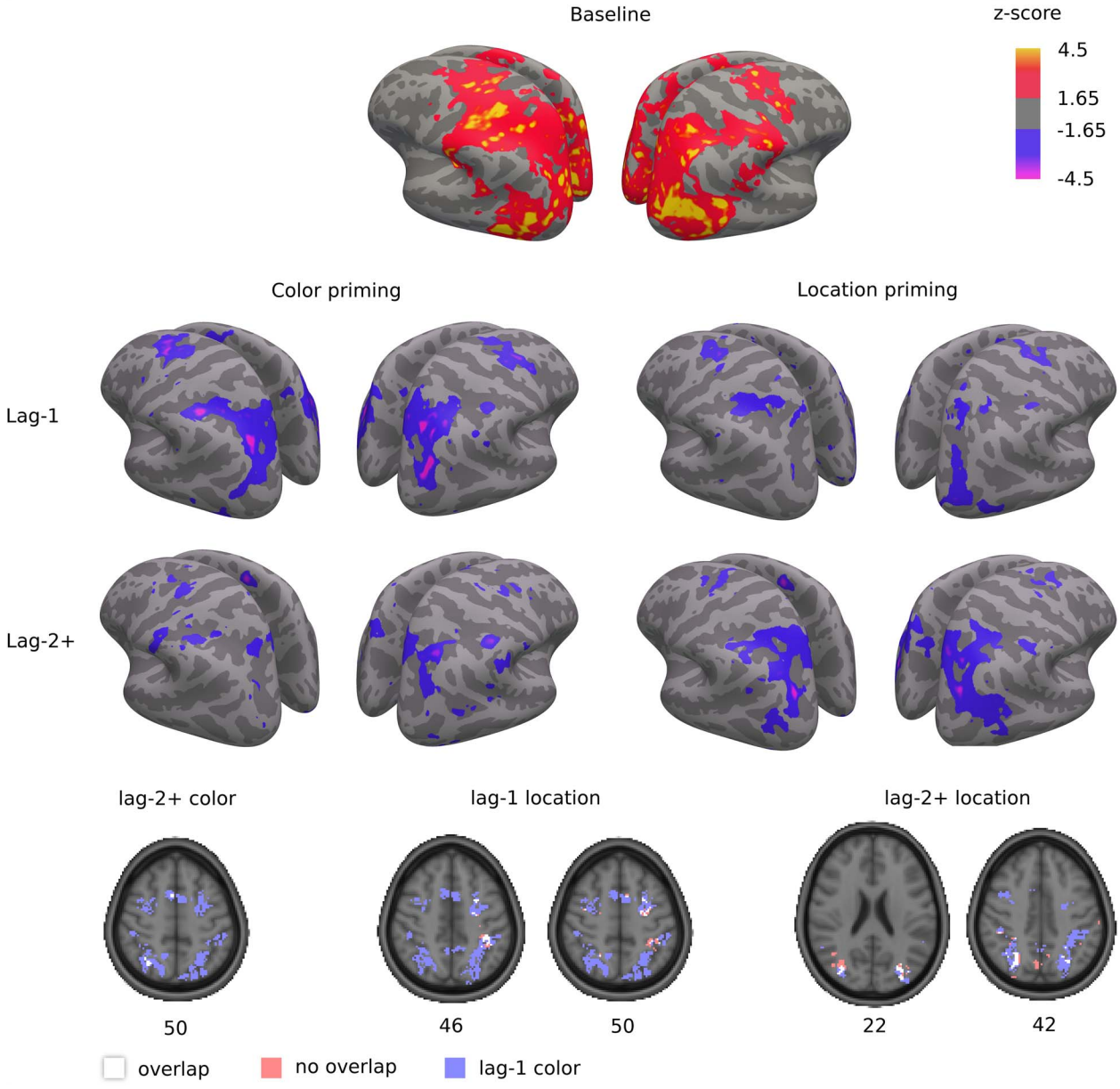

Figure 3. BOLD contrasts projected onto the surface showing stimulus-related activations as baseline (upper row) in frontoparietal regions and occipital areas. The second row displays a reduced BOLD response, broadly within the same regions, at stimulus onset for color priming (left) and for location priming (right) at a single lag, replicating Kristjánsson et al. (2007) and Rorden et al. (2011). The third row shows the lag-2+-related BOLD reductions at stimulus onset for color (left) and location (right) priming. Contrasts are thresholded at an uncorrected P-value of 0.05 for display purposes. The lower row shows axial slices from the lag-1 color priming contrast (blue voxels), intersected with the other priming contrasts (from left to right: lag-2+ color priming, lag-1 location priming and lag-2+ location priming), thresholded at the FDR (see text for details). White voxels show where significant voxels overlapped between the priming contrasts, whereas blue and red voxels show where there was no overlap. Cortical reconstruction was performed using Freesurfer image analysis suite (see Dale et al. 1999 for technical details on those procedures).

lag-1 priming and one regressor that covered the compound priming effects accumulated at all longer lags, which we will refer to as lag-2+ priming. This procedure enabled assessment of BOLD correlates of lag-1 facilitation and of longer-lasting facilitation independently. The model used in our primary analysis included 8 regressors: 4 regressors for target presence at each location; 2 lag-one priming regressors (one for color and one for location); and 2 regressors for longer-lasting priming (one for color and one for location). These sequences were then convolved with a standard hemodynamic response function (HRF) using FSL for the first level of fMRI analysis. Derivatives of each regressor were added to the model to account for small BOLD-response shifts relative to the standard HRF (Friston et al. 1998). The data for Figures 3 through 7 were obtained by contrasting parameter estimates from this model with an implicit baseline, meaning that parameter estimates were contrasted with zero.

Importantly, our approach allowed us to impose an unbiased priming state at the beginning of each scan. Given that there are 2 potential target colors, color priming as calculated based on the exponential kernels hovers around a neutral baseline of

$y = 0.5$. Similarly, location priming hovers around $y = 0.25$ because there are 4 locations. Preliminary analyses showed that simply starting with priming values of 0 at the start of each scan produced regressors in which a quick upstroke from 0 to these baselines produced correlations with BOLD signals that had nothing to do with the priming-related fluctuations around baseline that were the target of our analyses, but that were instead related to the onset of a new scan. For this reason, we imposed neutral priming values of 0.5 (for color) and 0.25 (for location) on the first trial of each scan for both our lag-1 priming regressors and during the iterative procedure for longer-term priming described above.

We verified the correct construction of these priming regressors by performing linear mixed effects analyses (using R; R Core Team, 2012 and the lme4 package; Bates et al. 2014) to assess the relation between the modeled priming level estimates and the actual, normalized, RT data. Observers were included as random effects and estimated priming levels were included as fixed effects. Specifically, we compared a model with lag-1 effects and, separately, one with longer-lasting effects, against a model without these fixed effects. The priming level estimates for target color and location were included within the same linear models. *P*-values were obtained with likelihood ratio tests. We found that the lag-1 priming signals for color and location significantly improved the model fit RTs ($\chi^2(1) = 2.32$, $P < 0.001$ and $\chi^2(1) = 104.21$, $P < 0.001$). The same was true for the slower priming signals ($\chi^2(1) = 48.97$, $P < 0.001$ and $\chi^2(1) = 73.91$, $P < 0.001$). Furthermore, the model that included both lag-1 and longer-lasting facilitation effects was a significantly better fit to the data than a model with only lag-1 facilitation ($\chi^2(2) = 143.93$, $P < 0.001$). These sanity checks confirmed that our priming regressors captured RT fluctuations as intended.

Next, the aforementioned ROIs were further analyzed to assess the extent of lag-2+ priming effects. We created 2 new priming models to capture lag-2+ effects. One model included 12 regressors for "color" repetition of 1–12 lags and the other model contained 12 regressors of "location" repetitions up to 12 lags. These regressors were then convolved with the HRF and each model was fitted to the BOLD signal using Python. To assess the extent of our significant results, we created ROIs based on significant voxels in our main analysis. Specifically, we again created spheres with a radius of 8 voxels, around the reported peak reductions related to the lag-1 color and location priming effects in the study of Kristjánsson et al. (2007). Within each sphere, we then selected the peak reduction in our own data and created a new sphere around that voxel with a smaller radius of 2 voxels. These smaller spheres were then transformed back from MNI space to the observer space, using FLS's "inv_warp." Next, we selected the BOLD time series per individual experiment run and averaged the signal across voxels within each ROI.

Finally, because the behavioral color and location priming kernels (Fig. 2c,d) were created once per observer based on the data of all experiment runs together, the fit of these kernels with RTs naturally varies across runs. Therefore, we conducted additional analyses to assess this variance across runs and its correspondence with the BOLD response effects. We first fitted a general linear model to normalized RTs using the same regressors as in our main fMRI analysis. Specifically, for each observer, we created lag-1 and lag-2+ priming regressors for color and location repetitions. The lag-2+ regressor was again composed of the summed effects of all lags beyond lag-1, given the derived priming kernels per observer in Figure 2c,d. However, in contrast with our fMRI analysis, these regressors were not convolved with the HRF. This resulted in 4 parameter estimates for each priming regressor per experiment run, but now for a model with behavioral RT, instead of BOLD response, as the dependent variable. We were then able, for each regressor, to compare these 4 RT parameter estimates per run with the 4 BOLD parameter estimates per run that were derived in the main fMRI analysis for each equivalent regressor. We only looked at significant fMRI results to assess how the variance of these parameter estimates across experiment runs corresponded between the model fits with BOLD and with RT data. To select these significant fMRI results, we filtered, for each regressor, the voxels that showed significant BOLD reductions within the ROIs reported in Tables 1 and 2 for color and location priming, respectively, and averaged the parameter estimates in these voxel selections per ROI. We then created one linear mixed model per priming model (i.e., color lag-1, location lag-1, color lag-2+, and location lag-2+), with observers as random factor and the averaged BOLD parameter estimates per ROI as fixed effects and RT parameter estimates as dependent variable. Each model was compared to a baseline model including only the intercept as fixed factor and subject as random factor, with likelihood ratio tests.

Code Accessibility

The full Python and R code of our experiments and analyses can be accessed through the following repository (https://www.github.com/manjebrinkhuis/attention-priming-decay).

Results

Behavioral

The average number of correct trials across all scans was 98.9% (SD = 0.009), although missed responses were not counted as incorrect in this calculation. The number of missed responses was artificially high (477 out of all 12 900 trials) because during 2 sessions, 1 for observer 1 and 1 for observer 5, 1 in 4 responses could not be registered due to a defective response button. Neither incorrect nor unrecorded responses were excluded from further analysis (except that a RT could not be computed in the case of unrecorded responses). Figure 2 shows the across-observer averaged changes in RTs (y-axis), for color (panel a) and location (panel c), on a given trial when its target color or location is repeated a certain number of trials later (*x*-axis). For each observer, both color repetition and location repetition caused a reduction in RT, and this reduction was larger when a recent target feature was repeated than when an earlier target feature was repeated (individual participants' data shown as dots in Figures 2b,d). The average rate of priming decay (the proportion by which search facilitation effects reduced per intervening trial) for color and for location repetitions was 50.1% (SD = 14.0) and 39.9% (SD = 15.4), respectively. Comparing these proportions in a paired sample *t*-test showed that color priming generally decayed at a faster rate than location priming ($t(5) = 2.85$; $P = 0.034$).

fMRI

Stimulus-Specific Effects

In addition to the regressors that modeled priming, we included regressors corresponding to the onset of targets at each stimulus position separately. Combined, these 4 regressors modeled

Table 1 Overlap between lag-1 color priming-related reductions in the BOLD response as reported in Kristjánsson et al. (2007) and lag-1 and lag-2+ color priming effects in the current study

	Region	Num. voxels	Num. voxels in ROI	Peak z-score	MNI coordinates		
					x	y	z
Lag-1 color priming	L FEF	475	595	−4.73	−28	0	54
	R FEF	640	957	−4.69	36	0	60
	L IPS	1169	1409	−5.88	−24	−70	58
	R IPS	88	915	−3.87	38	−58	46
	L lateral occipital cortex	0	657	−3.25	−42	−74	−6
	R occipital	0	665	−1.87	6	−98	2
	L frontal gyrus	0	127	−2.81	−44	−68	−8
	R ACC	0	653	−2.59	−2	2	52
Lag-2+ color priming	L FEF	0	595	−3.41	−30	−8	54
	R FEF	190	957	−3.72	38	2	42
	L IPS	102	1409	−3.67	−24	−66	54
	R IPS	8	915	−4.31	34	−58	48
	L lateral occipital cortex	0	657	−2.35	−22	−80	−4
	R occipital	0	665	−2.76	0	−82	−8
	L frontal gyrus	0	127	−1.51	−44	−68	−10
	R ACC	0	653	−2.32	−8	−4	48

Table 2 Overlap between lag-1 location priming-related reductions in the BOLD response as reported in Kristjánsson et al. (2007) and lag-1 and lag-2+ location priming effects in the current study

	Region	Num. voxels	Num. voxels in ROI	Peak z-score	MNI coordinates		
					x	y	z
Lag-1 location priming	L-FEF	159	1379	−4.01	−26	−10	50
	R FEF	112	862	−4.11	32	−12	56
	L IPS	0	1075	−3.2	−34	−48	48
	R IPS	0	1486	−3.53	22	−70	60
	L peristriate cortex	0	1157	−2.34	−10	−74	2
	R peristriate cortex	0	1331	−2.43	18	−74	6
	R anterior parietal	0	253	−2.13	38	−42	58
	R inferior parietal	0	698	−2.91	48	−28	44
Lag-2+ location priming	L FEF	184	1379	−3.62	−30	−4	52
	R FEF	247	862	−3.81	36	0	60
	L IPS	687	1075	−4.15	−30	−70	52
	R IPS	1136	1486	−4.79	26	−62	42
	L peristriate cortex	0	1157	−2.47	−4	−56	4
	R peristriate cortex	0	1331	−2.45	26	−64	26
	R anterior parietal	0	253	−2.79	46	−36	60
	R inferior parietal	135	698	−4.27	48	−36	5

responses to search display onsets, regardless of any priming. For a sanity check, we contrasted stimulus onset with an implicit baseline. Stimulus onset was associated with increased activity in bilateral visual cortex, IPS, inferior postcentral sulcus and superior precentral sulcus, and left central sulcus (subjects responded with their right hand) (Fig. 3). Furthermore, for each stimulus location, we contrasted regressors corresponding to target onset at that location with a compound regressor for trials at which the target appeared at other locations. This showed target location-specific activity in visual cortex and parts of IPS. Overlaying the voxel patterns of both these analyses with those of a separate stimulus, localizer procedure (see Methods) showed good correspondence between the 2.

Lag-1 Priming Effects

We next investigated lag-1 priming effects. We were interested in replicating earlier findings of a reduced BOLD response to repeated target and distractor properties relative to switched target and distractor properties. To get an impression of the overall distribution of priming-related activations, we started

with a whole-brain analysis. Figure 3, second row (left) shows contrasts for lag-1 color priming. We found that after correction for multiple comparisons, as described in Methods, lag-1 color repetition was associated with BOLD reductions bilaterally in FEF, IPS, and anterior cingulate cortex (ACC).

We also created contrasts for lag-1 location repetitions versus switches (Fig. 3, second row, right). However, no significant reductions of activity in voxels remained after correction for multiple comparisons, when thresholding the contrast at an FDR of $q = 0.1$. At a less conservative FDR of $q = 0.3$ (corresponding to a z-score of -2.68) meaning that 30% of significant results should be rejected as false-positive findings, we found reduced activity at stimulus onset in parts of left and right FEF, left IPS and in a few voxels in right IPS, extending into lateral occipital cortex. These regions included 431 voxels of which 213 overlapped with lag-1 color priming effects (white voxels in the lower images in Fig. 3 indicate overlap). When choosing an uncorrected threshold (z-score < 3.1, or equivalent: $P < 0.001$) corresponding to the threshold used by Kristjánsson et al. (2007), we find similar results showing that left and right FEFs and left IPS still reached the threshold for significance.

Lag2+ Priming Effects

Besides conducting a replication of earlier findings, our aim was to identify correlates of the temporal signature of priming that decays over a number of intervening trials. To reiterate, the statistical model used for analyzing the fMRI signal included regressors for the collective priming signal for all repetitions beyond lag-1 repetitions combined using a weighted sum, given an exponentially decaying priming signal as a function of the number of intervening trials (Fig. 2). Figure 3, in the third row, shows lag-2+ priming effects, for color (left) and for location (right). After correction for the FDR, significant priming-related reductions in stimulus onset-related activity were visible in parts of right IPS and ACC for lag2+ color repetition. A large portion of IPS (left and right) and portions of left and right FEF showed significant reductions in activity that were related to lag2+ location priming. Because of the strong lag-1 color priming effects, and the absence of a significant lag-1 location priming effect, we identified significant voxels of both lag2+ priming contrasts (i.e., both color and location) that overlapped with significant voxels in the lag-1 color priming contrast (Fig. 3, lower row). In total, 48 of 54 voxels that showed significant reductions following lag-2+ color priming overlapped with significant voxels in the lag-1 color priming contrast and 1263 of 2244 significant voxels within the lag2+ location contrast overlapped with significant voxels in the lag-1 color priming contrast. While color repetition effects are strong at lag-1, they are much weaker at lag-2+, whereas the location repetition effect is also strong at lag-2+. This may reflect that the decrease in color repetition effects is faster than the decrease in location repetition effects, which was also true for the behavioral results.

ROI Analyses

To verify that the whole brain effects corresponded to those found by Kristjánsson et al. (2007), as well as to identify significant voxels within smaller regions to increase statistical power, we next created ROIs based on peak reductions in the earlier study (with independent data), which focused on lag-1 color priming, by drawing a sphere at the peaks' coordinates and intersecting the spheres with the cortical mask and stimulus onset activations, as described in Methods. We then defined a threshold for significance using the FDR ($q = 0.1$) within that set of voxels. In Tables 1 and 2, we report the number of voxels below the derived threshold for significance after correcting for FDR, as well as peak z-scores and coordinates within the ROI. We only included the peak coordinates that overlapped with the field of view of our scans. We found that overall this ROI analysis confirmed the pattern of our whole brain analysis. Specifically, regions including left and right IPS and FEF showed correspondence with the findings in the former study, for lag-1 color priming. There was also overlap in left and right IPS and right FEF with the contrast for lag-2+ color priming, although this was smaller.

Similarly, we ran the analysis for lag-1 and lag-2+ location priming with ROIs derived from the lag-1 location priming activations in the study of Kristjánsson et al. (2007). We again saw a pattern that corresponded to our whole-brain findings. Notably, we found significant correspondence between the lag-1 location priming effects in right FEF and left FEF. We found significant overlap between lag-1 and lag-2+ location priming in left and right IPS, right inferior parietal and right FEF. In sum, regions where we observe priming effects, both for color and for location and both for lag-1 priming and for lag-2+ priming, show good correspondence with the regions where Kristjánsson et al. (2007) observed lag-1 priming effects. Note that, while we find lag-2+ location priming effects in left and right FEF in the whole brain analysis, we did not confirm overlap in left FEF with the Kristjánsson et al. (2007) results. Moreover, we did not find lag-2+ color priming effects in left FEF. This could reflect that statistical power was rather weak, and indeed, when we increased the FDR-threshold to $q = 0.2$, we saw a pattern of BOLD reductions that included the left FEF for both color and location lag-2+ priming, showing 195 and 184 significantly reduced BOLD activations in left FEF voxels, respectively.

Longer-Lasting Priming Effects

Because the lag-2+ priming effect relied on a regressor that was composed of many underlying factors (i.e., the lag-2 repetitions, lag-3 repetitions, and beyond), the effects could have been driven entirely by lag-2 repetitions, with no effects of repetitions at lag-3 and greater. To determine which specific repetition lag drove these combined lag-2+ repetition effects, we ran additional analyses using models that included independent regressors for 1–12 repetitions of the target color and the target location. We averaged the BOLD signal in each ROI per observer, as described in Methods, and calculated parameter estimates for these models in each region. Figures 4 and 5 show the BOLD parameter estimates per repetition lag for color and location, respectively. Note that in most regions, including the FEF and IPS, parameter estimates for early repetitions up to 4 or 5 lags are mostly below 0, whereas for later repetitions the parameter estimates are around 0, indicating that the lag-2+ contrasts mirror a longer-lasting priming effect than just 2 lags, in correspondence with our behavioral results.

Session-to-Session Variance

To further evaluate the relation between behavioral effects (i.e., RT reductions) and effects in the BOLD response, we selected the voxels in the ROIs reported in Tables 1 and 2 that were significant after correcting for multiple comparisons, as described in the last paragraph of Methods. We then assessed how the mean parameter estimates per ROI for each of the 4 priming regressors (lag-1 and lag-2+, color and location) predicted the

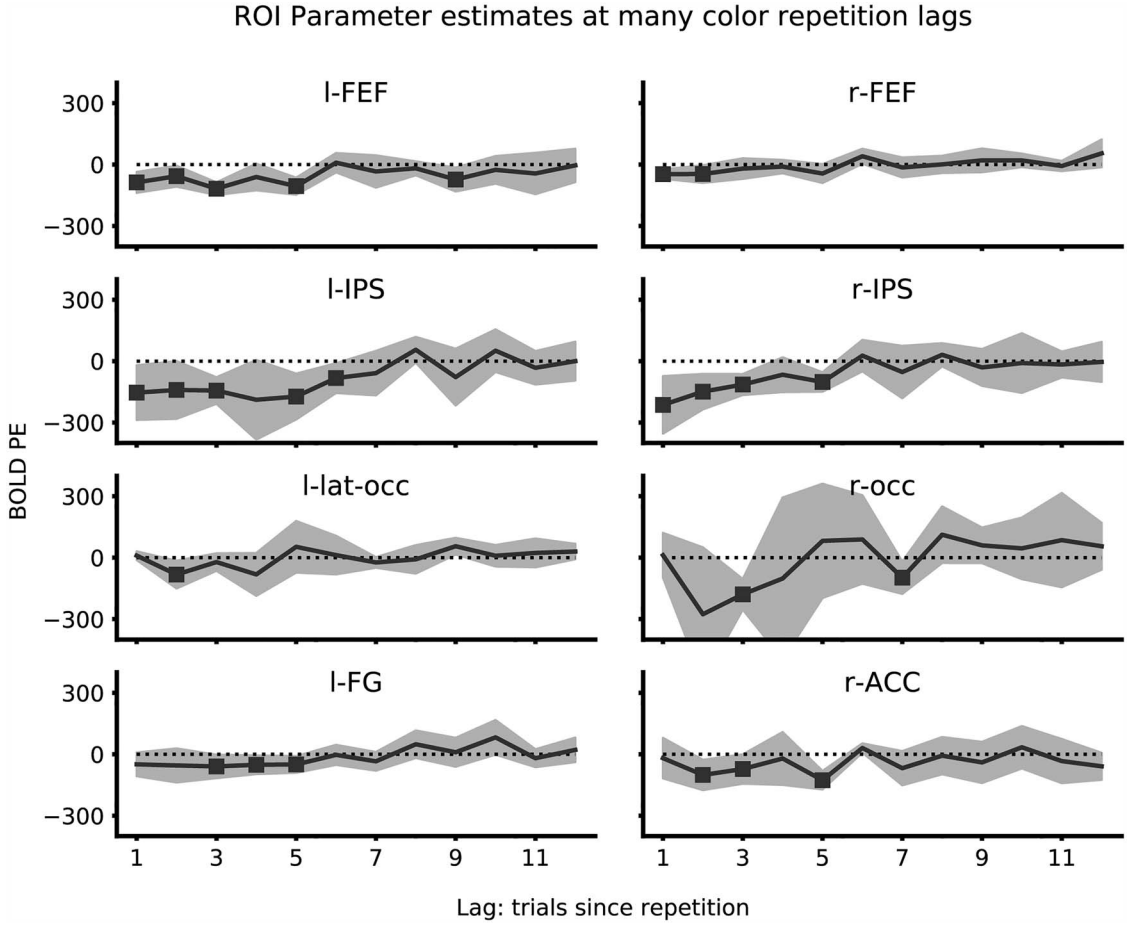

Figure 4. BOLD parameter estimates as a function of the number of trials between color repetitions in ROIs that were derived from Kristjánsson et al. (2007). The lighter area indicates the 90% confidence interval ($df = 5$). The square dots highlight parameter estimates that are below zero, given the confidence interval's upper boundary.

parameter estimates for the RT data and those regressors. We compared the parameter estimates per experiment run in one linear mixed model per priming regressor and found that, in 3 cases, the BOLD parameter estimates significantly predicted the RT parameter estimates (lag-2 color priming: $\chi^2(3) = 39.81$, $P < 0.001$; lag-1 location priming: $\chi^2(2) = 19.00$, $P < 0.001$; and lag-2 location priming: $\chi^2(5) = 29.54$, $P < 0.001$). Running the same analysis with each separate ROI yielded the same results (all P-values ≤ 0.003), except in the left FEF for location lag-1 priming ($P = 0.07$). This per-ROI analysis also revealed that the BOLD and RT parameter estimates were all positively correlated. Color lag-1 priming, however, was not significantly predicted by the BOLD parameter estimates ($\chi^2(4) = 6.3$, $P = 0.18$). Whereas the latter absence of a correlation between parameter estimates is perhaps surprising (since we found a strong signature of lag-1 color priming in the BOLD-signal), the results for lag-1 location priming and lag-2+ color and location priming further establish the relation between BOLD reductions in these ROIs and the RT signature of search priming. Figures 6 and 7 provide a more in-depth overview of the correlation coefficients across significant ROIs between BOLD and RT parameter estimates, within observers (Fig. 6), and across observers (Fig. 7). Note, that while the majority of these individual correlations was not significant, the overall trend suggests a positive correlation between behavioral effects and the BOLD effects within observers, except for lag-1 color priming. Across observers, the same positive trend was visible, but not for location lag-2+ priming, suggesting that the positive correlation between BOLD and RT parameter estimates, at least for lag-2+ location priming, is driven by within-observer and not across-observer variance. None of the across-observer correlations were significant.

Discussion

Our aim was to identify neural correlates of priming of feature-based and spatial attention. We specifically addressed how the priming of attention during visual search modulated the BOLD signal and task performance across time. We asked whether the longer-lasting priming effects of target and distractor features and locations on visual search are reflected in the same frontoparietal regions as immediate effects of trial repetitions to assess the proposed role of these regions in attentional priming (Kristjánsson et al. 2007). We first confirmed that a model based on the exponential decay of priming fitted the behavioral data well. Both repetitions of target color and repetitions of target location contributed to reduced RTs and these effects decayed over trials, in correspondence with previous findings (Maljkovic and Nakayama 1994; Maljkovic and Martini 2005; Martini 2010). We found evidence for reduced BOLD responses for repeated features and locations in frontoparietal regions, notably IPS and FEF, replicating previous imaging

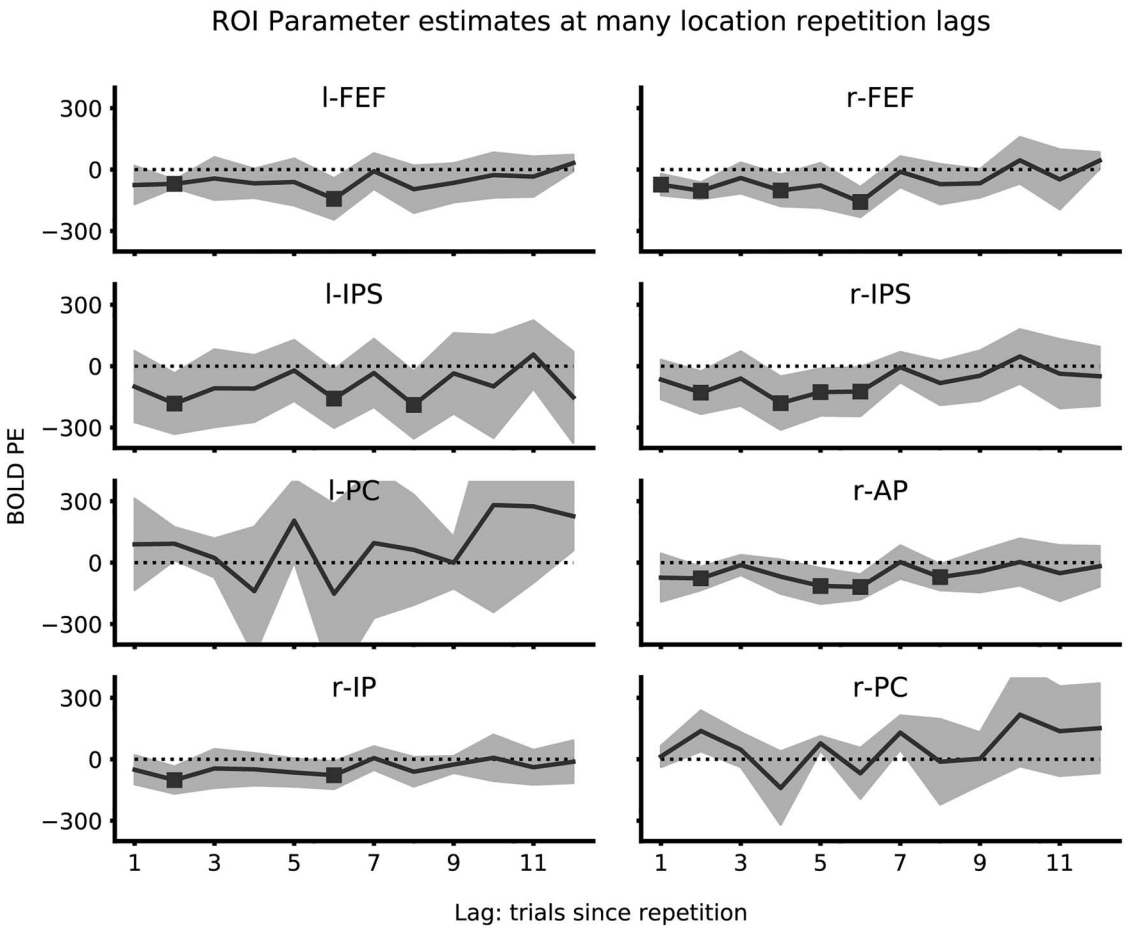

Figure 5. BOLD parameter estimates as a function of the number of trials between location repetitions in ROIs that were derived from Kristjánsson et al. (2007). The lighter area indicates the 90% confidence interval ($df = 5$). The square dots highlight parameter estimates that are below zero, given the confidence interval's upper boundary.

studies (Kristjánsson et al. 2007; Rorden et al. 2011), even though these effects only survived a correction for multiple comparisons over the whole brain for color. This difference might be due to lower statistical power for location priming effects, given that the probability of target location repetition (0.25) was lower than for target color repetition (0.5). Consistent with this, we found significant BOLD reductions associated with all priming regressors when we conducted ROI-based analyses, a more statistically powerful approach. Beyond this replication of earlier work with regard to lag-1 priming effects, we found evidence for repetition suppression within the same regions reflecting longer-lasting priming. This shows that activity in the same network is likely to reflect both immediate and longer-lasting characteristics of attentional priming, providing strong evidence that it is part of the neural basis of attentional priming and, more broadly, of selective attention that relies on the discriminability between items by feature or by location. Finally, by comparing fMRI BOLD reductions and RT reductions across experimental runs, we found that across-run differences in these 2 variables are significantly correlated, providing further evidence that these BOLD reductions form neural correlates of attention priming. However, the absence of a correlation between lag-1 color priming and a reduced BOLD-signal across sessions may suggest that the lag-1 color priming effect is indeed composed of 2 independent components (Martini, 2010). Specifically, a strong and fast decaying component, that is unrelated to the reduced activity in the frontoparietal network we show here, may have masked the correlation between lag-1 priming and the BOLD-signal in our session by session analysis. An interesting direction for future study, therefore, may be to disentangle these different components further and identify their neural correlates.

We have defined attention priming as a kind of search facilitation due to intertrial repetition of color or location, but another perspective is that it is a type of search impairment due to an intertrial change of color or location. Importantly, the direction of lag-1 priming-related BOLD signals is subject to a similar type of ambiguity. Regarding color priming, Rorden et al. (2011) suggested that, rather than repeated items eliciting a smaller BOLD response relative to baseline, role reversals of target and distractors specifically enhance the BOLD response above baseline. This idea is reminiscent of results in other paradigms, where increased BOLD activations in FEF and IPS are associated with attentional switches between feature dimensions (Liu et al. 2003) and between features within feature space (Serences and Yantis 2007). In this study, we have not attempted to resolve the dissociation between target–distractor switches and repetitions. The decaying priming signal might as well reflect a decaying impairment to perform the task after a switch. The current results fit well within other literature that relates priming to either repetition suppression or switch-related activations. Neu-

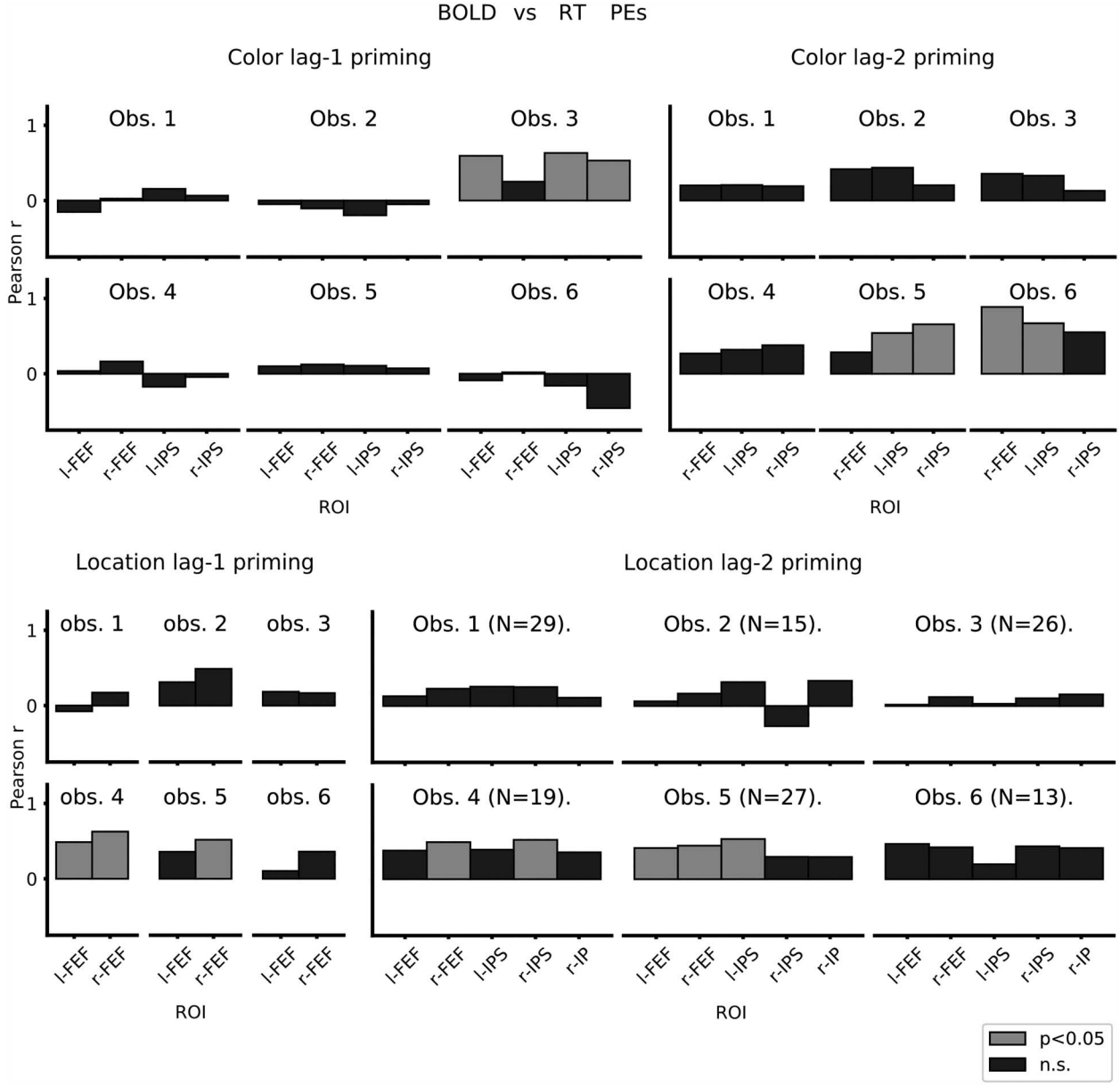

Figure 6. Pearson correlation coefficients of mean BOLD parameter estimates in significant voxels with the RT parameter estimates for lag-1 and lag-2+ priming of color and location. Light bars reflect significant correlation coefficients, while darker bars reflect correlation coefficients that were not significant.

roimaging studies show that the regions that show lag-1 effects in the BOLD-response show a decay of those effects that corresponds to the decay of behavioral priming effects. For example, in an object identification task, the occipitotemporal BOLD effect that was related to repetition decayed with the lag between trials (Henson et al. 2004). Similarly, activity in the ACC and pre-supplementary motor area decayed after switching between 2 types of Stroop tasks (Todd et al. 2005).

While the frontoparietal network highlighted in this study has been extensively related to selective spatial attention and to feature selective attention (Liu et al. 2011; Scolari et al. 2015), the specific influences of priming on feature encoding remain unknown. Previous evidence suggests that the FEF are involved in feature discrimination and are sensitive to priming. Bichot and Schall (2002) showed with single-cell recordings in monkeys that the ability of FEF neurons to discriminate between target and distractors increases as item features repeat across consecutive trials. Moreover, these neural effects were correlated with behavioral effects in terms of RT. Notably, while these behavioral effects relied on eye movements rather than on button presses, they showed similar characteristics as the current behavioral data. Specifically, facilitation through repetition appeared to asymptote after around 5 trials. The current results therefore suggest that an increased ability to discriminate between display items through repetition of stimulus features and stimulus locations while performing a feature-based search task may lead to a reduced BOLD response and that the effect scales with behavioral priming effects over longer trial runs (most prominently in right FEF), in correspondence with the findings from single-cell recordings.

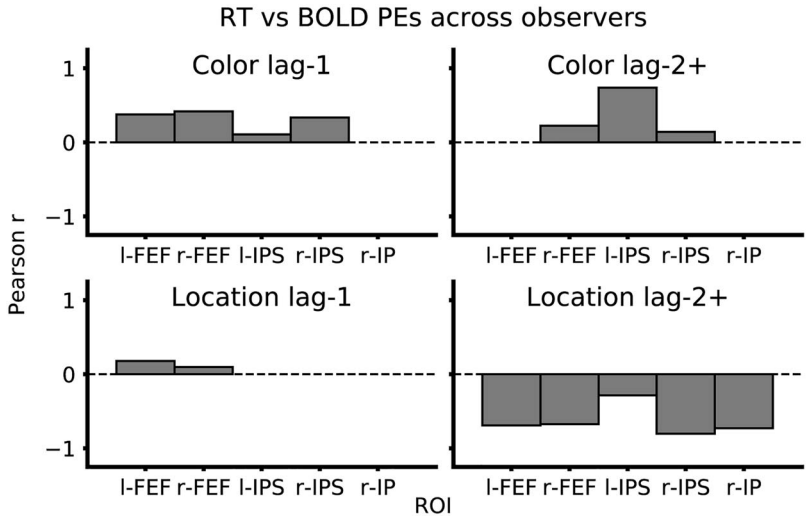

Figure 7. Pearson correlation coefficients across observers of mean BOLD parameter estimates in significant voxels, with the RT parameter estimates for lag-1 and lag-2+ priming of color and location.

While the paradigm in our study has been referred to as pop-out search in previous studies, we refer to the effect as attention priming. We have avoided calling the task pop-out search, because identifying a subtle feature such as the shape of the target (the notch's location) may require focal attention, compared to distributed attention across the entire search display when observers report whether a target is present (Bravo and Nakayama 1992). Just as priming effects on RTs may be different for identical search displays depending on the required response (Olivers and Meeter 2006), those priming effects may also show a difference in associated BOLD response. Attentional priming has been shown to occur for many types of search, ranging from easy to difficult (Ásgeirsson and Kristjánsson 2011). The results of Bichot and Schall (2002), which relied on a task without such a focal component, however, suggest that our findings rely on similar mechanisms as are involved in priming of pop-out, but we have little evidence that the current effects are unique to pop-out search. But importantly, the repetition of target-defining features underlies both our effects and the priming of pop-out effects found by Bichot and Schall (2002), suggesting a general mechanism for feature-based, exogenously cued attention in the frontoparietal network.

Conclusion

To summarize, we replicated earlier findings that color repetition and location repetition reduce the BOLD response associated with search display onset in the frontoparietal network, specifically in bilateral FEF and IPS. Beyond this, we found that the behavioral signature of these effects, a repetition-related RT reduction that exponentially decays as a function of the number of intervening trials, is mirrored by a similar pattern of BOLD repetition suppression in the same frontoparietal regions. This correspondence between the patterns found in the behavioral and the functional imaging data provides strong evidence that these brain areas form (part of) the cortical basis of attentional priming.

Funding

Icelandic Research Fund (Rannis, #130575-051 to M.B. and J.W.B.); the ERC (grant 643636 to A.K.); the Icelandic Research Fund (#130575-051, #152427-051 and #173947-051); and the Research Fund of the University of Iceland. Netherlands Organization for Scientific Research (grant #452.17.012 to B.M.) and Portuguese Foundation for Science and Technology (grant #IF/01405/2014 to B.M.).

Notes

We would like to thank our reviewers for valuable suggestions and Tomas Knapen for technical support and valuable input to our study design.

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