The Devil Is in the Detail: Brain Dynamics in Preparation for a Global–Local Task

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Abstract

When analyzing visual scenes, it is sometimes important to determine the relevant “grain” size. Attention control mechanisms may help direct our processing to the intended grain size. Here we used the event-related optical signal, a method possessing high temporal and spatial resolution, to examine the involvement of brain structures within the dorsal attention network (DAN) and the visual processing network (VPN) in preparation for the appropriate level of analysis. Behavioral data indicate that the small features of a hierarchical stimulus (local condition) are more difficult to process than the large features (global condition). Consistent with this finding, cues predicting a local trial were associated with greater DAN activation. This activity was bilateral but more pronounced in the left hemisphere, where it showed a frontal-to-parietal progression over time. Furthermore, the amount of DAN activation, especially in the left hemisphere and in parietal regions, was predictive of subsequent performance. Although local cues elicited left-lateralized DAN activity, no preponderantly right activity was observed for global cues; however, the data indicated an interaction between level of analysis (local vs. global) and hemisphere in VPN. They further showed that local processing involves structures in the ventral VPN, whereas global processing involves structures in the dorsal VPN. These results indicate that in our study preparation for analyzing different size features is an asymmetric process, in which greater preparation is required to focus on small rather than large features, perhaps because of their lesser salience. This preparation involves the same DAN used for other attention control operations.

INTRODUCTION

Our brain controls how we gather and use information from the environment. An example of such control is our ability to focus on the global features provided by a stimulus or on its details. This type of attentional control is often studied using “hierarchical” stimuli (i.e., large letters made up of smaller letters, which can be the same as or different from the large letters). Hierarchical stimuli can lead to different responses, depending on whether the participant’s task requires attention on the “global” (big picture) or “local” (detail) features of the stimuli (Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Van Kleek, 1989; Navon, 1977). During the last two decades, investigators have shown that this attention “focusing” process is carried out by a set of dorsal brain structures in the frontal and parietal cortex, which have been collectively labeled the “frontoparietal” or “dorsal attention network” (DAN; Ruge et al., 2005; Weissman & Woldorff, 2005; Brass & von Cramon, 2004; Braver, Reynolds, & Donaldson, 2003; Corbetta & Shulman, 2002; Weissman, Mangun, & Woldorff, 2002; Fink et al., 1997). In addition, areas in the visual processing network (VPN) are likely to be important for processing local and global features. In this case, an important distinction can be made between the set of areas most responsible for processing information coming from the magnocellular layers in the LGN (characterized by low visual acuity but fast processing) mostly contributing to the dorsal visual pathway and those largely responsible for processing information from the parvocellular layers in the LGN (characterized by high visual acuity but slow processing) mostly contributing to the ventral pathway (e.g., see Coleman et al., 2009, for a similar argument about the roles of these pathways in global–local tasks).

There is a large amount of evidence in support of the involvement of the DAN in the control of attention, coming from a variety of populations, paradigms, and conditions. These include patients with lesions in DAN regions (Ptak & Schneider, 2010; Corbetta, Kincade, Lewis, Snyder, & Sapir, 2005; Polster & Rapcsak, 1994; Lamb, Robertson, & Knight, 1989), functional brain imaging data (Bressler, Tang, Sylvester, Shulman, & Corbetta, 2008; Corbetta & Shulman, 2002; Hopfinger, Buonocore, & Mangun, 2000), and more recently data obtained with TMS (Capotosto, Babiloni, Romani, & Corbetta, 2009). More specific to the deployment of local versus global attention, Weissman and colleagues (2002) have shown, using fMRI, that the DAN is engaged in following cues.

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that indicate whether upcoming hierarchical stimuli should be responded to on the basis of the large or small letters. This activity is considered preparatory for processing the upcoming stimuli. In addition, in a companion paper (Weissman & Woldorff, 2005), they observed that a DAN region near the intraparietal sulcus exhibited lateralized activity, with greater up-regulation in the left hemisphere to cues requiring preparation for processing local features than to those requiring preparation for global features in the upcoming trial. The response in the right hemisphere did not significantly distinguish local and global cues.

This finding is consistent with two observations that are commonly present in the literature. First, the local and global tasks are not equivalent: Participants have a bias to respond on the basis of global rather than local information, as demonstrated by faster RTs, higher accuracy, and smaller conflict effects when the global and local features are associated with different responses (Han, Fan, Chen, & Zhuo, 1999; Heinze & Munte, 1993; Van Kleek, 1989; Navon, 1977). These findings have been modeled as the result of a competitive process between the analysis of global and local information, with a speed advantage for the global analysis (Heinze et al., 1998; Van Kleek, 1989). In Weissman and colleagues’ (Weissman & Woldorff, 2005; Weissman et al., 2002) studies, the global bias is reflected by a greater need for preparation after local cues than after global cues. Thus, there is substantial indication that the brain’s default mode is oriented toward a global analysis. The data also suggest that there may be a hemispheric specialization, with the left hemisphere specialized for local processing and the right hemisphere specialized for global processing (Heinze et al., 1998; Heinze & Munte, 1993; but see also Volberg & Hübner, 2007, for findings contrary to such specialization). This is consistent with evidence from lesion studies (Lamb et al., 1989; Robertson, Lamb, & Knight, 1988; Delis, Robertson, & Efron, 1986) and to some extent with data from ERP studies (Evans, Shedden, Hevenor, & Hahn, 2000; Yamaguchi, Yamagata, & Kobayashi, 2000; Han et al., 1999; Heinze et al., 1998; Heinze & Munte, 1993). In Weissman et al.’s (2002) study, hemispheric specialization could account for the differences observed in the left, but not the right, hemisphere during preparation for the local task. The left/local–right/global processing specialization is also consistent with theories proposing a categorical (corresponding to larger receptive fields in the right hemisphere) versus coordinate (corresponding to smaller receptive fields) processing distinction between the two hemispheres (e.g., Jager & Postma, 2003), thus framing this finding into a more general theory of hemispheric specialization.

An alternative way in which participants may get ready for the local or global task is by maintaining the preparatory set used in the previous trial, whichever it was. In this case, the preparatory processes would be dominated by the need to change the attention set whenever the cue signaled a switch (i.e., task switching, Monsell, 2003; Wylie & Allport, 2000; Allport, Styles, & Hsieh, 1994; Jersild, 1927). In this case, we would expect greater brain activity when the cue signals a switch than when it does not (as in Hopfinger et al., 2000; Meiran, 2000; Sohn, Anderson, Stenger, & Carter, 2000; for a review, see Karayanidis et al., 2010).

Although this provides a general frame of reference for understanding how individuals may prepare for processing global or local information, several questions remain unanswered. First, what is the relationship between the frontal and parietal structures composing DAN? Are they activated simultaneously or at different times? Latency differences may provide information about the flow of activation across different DAN structures, which is a rationale used in previous studies (Mathewson et al., 2014; Baniqued, Low, Fabiani, & Gratton, 2013). Given the relative temporal and spatial proximity of the phenomena involved, a prerequisite for this analysis is to employ a technique that is able to identify both the timing (with a resolution of the order of 100 msec) and the location (with a resolution of 1–2 cm) of cortical activation. In this article, we used the event-related optical signal (EROS; Gratton & Fabiani, 2010; Gratton, Corballis, Cho, Fabiani, & Hood, 1995). This technique has been employed in studies of response preparation during task switching (Baniqued et al., 2013; Gratton, Rykhlevskaia, Wee, Leaver, & Fabiani, 2009), showing that it can temporally and spatially separate brain activations associated with different phases of preparation. To provide appropriate spatial and temporal resolution, here we used an extended recording montage based on 1024 channels (across different recording montages) covering the entire scalp, with a spatial density of approximately one channel every 0.2 cm² and a temporal sampling of 25.6 msec.

A second question we address in this article is about the functional significance of the preparatory brain activity. Is this activity relevant to or at least predictive of subsequent behavior? In other words, if the DAN activity is important for subsequent behavior, its amplitude should predict the extent to which participants are better prepared for the upcoming stimuli. Specifically, we hypothesize (a) that preparatory activity should lead to a reduction in the difference between local and global RTs (or accuracy) by providing a head start for the relevant processing stream and (b) that by providing this processing head start, it should also lead to a reduction in the conflict effect obtained when the irrelevant dimension provides incongruent information with respect to the relevant dimension. Although this analysis can be carried out by considering the entire DAN network as a unit, it can also be carried out separately for each of its components, thus providing information about which of these structures is more directly related to the control of the processing of the upcoming stimulus.

Recent research (Romei, Thut, Mok, Schyns, & Driver, 2012; Romei, Driver, Schyns, & Thut, 2011) indicates that global–local task biases may interact with oscillatory brain activity. These authors showed that the rhythmic TMS
(rTMS) of parietal cortex could influence these biases, with 5-Hz stimulation favoring global processing and 20-Hz stimulation favoring local processing. In addition, 10-Hz stimulation in the right hemisphere appears to affect global processing more than local processing, whereas the same stimulation in the left hemisphere appears to have an opposite effect. It is possible that rTMS at these frequencies may induce brain rhythms of corresponding frequencies, which in turn could mediate the global or local bias effects. To test this hypothesis, we carried out a time–frequency analysis of the fast optical signal data to determine if the global–local cues could induce the occurrence of preparatory theta, alpha, and beta activity in the DAN. Furthermore, we were interested in determining whether lateralization of alpha activity in visual processing areas could be associated with local–global preparation.

Finally, we were interested in demonstrating a correspondence between the locations of preparatory processes for local and global cues and the subsequent processing pathways that are engaged to process the actual response stimuli. To this end, we analyzed the EROS responses after the presentation of the response stimuli. Specifically, we were interested in determining whether the local or global task would preferentially involve visual processing areas in the left or right hemisphere and in the dorsal or ventral pathways.

In summary, in this article we are interested in analyzing the spatiotemporal dynamics of the brain networks associated with preparation for processing local and global information. We use cues predicting which of the information levels of an upcoming hierarchical stimulus (global or local) is relevant on a particular trial. We examine the brain activity following the cues using EROS from an extended, high-density montage to provide data about brain activity combining high spatial and temporal resolution. We further analyze the relationship between the preparatory brain activity in the DAN network and subsequent behavior. Finally, we analyze the EROS activity following the response stimuli to assess its relationship with the preparatory activity.

METHODS
Participants
Sixteen young adults (eight men; age range = 18–30 years) participated in this study and received compensation of $10/hr. All participants were native English speakers, were right-handed, and had normal or corrected-to-normal vision. All participants reported being in good health and were free from medications affecting the CNS. Participants were run in four separate sessions: (1) 3-D digitization of the locations of optical sources and detectors; (2) structural MRI recording for anatomical coregistration; and EROS data collection during the (3) global–(4) local task. The study was approved by the institutional review board of the University of Illinois, and all participants provided informed consent.

Stimuli and Procedures
A schematic of the paradigm is shown in Figure 1A. Participants performed a global–local task in which a cue informed them whether they had to attend to the local (L = little) or the global (B = big) features of the upcoming target stimulus. Cues were randomized, with equal probability of occurrence. Thus, some trials involved switching from one level of analysis to another (switch), whereas others involved attending to the same level as the previous trial (no switch).

Participants were seated at an 80-cm distance from the screen. Stimuli were presented at the center of a 15-in. computer monitor. Both cues and targets were presented for 400 msec, with a SOA of 2000 msec for both cue-to-target and target-to-cue. Cue stimuli were presented at a visual angle that subtended 1.22° horizontally and 1.6° vertically. The target stimuli were the letters H and S, composed of smaller Hs and Ss, resulting in four trial types: two congruent (large H made up of small Hs and large S made up of small Ss) and two incongruent (large H made up of small Ss and large S made up of small Hs; see Figure 1B). The presentation order of the four target stimuli was randomized, with equal probability for each stimulus type. The stimuli appeared in san serif font with the size of the global letters corresponding to font size 210 (visual angle subtended 3.5° horizontally and 5.36° vertically) and the local letters to font size 12 (visual angle subtended 0.24° horizontally and 0.28° vertically).

Participants responded to the target stimuli by pressing the “m” key with the right hand or the “z” key with the left hand on the computer keyboard. The key-hand response mapping was counterbalanced such that half the participants indicated “H” with a left-handed response (and “S” with a right-handed response) whereas the other half did the opposite. Participants were presented with 20 blocks of 24 trials for each of four recording montages (see Optical Recordings section below). The start of each block was self-paced, in that the participant pressed the space bar to begin each block of trials. Participants were told to respond as quickly and accurately as possible. The first trial of each block was excluded from all analyses, as it could not be classified as either switch or no switch.

To ensure that participants understood the task and reached a stable performance level before the optical recording, they were each given a training session. The training session consisted of two blocks of 24 trials presented at a slowed pace to allow the participant to adapt to the demands of the task. Five blocks of 24 trials presented at the same pace as the actual experimental trials immediately followed the slow blocks to complete the practice.
Optical Recording and Analysis

Optical Recordings

The optical data were recorded continuously using two independent Imagent frequency domain systems manufactured by ISS, Inc. (Champaign, IL), each with 64 sources and eight detectors. Sources were laser diodes coupled with 0.4-mm optic fibers, emitting near infrared light (830 nm). Detectors were 3-mm fiber-optic bundles coupled to photomultiplier tubes (PMTs). The current feeding into the PMTs was modulated at 110.00625 MHz over frontal and central brain regions and at 300.00625 MHz over parietal and occipital regions (frontal/parietal regions were always recorded simultaneously, as were central/occipital regions). Maclin, Low, Fabiani, and Gratton (2007) showed that these two modulation frequencies yield similar EROS responses once the phase delay data are transformed into picoseconds. The sources and PMTs were modulated and synchronized with one another, allowing for the two frequencies to be multiplied to generate a 6.25-kHz heterodyne frequency. This frequency was slow enough to be appropriately sampled and analyzed.

The output current from the PMTs was Fourier transformed using the fast Fourier transform algorithm for computation of DC (average) intensity, relative phase delay (picoseconds), and AC (amplitude) measures. The final sampling rate was 39.0625 Hz. A modified motorcycle helmet was used to secure the source and detector fibers on the participant’s head.

Four recording montages were devised to effectively record optical data from a majority of the cortex while avoiding cross-talk. The montages were based on front–back pairs of rows of sources and detectors, with sources and detectors approximately equidistant along the front–back direction and rows being equidistant and concentric with respect to the ear canal. Two interdigitized montages investigated frontal and parietal areas (using the left row of each pair in one session and the right row in the other session), and two investigated central and occipital/temporal areas (using the same approach). The order of the different montages (left vs. right rows, front/parietal vs. central/occipital region) was counterbalanced across participants. Each EROS montage included 16 detectors corresponding to each of 16 multiplexed sources allowing
for the recording of 256 channels per montage for a total of 1024 channels across montages. Source–detector distances ranged between 10 and 170 mm, but channels with distances less than 20 mm or greater than 55 mm were excluded from further analysis because they were either unlikely to pass through the cortex (distances < 20 mm) or were too noisy because of the large source–detector distance (distances > 55 mm).

Coregistration

For each participant, the locations of all sources and detectors in relation to the nasion and preauricular points (fiducial points) were digitized using a Polhemus 3-Space Fastrak 3-D digitizer (Polhemus, Colchester, VT). Note that the optical and digitization sessions were actually run consecutively within a single day. The optical locations were digitized first, and then fibers were attached for Session 1. For Session 2, each of the source and detector fibers was moved to new locations, but the helmet used to keep the fibers in place was never moved. We keep the helmet securely strapped on the head with a chin strap to reduce the likelihood of movements. This approach limits fiber location movements across sessions to less than a few millimeters. Furthermore, volumetric T1-weighted structural MRI data (MPRAGE) were collected on all participants in a separate session. The same fiducial landmarks used for optical digitization and recording were identified during the scans with vitamin E pills. The digitized images of the light source and detector locations were spatially aligned with the MRI image using the three fiducial points as markers followed by surface fitting of the digitized recording points to the scalp surface using a Levenberg–Marquardt algorithm (least-squares fit) and standard Talairach transformation (Whalen, Maclin, Fabiani, & Gratton, 2008) to permit the computation of statistics across participants. The locations of the sources and detectors relative to an anatomical image for a representative participant are presented in Figure 2.

EROS Analysis

The phase data were corrected for phase wrapping, converted from degrees to picoseconds and adjusted to a mean of zero. Pulse artifacts were removed according to a previously described algorithm (Gratton & Corballis, 1995). After the application of a band-pass filter of 0.5–6 Hz, the data were segmented into 2200-msec epochs around the cue, with 180 msec prestimulus baseline and 2020 msec poststimulus. A comparable analysis, with similar temporal properties, was also conducted around the response stimulus. The time series were averaged for each participant and channel to create a 2 (global vs. local) × 2 (switch vs. no switch) set of EROS averages.

Channels with standard deviations of the phase greater than 80 psec were excluded from further analysis. In-house software “OPT-3D” (Gratton, 2000) was used to combine channels whose mean diffusion paths intersected for a given brain volume and to compute group level statistics. A two-dimensional reconstruction algorithm was used to generate maps of surface activation. An 8-mm Gaussian filter (based on a 2-cm kernel) was used to spatially filter the data.

To analyze activity in the DAN, we selected four ROIs for each hemisphere comprising BA 8, BA 9, BA 7, and BA 40. The specific boundaries of the ROIs were derived from previous fMRI research using cueing global–local manipulations (Weissman et al., 2002; see also Corbetta & Shulman, 2002; Hopfinger et al., 2000, for other work identifying DAN) and optical imaging research investigating top–down attention control processes (Baniqued et al., 2013). In addition, we selected two areas along the ventral visual pathway (the ventral section of BA 19 and BA 37), which were chosen because they are typically involved in letter processing (e.g., Heinzel et al., 2008). The boundaries of each ROI are presented in Table 1.

Group level t statistics for each voxel were calculated using an error term pooled across time. These t values

Table 1. ROI Boundaries (in Talairach Coordinates, mm)

<table>
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<tr>
<th>Area</th>
<th>Left</th>
<th>Right</th>
<th>Back</th>
<th>Front</th>
<th>Bottom</th>
<th>Top</th>
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<tbody>
<tr>
<td>BA 9</td>
<td>−60</td>
<td>60</td>
<td>−10</td>
<td>25</td>
<td>25</td>
<td>45</td>
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<tr>
<td>BA 8</td>
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<td>60</td>
<td>30</td>
<td>50</td>
<td>35</td>
<td>55</td>
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<tr>
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<td>60</td>
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<td>−50</td>
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<td>55</td>
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<td>−30</td>
<td>−35</td>
<td>−5</td>
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</table>
were then converted to Z scores, with appropriate correction for multiple comparisons using random field theory based on the number of independent resolution elements (resels) within each ROI (Kiebel, Poline, Friston, Holmes, & Worsley, 1999). Z scores were orthogonally projected onto axial, sagittal, and coronal surfaces of a brain in Talairach space.

**Time–Frequency Analysis**

A time–frequency analysis of the fast optical data was conducted by generating four different time series for each channel and block, each obtained by filtering the data using different band-pass frequencies: 1–4 Hz (delta band), 4–7 Hz (theta band), 8–13 Hz (alpha band), and 13–19 Hz (beta band; the 19-Hz upper limit corresponds to the Nyquist frequency of the data). Each of these time series was then rectified and low-pass filtered using the upper limit of the corresponding frequency band. The data were then segmented starting 154 msec before cue onsets and continuing for 1305 msec after the cues. A prestimulus baseline (corresponding to the last 154 msec before cue onset) was subtracted from the data. The data were then averaged across trials. The resulting waveforms were used for 3-D reconstruction and plotting. For quantification, we used an ROI approach based on a back projection of the data. Separate analyses were conducted for DAN (using the same four ROIs for each hemisphere used for the EROS analysis) and for VPN (using back projections and left and right ROIs corresponding to posterior parietal cortex [left: x: −55, −25; z: 35, 55, right: x: 25, 55; z = 35, 55] and left and right inferior temporal [left: x: −60, −40; z: −35, −5, right: x: 40, 60; z = −35, −5]). Data were then averaged separately for each of four latency intervals: 0–256 msec after the cue, 256–512 msec after the cue, 512–768 msec after the cue, and 768–1024 msec after the cue.

**EROS Analysis of Brain Activity Elicited by Response Stimuli**

This analysis was conducted in a manner completely analogous to that used to analyze the EROS activity elicited by the cues, with the only difference being that the time-locking events were the response stimuli.

**RESULTS**

**Behavioral Data**

Performance data were analyzed with a 2 × 2 × 2 repeated-measure ANOVA with Congruency (incongruent vs. congruent), Analysis level (local vs. global), and Switch status (switch vs. no switch) as factors. Tests were conducted for RT, accuracy (proportion correct), and inverse efficiency (i.e., RT/accuracy; Townsend & Ashby, 1983). The grand-averaged RT and accuracy data are presented in Figure 3.

A main effect of Analysis level was observed for RT, $F(1, 15) = 24.27, p < .001$, in that global trials resulted in significantly shorter RTs (515 msec) as compared to local trials (545 msec). However, there was no significant difference in accuracy between global and local trials, $F(1, 15) = .25, ns$. Furthermore, there was a main effect of Congruency for both RT, $F(1, 15) = 17.05, p < .001$, and accuracy, $F(1, 15) = 62.86, p < .0001$. As expected, participants were faster and more accurate on congruent than on incongruent trials. Finally, a main effect of Switch for RT, $F(1, 15) = 5.48, p < .05$, and accuracy, $F(1, 15) = 22.29, p < .001$, was also observed such that participants were faster and more accurate on no-switch trials.

In addition to the main effects described above, we observed a significant Analysis level × Switch interaction for accuracy, $F(1, 15) = 10.39, p < .01$: The switch cost was greater when switching to the local (.033, $t(15) = 4.89, p < .001$) than when switching to the global task (.011, $t(15) = 2.16, p < .05$). The inverse efficiency analysis revealed main effects of Congruency, $F(1, 15) = 87.27, p < .001$, Switch, $F(1, 15) = 34.79, p < .001$, and Analysis level, $F(1, 15) = 10.29, p < .01$, with no interaction.

**EROS Data**

Maps depicting the contrasts between the EROS responses elicited by local and global cues are presented in Figure 3. Behavioral data. Left: Average RTs (msec). Right: Average accuracy (proportion correct). The error bars refer to SEM.
in Figure 4. These maps use color to indicate the timing of peak activity at locations for which the contrasts “local > global” (top) and “global > local” (bottom) yielded a peak Z score greater than 2.5 (corresponding to \( p < .006 \), uncorrected for multiple comparisons) from 230 to 538 msec after cue presentation. This interval was chosen based on extant ERP results (Evans et al., 2000; Yamaguchi et al., 2000; Han et al., 1999; Heinze et al., 1998; Proverbio, Minniti, & Zani, 1998; Heinze & Munte, 1993). The colors used at each location correspond to the latency of the peak activity at that particular site. These maps also indicate that the locations of peak activity largely corresponded to the ROIs (also displayed on the maps).

Three types of analyses were performed to determine the statistical significance of the effects. The first analysis was designed to demonstrate which areas showed significant activation with respect to baseline and focused on the peak location for each ROI. In this case, the peak value (expressed as a Z score) was compared to a critical Z score \( (p < .05) \) adjusted for multiple comparisons based on the random field theory (Kiebel et al., 1999). The results of this analysis are presented in Table 2. They indicate significantly larger activity after the local than the global cues in four out of eight of the DAN ROIs (BA 8, BA 9, BA 7, and BA 40 in each hemisphere), but none for the reverse contrast. In the left hemisphere, these activities were temporally ordered from frontal to parietal regions; in the right hemisphere, this temporal ordering was less obvious. Significant activation was apparent for both the local > global and global > local contrasts, albeit at different time points, in the right BA 37. We also repeated this same analysis for switch versus no switch trials. No significant peaks were observed in either the DAN or the visual network as a function of the requirement to switch task.

In the second analysis, we were interested in determining whether there were significant differences in the time course of activity across conditions and ROIs. Therefore, we evaluated the amplitude of the EROS activity following local and global cues, averaged across an entire ROI and separately for each of five 100-msec intervals from

<table>
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<th>ROI</th>
<th>Latency</th>
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<td>−51</td>
<td>47</td>
<td>1.88</td>
<td>2.86</td>
</tr>
<tr>
<td>BA 40L</td>
<td>409</td>
<td>61</td>
<td>−41</td>
<td>27</td>
<td>2.75</td>
<td>2.78</td>
</tr>
<tr>
<td>BA 19L</td>
<td>384</td>
<td>56</td>
<td>−61</td>
<td>−8</td>
<td>1.73</td>
<td>3.14</td>
</tr>
<tr>
<td>BA 37L</td>
<td>435</td>
<td>62</td>
<td>−48</td>
<td>−6</td>
<td>2.52</td>
<td>2.87</td>
</tr>
<tr>
<td>BA 8R</td>
<td>563</td>
<td>−24</td>
<td>47</td>
<td>34</td>
<td>1.99</td>
<td>3.06</td>
</tr>
<tr>
<td>BA 9R</td>
<td>256</td>
<td>−49</td>
<td>2</td>
<td>44</td>
<td>2.32</td>
<td>2.95</td>
</tr>
<tr>
<td>BA 7R</td>
<td>435</td>
<td>−45</td>
<td>−71</td>
<td>34</td>
<td>2.20</td>
<td>2.81</td>
</tr>
<tr>
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<td>486</td>
<td>−66</td>
<td>−31</td>
<td>24</td>
<td>2.16</td>
<td>2.76</td>
</tr>
<tr>
<td>BA 19R</td>
<td>358</td>
<td>−52</td>
<td>−73</td>
<td>−21</td>
<td>2.36</td>
<td>3.32</td>
</tr>
<tr>
<td><strong>BA 37R</strong></td>
<td><strong>435</strong></td>
<td><strong>−63</strong></td>
<td><strong>−23</strong></td>
<td><strong>−18</strong></td>
<td><strong>3.34</strong></td>
<td><strong>3.13</strong></td>
</tr>
</tbody>
</table>

ROI/Time points with Z scores above the \( p < .05 \) threshold are presented in bold. Latency is expressed in milliseconds after cue presentation, \( x, y, \) and \( z \) coordinates are expressed in millimeters (Talairach coordinates).
200 to 700 msec after cue presentation (see Figure 5, left). These values were then entered in a four-way repeated-measure ANOVA, including Analysis level (global vs. local), Hemisphere, ROI, and Time Interval as factors. The ANOVA indicated a three-way interaction between Analysis level, ROI, and Interval, $F(20, 300) = 1.82, p < .05$, indicating a different time course of the Analysis level effect across ROIs. To clarify the meaning of this interaction, we carried out separate analyses for each ROI. A significant interaction was observed in BA 40 between Analysis level and Interval, $F(4, 60) = 2.96, p < .05$, with greater activation for local during the 200–300 msec, 300–400 msec, and 500–600 msec intervals and greater activation for global during the 400–500 msec interval. In BA 9, there was a trend toward an Analysis level × Hemisphere × Interval interaction, $F(4, 60) = 2.06, p < .10$, with a general tendency to greater activity in preparation for the global task, apart from the very early and late intervals, in right hemisphere. A similar trend was observed in BA 7, $F(4, 60) = 2.17, p < .10$, but with generally greater activity in preparation for the local task, apart from very early and late intervals, in the left hemisphere. No significant effect was observed in the other areas. Thus, these findings indicate generally greater EROS responses in preparation for the local than for the global task, although these changes were significant only in regions belonging to DAN and not in the visual processing areas.

To better display the differences in time course between regions, the difference waveforms (local–global) computed across each ROI are presented in Figure 5 (right, left hemisphere only). These waveforms indicate that in the left hemisphere the latency of the peak response varied across ROIs, with shorter latency in the frontal regions (BA 8 and BA 9), intermediate latencies in parietal regions (BA 40 and BA 7, although BA 40 also showed very early activity), and the longest latencies in the visual areas (BA 19 and BA 37), reflecting a general anterior-to-posterior preparatory processing flow. This is consistent with the idea that these activities correspond to top–down preparatory control processes elicited by the local cue (when compared to the global cue).

Although overall the data did not exhibit a significant Analysis level by Hemisphere interaction, we were interested in determining whether such effects would become visible if we restricted our analyses to the parietal regions, as was done by Weissman and colleagues (2002). We therefore repeated the ANOVA using only the two parietal ROIs. In this case, the data indicated a significant two-way (Analysis level × Time interval) interaction, $F(4, 60) = 3.98, p < .01$, but no significant Analysis level × Hemisphere interaction. We thus did not find a direct support for an Analysis level × Hemisphere interaction.

A third type of analysis was related to investigating more directly the dynamics of the brain network associated with preparation for local processing, relative to those involved in global processing. To this end, we used a lagged cross-correlation approach (see Baniqued et al., 2013; Rykhlevskaia, Fabiani, & Gratton, 2006), in which we examined the lagged cross-correlations between a seed location and other locations to determine the extent to which activity in the seed location “predicted” the subsequent activities at other locations. We chose a voxel in BA 8 as...
the seed location, in which the difference between the activity for the local and global cues was greatest. This selection was made because the latency maps (see Figure 3) indicated that this location was one of the first to systematically show differential activation between local and global processing. Homologous locations were chosen in the two hemispheres ($Y = 44, Z = 42$). For each participant, we computed the correlations between the local versus global waveform at this voxel (in the left and right hemisphere) and that at all other voxels within the same hemisphere, with lags varying between 0 and 358 msec (in steps of 25.6 msec). These correlations were Fisher-transformed, and across participants, a $t$ test (with an associated $z$ score) was used to determine whether the correlation was greater than 0. Although correlations were computed for all voxels (to produce the $z$ score maps presented in Figure 6), the statistical analysis was restricted to the six ROIs used for the other analyses. To account for the problem of multiple comparisons (derived from using multiple lags and multiple ROIs), we used an alpha value of .005. In Figure 6, only the peak correlation values for the various ROIs are presented, separately for the left and right hemisphere. This figure indicates that the first area to show a significant lagged activation after BA 8 is BA 9 (with a lag of 26–51 msec, visible in both hemispheres), followed by BA 40 (with a lag of 153–179 msec, also visible in both hemispheres), consistent with a frontal-to-parietal progression of the activation. However, only BA 7 showed significant lagged activation (with a lag of 102 msec) in the right hemisphere, but not in the left hemisphere. The lagged correlations also suggested activation of the ventral visual processing stream; this activation was partly overlapping, but with an overall longer latency, with that of DAN.

**Correlations between EROS and Subsequent Behavior**

To determine the functional significance of the preparatory EROS activities described above, we computed their correlations with subsequent behavior. To reduce the number of correlations, we computed the average EROS activity for local and global trials over the entire DAN network (i.e., we averaged the values across the four DAN ROIs and across the five intervals between 200 and 700 msec, separately for left and right hemisphere, as well as the difference between the two hemispheres) for each participant and correlated these values with various indices of successful (or unsuccessful) preparatory behavior (also obtained for each participant). Specifically, these measures included the accuracy and RT difference between local and global trials (expressed in terms of local cost, with positive values indicating longer RTs and lower accuracy for local vs. global trials), the size of the RT conflict cost for local and global trials (as only incongruent trials would really reveal inappropriate preparation), and the difference between the conflict cost for local and global trials. Note that, for all these behavioral variables, a higher value
indicates greater costs (lower performance). For all these correlations, therefore, a negative value indicates that the EROS activity after the cue predicts reduction in the subsequent performance costs associated with a local level of analysis or with incongruent stimulus information.

The results are presented in Table 3. They indicate the presence of several significant relationships between the amplitude of DAN activity (as measured by EROS) during the interval between 200 and 700 msec after the cue and subsequent behavior. In general, DAN activity predicted very different effects in the left and right hemisphere. DAN activity in the left hemisphere after local cues predicted smaller subsequent local condition costs and greater global costs. DAN activity in the right hemisphere, however, was not predictive of opposite effects. This suggests that preparing the left (but not necessarily the right) hemisphere for local trials may help reduce local costs. In general, the more participants are using the left (rather than the right) hemisphere DAN to prepare for local trials, the better their performance in the local task, but at some cost for the global task. This may reflect some degree of differential specialization of the left and right hemisphere for processing local and global information and some level of competition between the two tasks.

The inverse efficiency results are in general very consistent with the RT data but, in several cases, show stronger effects. This indicates that the effects observed do not reflect a speed-accuracy trade off, but rather true changes in the speed and efficiency of processing local and global stimuli.

**Time–Frequency Analysis**

The results of the time–frequency analysis of the global versus local contrast are presented in Figures 7 (DAN) and 8 (VPN). The statistical analysis was based on a repeated-measure ANOVA design with four factors (Analysis level, Hemisphere, Region, and Interval), conducted separately for each frequency band (delta, theta, alpha, and beta) and network (DAN, encompassing ROIs in BA 8, BA 9, BA 7, and BA 40, and VPN, encompassing ROIs in the posterior parietal cortex and the inferior temporal cortex).

Figure 7 suggests that left frontal and parietal structures showed increased theta activity for global (relative to local) cues (shown in green and blue in the time–frequency plots) at latencies between 256 and 1024 msec after the cue. This visual impression was supported by a significant four-way interaction (Analysis level × Hemisphere × Region × Interval), $F(9, 135) = 3.54, p < .001$. Analyses of simple main effects showed significant lateralized Analysis level effects in BA 9 for the 256–512, 512–768, 768–1024 msec intervals and in BA 7 for the 0–256 msec interval (all $|r| > 2.26, p < .05$), with increases in theta in the left hemisphere for global, relative to local, cues. Similar, but not significant, effects were observed in the alpha band.

**Table 3.** Correlations between DAN EROS Measures (Averaged across Different ROIs and Time Points) and Subsequent Behavior

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td><strong>Local Cost</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Accuracy (0.5%)</td>
<td>$-0.03$</td>
<td>$-0.37$</td>
<td>$0.40$</td>
<td>$0.54$</td>
<td>$-0.38$</td>
<td>$0.62$</td>
</tr>
<tr>
<td>RT (33 msec)</td>
<td>$0.07$</td>
<td>$-0.36$</td>
<td>$0.07$</td>
<td>$0.63$</td>
<td>$-0.02$</td>
<td>$0.67$</td>
</tr>
<tr>
<td>IE (41 msec)</td>
<td>$-0.02$</td>
<td>$-0.45$</td>
<td>$0.29$</td>
<td>$0.70$</td>
<td>$0.24$</td>
<td>$0.78$</td>
</tr>
<tr>
<td><strong>RT Conflict Cost</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Local (27 msec)</td>
<td>$-0.07$</td>
<td>$-0.15$</td>
<td>$0.15$</td>
<td>$-0.11$</td>
<td>$-0.19$</td>
<td>$0.01$</td>
</tr>
<tr>
<td>Global (16 msec)</td>
<td>$-0.01$</td>
<td>$0.34$</td>
<td>$0.08$</td>
<td>$-0.23$</td>
<td>$-0.08$</td>
<td>$0.57$</td>
</tr>
<tr>
<td>Local–global (10 msec)</td>
<td>$-0.06$</td>
<td>$-0.48$</td>
<td>$0.08$</td>
<td>$0.12$</td>
<td>$-0.11$</td>
<td>$-0.37$</td>
</tr>
<tr>
<td><strong>IE Conflict Cost</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Local (88 msec)</td>
<td>$0.25$</td>
<td>$-0.28$</td>
<td>$0.32$</td>
<td>$-0.05$</td>
<td>$-0.10$</td>
<td>$-0.21$</td>
</tr>
<tr>
<td>Global (62 msec)</td>
<td>$0.01$</td>
<td>$0.32$</td>
<td>$0.05$</td>
<td>$-0.66$</td>
<td>$-0.04$</td>
<td>$0.68$</td>
</tr>
<tr>
<td>Local–global (25 msec)</td>
<td>$0.20$</td>
<td>$-0.44$</td>
<td>$0.23$</td>
<td>$0.49$</td>
<td>$-0.05$</td>
<td>$0.62$</td>
</tr>
</tbody>
</table>

**Bold font indicates significance ($p < .05$).**

Global LH = EROS activity across all left hemisphere DAN areas after global cues; Local LH = EROS activity across all left hemisphere DAN areas after local cues; Global RH = EROS activity across all right hemisphere DAN areas after global cues; Local RH = EROS activity across all right hemisphere DAN areas after local cues; Global LH–RH = hemispheric EROS difference across all DAN areas after global cues; Local LH–RH = hemispheric EROS difference across all DAN areas after local cues; IE = inverse efficiency (RT/Accuracy).
Figure 8 suggests that local cues elicited left-lateralized effects and global cues elicited right-lateralized effects in temporal visual processing areas in the theta and alpha bands. This was confirmed by a three-way (Analysis level × ROI × Hemisphere) interaction, $F(1, 15) = 7.96$, $p < .05$. Post hoc analyses indicated that, in temporal areas, there was increased activity for local (with respect to global) theta activity in the left hemisphere and for global (with respect to local) in the right hemisphere, $t(15) = 2.56$, $p < .05$. In parietal regions, instead, the effect was mostly due to increases in global (with respect to local) in the theta and alpha bands, $t(15) > 1.94$, $p < .05$ in both bands.

Figure 8 also indicates an increase activity in the delta band in the right hemisphere for the local task than for the global task. However, the ANOVA revealed no significant interaction between Task and Hemisphere or ROI, but only a main effect of Task, $F(1, 15) = 6.67$, $p < .05$. This may reflect the greater difficulty (and therefore greater effort required) for the local task than the global task.

Analysis of EROS Associated with the Response Stimulus

The peaks of the EROS activity elicited by the response stimuli are presented in Figure 9 (posterior view). These maps indicate that the brain activity differed depending on whether the stimuli were to be analyzed using local or global dimensions. A peak with a latency of 307 msec was observed in the left inferior temporal cortex for the local task ($y = -61$, $z = -21$, $z = 2.91$, critical $Z = 2.86$) and in the right posterior parietal cortex for the global task ($y = 24$, $z = 42$, $z = 3.14$, critical $Z = 3.07$).

DISCUSSION

The behavioral results of the current study support the idea that the global level of analysis is carried out faster and more accurately than the local level of analysis, consistent with “race models” of the global–local paradigm (Heinze et al., 1998; Van Kleek, 1989). In this sense, a “global-first” mode of processing could be considered as the “default” processing strategy. Hence, we can also expect that preparation will be more important for local than for global processing and that therefore local cues should elicit larger brain activity than global cues. This is in fact what we observed: Consistent with previous work (Weissman & Woldorff, 2005; Weissman et al., 2002; Han et al., 1999; Heinze et al., 1998; Fink et al., 1997), frontal and parietal structures corresponding to the DAN were activated following local cues but not global cues.
The data also support the idea that this preparatory activity is related to getting ready for local cues rather than to task switching. In fact, no significant up-regulation of brain activity was present after cues signaling a task switch, relative to trials in which no switch was required. This suggests that participants up-regulated their processing when confronted with a “nondominant” task, rather than when they needed to switch task with respect to the previous trial.

It should be noted, however, that Mevorach, Humphreys, and Shalev (2006) showed that preference for global or local task conditions observed in patients with posterior parietal lesions could be reversed by manipulating the salience of the local or global cues. It can therefore be argued that the global advantage observed in the current study may be a result of its greater salience, rather than an inherent advantage for global processing. As no direct manipulation of salience was used in the current study, this account cannot be excluded. In any case, the data support the idea that, in the presence of asymmetric processing, task dominance is more important than task switching in governing the brain activity following the cues. In the current study, significant DAN activation occurred in an interval between 200 and 700 msec after stimulation, starting in medial/superior frontal regions (latency: 230 msec) and then extending to more lateral frontal regions (latency: 307 msec) and finally to parietal regions (latency: 512–537 msec), as supported by both the peak and seeded cross-correlation analyses. These latencies are consistent with ERP studies of cued paradigms, which generally show both frontal and parietal activation within the same interval as those obtained here (Yamaguchi et al., 2000; Han et al., 1999; Heinze et al., 1998; Heinze & Munte, 1993). The frontal-then-parietal order of activation is consistent with that observed with MEG in task-switching paradigms (Periániz et al., 2010). The middle frontal gyrus activation latency is also consistent with that reported by Gratton and colleagues (2009), also using EROS in a similarly constructed cued paradigm.

The frontal-then-parietal order of activation, however, is inconsistent with that reported in Baniqued and colleagues (2013), also using EROS. In that study, the cues indicated which of two possible response modalities (hands vs. voice) had to be used in a particular trial. In that case, the parietal activity preceded the frontal activity. A possible interpretation of this discrepancy is that changes in response modality may involve a different circuit than that used in changing stimulus-processing modalities (as in the current study). Another interpretation is that the parietal activity may occur twice: one concurrent with the frontal activity (around 300 msec after the cue) and one at a longer latency (around 500 msec). A hint that this might be the case is given by the activation waveform for the BA 40 ROI peak, reported in Figure 5 and Table 2, which shows two peaks with the appropriate latencies. Thus, the presence of double peaks may explain the difference in the timing of the activations in the left and right hemisphere in the current study. The presence of multiple peaks may represent a complex “hand-shake” process, involving bidirectional innervation, between anterior and posterior regions.

An important question in the global–local literature is the extent to which the two hemispheres may be differentially specialized for these two levels of analysis (Heinze et al., 1998; Heinze & Munte, 1993). In general, it is assumed that the left hemisphere is specialized for processing local details and the right hemisphere for processing the global picture. This is consistent with a presumed smaller size of receptive fields in the left hemisphere than in the right hemisphere (Jager & Postma, 2003). In our study, however, we found scant evidence in favor of this hypothesis. In fact, although the largest effects were observed for local preparation in the left hemisphere, there was no evidence of corresponding greater activation for global preparation in the right hemisphere. This lack of evidence for global preparation, however, could result from the fact that participants do not really need to prepare extensively for this condition, if the global mode of processing is in fact the default processing condition. Consistent with this interpretation is the observation that, in the Weissman et al. (2002) fMRI study, most of the interaction between hemisphere and analysis level was restricted to modulation of the left
hemisphere response between local and global cues, with little variation in the right hemisphere.

The correlation analyses between EROS preparatory activity and behavior, conducted across participants, clearly indicated that the preparatory activity is related to subsequent behavioral performance. The data indicate that those participants who generate the greatest activation within DAN in response to local cues are also the participants who have less differential RT between local and global trials and are less sensitive to conflict in local trials. Both of these findings are consistent with the interpretation that a function of the DAN is to up- or down-regulate processing streams in a fashion that is appropriate for the upcoming task. This view is consistent with extant models of attention control (Corbetta & Shulman, 2002). Interestingly, however, some of these models (Banich et al., 2000) emphasize the role of frontal structures in determining attention biases, whereas in our study the best prediction is obtained from activity at parietal locations. This may reflect the fact that the parietal structures may also be directly involved in the processing of the hierarchical stimuli. This is consistent with recent TMS evidence (Romei et al., 2012) and with EEG studies of alpha activity following cues (Volberg, Kliegl, Hanslmayr, & Greenlee, 2009). A similar prediction, however, was not observed in the visual areas analyzed in the current study.

The results of the time–frequency analysis provide additional insights into the effects of the cues on preparatory processes. The clearest phenomena were observed in the theta band in frontoparietal regions and theta and alpha bands in visual processing areas. In DAN, global cues were associated with an increase (with respect to the baseline level) of frontal and parietal theta activity, whereas a decline of theta activity in these areas was observed after local cues. This is consistent with previous findings obtained with rTMS (Romei et al., 2011, 2012; Smith, Gosselin, & Schyns, 2006). A similar prediction, however, was not observed in the left hemisphere. The association of the parietal structures with respect to the local condition, which appears to be associated with processing involving areas along the dorsal visual pathway (see Coleman et al., 2009). The association of the global condition with the dorsal pathway (which is associated with processing magnocellular information) may help explain its greater salience and temporal advantage with respect to the local condition, which appears to be associated with the ventral pathway (which is processing parvocellular information).

Finally, in the current study, we did not find much EROS evidence of preparatory activity related to task switching per se, differently from other previous studies (e.g., Gratton et al., 2009). This may reflect the special nature of the global–local task: The large advantage for global processing observed in this study may be best viewed as a situation in which this is the default processing mode. In this sense, only changes to the local cue, rather than any cue change, would induce “task switching.” The observation of task-switching effects on RT and accuracy would then reflect residual activation of processing modes used in a previous trial: When the same rule is used on two consecutive trials, performance is facilitated. The persistence of this residual activation may occur in the absence of preparatory effects elicited by the cue.

In summary, the results of this study support an asymmetric view of the global–local task, in which global processing is the default attention mode, and effortful preparation is required to instantiate local processing in advance of local trials. This effortful preparation involves activation of a set of frontoparietal structures corresponding to the DAN, a network normally activated when attention control is required. To the extent that the DAN is activated, the RT on local trials and the related conflict costs (when global and local cues are incongruent) are minimized. In our study, the DAN was activated in a frontal to parietal direction. The parietal activation was the best predictor of successful preparation. These findings are consistent with extant theories of attention control.

Acknowledgments

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Notes

1. Given the band-pass filters used, the time–frequency analysis had a frequency resolution of approximately 4 Hz.
2. These intervals were chosen to have round numbers (100 msec), with epochs made up of the same number of recording points (four for each interval).
3. Notice that the major effects were observed in theta and alpha rather than in the beta band. This may occur because the sampling frequency (59 Hz) only afforded us a very limited range within this band.

REFERENCES


