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Pitting binding against selection: electrophysiological measures of feature-based attention are attenuated by Gestalt object grouping

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Abstract

Humans have limited cognitive resources to process the nearly limitless information available in the environment. Endogenous, or “top-down”, selective attention to basic visual features such as color or motion is a common strategy for biasing resources in favor of the most relevant information sources in a given context. Opposing this top-down separation of features is a “bottom-up” tendency to integrate, or bind, the various features that constitute objects. We pitted these two processes against each other in an electrophysiological experiment to test if top-down selective attention can overcome constitutive binding processes. Our results demonstrate that bottom-up binding processes can dominate top-down feature-based attention even when explicitly detrimental to task performance.

Keywords

Object-processing; Attention; Feature-based selection; binding; ERP

INTRODUCTION

It has been estimated that approximately 10^7 bits of data travel down the optic nerve each waking second (Koch et al., 2006), and while our perception is impressive and creates an illusion of continuity, we consciously register but a fraction of that information. Every day we must extract useful signals from among the information in our environment if we are to perceive, learn, remember, and plan actions useful to our survival. This filtering of information from the environment is achieved through a combination of endogenous (“top-down”) and exogenous (“bottom-up”) biasing that resolves the competition for limited processing resources. The top-down form of this biasing, known as “selective attention”, involves allocating processing resources such that sources or classes of information expected to be relevant in a given context are given priority at the expense of irrelevant or distracting information (e.g. Broadbent, 1958, Kahneman, 1973; Schneider and Shiffrin, 1977, Shiffrin and Schneider, 1977; Neely, 1977; Schneider and Fisk, 1982). In this article we focus on selective attention to basic visual features, such as color and motion (Snyder and Foxe, 2010). Feature-based selective attention is an efficient way to guide visual search, as when

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meeting a friend at a crowded train station who has mentioned in advance, “I’ll be wearing red.” Experimentally, people informed in this way about the likely color of an upcoming task-relevant stimulus are faster to respond if the stimulus does in fact appear with the expected color than if it appears with another color (e.g., Most and Astur, 2007; Egner et al., 2008. See also Hopf et al., 2004).

Seemingly in opposition to this intentional boost in processing of separable features is an inherent bias to integrate (or “bind”) features that co-occur in time and space. Previous literature has demonstrated that enhanced processing spreads from an object’s task-relevant features to its irrelevant features (O’Craven et al., 1999; Schoenfeld et al., 2003; Wylie et al., 2004; Molholm et al., 2007; Katzner et al., 2009; Fiebelkorn et al., 2010a, 2010b). What’s more, this spreading of attention across the features of an object seems to be highly automatic (i.e., “bottom-up”; Fiebelkorn et al., 2010a).

We reasoned that such a spreading of attention across the features of an object might undermine attempts at feature-based selective attention. Selective attention entails a segregation of features whereas binding entails an integration of features, so the two processes have opposing aims. Our prediction was that binding, as an exogenous process, would dominate the more endogenous feature-based selective attention.

We tested this prediction in a prior behavioral study (Snyder and Foxe, 2011), which used response time facilitation to measure attentional biasing effects. Visual cues directed attention to one of two basic visual features (color or motion), and a non-informative neutral cue was used as a reference condition. Following the cue, participants tried to detect a subtle variation in either the color or motion of a field of moving dots. The cue correctly indicated which feature contained the target 80% of the time (i.e., valid cues), but participants had to respond to all targets, including those that were invalidly cued. Moreover, we pinned performance below ceiling levels, such that processing resources were limited, and any attentional enhancement of one feature would necessarily come at the expense of some other process. On top of this biased attention task, we used well-established Gestalt grouping principles to manipulate the degree to which the imperative stimulus was perceived as a single coherent object. In the ‘STRONG’ binding condition, all dots moved at the same speed and in the same direction, which leads to the percept that the dots are ‘painted’ on a single transparent surface that is itself sliding past an aperture. In the ‘WEAK’ binding condition dots moved in the same direction but each at a unique rate, which unlike the STRONG condition does not lead to the percept of a single object. We found that for WEAK stimuli, valid cue information could be utilized to speed responses relative to neutral cues, but no such response time benefit was found for STRONG stimuli (Fig. 1). In other words, increasing the tendency to perceive the stimulus as a single coherent object eliminated the behavioral signature of biased attention.

Using a similar design, the current experiment follows up on our earlier behavioral results by using event-related potential (ERP) methods to examine the neurophysiological underpinnings of the observed interference between selective attention and binding processes. Use of ERP methods affords several advantages that complement and expand the behavioral approach just described. Most obviously, ERPs provide information regarding the spatiotemporal dynamics of the brain activity underlying the observed behavior. Additionally, ERPs enable the use of an experimental design in which the uncued feature can be completely ignored (rather than merely ‘less attended’). This is in contrast to behavioral approaches, which require overt responses to all targets, including those that were not indicated by the cue. Because of this, the uncued feature is always task-relevant, and should be attended to some degree, if only less so than the cued feature. ERPs, which provide measures of brain activity that are not dependent on overt behavior do not have this

drawback. Use of a design in which the unattended feature is completely irrelevant creates the greatest advantage for strongly biasing attention and creates the most powerful context for testing our predictions regarding the automaticity of binding.

Previous research into feature-based selective attention has reported ERP differences emerging around 200ms post-stimulus onset that localize to brain regions implicated in processing the attended feature (e.g., Anllo-Vento and Hillyard, 1996; Schoenfeld et al., 2007; Hopf et al., 2004). While the current experiment differs in several key respects from these preceding examples, a similar sort of effect might be expected for this experiment when feature-based selective attention is effective (i.e., for WEAK stimuli). The key prediction of the current experiment, however, is that attention effects in the ERP should be diminished, delayed, or entirely absent for STRONG stimuli, as enhanced processing is reallocated to support binding across all the features of the object, including the task-irrelevant features. Because processing capacity is limited in this experiment, such a reallocation of processing resources should involve a withdrawal of resources from the attended feature, leading to a less-biased processing state.

METHOD

Participants

Sixteen adults (11 male, 3 left-handed) aged 20 to 47 years (mean $\pm$ s.d.: 27.19 $\pm$ 6.75 y) participated in the experiment. Three participants were excluded due to data quality concerns. The resultant sample contained 10 males and 3 females aged 20 to 47 years (27.92 $\pm$ 7.32y), three of whom were left-handed. Participants were sourced from the undergraduate and graduate student populations of The City College of New York, and from the local community. None of the participants had any history of brain injury or disease, per self-report. Participants had normal or corrected-to-normal visual acuity and normal color vision per self-report. All participants provided informed consent prior to the experiment. All materials and procedures were approved by the institutional review board of The City College of New York in accordance with the United States Public Health Service Act (US 45 CFR 46) and the Declaration of Helsinki.

Stimuli

The experiment was administered in a light- and sound-attenuated chamber using Presentation software version 14.4 (Neurobehavioral Systems, Albany, California). All stimuli were presented on a 34.5 $\times$ 55.0 cm LCD monitor with a 60 Hz refresh rate (ViewSonic, model VP2655wb). Trials began with a warning cue consisting of a white fixation dot on a black background for 1 s, followed by a cue word ('COLOR', 'HUE', 'MOTION', or 'DIRECTION') in white block capitals for 1 s. The words 'color' and 'hue' both directed attention to the color of the upcoming imperative stimulus (the second stimulus, or "S2"). Likewise, 'motion' and 'direction' both directed attention to the motion of the stimulus. The use of multiple cue words for each feature was to reduce the automatization of the task through implicit learning, with an aim to maintain the engagement of endogenous orienting mechanisms throughout the session. After an interval of 1.7 to 2.3 s (random, and evenly distributed) during which only a black screen was displayed, the S2 was presented for 0.2 s. Each S2 was followed by a 1 s response interval. Each subsequent trial began immediately following the response interval (Fig. 2a).

The S2 consisted of an array of one thousand dots, each subtending 0.05 degrees of visual angle, constrained to a square aperture subtending 5 degrees of visual angle. In one condition, designed to engage Gestalt grouping processes, all dots moved in the same direction at a speed of 21 degrees of visual angle per second. We refer to this condition as

the STRONG condition, indicating that Gestalt processes are strongly engaged. A common percept of this type of stimulus is that the dots are ‘painted’ on a single transparent surface that is itself sliding past the aperture. In another condition, designed to minimize the engagement of Gestalt grouping processes, each dot moved at a unique speed between 14 and 28 degrees of visual angle per second, and all dots moved in the same direction. For this type of stimulus the dots are not perceived as parts of a single object as is the case when the dots all move at the same speed. We refer to this condition as the WEAK condition, indicating that Gestalt processes are weakly engaged (relative to the STRONG condition). Dots ‘wrapped around’ the edges of the square aperture, so that the total amount of illumination was held constant. STRONG and WEAK S2’s each occurred on 50% of trials in an unpredictable order. It should be emphasized that the STRONG/WEAK manipulation was irrelevant to the task. Participants were not informed by the experimenter of this manipulation until debriefing, at which point several participants expressed that they were unaware of the STRONG/WEAK distinction during the experiment.

Dots were colored with hues from an isoluminant plane of DKL color-space (Derrington et al., 1984). This color-space uses the response properties of neurons in macaque lateral geniculate nucleus to create a subjective luminance axis, planes orthogonal to which are approximately isoluminant. The use of this color-space enables the continuous variation of hue needed to derive hue discrimination thresholds while controlling for subjective luminance.

Task

The task was adapted from previously reported experiments (Snyder and Foxe, 2010, 2011). Half of the trials consisted of uniformly-colored S2’s (color standard), whereas for the other half of trials 20% of dots had a slightly different color from the majority (color target). Orthogonally to this color manipulation, half of trials contained S2’s for which all dots moved on a common linear trajectory (motion standard) and the other half contained S2’s for which the dots moved on a curved trajectory (motion target). Schematized examples of targets are illustrated in figure 2b. The degree of difference for each of the relevant targets was titrated on a per-subject basis to 80% detection rate prior to beginning each experiment using an up-down transformed response (UDTR) modified staircase procedure (Wetherill & Levitt, 1965). No particular value of any feature indicated a target: subjects had to detect a particular feature *variation* in the stimulus. This strategy was used to reduce competition within a feature processing area (if subjects were attending to red and suppressing green, for example). The goal, rather, was to have subjects attend to *color* and suppress *motion*, or vice versa as the cue indicated.

Participants were instructed to attend to the cued feature only, ignoring the uncued feature entirely, and to respond by pressing a computer mouse button with the right index finger upon detection of a target in the cued feature. The requirement to ignore the uncued feature was intended to make any target properties appearing in the uncued feature distracting, so that object-related spreading of attention could provide no task-related benefits. Participants completed 10 ten-minute blocks, which included breaks every 12 trials to reduce fatigue and maintain a high level of alertness throughout the session.

EEG Recording

Continuous EEG was acquired through the ActiveTwo BioSemi (Amsterdam) electrode system from 168 scalp electrodes, digitized at 512 Hz with a 31.25 nV quantization resolution. Data were band-pass filtered during acquisition from 0.1–100 Hz. With the BioSemi system, every electrode or combination of electrodes can be assigned as the reference, which is done purely in software after acquisition. BioSemi replaces the ground

electrodes that are used in conventional systems with two separate electrodes: Common Mode Sense (CMS) active electrode and Driven Right Leg (DRL) passive electrode. These two electrodes form a feedback loop, which drives the average potential of the subject as close as possible to the reference voltage of the analog-to-digital converter, thus rendering them references. One electrode placed 1 cm posterior to each orbital canthus and one electrode placed on the nasion were used to monitor eye movements.

Data processing

EEG data were processed using the FieldTrip toolbox (Donders Institute for Brain, Cognition and Behaviour, Radboud University Nijmegen, the Netherlands) for MATLAB (The MathWorks Inc., Natick, Massachusetts). Only trials with correct behavior (responses to targets and withheld responses to non-targets) were included in the analysis. Data were epoched from 100ms pre-S2 onset to 500ms post-S2 onset. Each trial was first visually inspected, and channels showing transient, large-amplitude electronic artifacts were linearly interpolated on a per-trial basis. Trials with more than 5 interpolated channels were excluded from further analysis. Then, the data were decomposed into independent components that were used for correction of muscular and ocular artifacts.

To perform the independent components analysis (ICA), we first concatenated all the trials for each individual participant. This resulted in very large datasets, and so we next downsampled the data by a factor of 4 for efficiency of the ICA algorithm. The concatenated, downsampled data were then used to derive unmixing matrices using the FastICA algorithm with default settings (Hyvärinen, 1999). The downsampled data were then discarded, and the unmixing matrices were used to unmix the original, undownsampled data for each participant into independent components. Components reflecting artifacts were identified using an automated approach described by Whittingstall and colleagues (2010). Artifacts were identified based on temporal and spatial characteristics. For the temporal criterion, component time courses were rectified and then converted to z-scores, and components containing z-scores exceeding a value of 7 were discarded. This criterion identifies infrequently-occurring, large amplitude, transient artifacts. For the spatial criterion, each component topography (i.e., each column of the unmixing matrix) was converted to z-scores, and components for which the largest z-score exceeded a value of 9, or for which the sum of the two largest z-scores exceeded 15, were discarded. This criterion identifies artifacts that are limited to one or two electrodes. The choice of z-score threshold values was adopted from the report by Whittingstall and others (2010). In a preliminary stage, we tested this method with several z-score thresholds and found that the particular set of components rejected was consistent across a moderate range of threshold values. After rejecting components reflecting artifacts, the remaining components were remixed into sensor-space and re-divided into individual epochs for further processing and analysis.

Artifact-corrected data were re-referenced to a frontopolar electrode equivalent to Fpz in the 10–20 system. This reference was chosen because it was a clean recording site in all participants far from occipital cortices, which were hypothesized to be the regions likely to show maximal effects in this visual paradigm. Data were then low-pass filtered below 30 Hz and then high-pass filtered above 0.3 Hz. In each case a 6th-order zero-phase digital Butterworth filter was used. Expanded epochs (2s pre-S2 to 2s post-S2) were used for filtering to avoid contamination by artifacts introduced by discontinuities at the edge of the epochs. Subsequent to filtering, the epochs were trimmed back to 100ms pre-S2 onset to 500ms post-S2 onset and averaged across trials. A mean of 161 trials (± 25.4 s.d.) were included in the ERP for each condition for each participant.

Analysis

Behavioral Analysis—We analyzed both performance accuracy and response times. In each case we used a repeated-measures ANOVA with factors of ‘feature’ (two levels: color and motion) and ‘S2 type’ (two levels: WEAK and STRONG). Our dependent measure for performance accuracy was the discriminability index (d'), a measure of performance which takes into account response bias. For response time (RT), we tested the median RT’s across trials for each participant for each cell of the ANOVA design matrix. We chose the median as the measure of central tendency because it is robust to outliers, which were likely in this case because participants were not instructed to respond rapidly. Behavioral statistics were analyzed using PASW version 18.0.0 (SPSS Inc., Somers, New York). We should mention that unlike our prior study (Snyder and Foxe, 2010) in which behavioral effects of biased attention were explicitly measured, no behavioral differences were predicted for the current study. The reasons for this are two-fold: 1) responses were only made to the cued feature, so there were no “valid” or “invalid” cues between which response time would differ, and 2) we explicitly titrated performance to equate task difficulty across all conditions. Therefore, our aim in analyzing behavioral outcomes for this study was simply to confirm that task difficulty was equated across conditions.

Statistical Hypothesis Testing of ERP Differences—We had a directed hypothesis that the ERP indices of attentional biasing would be greater for WEAK S2s than for STRONG S2s. To identify the ERP indices of our feature-based attention manipulation, we performed a running dependent samples t -test between conditions of attention-to-motion and attention-to-color for all channels and time points. We used a clustering approach to control for inflation of type I error due to multiple comparisons (cf. Guthrie and Buchwald, 1991). The rationale for this method is that type I errors are unlikely to occur simultaneously at adjacent electrodes and unlikely to endure for several consecutive time points. Since the EEG signal does not change arbitrarily fast, however, there is some dependence between consecutive time points. We examined the autocorrelation of the noise in the baseline interval of the ERP to determine the minimum time delay at which time points in the EEG are not significantly correlated, which we found to be 15 samples (29ms). We thus required two-tailed p values below 0.05 to be simultaneously present at two or more adjacent electrodes and to persist for at least 15 samples to consider the effects significant. This statistical analysis was applied separately to the STRONG and WEAK conditions. The results of this analysis indicated whether a significant attention effect was present for either STRONG or WEAK stimuli. We also performed an orthogonal comparison of feature-based attentional deployment across binding conditions. To do this, we first derived difference waves for each subject by subtracting the ERPs when motion was attended from the ERPs when color was attended, separately for each binding condition. We then tested for significant differences between these difference waves using a nonparametric repeated-measures randomization procedure as follows: (1) we first measured the mean difference for each channel and timepoint between the observed WEAK and STRONG difference waves, (2) we then selected a random subset of our sample and swapped the categorization of the WEAK and STRONG difference waves for those participants (this swapping reflects the null hypothesis that the WEAK and STRONG conditions are equivalent), and (3) we noted the difference between the two randomly repartitioned groups. This random repartitioning procedure was repeated 1000 times to generate a distribution of such differences. The probability (p -value) that the observed difference between the WEAK and STRONG attention-related difference waves is due to chance (under the null hypothesis) is equal to the proportion of the distribution that exceeds that observed difference. We also performed a running dependent samples t -test comparing all STRONG to WEAK responses, regardless of which feature was attended, to characterize main effects of the Gestalt grouping manipulation.

Source Estimation—To visualize the cortical regions most likely to be contributing to effects observed at the scalp, we employed a minimum norm current source estimation (MNE) method using Brain Electrical Source Analysis software (BESA GmbH, ver. 5.1.8), using the following settings: depth weighting and spatiotemporal weighting using subspace correlation (dimension = 7); and noise estimation using the 15% lowest values, weighted by averaging over channels. Source localization was applied to subtraction waveforms representing effects of interest. Subtractions were made as follows: 1) attend-color WEAK minus attend-motion WEAK; 2) attend-color STRONG minus attend-motion STRONG; and 3) STRONG minus WEAK.

RESULTS

Behavior

Performance Accuracy (Fig. 3a)—Discriminability scores ranged from $d' = 0.88$ to $d' = 4.22$ (mean $\pm$ s.d.: 2.44 ± 0.76), indicating that all participants performed above chance (i.e., $d' > 0$) and below ceiling (i.e., $d' < 4.65$, which reflects a 99% hit rate and 1% false alarm rate). There were no main effects or interactions for the factors of 'feature' and 'S2 type' on d' scores (all p 's > 0.12). The lack of significant differences was consistent with our aim to equate task difficulty across conditions.

Response Times (RT's; Fig. 3b)—Median RT's ranged from 511.7 ms to 957.0 ms (698.8 ± 113.9 ms). There was a main effect of 'feature' ($F_{1,12} = 6.593$, $p = 0.025$). A post-hoc paired-samples t -test showed that responses to motion targets were slower than responses to color targets ($p = 0.025$). Overall, participants responded 42.2 ms (s.d.: 59.3 ms) slower to motion than color, and 10 out of 13 participants showed this general pattern. Slower RT's for motion judgments compared to color judgments are not uncommon in feature-based attention studies (e.g., Anllo-Vento and Hillyard, 1996; Schoenfeld et al., 2007), and likely reflect the integrative nature of motion processing.

No main effect was found for the factor of 'S2 type' ($F_{1,12} = 1.241$, $p = 0.287$). The 'feature' by 'S2 type' interaction was not significant ($F_{1,12} = 0.207$, $p = 0.657$).

Statistical Testing of ERP Differences

For WEAK stimuli, ERP differences between attend-color and attend-motion were found at 11 parieto-occipital electrodes from 180 ms to 221 ms post-stimulus onset (Fig. 4, 5a). The ERP was more negative for attend-color than for attend-motion at these locations for this time period. In contrast, no attention effects for STRONG stimuli were found (Fig. 4).

We compared attention effects between WEAK and STRONG stimuli using a nonparametric randomization test. Difference waves reflecting feature-based attention were compared across binding conditions. Significant differences were found from 174–219 ms, which closely overlaps the period of significant attention effects within the WEAK condition. Figure 6 illustrates the spatial extent of the effect during the overlapping time period. We found that attention-related differences for WEAK stimuli were greater than those for STRONG stimuli at 6 of the 11 electrodes that showed an attention effect within the WEAK condition ($p < 0.05$, Fig. 6). There was a trend towards significance at another 9 nearby electrodes ($p < 0.1$).

A comparison between the ERP's for STRONG and WEAK stimuli revealed a robust effect at parieto-occipital electrodes from 273 ms to 404 ms (Fig. 7a,b). The ERP was more positive for STRONG stimuli than for WEAK stimuli at these times and locations.

It is reasonable to suppose that the moving dot stimuli used for this experiment might induce eye movements that could potentially confound the electrophysiological results reported here. We examined the bipolar-referenced EOG channels prior to artifact correction, and found that eye movements were not made prior to 400ms, and even thereafter, any eye movements that were seen did not differ across conditions. Thus, it seems unlikely that eye movements are confounding the observed effects.

Source Estimation

The minimum norm source estimate (MNE) analysis localized the early (180–221 ms) attention effect for WEAK stimuli to occipital pole regions and posterior ventral occipito-temporal cortex bilaterally (Fig. 5b). The general Gestalt binding effect (i.e., STRONG vs. WEAK) localized to right lateral occipital cortex and left dorsolateral prefrontal cortex (Fig. 7c).

DISCUSSION

Here we tested whether the electrophysiological effects of feature-based selective attention persist despite environmental cues (i.e., common fate) that typically lead to object-based integration through the bottom-up spreading of attention (O'Craven et al., 1999; Schoenfeld et al., 2003; Busse et al., 2010; Fiebelkorn et al., 2010a). In other words, we examined whether the well-established ability to bias processing toward a specific feature (color or motion) would be counteracted by the well-established bias to form coherent objects. To test the automaticity of the spreading of attention, which is thought to reflect feature binding, we designed a task where object-based integration would be detrimental to performance.

On each trial, participants' were cued to detect either color or motion targets, while overall performance was held near 80 percent. Pinning performance below 100 percent accuracy served to saturate attentional resources, such that any boost in the processing the irrelevant feature would necessarily detract from processing the relevant one. If Gestalt principles in the STRONG condition led to a spreading of attention from the relevant feature to the irrelevant feature, we would predict that the two features would be processed with greater parity. In other words, any differences in the ERPs between attention to motion and attention to color should be smaller for STRONG than for WEAK stimuli. Evidence of decreased feature-based selectivity in the presence of environmental cues for binding would suggest that the inherent bias to process objects as wholes supersedes task-driven attempts to bias processing toward a particular feature in order to optimize performance.

Our electrophysiological measure of feature-selective processing was the difference between ERPs when color was attended compared to when motion was attended. For the WEAK condition, robust evidence of biased processing for the cued feature was evident around 180 ms; whereas, for the STRONG condition, evidence of biased processing for the cued feature was not observed. We therefore conclude that feature-based selective attention is substantially attenuated by object-based binding processes. These data emphasize the strength of the tendency to integrate features that share a common fate, even when doing so will interfere with the task at hand, as was demonstrated by our earlier behavioral report (Snyder and Foxe, 2011; Fig. 1).

In addition to providing confirmatory support for the previously reported behavioral effects, the results of the current experiment provide important additional information. Firstly, the use of an instructional cue in the current experiment speaks to the robustness of the effect. In our prior experiment, participants were required to respond to all targets, including the infrequent cases when the target appeared in the uncued feature. Thus, the optimal strategy in that case would not have been to *completely ignore* the uncued feature, but merely to

attend to it *less*. Thus, biasing might not have been particularly strong to begin with, increasing susceptibility of feature-based attention to interference by binding. In the current design, however, the uncued feature never warranted a response, and could in fact be a source of distracting information. Thus, the optimal strategy would be to *actively ignore* the uncued feature. In this way, the strongest anticipatory biasing is encouraged. That disruptions of feature-based attention by binding were still observed in this extreme case of attentive biasing indicate the robustness of the effect.

Moreover, the ERP method provides information regarding the spatiotemporal dynamics of the brain activity underlying the effect. The significant differences that we observed between attention to color and attention to motion for the WEAK condition are similar in terms of latency and topography to previously observed feature-specific attention effects (Anllo-Vento and Hillyard, 1996; Schoenfeld et al., 2007; Hopf et al., 2004). Source localizations implicated ventral temporal lobes bilaterally, with additional contributions from occipital pole regions. Because color processing has been previously localized to the ventral occipito-temporal regions (Corbetta et al., 1991; Vaina, 1994), we interpret this pattern of results as enhanced processing in color-related cortical areas when color is attended compared to when motion is attended.

Because the evidence of feature-based selective attention was present for WEAK stimuli at 180 ms, but absent for STRONG stimuli at that time, we can conclude that object-based binding effects within STRONG stimuli must have onset prior to 180 ms. An obvious question is how the timing of our current effects accord with timing of known binding processes. Evidence for the timing of object binding comes from several electrophysiological investigations of the canonical “illusory contour” stimulus class. These studies have utilized Kanisza illusory figures (cf. Kanisza, 1976), which are composed of arrays of Pacman shaped inducers oriented with their “mouths” aligned toward a common point, such that the region interior to the inducers is perceived as a geometric shape superimposed on the background, although no such shape actually exists. If the inducers are sufficiently misaligned the illusion is destroyed. By comparing the ERP to the Kanisza figures to their non-illusion-inducing counterparts, an “illusory contour effect” has been identified that onsets around 100 ms and peaks around 170 ms (Herrmann, et al., 1999; Murray, et al., 2002, 2004, 2006; Foxe, et al., 2005; Shpaner, et al., 2009; Fiebelkorn, et al., 2010b), the effect is taken to indicate binding of the disparate inducers into a single Gestalt, as in the current experiment.

While our inference that binding effects occurred prior to 180ms was indirect, we directly observed effects of our Gestalt grouping manipulation during later time periods (273 ms to 404 ms). This effect was characterized by greater positivity at posterior electrodes, and implicated a robust current source in right lateral occipital cortex. Lateral occipital cortex has previously been implicated in object-related processing (e.g., Martinez et al., 2006, 2007b; Lucan et al., 2010), particularly with regards to integrating fragmented images (Doniger et al., 2000, 2001; Sehatpour, et al., 2006) and illusory contours (Murray et al., 2002, 2004; Martinez et al., 2007a; Shpaner et al., 2009).

We found that participants were successfully able to bias processing resources between the features of color and motion. This biased attentional state was evident in differences in the ERP’s between when motion was attended and color was attended. These effects were relatively early (180ms) and attributed to feature-specific cortical processing regions. However, these differences were only evident when environmental cues for object-based binding were weak. When environmental cues for binding were strong, evidence for biased feature-specific processing was not observed. We therefore conclude that bottom-up binding

processes supercede top-down feature-based selective attention, even when explicitly detrimental to task performance.

Our results provide insight into how attention and binding processes are used to guide interaction with the environment in a natural setting. We propose the following model: First, feature-based attention, which is not spatially-specific, highlights objects with the attended feature for subsequent spatial selection. Binding processes then take over, which leads to a spread of attention between the attended object's constituent features, and an object-based attentional selection is formed. The attended object can then be scrutinized with respect to the individual features, but this scrutiny is likely deferred to post-perceptual timeframes.

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Figure 1.

Response time results from Snyder and Foxe (2011). For the depicted experiment, participants responded to all targets, including those that were invalidly cued. Benefits for valid cue information were seen for WEAK stimuli, but not for STRONG stimuli. That task-irrelevant binding processes led to behavioral costs suggests that binding is automatic and interferes with successful feature-based selective attention.

Figure 2.

Task. A) Schematic of task procedures. For each trial, subjects first viewed a fixation dot for 1s, followed by a cue word in block capitals for 1s. The cue (S1) was followed by an interval of 1.7–2.3s with no stimulation. After the cue-target interval, the random dot stimulus (S2) was shown for 0.2s, followed by a 1s response period. The next trial began immediately following the response interval. The arrow in the S2 represents the motion of the dots and was not actually present in the stimulus. Details have been enhanced for clarity of illustration. Timeline is not to scale. B) Schematized illustration of target examples.

Arrows represent motion and were not actually present in the stimulus. The length of each arrow represents the speed of the adjacent dot. Color targets were defined by the presence of two colors of dots. Motion targets were defined by the presence of curved motion (i.e., sequential presentation of different motion directions). Note that no one particular color or motion direction was indicative of target presence, and that the examples given here are not exhaustive. Both color and motion targets could be present in a single stimulus. Stimuli are shown here on a white background for illustration; stimuli were on a black background in the experiment. Color and motion differences are enhanced for clarity. Dots in the actual stimuli were smaller and more numerous.

Figure 3. Summary of behavioral results for the current experiment. A) Performance accuracy in d' scores. B) Response times in milliseconds. *: $p < 0.05$ (repeated-measures ANOVA). Error bars indicate 2 standard errors of the mean.

Figure 4.

Feature-based attention effects for WEAK and STRONG stimuli. ERPs in response to S2's are plotted for a representative electrode (electrode location highlighted in insets) above the p -values for a running t-test of the comparison 'color vs. motion.' The green dashed line represents $p = 0.05$. The light green rectangle highlights the time period of significant difference.

Figure 5. Maps of feature-based attention effects. A) Scalp topography of attend-color ERP minus attend-motion ERP for WEAK stimuli for the time period of significant difference. Black circles depict significant channels. B) Minimum norm current source estimates for time period with significant attention effects for WEAK stimuli (L = left, P = posterior, R = right, V = ventral).

WEAK attention effect vs. STRONG attention effect (180-221ms)

Figure 6.

Results of nonparametric statistical test for the comparison 'WEAK attention effect > STRONG attention effect'. Shading denotes p values with a threshold of $p < 0.1$. A cluster of 12 contiguous electrodes can be seen over parietal occipital scalp where the effect of attention for WEAK stimuli is significantly greater than the effect of attention for STRONG stimuli.

Figure 7.

General Gestalt grouping effect (i.e., STRONG minus WEAK). A) ERPs for representative electrode (location depicted in inset. Shaded rectangle indicates time period of significant difference. B) Representative topography of the difference 'STRONG minus WEAK' during significant period. Black circles indicate significant electrodes. D) Minimum norm current source estimate for time period with significant effect.