

Local or Global? Attentional Selection of Spatial Frequencies Binds Shapes to Hierarchical Levels

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Abstract

Contrary to the traditional view that shapes and their hierarchical level (local or global) are a priori integrated in perception, recent evidence suggests that the identity of a shape and its level are encoded independently, implying the need for shape-level binding to account for normal perception. What is the binding mechanism in this case? Using hierarchically arranged letter shapes, we obtained evidence that the left hemisphere has a preference for binding shapes to the local level, whereas the right hemisphere has a preference for binding shapes to the global level. More important, binding is modulated by attentional selection of higher or lower spatial frequencies. Attention to higher spatial frequencies facilitated subsequent binding by the left hemisphere of elements to the local level, whereas attention to lower spatial frequencies facilitated subsequent binding by the right hemisphere of elements to the global level.

Keywords

local processing, global processing, hemispheric asymmetries, spatial frequencies, visual feature binding

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One question that has been pervasive across cognitive, computational, neuropsychological, and neurophysiological studies is how local elements in a visual scene (e.g., branches, leaves, trunk) are integrated to produce global percepts (e.g., tree). From Gestalt psychology to more recent studies of functional hemispheric differences, a central question has been how local parts are integrated into global wholes. Within this context, one issue that has been largely ignored is how the level of processing (local or global) is perceptually integrated with the shapes in the display. This issue may have been overlooked because an implicit assumption in much of the literature on hierarchical perception has been that the hierarchical level is not processed separately from the identity of the perceived shape at that level (e.g., Navon, 1977; Robertson, 1996). In other words, when the tree is defined as the global level, its representation as being global is assumed to be intrinsic to the perceptual process. In this traditional view, shape and level are bound throughout visual processing, although one level may be processed before another (Navon, 1977).

The traditional view may appear reasonable when one considers the displays used to study hierarchical perception. These often consist of a series of smaller (local) shapes spatially arranged to form a larger (global) shape (“Navon” displays;

see Fig. 1). Intuitively, the local and global levels seem unambiguous. However, when one considers hierarchically structured objects in the natural environment, the traditional view warrants reconsideration because the same element might be a local percept in one instance (e.g., local tree in a global forest) and a global percept in a different instance (e.g., global tree composed of local branches), depending on the focus of attention. In line with this observation, Hübner and Volberg’s (2005) hierarchical integration theory suggests that visual information at different levels is initially represented independently of level and only later bound to form an integrated representation at a particular level. They adopted the framework of feature integration theory (FIT), which posits attentional selection of a spatial location as the medium by which individual representations of surface features (e.g., color, shape, and orientation) are bound into a coherent whole (Treisman, 1999; Treisman & Gelade, 1980). Evidence for FIT lies in the fact that deficits in spatial attention after brain injury lead to

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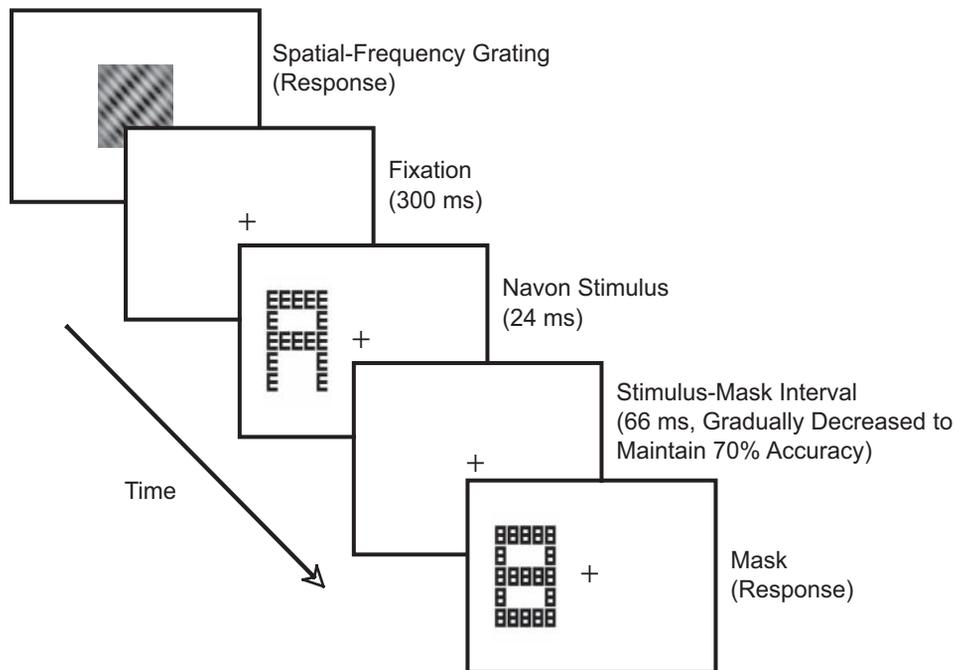


Fig. 1. Example trial from the primary experiment. First, a compound spatial-frequency grating was displayed until participants reported the orientation (left or right) of the lower or the higher spatial-frequency component (separate blocks of trials). Next, after a fixation display, a Navon stimulus was flashed for 24 ms to the left or right of fixation. After a predetermined interval, a figure-eight mask appeared at the location of the Navon stimulus. Participants reported the identity of the global or local letter (in separate blocks of trials) by selecting from among four alternatives. The stimulus-mask interval started at 66 ms and was gradually decreased after each block in which a participant was more than 70% accurate. In the control experiment, there was no prime task, so trials began with a 300-ms fixation cross.

incorrect perceptual feature combinations known as *illusory conjunctions* (e.g., mistakenly reporting a red *X* when presented with a blue *X* and a red *T*; Robertson, Treisman, Friedman-Hill, & Grabowecy, 1997). Illusory conjunctions also occur in normal perception when attention is diverted and the stimuli are briefly presented (Treisman & Schmidt, 1982).

Addressing the question of how shape and level (local vs. global) are bound, Hübner and Volberg (2005) interrupted processing of Navon displays by masking them after randomly presenting them in the left visual field (LVF) or right visual field (RVF). Participants' task on each trial was to identify the letter at either the local or the global level. The rationale in this design was that if shape and level were initially represented separately, then an interruption in processing would lead to instances in which binding failed, and illusory conjunctions of shape and level would result (i.e., participants would identify the letter at the unattended level and report it as the letter at the attended level). Indeed, Hübner and Volberg found a high incidence of shape-level conjunction errors that exceeded chance and could not be explained by guessing.

In addition, by presenting the displays in the LVF or RVF, Hübner and Volberg (2005) examined whether there was a visual-field asymmetry in conjunction errors consistent with evidence for functional hemispheric differences in hierarchical processing (e.g., Delis, Robertson, & Efron, 1986; Martin, 1979; Martinez et al., 1997; Robertson & Delis, 1986; Robertson,

Lamb, & Knight, 1988; Robertson, Lamb, & Zaidel, 1993; Weissman & Woldorff, 2005). Although some studies have not found these differences (Fink et al., 1997; Heinze, Hinrichs, Scholz, Burchert, & Mangun, 1998; Polster & Rapcsak, 1994), a meta-analysis showed that overall there is strong evidence for a left-hemisphere (LH) bias toward local processing and a right-hemisphere (RH) bias toward global processing (Van Kleeck, 1989). This meta-analysis also showed that the hemispheric differences found in speed and accuracy at reporting targets at the local versus global level were more pronounced when the stimuli were incongruent (i.e., letter identity differed at the local and global levels). In line with the integration theory, incongruent displays would yield more illusory conjunctions than congruent displays (i.e., congruent displays do not require accurate binding because the same element is represented at both the local and the global level).

Hübner and Volberg (2005) found that participants made significantly more conjunction errors in response to local targets (i.e., when asked to report local letters, they reported global ones) when the stimulus was presented in the LVF (projected to the RH), and they made significantly more conjunction errors in response to global targets (i.e., when asked to report global letters, they reported local ones) when the stimulus was presented in the RVF (projected to the LH). These results provide evidence that shape and level are represented separately during some early visual processing stage, that this

stage is followed by a binding stage, and that the rate of binding errors depends on the visual field in which the hierarchical displays are presented. However, the mechanism underlying shape-level binding is unknown. In FIT (Treisman & Gelade, 1980), features must be collocated (through spatial attention) to be properly bound. In contrast, the integration theory formulated by Hübner and Volberg does not offer a binding mechanism.

The goal of the present study was to examine whether the medium of hierarchical binding is attentional selection of task-relevant spatial frequencies. Specifically, we sought to investigate if hemispheric asymmetries in hierarchical binding are mediated by attentional selection of relatively high versus low spatial frequencies. This hypothesis is based on previous data suggesting that spatial frequencies cue the level of representation (Robertson, 1996) and that the task-relevant spatial frequencies in a stimulus can drive hemispheric differences in performance (Ivry & Robertson, 1998). Studies involving discrimination of sinusoidal gratings have demonstrated that the LH is biased to select higher spatial frequencies, whereas the RH is biased to select lower spatial frequencies (Christman, Kitterle, & Hellige, 1991; Flevaris, Bentin, & Robertson, 2009a, 2009b; Kitterle, Christman, & Hellige, 1990); the same biases have been found for processing of letters, faces, scenes, and objects (Iidaka, Yamashita, & Yonekura, 2004; Jonsson & Hellige, 1986; Keenan, Whitman, & Pepe, 1989; Parker, Lishman, & Hughes, 1996; Peyrin et al., 2005). Studies have also demonstrated that global perception relies more on the selection of relatively low spatial frequencies in the stimulus, whereas local perception relies more on the selection of relatively high spatial frequencies (Han, Yund, & Woods, 2003; Hughes, Fendrich, & Reuter-Lorenz, 1990; Hughes, Nozawa, & Kitterle, 1996; Jian & Han, 2005; Robertson, 1996; Shulman, Sullivan, Gish, & Sakoda, 1986; Shulman & Wilson, 1987; Yoshida, Yoshino, Takahashi, & Nomura, 2007). Perhaps most important, spatial-frequency processing is flexible and contingent both on bottom-up factors, such as image information, and on top-down factors, such as attention and task constraints (Peyrin, Mermillod, Chokron, & Marendaz, 2006; Sowden & Schyns, 2006).

Given this evidence, our hypothesis was that spatial frequency is the medium for hierarchical binding, such that attentional selection of relatively high spatial frequencies facilitates shape-level binding by the LH, and attentional selection of relatively low spatial frequencies facilitates binding by the RH. To test this hypothesis, we used a priming paradigm designed to examine how directing attention to spatial frequency (relatively high or relatively low) modulates shape-level conjunction errors in a hierarchical display. On each trial, participants first discriminated the orientation of either the lower or the higher spatial frequencies in a centrally presented compound grating (e.g., Olzak, 1986). A Navon display was then briefly flashed in the LVF or RVF and was subsequently masked. Participants indicated which of four possible letters appeared at either the local or the global level. They were

informed that each display would be constructed of two different letters, so if they identified only the letter at the unattended level, they should guess from the remaining three alternatives. Inadvertently reporting the letter at the unattended level was considered to be a *shape-level conjunction error*, and reporting one of the two letters that were not presented at any level was considered to be a *feature error*.

If letters and levels are bound a priori (i.e., the traditional view), then the number of conjunction errors in this paradigm should be approximately equal to the number of each possible feature error (i.e., with three possible erroneous responses, conjunction errors should not exceed 1/3 of the total errors). In order to verify the predictions of integration theory within our experimental design, we first replicated Hübner and Volberg's (2005) findings, showing that the number of conjunction errors was much larger than the number of other errors, that conjunction errors in response to local targets were greater when the stimulus was projected to the RH than when it was projected to the LH, and that conjunction errors in response to global targets were greater when the stimulus was projected to the LH than when it was projected to the RH. More important, the attended spatial frequency in the prime task modulated the hemispheric asymmetry of conjunction errors such that attentional selection of higher spatial frequencies reduced the hemispheric asymmetry in conjunction errors in response to local targets, and attentional selection of lower spatial frequencies reduced the hemispheric asymmetry in conjunction errors in response to global targets.

Method

Participants

Twenty-four undergraduates from the University of California, Berkeley, participated in the experiment for course credit. Sixteen participants (12 women and 4 men) were tested in the primary experiment and 8 (5 women and 3 men) were tested in a subsidiary control experiment (see the Procedure section). All were right-handed and had normal or corrected-to-normal vision. All gave informed consent as approved by the committee for the protection of human subjects at the University of California, Berkeley.

Stimuli

The compound gratings were generated in MATLAB (Mathworks, Natick, MA) with a sinusoid function for each spatial frequency. Each compound grating subtended 6.6° of visual angle and was composed of both a 3.6-cycle/deg grating (the high-spatial-frequency component) and a 1.2-cycle/deg grating (the low-spatial-frequency component) at 100% contrast. One spatial-frequency component was oriented at +45° (tilted to the right), and the other was oriented at -45° (tilted to the left).

The Navon displays consisted of black letters, presented on a white background. They were created using Adobe Photoshop.

Seen from a distance of 57 cm, each local letter subtended 0.9° of visual angle; the local letters were spatially arranged on a 5×5 grid to form a global letter that was 4.5° wide by 6° high. The letters used were squared (i.e., constructed with only straight lines) *A*, *E*, *H*, and *S* in all their local and global combinations, with the exception of congruent combinations (e.g., a global *A* composed of local *As*). Thus, 12 distinct Navon displays were used. The mask was composed of local figure eights arranged on the same grid to form a global figure eight, such that the symbols overlapped with the lines in all possible letter combinations.

Procedure

The stimuli were shown on a 17-in. color monitor with a vertical refresh rate of 60 Hz and a resolution of 1024×768 pixels. Trial timing was controlled by Presentation (Neurobehavioral Systems, Albany, CA) and is depicted in Figure 1.

On each trial, a compound spatial-frequency grating (prime) appeared until participants reported the orientation of the bars of a given spatial frequency. In separate blocks of trials, participants reported the orientation of either the “thin bars” (higher spatial frequency) or the “thick bars” (lower spatial frequency). They were instructed to respond quickly but accurately, without moving their eyes over the grating. The grating was then replaced by a central fixation cross for 300 ms. Next, a Navon display was flashed for 24 ms. Its medial edge was 1° to the left or right of fixation and 3.25° from the midline. Visual field of presentation was randomized within each block. After a predetermined interval, the mask appeared in the same location as the Navon display. The mask remained on the screen until participants provided a response. In separate blocks of trials, participants were asked to indicate the identity of the local or the global letter. The stimulus-mask interval (SMI) was initially 66 ms (i.e., the mask appeared 66 ms after the offset of the Navon stimulus) and was gradually decreased to maintain approximately 70% accuracy in letter identification. The SMI was adjusted separately for local and global blocks. For example, if participants started with the local condition, the SMI was adjusted for blocks in that condition and was reset to 66 ms when they started the global condition.

Participants were instructed to guess if they did not know the target letter. They were told that each Navon display would be composed of two different letters (selected from *A*, *E*, *H*, and *S*), and if they did not see the letter at the target level, they should not report the nontarget letter but should instead guess from the remaining three alternatives. There were four blocks of 48 trials for each combination of the prime (high vs. low spatial frequency) and probe (local vs. global), and participants performed all four blocks for a given prime-probe combination before moving on to the blocks for the next combination. The order of the conditions was counterbalanced across participants. We used this blocked design rather than cuing participants to a specific

level on a trial-by-trial basis to lessen confusion about the dual task.

Eight participants used their left hand for the prime task and their right hand for the probe task; the other 8 participants used the reverse pairing. For the prime task, participants used the index and middle finger of the response hand to indicate their response; the left finger was used to indicate a “left” orientation of the target spatial frequency, and the right finger was used to indicate a “right” orientation. For the probe task, tabs indicating “A,” “E,” “H,” and “S” were placed over keys on the keyboard, and participants pressed the corresponding button to indicate their response.

Prior to the main experiment, a control experiment was run (with 8 different participants from the same population) in order to ensure that we could replicate Hübner and Volberg’s (2005) findings with the attended level (local vs. global) varied between blocks and using our stimuli. We used the same design in the control experiment as in the primary experiment except that there was no prime. Thus, there were only two blocked conditions (probe: local or global). The control experiment was successful, and its results are presented at the end of the Results section.

Results

Main experiment

Participants had no trouble performing the priming task: Average accuracy in reporting the orientation of the target spatial frequency was 98%. We were therefore confident that attention was directed to the relevant spatial frequency in each block.

We established the separate representation of letter identity and hierarchical level, as predicted by integration theory, by comparing the observed distribution of errors with the distribution predicted by the traditional view (Fig. 2). The mean error rate across all conditions was 42%. These errors were evenly split between conjunction errors (21%) and feature errors (21%). As in Hübner and Volberg’s (2005) study, the distribution of errors was significantly different from that predicted by the traditional view, as indicated statistically by a significant Model (traditional vs. observed) \times Error Type (feature vs. conjunction) interaction, $F(1, 15) = 56.2$, $MSE = 13.0$, $p < .0001$, $p_{\text{rep}} = 1.0$, $\eta_p^2 = .79$. Follow-up t tests (all follow-up t tests described in the Results section used the Bonferroni correction) indicated that the rate of conjunction errors was significantly greater than the rate predicted by the traditional view, $t(15) = 7.5$, $p < .0001$, $p_{\text{rep}} = 1.0$, $d = 2.5$, and the rate of feature errors was significantly smaller than the rate predicted by the traditional view, $t(15) = 7.5$, $p < .0001$, $p_{\text{rep}} = 1.0$, $d = 1.0$.

An analysis comparing the observed pattern of errors with the pattern predicted by the traditional view for the local and global blocks separately mirrored the overall analysis. For local blocks, the significant Model \times Error Type interaction, $F(1, 15) = 130.9$, $MSE = 5.2$, $p < .0001$, $p_{\text{rep}} = 1.0$, $\eta_p^2 = .89$, reflected significantly more conjunction errors (18%) than

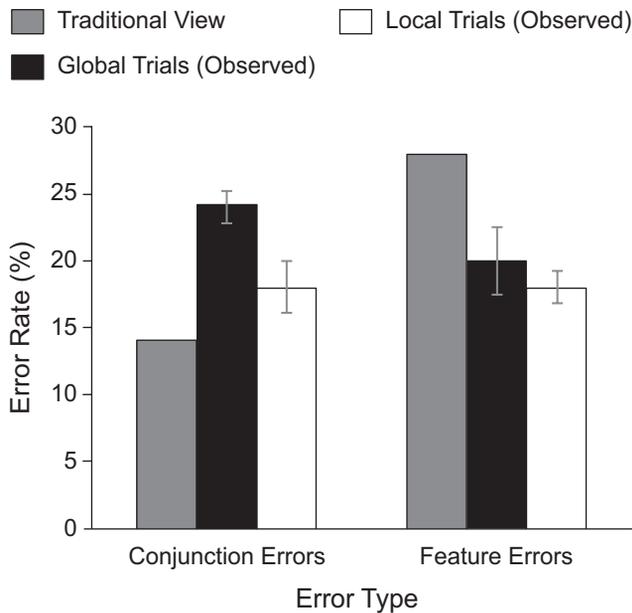


Fig. 2. Percentages of conjunction and feature errors predicted by the traditional view of shape-level binding and observed percentages of these errors on global and local trials. Error bars reflect standard errors of the mean.

predicted by the traditional view (13%), $t(15) = 6.7, p < .0001, p_{\text{rep}} = 1.0, d = 0.93$, and significantly fewer feature errors (18%) than predicted by the traditional view (26%), $t(15) = 6.7, p < .0001, p_{\text{rep}} = 1.0, d = 1.0$. Likewise, for global blocks, the significant Model \times Error Type interaction, $F(1, 15) = 52.0, MSE = 26.2, p < .0001, p_{\text{rep}} = 1.0, \eta_p^2 = .78$, reflected significantly more conjunction errors (24%) than predicted by the traditional view (16%), $t(15) = 7.2, p < .0001, p_{\text{rep}} = 1.0, d = 2.2$, and significantly fewer feature errors (20%) than

predicted by the traditional view (29%), $t(15) = 7.2, p < .0001, p_{\text{rep}} = 1.0, d = 1.1$. These results replicate those of Hübner and Volberg (2005), showing that when participants made an error, they were more likely to report the letter at the unattended level as being the target letter than to report a letter that was not present.

To examine our primary prediction that attentional selection of spatial frequencies would modulate shape-level binding differently depending on the visual field of presentation, we analyzed the conjunction errors in a $2 \times 2 \times 2$ analysis of variance (ANOVA), with attended spatial frequency in the prime (high vs. low), attended target level (local vs. global), and hemisphere (left vs. right) as factors. This analysis revealed a Level \times Hemisphere interaction, $F(1, 15) = 9.3, MSE = 52.8, p = .008, p_{\text{rep}} = .98, \eta_p^2 = .38$, which is depicted in Figure 3. There were significantly more conjunction errors for local targets projected to the RH (19%) than for local targets projected to the LH (15%), $t(15) = 2.5, p = .03, p_{\text{rep}} = .95, d = 0.73$, and significantly more conjunction errors for global targets projected to the LH (26%) than for global targets projected to the RH (22%), $t(15) = 2.4, p = .03, p_{\text{rep}} = .95, d = 0.65$. There was no Level \times Hemisphere interaction for feature errors, $F > 1$ (see Fig. 3), and no other effects in the feature-error analyses were close to significant levels.

The analysis of the conjunction errors also revealed a Spatial Frequency \times Level \times Hemisphere second-order interaction, $F(1, 15) = 8.2, MSE = 5.6, p = .01, p_{\text{rep}} = .97, \eta_p^2 = .35$. To examine this interaction, we conducted Level (local vs. global) \times Hemisphere (left vs. right) ANOVAs for the low-spatial-frequency and high-spatial-frequency conditions separately. For the low-spatial-frequency condition, there was a significant Level \times Hemisphere interaction (see Fig. 4), $F(1, 15) = 5.1, MSE = 24.4, p = .04, p_{\text{rep}} = .93, \eta_p^2 = .25$. As predicted,

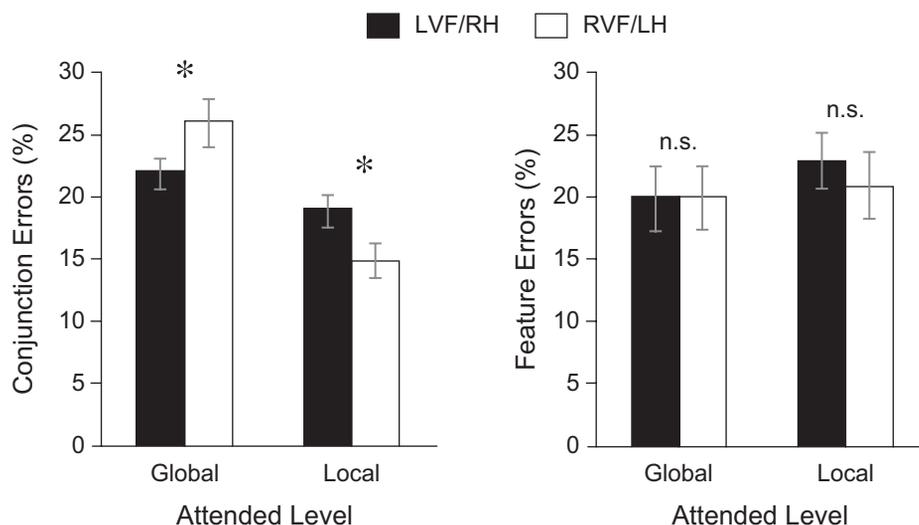


Fig. 3. Percentage of conjunction errors (left panel) and feature errors (right panel) as a function of level of the target (global vs. local) and visual field of presentation (left visual field/right hemisphere, LVF/RH, vs. right visual field/left hemisphere, RVF/LH). Error bars reflect standard errors of the mean. Asterisks indicate significant differences in the error rate at the $p < .05$ level.

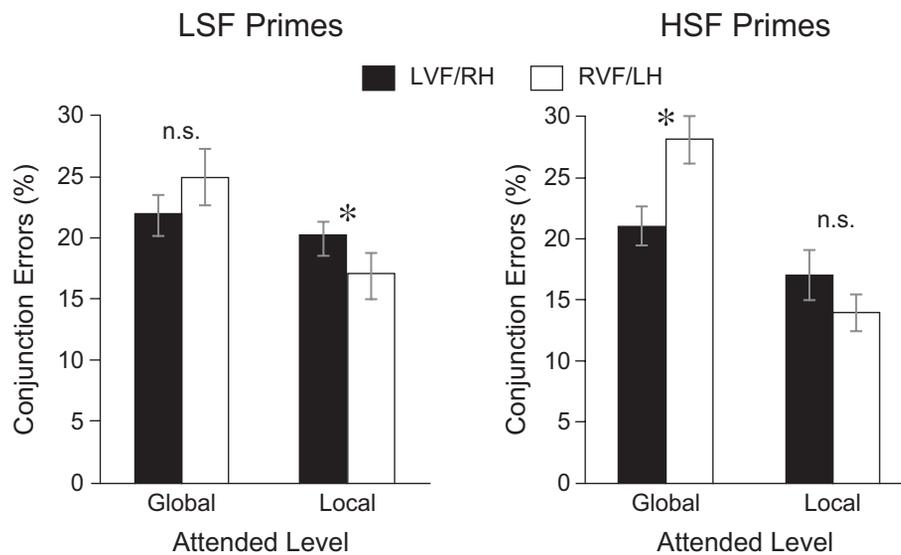


Fig. 4. Percentage of conjunction errors as a function of level of the target (global vs. local) and visual field of presentation (left visual field/right hemisphere, LVF/RH, vs. right visual field/left hemisphere, RVF/LH), separately for trials following low-spatial-frequency (LSF) primes (left panel) and for trials following high-spatial-frequency (HSF) primes (right panel). Error bars reflect standard errors of the mean. Asterisks indicate significant differences in the error rate at the $p < .05$ level.

follow-up t tests showed that following low-spatial-frequency selection, there were significantly more conjunction errors for local targets projected to the RH (20%) than for local targets projected to the LH (17%), $t(15) = 2.8, p = .01, p_{\text{rep}} = .97, d = 0.44$ (significant using Bonferroni correction), whereas there was no significant hemispheric difference for global targets, $t(15) = 1.3, p = .22, p_{\text{rep}} = .81, d = 0.30$. The Level \times Hemisphere ANOVA for the high-spatial-frequency condition also revealed a significant Level \times Hemisphere interaction (see Fig. 4), $F(1, 15) = 12.0, MSE = 34.9, p = .004, p_{\text{rep}} = .99, \eta_p^2 = .44$. As predicted, follow-up t tests showed the pattern opposite that found for low-spatial-frequency primes. That is, following attention to high-spatial-frequency primes, there were significantly more conjunction errors for global targets projected to the LH (28%) than for global targets projected to the RH (21%), $t(15) = 3.2, p = .006, p_{\text{rep}} = .98, d = 0.96$ (significant using Bonferroni correction), whereas there was no statistically significant difference between the hemispheres for local targets, $t(15) = 1.8, p = .09, p_{\text{rep}} = .89, d = 0.46$.

Control experiment

The results from the control experiment were similar to the overall results for probes in the primary experiment (i.e., collapsed over spatial frequency). The overall error rate was 37%, with feature errors occurring in 17% of trials and conjunction errors occurring in 20% of trials. Participants made significantly more conjunction errors (20%) than predicted by the traditional view (12%), as indicated by a significant Model (traditional vs. observed) \times Error Type (feature vs. conjunction) interaction, $F(1, 15) = 46.6, MSE = 10.7, p < .0001, p_{\text{rep}} = 1.0, \eta_p^2 = .87$. As in the primary experiment, the rate of conjunction

errors was significantly greater than that predicted by the traditional view, $t(15) = 6.8, p < .0001, p_{\text{rep}} = 1.0, d = 2.8$, and the rate of feature errors was significantly smaller than that predicted by the traditional view, $t(15) = 6.8, p < .0001, p_{\text{rep}} = 1.0, d = 1.8$.

The Level (local vs. global) \times Hemisphere (left vs. right) ANOVA was also consistent with the results from the primary experiment, revealing a Level \times Hemisphere interaction, $F(1, 7) = 18.7, MSE = 14.5, p = .003, p_{\text{rep}} = .99, \eta_p^2 = .73$. There were significantly more conjunction errors for local targets projected to the RH (18%) than for local targets projected to the LH (13%), $t(7) = 2.7, p = .03, p_{\text{rep}} = .95, d = 1.0$, and significantly more conjunction errors for global targets projected to the LH (28%) than for global targets projected to the RH (21%), $t(7) = 4.3, p = .004, p_{\text{rep}} = .99, d = 1.1$. There was no Level \times Hemisphere interaction for feature errors, $F > 1$, and no other effects in the feature-error analyses approached significant levels.

Discussion

The results of this study demonstrate that the selected spatial frequency in a previously presented stimulus facilitates shape-level binding in hierarchical displays. We replicated the disproportionately large incidence of conjunction errors relative to feature errors and the modulation of these errors across the two hemispheres (Hübner & Volberg, 2005). Most important, attentional selection of spatial frequency modulated shape-level binding in a manner consistent with hierarchical integration theory and the literature on functional hemispheric differences. Attentional selection of relatively low spatial frequencies reduced the hemispheric asymmetry for global

conjunction errors and facilitated binding of letters to the global level in the right hemisphere. Conversely, selection of relatively high spatial frequencies reduced the hemispheric asymmetry for local conjunction errors and facilitated binding of letters to the local level in the left hemisphere. This modulation by spatial frequency occurred despite any habituation effects that may have occurred from presenting the same spatial-frequency gratings throughout the experiment (albeit in different orientations).

Although by their nature high-spatial-frequency stripes are smaller than low-spatial-frequency stripes, a recent study provided evidence that relative spatial frequency, rather than attentional window size, is the critical factor for this facilitation effect (Flevaris et al., 2009b). In that study, compound gratings similar to those used here were presented as target stimuli, preceded by hierarchical Navon letters as primes. Attention to the global level in the prime improved discrimination of the low spatial frequencies in the compound grating, whereas attention directed to the local level improved discrimination of the high spatial frequencies. This pattern was observed despite differences in the retinal location of the hierarchical displays and the grating. Most important, these effects were determined by the relationship between the two spatial frequencies in the grating, rather than by absolute spatial frequency: Discrimination of a 1.8-cycles/deg grating was facilitated by local attention when it was paired with a 0.9-cycles/deg grating (lower spatial frequency), but was facilitated by global attention when it was paired with a 5.3-cycles/deg grating (higher spatial frequency). These findings strongly suggest that the current results cannot be attributed to the size of the attentional window.

The results from the current study are consistent with the double-filtering-by-frequency (DFF) theory of hemispheric specialization posited by Ivry and Robertson (Ivry & Robertson, 1998; Robertson & Ivry, 2000), but with a new twist. According to DFF theory, the two cerebral hemispheres differ in how they amplify relative spatial-frequency information in the stimulus. Attention first selects the task-relevant spatial-frequency range, and the frequencies in this range are projected to both cerebral hemispheres. The RH selectively emphasizes the relatively low spatial frequencies within that range, and the LH selectively emphasizes the relatively high spatial frequencies. The current data, together with Hübner and Volberg's (2005) initial findings, suggest that the asymmetry in selective tuning to spatial frequencies provides the basic features that segregate local and global levels, but that when attention is overtaxed and biased toward one spatial frequency, shapes are more likely to be perceptually bound incorrectly to the wrong level (as reflected by illusory shape-level conjunctions). An important tenet of DFF theory is that both hemispheres have access to the initial task-relevant selection of the spatial-frequency spectrum, so that hemispheric asymmetry in spatial-frequency filtering is a higher-level mechanism. That we did not find an interaction between spatial frequency and hemisphere is consistent with this idea. That is, attention to

relatively high spatial frequencies or low spatial frequencies did not generally facilitate processing by the LH or RH, respectively. Rather, attention to spatial frequency modulated specific, task-relevant processing in each hemisphere—namely, the binding of letter identity to hierarchical level.

Although spatial frequencies are involved in parsing information into global and local levels (Robertson, 1996), studies have shown that other features of a stimulus can also be valuable in parsing levels when spatial-frequency differences are degraded (Lamb, Yund, & Pond, 1999). Whether image properties such as size can also facilitate binding of identity and hierarchical level and whether binding varies as a function of the spatial-frequency differences present in the display are interesting avenues for future research. Moreover, given that attention to spatial location plays a key role in binding surface properties into integrated object percepts (Treisman & Gelade, 1980), it will also be important to determine how spatial attention interacts with the mechanisms underlying the binding of individual objects to the relative scale at which they exist in the visual environment. The results from the current study open the door for these explorations by showing that attentional selection of spatial-frequency information plays a key role in binding elements of hierarchical displays to the levels at which they occur.

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Declaration of Conflicting Interests

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