

The Role of Spatial Frequency Selection in Local versus Global Perception

by

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Abstract

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The aim of this research is to investigate the extent to which selective attention to spatial frequency (SF) mediates local versus global perception in general and in the context of face perception. Previous research has suggested a relationship between processing high versus low SFs and local versus global perception, respectively, but the nature of this relationship is debated. The experiments reported here demonstrate that attention to local and global aspects of a hierarchical display biases the flexible selection of *relatively* higher and *relatively* lower SFs during image processing. Moreover, the attentional selection of relative SF mediates the perceptual integration of the identity of elements in a hierarchical display with the level (local/global) at which they occur. Finally, the attentional selection of SF is shown to modulate early stages of face perception reflected in the N170-effect, a neurobiological index of face categorization that is particularly sensitive to face features. The N170-effect is found to be equally robust in response to the selection of *both* HSFs and LSFs in face-related stimuli, but the reliance on one SF scale or another is contingent upon the nature of the attended face-related stimulus, and whether its configuration is intact. Taken together, this investigation provides clear evidence that the flexible, top-down selection of low-level SF channels mediates the perception of local and global elements of visual displays, both for tightly controlled experimental stimuli as well as faces, a natural and frequently viewed hierarchical object category.

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1. Introduction

We perceive our environment as being hierarchically organized, such that scenes are composed of objects, which are composed of parts, and so on. Accurate visual perception thus requires the ability to represent elements at multiple levels of hierarchical structure. At any given moment, we can selectively attend to the level of the components, which is referred to as “local processing”, or to the level of the whole, which is referred to as “global processing.” Studies across cognitive, computational, neuropsychological and neurophysiological domains have established functional hemispheric differences in hierarchical perception¹, with the left hemisphere (LH) of the brain demonstrating a local processing bias and the right hemisphere (RH) demonstrating a global processing bias. However, though it is accepted that distinct but overlapping neural and perceptual mechanisms underlie local and global perception, the nature of these mechanisms is debated.

The picture becomes more complicated when we consider the fact that the level at which a particular object is perceived can vary depending on the focus of attention. For example, when viewing a forest, a tree in the forest is a local element in the global scene, but if we focus our attention on the tree, it becomes a global element of which its leaves, branches, and trunk are local elements. Any theory of hierarchical perception must therefore provide an account for how the local and global levels are initially determined. Some researchers have associated the processing of high spatial frequencies (HSFs) versus low spatial frequencies (LSFs) with local versus global perception, respectively, but it is debated whether the association with spatial frequency (SF) reflects a lower-level perceptual mechanism (e.g., Sasaki, 2001; Sergent, 1982) or a higher-level attentional process that interacts with low level SF channels (e.g., Ivry & Robertson, 1998). Other researchers have questioned if SF processing underlies hierarchical perception at all, providing alternative accounts for the hemispheric asymmetry observed in local versus global processing (e.g., Hübner & Volberg, 2005).

The present research investigates the role of SF selection in hierarchical perception. This investigation is three-fold: (1) In Chapter 2, I evaluate whether the association between SF processing and hierarchical perception reflects a higher-level attentional mechanism involved in the selection of *relative* SF, rather than the low-level perceptual processing of *absolute* SF. Experiments 1-4 provide evidence for a higher-level mechanism by demonstrating that attention directed to the local versus global level of hierarchical displays facilitates attentional selection of *relatively* HSFs versus *relatively* LSFs, respectively. (2) In Chapter 3, I consider a theory of hemispheric asymmetry in local versus global processing that was recently proposed as an alternative to theories associating SF processing with hierarchical perception, which I will refer to as “Hierarchical Integration” (HI) theory (Hübner & Volberg, 2005). HI proposes that the two hemispheres differ in how they perceptually bind the shapes of elements in a hierarchical image with the level at which they occur (i.e., local or global): HI proposes that the LH is more involved in perceptually binding elements with the local level and the RH is more involved in perceptually binding elements with the global level. However, the nature of the integration

¹ Unless otherwise noted, the phrase “hierarchical perception” will refer to the perception of hierarchically arranged visual stimuli, not to be confused with the hierarchical organization of the visual system in the brain.

mechanism involved has not been characterized. Although HI was proposed in contrast to theories relating SF processing with hierarchical perception, I propose that these two ideas can be incorporated into a unified framework such that attentional selection of SF may be the medium by which HI occurs. Experiment 5 assesses this possibility. (3) In Chapter 4, I examine the role of SF processing in the perception of an arguably unique hierarchical stimulus, the face. Studies of face perception have revealed that analysis of the global structure, the features, and their second order relationships all contribute to normal face perception, but the extent to which different stages of face perception rely on these computations is disputed. Experiment 6 explores how SF scales are used to perform the computations that allow for face detection by examining how SFs in the stimulus modulate the N170-effect, a relatively early face-selective ERP difference associated with face categorization.

2. Evaluation of the relationship between SF processing and hierarchical perception: Higher-level attentional mechanism?

2.1. Hierarchical perception: Relevant background

From Gestalt psychology to more recent studies of functional hemispheric differences, a central question has been how local parts are integrated into global wholes. To explore questions of visual hierarchical processing, many studies have employed hierarchical letter displays that were first developed by David Navon (1977) and thus referred to as “Navon” stimuli (Figure 1). In such displays, a series of local elements (usually letters, though studies have shown similar results using non-letter shapes, e.g., Kimchi & Merhav, 1991) are spatially arranged to form a global element of the same type. By presenting the same type of object at the local and global levels, hierarchical processing can be isolated from other object recognition processes that concurrently occur during normal perception of hierarchical images (e.g., an E can be global on one trial and local on another).



Figure 1. Example Navon display. In this example a global A is composed of local E's.

2.1.1. Distinct but overlapping mechanisms underlying local and global perception: Hemispheric lateralization

When presenting Navon displays in one visual field or the other, Martin (1979) was the first to report a functional hemispheric difference in local versus global perception by demonstrating that participants were faster to identify the letters at the local level when the displays were projected directly to the LH (i.e., presented in the right visual field/RVF) and they were faster to identify the letters at the global level when the displays were projected directly to the RH (i.e., presented in the left visual field/LVF).

The RH dominance for global processing and LH dominance for local processing was later corroborated by neuropsychological investigations of brain-damaged patients (Delis, Robertson & Efron, 1986; Lamb, Robertson & Knight, 1989; Robertson & Delis, 1986; Robertson & Lamb, 1991; Robertson, Lamb & Knight, 1988; Robertson, Lamb & Zaidel, 1993). These studies found that patients with lesions in the left temporal-parietal junction (TPJ) were selectively impaired at perceiving local elements in Navon displays, whereas patients with lesions in the right TPJ were selectively impaired at perceiving global elements. Similar regions were later implicated in neurologically intact participants using fMRI, demonstrating a hemispheric asymmetry in the BOLD response in the superior temporal gyrus (STG) when participants identified local versus global elements of Navon displays (Weissman & Woldorff, 2005). However, there have also been functional imaging studies which have found hemispheric

asymmetries in local versus global processing in earlier, occipito-temporal regions (e.g., Fink et al., 1997; Han et al., 2002, Martinez et al., 1997). Despite differences in the specific regions implicated, studies have replicated and converged on evidence that LH function is biased toward local perception and RH function is biased toward global perception.

Importantly, the lateralized effects have not been found in the primary visual cortex, but in later visual areas, suggesting that the hemispheric functional asymmetry in hierarchical perception reflects a higher-level mechanism than the mere perceptual processing of low-level features in the displays. Findings from ERP studies (e.g., Han & Chen, 1996; Han, Liu & Woods, 2000; Heinze et al., 1998; Volberg & Hübner, 2004) corroborate this notion because hemispheric asymmetries in local versus global perception have most often been reported in later components such as N2 (260ms-350ms) and P3 (320ms-400ms) rather than in earlier components such as C1 (55ms-80ms), P1 (80ms-150ms) and N1 (130ms-210ms).

2.1.2. Role of SF processing in hierarchical perception

Broadbent (1977) first proposed that the important functional distinction between local and global levels of hierarchical displays is in their SF content. That is, HSFs are more important for resolving the local than global level and LSFs are more important for resolving the global than local level. The visual system filters incoming information into channels that are tuned for different SF bands (De Valois & De Valois, 1990), and it is thus possible that different SF channels are utilized for local and global processing. Corroborating this view, Shulman and colleagues (1986, 1987) provided evidence associating local perception with HSF processing and global perception with LSF processing. For example, when detecting SF gratings following a local/global task using Navon patterns, participants were faster at detecting HSF gratings when they had just reported a target at the local level, and they were faster at detecting LSF gratings when they had just reported a target at the global level.

According to these initial characterizations, the hemispheric asymmetry in local versus global perception was thought to reflect slightly different tuning of HSF or LSF channels in the LH and RH, respectively. However, subsequent studies (Christman, Kitterle & Hellige, 1991; Kitterle, Christman & Hellige, 1990; Kitterle, Hellige & Christman, 1992) suggested that the hemispheric asymmetry in SF processing arose when the output of multiple SF channels needed to be compared, suggesting that it was not a low-level mechanism in SF processing *per se*. When participants were asked to identify sinusoidal gratings of a different SF, they were faster to *identify* HSFs projected directly to the LH and LSFs projected directly to the RH, but no such hemispheric differences were found when participants merely *detected* the presence of the gratings. Moreover, the difference was one of relative SF rather than absolute SF. That is the RH advantage for the lower SF grating of a set, e.g., 3 versus 9 cycles/degree (c/d) changed to a LH advantage when the same grating (3c/d) became the higher SF of the set, e.g., 1 versus 3c/d.

The relationship between SF selection and processing targets in hierarchical displays was further studied by Robertson (1996) with Navon patterns that varied in their SF content. In that study participants discriminated letter targets that could appear at either the global or local level of Navon patterns and were faster at reporting a target in trial N when it appeared at the same level as in trial N-1 (i.e., same-level priming). Importantly, same-level priming occurred whether

or not the color, shape, contrast, polarity, or location of the displays changed from trial to trial, but was eliminated when the SF content of the displays changed between trials. In alternating trials, the Navon patterns were contrast-balanced to filter out the lower SFs. This was done by adding a set of darkened dots to each pixel of the display such that the mean luminance across each set of dots (including the central brightened pixel) summed to the mean luminance of the background. Importantly, when the trials alternated between contrast-balanced and full spectrum displays, same-level priming disappeared. That is, SF was the only dimension that required consistency across trials for the same-level priming to occur. Robertson concluded that SFs are used to guide attention to one or the other level of hierarchical displays. In a later study, Lamb, Yund and Pond (1999) replicated this finding, but found that if participants had previous experience in a block of contrast-balanced displays, same-level priming was then observed in an alternating (between contrast balanced and full spectrum) condition. On the basis of these findings Lamb et al. (1999) argued that hierarchical displays are not necessarily parsed on the basis of their SFs as Robertson (1996) had proposed. However, as Robertson (1999) pointed out in a response article, although these results may constrain the attention-guiding hypothesis, they do not entirely explain her earlier findings. It is clear that SFs are involved in parsing information into global and local levels when SF differences between the levels are present, though other features of a stimulus can also be valuable in parsing hierarchical levels under conditions when SF differences are not present.

2.1.3. Double Filtering by Frequency (DFF) theory

The hemispheric lateralization in processing relatively low versus relatively high SFs, and the association of HSFs with local processing and LSFs with global processing led Ivry and Robertson (1998; Robertson & Ivry, 2000) to posit the DFF theory of hemispheric specialization. According to this theory, there are two stages based on SF processing, and the two hemispheres differ in how they amplify SF information after the initial stage. According to DFF theory, attention first selects a SF range from the incoming spectra that is most suited for the current task (e.g., what range of spatial scales is most likely to contain the target?; see Watt, 1988 for a model of how this might work). This SF range is then fed forward to both cerebral hemispheres. It is at this stage that the hemispheres differ, with the LH acting as a relatively high-pass filter, emphasizing information from higher SFs within the range, and the RH as a relatively low-pass filter, emphasizing the lower SFs within the range. Hence, the critical distinction between DFF and other conceptualizations of the role of SF processing in hierarchical perception is that DFF theory proposes a flexible mechanism to underlie the observed hemispheric asymmetries. That is, a particular portion of the SF spectra may be preferred by the LH in one instance and by the RH in a different instance depending on the stimuli present and the task. In contrast, other models assume a lower-level mechanism by suggesting that the hemispheres receive different input (or asymmetrically emphasize different input) from lower-level visual areas and thus differ in absolute SF biases (e.g., Jacobs & Kosslyn, 1994; Sasaki et al., 2001; Sergent, 1982).

In accord with the flexible mechanism posited by DFF theory, researchers exploring the use of SF scales during visual perception have shown that SFs can be flexibly used to influence responses depending on the task (e.g., Goffaux et al., 2005; Loftus & Harley, 2004; Morrison & Schyns, 2001; Schyns & Oliva, 1999). For example, in the context of face perception, Schyns & Oliva (1999) demonstrated that the initially perceived SFs (HSF versus LSF) vary as a function

of the face perception task (determining if a face is expressive or not versus identifying the specific expression, respectively). Nonetheless, whether the hemispheric biases in SF processing reflect the flexible mechanism proposed by DFF theory has not yet been directly tested, and is the aim of Experiments 1-4.

2.2. Aim of Experiments 1-4: Appraising the flexible mechanism posited by DFF theory

Experiments 1-4 ask if *selection* of higher or lower SFs in a compound grating is influenced by previously attending to the local or global level of a Navon pattern. In all four experiments participants viewed pairs of Navon patterns as the “prime” display (one in each visual field) and were asked to make same/different judgments on either the local or the global level. Following the response to the Navon patterns on each trial, one or two compound gratings with two orthogonally oriented SFs appeared as the “probe” display and participants were instructed to make an orientation judgment about either the “thin lines” (HSFs), or the “thick lines” (LSFs). The local/global and the HSF/LSF conditions were orthogonally associated forming four possible combinations that were presented in a counterbalanced blocked design. In Experiment 1, two identical compound gratings were presented in the periphery at the same locations as the two Navon patterns. In Experiment 2, only one compound grating was presented after the two peripheral Navon patterns, and it was centrally located. Experiment 3 was identical to Experiment 2 but used single letters (either small or large) as primes, to rule out the possibility that adjusting the size of the attentional “spotlight” drove the effects in Experiments 1 and 2 (i.e., due to the size correspondence between the local level and HSFs and global level and LSFs, respectively). Experiment 4 directly examined if attention to hierarchical level biases attention to relative and/or absolute SF by presenting a 1.8 cycle/degree grating as the relatively *higher* SF in the compound grating during half of the blocks and as the relatively *lower* SF in the compound grating during the other half.

In all four experiments, the two SFs within the compound grating differed in orientation, forcing participants to selectively attend to the task-relevant SF in order to report its orientation. Thus, in contrast to the previous studies (e.g., Shulman et al., 1987; Robertson, 1996), the priming effects examined in the present studies concerned the influence of hierarchical perception on selective attention to SF rather than the perceptual processing of high versus low SFs *per se*. If selection of SFs is, indeed, influenced by attending to local versus global levels, participants should be faster at selectively reporting the orientation of relatively HSF than relatively LSF gratings during the local attention block, and they should be faster at selectively reporting the orientation of the relatively LSF than relatively HSF gratings during the global attention block.

2.3. Experiment 1

2.3.1. Experiment 1 Methods

Participants

Sixteen students from the University of California, Berkeley (eight female) participated in the experiment for course credit. All had normal or corrected-to-normal vision. The experiment was approved by the University of California, Berkeley Committee for the Protection

of Human Subjects (CPHS), and all participants gave informed consent before participating. The CPHS protocol number was 2004-3-35.

Stimuli

The Navon patterns were generated using Adobe Photoshop™. Seen from a distance of 1m, each local letter subtended 0.7° of visual angle and was black Helvetica bold font presented on a gray background, arranged to form a global letter that was 4.0° wide by 5.7° high. The letters used were A, C, D, E, F and H, in all their global and local combinations, with the exception of congruent combinations (e.g., a global A made up of local A's). This resulted in 30 different Navon displays.

The compound gratings were generated in Matlab™ (Mathworks, Natick, MA) with a sinusoid function for each SF. Each compound grating subtended 5.4° of visual angle and was composed of a 2.4c/d (13 cycles/image; c/i) grating (the relatively HSF component) and a 0.7c/d (4c/i) grating (the relatively LSF component). Both SF gratings were at 100% contrast. The relatively HSF component was oriented either at 45° (tilted to the right) or at 135° (tilted to the left) and the relatively LSF component was oriented in the opposite direction (Figure 2).

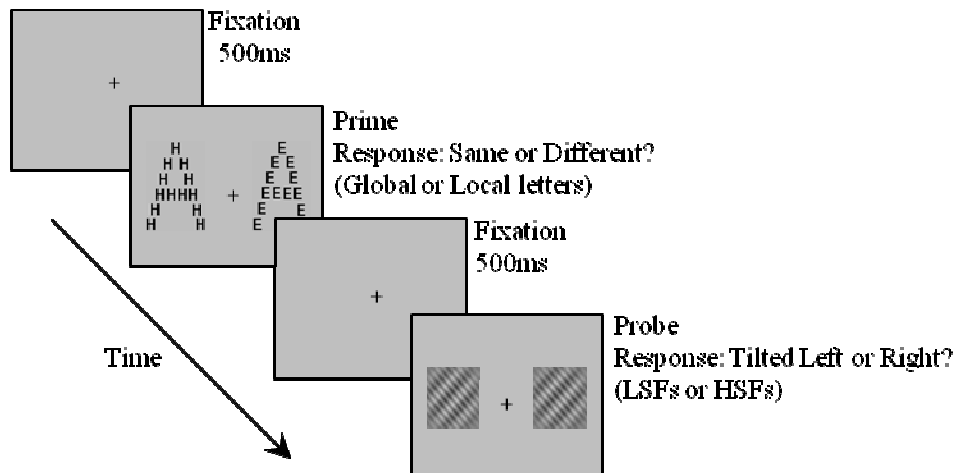


Figure 2. Example trial from Experiment 1. Participants performed two tasks in alternating sequence. First, two Navon figures appeared on each side of fixation until response (prime). Participants indicated if they differed at the global or local level (in separate blocks of trials). Following the prime, two identical compound frequency gratings appeared until response (probe). Participants reported the orientation of the LSFs or HSFs in the gratings (in separate blocks of trials).

Procedure

The stimuli were shown on a Dell 17 inch color monitor with a vertical refresh rate of 60 Hz at a resolution of 1024 x 768 pixels. Participants were seated 1m from the screen in a dimly lit room. Trial timing was controlled by Presentation™ (Neurobehavioral Systems, Albany, CA) and is depicted in Figure 2. Each trial began with a central fixation cross presented for 500ms, followed by two Navon patterns (the prime), one in the left and one in the right visual field, with

the medial edge 1° from fixation. The letters remained on the screen until response. Participants indicated if the two Navon displays were the same or different at the local level during half of the trials and they indicated if the Navon displays were the same or different at the global level during the other half of trials. Responses were made by pressing one of two keys on the keyboard (either “S” for same or “D” for different, or “J” for same or “K” for different) with either the left or right hand, which was also counterbalanced across participants. That is, half of the participants used the S and D keys (left hand) while the other half used the J and K keys (right hand) for the prime task. Immediately following the Navon prime, two identical compound gratings (the probe) appeared until response in the same spatial locations as the Navon patterns.

Participants indicated whether the relatively HSF components (referred to as “thin bars”) were oriented to the left or right in half of the trials and they indicated whether the relatively LSF components (referred to as “thick bars”) were pointing to the left or right in the other half of the trials. Responses to the grating probe were made by pressing one of two keys on the keyboard (the opposite pair of keys than were used for the prime task) by the opposite hand than that used for the prime task. Participants thus performed four blocks of 120 trials each, the order of which was counterbalanced. A different combination of prime and probe tasks was used in each block. In one block participants responded to the local level and then indicated whether the HSF was oriented left or right. In another block they responded to the global level and then indicated whether the HSF was oriented left or right. In another block of trials they responded to the local level and then indicated whether the LSF was oriented left or right. Finally, in another block they responded to the global level and then indicated whether the LSF was oriented left or right. Prior to each experimental block participants were given 30 practice trials to get them used to the task. Each session lasted about 30 minutes.

2.3.2. Experiment 1 Results

Probe RTs

Across priming conditions probe-performance accuracy was at ceiling (97%) and was not analyzed further. RTs to the designated SF in the probe were analyzed with a 2 x 2 analysis of variance (ANOVA) with repeated measures. The factors were primed level (local vs. global) and attended SF (HSF vs. LSF). Reaction times (RTs) to incorrect responses, either to the prime or to the probe, and those above or below two standard deviations of the mean (calculated within-subject and within-condition) were excluded (~16% of total trials; 11% for incorrect responses and 5% for outlier RTs).² This analysis revealed a significant interaction between the primed level and attended SF, [$F(1,15) = 7.1$, $MSe = 1293.3$ $p < .05$; partial $\eta^2 = 0.32$], but no significant main effects of SF or primed level. That is, while the overall means were statistically equivalent across the two SF conditions (534 ms to HSF and 530 ms to LSF) and across the two primed levels (531 ms in the local attention blocks and 534 ms in the global attention blocks), mean RTs

² The same analysis performed without excluding trials showed a similar pattern albeit noisier. The mean RTs were: 522 ms and 542 ms following global and local processing, respectively, in the LSF blocks and 547 ms and 536 ms following global and local processing, respectively, in the HSF blocks.

were faster to HSF probes following local (520ms, SE = 26ms) than global (548ms, SE = 35ms) primes, and faster to LSF probes following global (519ms, SE = 22ms) than local (540ms, SE = 23ms) primes (Figure 3). While some subjects showed both simple effects (faster RTs to HSF probes in the local block and to LSF targets in the global block), other subjects demonstrated only one of the simple effects (e.g., faster RTs to LSF probes in the global block but no difference in the local block or vice versa). Nonetheless, the significant interaction shows an overall pattern of better performance for HSF than LSF probes when attending to the local level and for LSF than HSF probes when attending to the global level. In Figure 4, the difference between RTs to LSF and HSF probes are plotted for each individual. All but two participants (shown in gray) had an increased mean difference in the local than global attention blocks, reflecting the consistency of the overall pattern of priming effects.

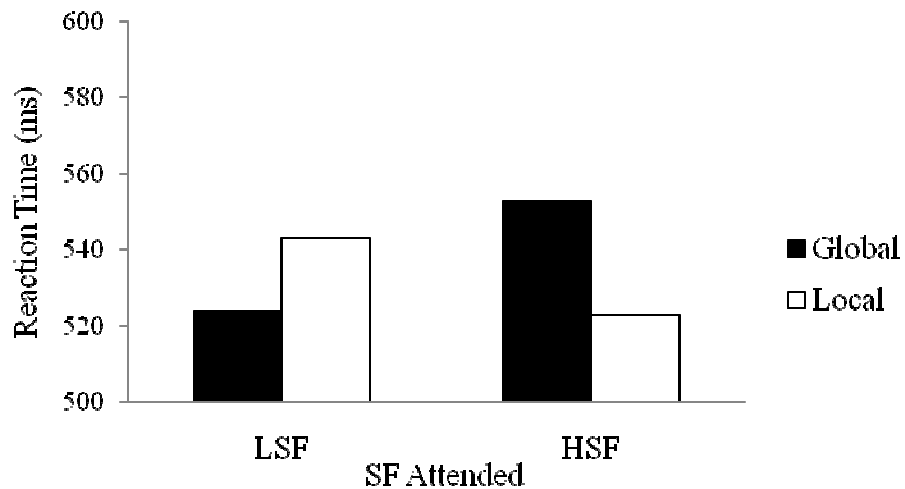


Figure 3. Average reaction times (RTs) to LSF and HSF targets in compound grating probes during the global and local attention blocks in Experiment 1.

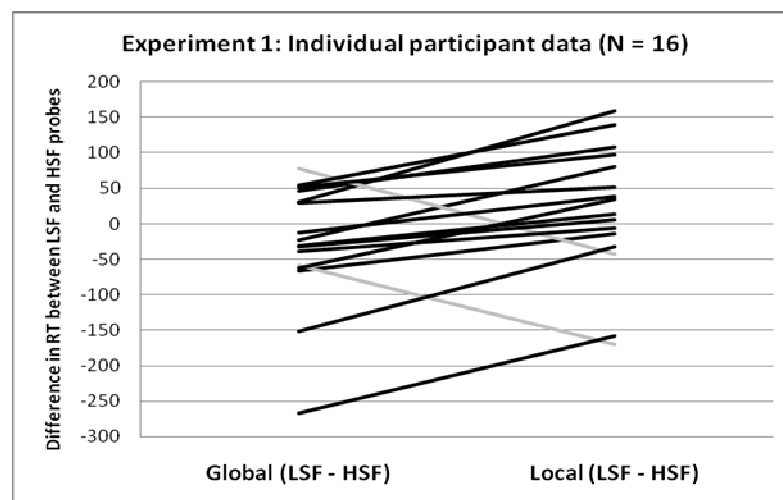


Figure 4. Individual participant data from Experiment 1 showing the difference between reaction times (RTs) to low spatial frequency (LSF) targets minus high spatial frequency (HSF) targets in the global and local attention blocks. For all but two participants, this difference was greater in the local than global block, as evidenced by the increasing slope. The two participants who showed the opposite effect are shown in gray.

Prime RTs

I also analyzed RTs to the primes with a 2 x 2 ANOVA for repeated measures. The factors were attended hierarchical level (local vs. global) and whether the attended probe frequency was high or low. This analysis revealed a main effect of prime, [$F(1,15) = 7.3$, $MSe = 9719.5$, $p < .05$; partial $\eta^2 = 0.33$], indicating that participants were faster when responding to global (683ms) than local (746ms) primes. Although the direction of this effect is consistent with global precedence (Navon, 1977), there was evidence of a speed accuracy tradeoff in the prime responses: Accuracy was greater for local than global responses (94.6% and 89.9% respectively) as revealed in a main effect of attended level, [$F(1,15) = 101.6$, $MSe = 3.8$, $p < .0001$; partial $\eta^2 = 0.87$]. Importantly, this difference in prime accuracy did not interact with the (forthcoming) probe's frequency [$F(1,15) < 1$]. When I combined RT and accuracy into a single measure by dividing RT by proportion correct (Townsend & Ashby, 1983) and re-ran the analyses using this measure, I found no effects in the prime data, thus, no global precedence.

2.3.3. Experiment 1 Discussion

The results of Experiment 1 demonstrate that attention to a given hierarchical level of a Navon pattern influences the time it takes to selectively respond to the relatively high or low SFs in a subsequent compound grating. RTs to the relatively HSF were facilitated following attention to the local level of the Navon patterns, and response times to the relatively LSF in the same compound gratings were facilitated following attention to the global level. The current results extend the previous findings of Shulman and colleagues (1986, 1987) because the present study required participants to select a SF within a stimulus compound containing both relatively high and relatively low SFs, whereas in their studies participants were presented with simple gratings (either HSF or LSF). Moreover, the two SFs in the present compound grating are not considered HSF and LSF in the absolute sense. Rather, the 2.4c/d HSF grating used here is a lower or mid-level SF in the spectrum (DeValois & DeValois, 1988). Indeed, Shulman and colleagues found that a 2c/d grating was associated with global perception whereas higher SF gratings of 8c/d and 16c/d were associated with local perception. This is an important distinction because it is consistent with models claiming that the relationship between SF and attention to hierarchical level is more than an automatic early perceptual effect. A bottom up priming effect would occur through stimulation of the same SF channels as biased by the prime rather than be contingent on the need to parse and then select relatively higher or lower SFs in the probe.

Before considering the implications of these findings, it is necessary to rule out a simple explanation of the results based on a prime-induced bias of the distribution of attention in space. Specifically, it is possible that the span of attentional focus varied between local and global blocks. Participants may have adopted a wide and more distributed attentional distribution when responding to the global level and a narrow, more focused attentional distribution when responding to the local level. Although I attempted to mitigate this problem by presenting hierarchical patterns in the periphery and asking participants to make same/different judgments at either the global or local level across the visual field, there was no need to change the spatial span of attention established by the prime in order to respond to the grating probes, since the grating probes were presented in the same spatial locations as the primes. Furthermore, it is also

possible that stimulus size was the critical dimension, rather than attention to hierarchical level. For example, if participants adopted a wider or narrower attentional window to perform the global versus local task, respectively, a larger attentional window could prime the larger LSFs whereas a smaller attentional window could prime the smaller HSFs. Finally, I did not monitor eye movements in Experiment 1 and thus I could not rule out the possibility that participants made more eye movements in one condition than another. These alternative hypotheses were tested and ruled out in Experiments 2 and 3.

2.4. Experiment 2

In Experiment 2, a single compound grating was presented as the probe at fixation after the same/different response to the pair of peripherally presented Navon patterns, and I monitored eye movements to verify that participants maintained central fixation during the prime task. In so doing, I assured that the spatial window required to perform the local prime task was actually closer in size to the window required for the LSF grating task than the window required to perform the global prime task. Since the prime task required a comparison of the two peripheral Navon patterns, the minimum spatial window required for the local attention block would need to span the nearest two local letters in the two displays. In Experiment 2 each local letter subtended $.7^\circ \times .7^\circ$ of visual angle, and their edges were located 1° to the left and right of fixation, resulting in a spatial window with a 3.4° diameter for the local prime task. For the global attention block, the spatial window would need to span nearly the whole $5.7^\circ \times 4^\circ$ global letters, resulting in a spatial window with a diameter somewhere between $11.4^\circ \times 6^\circ$. Importantly, the compound grating probe had a diameter of 5.4° centered at fixation, making it closer in size to the spatial window required for the local than global block. Thus, in a local block participants would not need to alter the span of their spatial window to perform either the LSF or HSF grating orientation task since the central grating was presented within the span of spatial attention. If local primes facilitate performance on HSF rather than LSF grating probes, a pure spatial account of the results is unlikely.

In addition to presenting a single compound grating probe at fixation and monitoring eye movements during both prime and probe, the Navon patterns in Experiment 2 were presented for 300ms rather than until response as in Experiment 1 to facilitate the maintenance of central fixation. It is important to note that the compound grating included the same SFs as in Experiment 1 as measured in the probe, but the change in its location from the peripheral to central visual field changed the spectral sensitivities of the visual response. In this way, the *relative* frequencies in the probe remained the same, while the input visual frequencies were vastly different.

2.4.1. Experiment 2 Methods

Participants

Sixteen students from the University of California, Berkeley (eight female) participated in Experiment 2. They received course credit for their participation. All had normal or corrected-to-normal vision. The experiment was approved by the University of California, Berkeley CPHS (#2004-3-35), and all participants gave informed consent before participating.

Stimuli

The stimuli in Experiment 2 were identical to those used in Experiment 1 except that only one grating probe was presented (see Figure 5). The grating subtended 5.4° in diameter and appeared at central fixation.

Procedure

The procedure in Experiment 2 was similar to Experiment 1 with three differences. First, the Navon/letter pairs were presented for 300ms followed by the reappearance of the fixation cross until response. Second, eye movements were monitored to verify that the participants maintained fixation while the primes were present. Third, only one compound grating probe followed the primes and it was centered at fixation. The grating probe remained on the screen until response. Other than those three differences, the procedure was identical to Experiment 1. Participants performed the same four blocks of 120 trials each, in counterbalanced order and performed the same two tasks with the same counterbalanced response mappings.

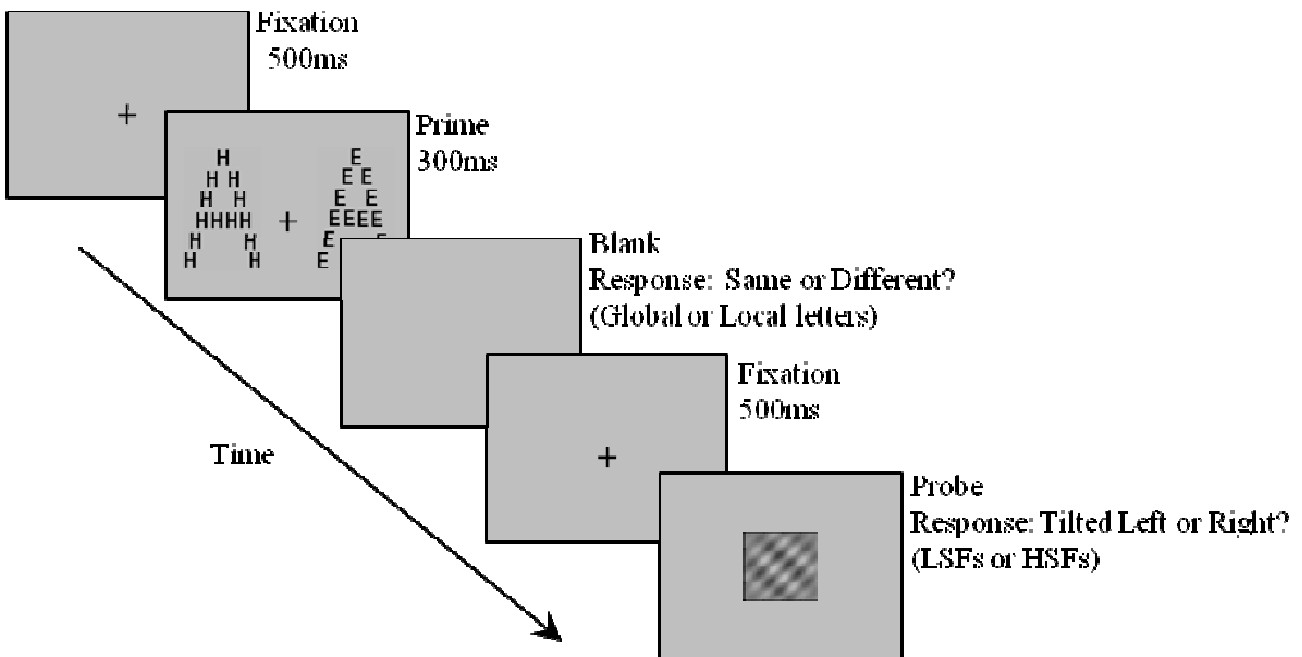


Figure 5. Example trial from Experiment 2. Participants performed two tasks in alternating sequence. First, two Navon figures appeared on each side of fixation until response (prime). Participants indicated if they differed at the global or local level (in separate blocks of trials). Following the prime, one compound frequency grating appeared at fixation until response (probe). Participants reported the orientation of the LSFs or HSFs in the grating (in separate blocks of trials).

2.4.2. Experiment 2 Results

Probe RTs

Similar to Experiment 1, probe-performance accuracy was at ceiling (97%) and therefore not analyzed further. RTs to the grating probes were analyzed with a 2 x 2 ANOVA with repeated measures; the factors were primed level (local vs. global) and attended SF (high vs. low). RTs to incorrect responses, either to the prime or to the probe, and those above or below two standard deviations of the mean were excluded, as well as any trials in which participants moved their eyes prior to the presentation of the grating probe (~15% of total trials; 10% for incorrect responses and 6% for outlier RTs).³ Participants had no trouble maintaining fixation, and eye movements accounted for almost none of the excluded trials (i.e., the highest number of eliminated trials due to eye movements for a single participant was 2). As found in Experiment 1, there was a significant interaction between primed level and SF [$F(1,15) = 5.5$, $MSe = 1380.9$, $p < .05$; partial $\eta^2 = 0.27$], and there were no significant main effects. That is, while RTs did not significantly differ across the two SF conditions (536ms for HSF probes and 551ms for LSF probes), or across the two prime conditions (543ms for both local and global primes), participants were faster reporting HSF orientation following local (525ms, $SE=27ms$) than global (546ms, $SE=30ms$) primes, and they were faster reporting LSF orientation following global (540ms, $SE=19ms$) than local (562ms, $SE=19ms$) primes (Figure 6). Figure 7 presents the difference between mean RTs to LSF and HSF targets for each individual subject in Experiment 2, showing a similar pattern to Experiment 1, although slightly more variable.

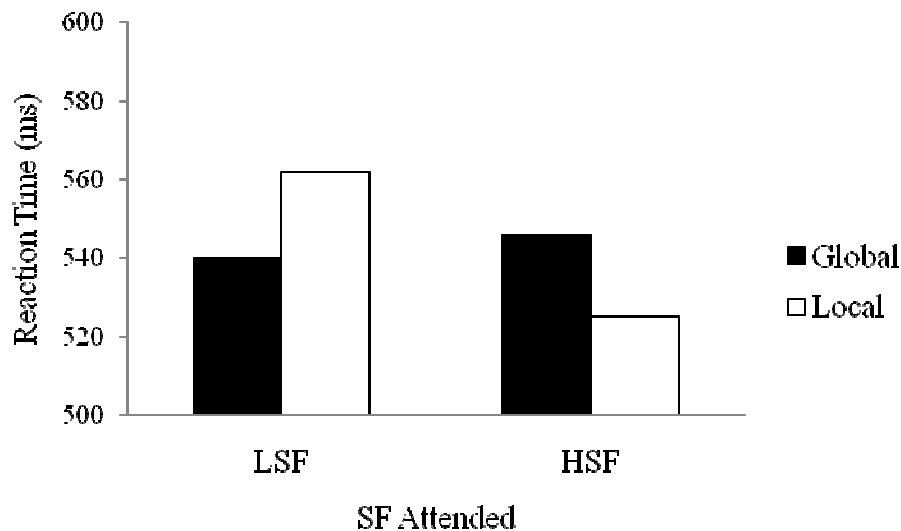


Figure 6. Average RTs to LSF and HSF targets in compound grating probes during the global and local attention blocks in Experiment 2.

³ The same analysis performed without excluding trials showed a similar pattern. The mean RTs were: 535ms and 560 ms following global and local processing, respectively, in the LSF blocks and 546 ms and 529 ms following global and local processing, respectively, in the HSF block.

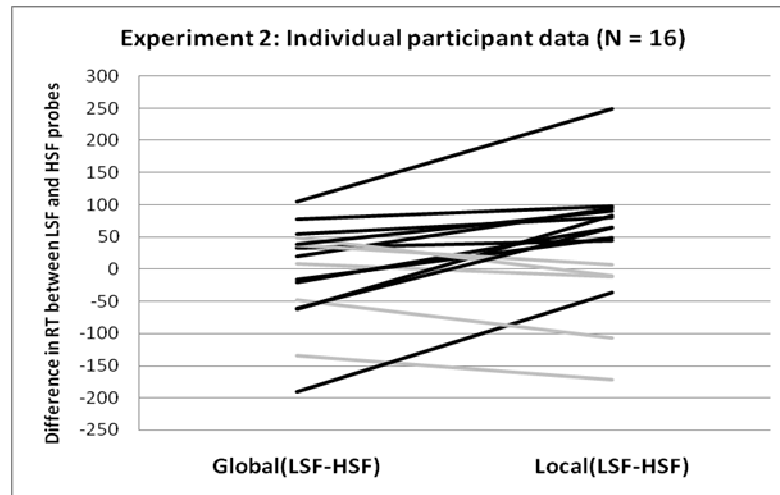


Figure 7. Individual participant data from Experiment 2 showing the *difference* between RTs to LSF targets minus HSF targets in the global and local attention blocks. For most participants (shown in black) there is an increasing slope, indicating an increased difference in the local than global block. Participants who did not reflect this pattern are shown in gray.

Prime RTs

I also analyzed mean RTs to the Navon primes with a 2 x 2 ANOVA for repeated measures with attended level (local vs. global) and attended SF in the probe (HSF vs. LSF target) as factors. This analysis revealed a main effect of attended level [$F(1,15) = 8.0$, $MSe = 13695.6$, $p < .05$; partial $\eta^2 = 0.35$], indicating that participants were faster responding to global (755ms) than local (849ms) primes as in Experiment 1. Again, there was no effect of the probe's SF and no interaction between attended level and SF of the probe ($F(1,15) < 1$).

The analysis of prime accuracy revealed that, similar to Experiment 1, the main effect of attended level was qualified by a speed-accuracy tradeoff. Although accuracy was high at both processing levels, the 2 (attended level) x 2 (SF) repeated measures ANOVA for prime accuracies resulted in a main effect of prime level, [$F(1,15) = 98.9$, $MSe = 15.1$, $p < .0001$; partial $\eta^2 = 0.87$], with the responses to local (95%) more accurate than to global (85%) primes. As in Experiment 1 I also ran the prime analyses using the combined measure (RT/proportion correct) and found no effects of primes using this measure. However, despite the speed-accuracy tradeoff found for the main effect of attended level, there was also a marginal interaction between attended level and SF [$F(1,15) = 4.5$, $MSe = 12.7$, $p = .051$; partial $\eta^2 = 0.23$], which had the same pattern as the RTs. That is, accuracy to local primes was higher in the HSF (96%) than LSF (93%) probe conditions, and accuracy to global primes was higher in the LSF probe condition (86%) than HSF (84%) probe condition (see Table 1).

Table 1. RT and accuracy to the primes in Experiments 1 and 2. In Experiment 2, the marginal prime level x SF interaction ($p = .051$) found for the prime accuracies showed the same pattern as the prime RTs. Importantly, this is the same pattern as the prime level x SF interaction found for the probe RTs. Although the prime level x SF interaction was not statistically significant for prime RTs or for prime accuracy in Experiment 1, inspection of the means showed a similar pattern.

	Experiment 1: RT and accuracy to the primes				Experiment 2: RT and accuracy to the primes				
	RTs (ms)		Accuracy (% correct)		RTs (ms)		Accuracy (% correct)		
	Global	Local	Global	Local	Global	Local	Global	Local	
LSF	671	746	85	94	LSF	764	849	86	94
HSF	694	746	84	95	HSF	767	848	84	96

Statistical Comparison of Experiments 1 and 2

To explore if the change in probe location from peripheral to central vision affects performance, I conducted a statistical comparison of Experiments 1 and 2 by running a mixed-model ANOVA with experiment (1 vs. 2) as a between-participant factor, and prime level (local vs. global) and SF (HSF vs. LSF target) as within-participant factors. For the probe RTs, this analysis revealed no interactions with experiment. The only significant effect was the interaction between prime level and SF [$F(1,30) = 12.5$, $MSe = 1337.1$, $p < .001$; partial $\eta^2 = 0.29$], reinforcing the outcome of the individual experiments.

The same analysis conducted on the prime RTs and on the prime accuracies also mirrored the results found in the individual experiment analyses and did not reveal any interactions with experiment. For the prime RTs, there was a main effect of attended level, [$F(1,30) = 15.2$, $MSe = 11207.5$; $p < .001$; partial $\eta^2 = 0.34$], reflecting the fact that RTs to global primes were faster (724ms) than RTs to local primes (797ms). For the prime accuracies, as was found in both experiments, there was a main effect of attended level [$F(1,30) = 164.5$, $MSe = 19.1$, $p < .001$; partial $\eta^2 = 0.85$], indicating that participants were more accurate in the local (94.6%) than global (84.6%) task (which, in concert with the RT results, might indicate a speed-accuracy tradeoff). There was also an interaction between prime and the attended SF in the probe [$F(1, 30) = 5.1$, $MSe = 10.3$, $p < .01$; partial $\eta^2 = 0.15$]. Follow-up t-tests revealed a trend for responses to global primes to be more accurate in the LSF than HSF block, [$t(31) = 1.871$, $p = .07$; $d = 1.9$], while there was no such difference for responses to local primes. In sum, the statistical comparison of Experiments 1 and 2 mirrored the results of the individual experiments' analyses and, most importantly, did not show any interaction with experiment.

2.4.3. Experiment 2 Discussion

The results of Experiment 2 replicated those of Experiment 1. Responses to HSFs in compound gratings were faster following attention to local than global levels in the primes, whereas responses to LSFs in the same gratings was faster following attention to global than local levels in the primes. Hence, the influence of attending to a particular hierarchical level on

SF selectivity was found despite a change in spatial location of the probe from periphery to central vision and despite the fact that the location of the hierarchical primes and compound grating probes changed. These findings question a simple spatial focus account of the results, and by monitoring eye movements I assured that the Navon patterns and the compound gratings appeared at different regions on the retina.

Importantly, the same pattern of priming was found in Experiments 1 and 2 despite the fact that perceptual sensitivity to different SFs varies between the periphery and the fovea, with a better resolution of HSFs in the fovea than the peripheral visual field (De Valois & De Valois, 1990). Moreover, it is noteworthy that both SFs that I used in the compound grating were at the lower end of the human visible spectrum and, without priming, both have been previously associated with global processing when presented alone (Shulman et al., 1986, 1987). Hence, the complex grating stimulus in the current study required participants to selectively attend to the *relatively* lower or *relatively* higher of two objectively LSF gratings. Nevertheless, relations between the hierarchical patterns and SF might have been different here than in previous studies, so it is important to directly examine hierarchical attention and its relationship to relative SF and absolute SF (see Experiment 4). It is also important to consider the possibility that the priming effects seen here have nothing to do with attentional selection of SF, but instead reflect an adjustment in the size of the attentional “spotlight”. In Experiments 1 and 2, there was a correspondence in size between the local level and HSFs, and between the global level and LSFs, and it is important to rule out the possibility that these effects were due to the priming of relative size rather than SF. This was done in Experiment 3.

2.5. Experiment 3

To rule out the possibility that adjusting the size of the attentional “spotlight” drove the effects in Experiments 1 and 2, Experiment 3 was identical to Experiment 2 in all respects except that the primes in Experiment 3 were single letters that were either the same size as the local letters in Experiment 2 or the same size as the global letters. The letters were either the same or different and, as in Experiments 1 and 2, the response was to report whether they were the same or different letter as rapidly as possible. If size rather than SF was the critical factor in Experiments 1 and 2, then small letters should prime HSFs and large letters should prime LSFs. However, if attention to hierarchical level is critical, then there should be no priming effects of size on SF.

2.5.1. Experiment 3 Methods

Participants

Sixteen students from the University of California, Berkeley (twelve female) participated in Experiment 3. They received course credit for their participation. All had normal or corrected-to-normal vision. The experiment was approved by the University of California, Berkeley CPHS (#2004-3-35), and all participants gave informed consent before participating.

Stimuli

The prime stimuli in Experiment 3 were single letters in black Helvetica bold font presented on a gray background. The small letters subtended 0.7° of visual angle and were identical to those that appeared at the local level in Experiments 1 and 2A. The large letters were the same size as the global letters in Experiments 1 and 2A, $4.0^\circ \times 5.7^\circ$ high. The grating probe in Experiment 3 was identical to that used in Experiment 2.

Procedure

The exact same procedure used for Experiment 2 was used for Experiment 3, the only difference being that single letters (small or large) appeared as the primes (see Figure 8).

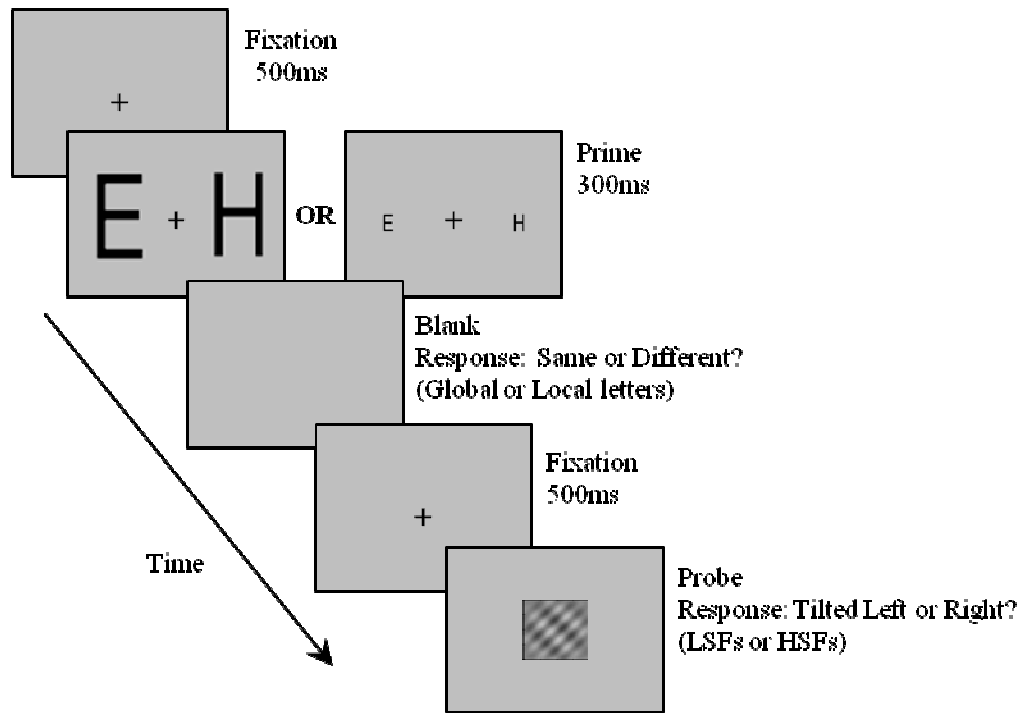


Figure 8. Example trial from Experiment 3. Participants performed two tasks in alternating sequence. First, two letters appeared on each side of fixation until response (prime). The letters were either large (same size as global letter in Experiment 2) or small (same size as local letters in experiment 2) and participants indicated if they were the same or different letter. Large and small letters appeared in separate blocks of trials. Following the prime, one compound frequency grating appeared at fixation until response (probe). Participants reported the orientation of the LSFs or HSFs in the grating (in separate blocks of trials).

2.5.2. Experiment 3 Results

Accuracy rates to both the grating probes and to the letter primes in Experiment 3 were at ceiling (96% and 95%, respectively) and were therefore not analyzed further. RTs to the grating

probes and to the letter primes were analyzed with a 2 x 2 ANOVA with repeated measures; the factors were primed size (small vs. large) and attended SF (high vs. low). RTs to incorrect responses, either to the prime or to the probe, and those above or below two standard deviations of the mean were excluded, as well as any trials in which participants moved their eyes prior to the presentation of the grating probe (~6% of total trials). No significant main effects emerged. More importantly, there was not even a trend toward an interaction between size and SF.

Statistical Comparison of Experiments 2 and 3

To compare Experiments 2 (Navon prime) and 3 (size prime) I conducted a mixed-model ANOVA with Experiment (2 vs. 3) as a between-participant factor, and prime level/size (local/small vs. global/large) and SF (HSF vs. LSF target) as within-participant factors. For the probe RTs, this analysis revealed a 3-way interaction between the factors SF, level/size, and Experiment, [$F(1,30) = 4.1$, $MSe = 11353.8$, $p = .05$; partial $\eta^2 = 0.12$]. This interaction reflects the fact that I found a significant interaction between primed level and attended SF in Experiment 2 (with Navon patterns as primes) and no such interaction between primed size and attended SF in Experiment 3 (with large or small letters as primes). No other effects were significant for the probe RTs. For the prime RTs, the same analysis revealed a main effect of size/level [$F(1,30) = 4.9$, $MSe = 11714.2$, $p < .05$; partial $\eta^2 = 0.14$], reflecting the fact that participants were faster at global/large primes (548ms) than local/small primes (553ms). However, as I found in the individual experiment analyses, this difference was only significant in Experiment 2 for the local versus global primes (though qualified by a speed-accuracy tradeoff) and not in Experiment 3 for the small vs. large primes. This was corroborated by a 2-way interaction between size and Experiment [$F(1,30) = 4.5$, $MSe = 11714.2$, $p < .05$; partial $\eta^2 = 0.13$]. There were no other significant effects in the prime RT analyses.

2.5.3. Experiment 3 Discussion

In Experiment 3, when single letters of identical size to the local and global letters in Experiment 2 were presented as primes, I did not find priming of size on SF. This is strong evidence that attention to hierarchical level was the critical factor in priming the selection of a SF, and not attention to size *per se*.

Taken together, Experiments 1-3 provide strong evidence that attention to the local level of a hierarchical display involves attentional selection of relatively HSFs, and attention to the global level involves attentional selection of relatively LSFs. In Experiment 4, I directly examined if hierarchical level primes relative or absolute SF by presenting the same 1.8c/d grating as the relatively higher SF of the compound grating probe during half of the blocks and as the relatively lower SF of the compound grating probe during the other half of the blocks. If attention to hierarchical level triggers a process that biases attentional selection of relative SF rather than absolute SF, attention to local primes should facilitate attention to the 1.8c/d grating when it is relatively higher and attention to global primes should facilitate attention to the same 1.8c/d grating when it is relatively lower.

2.6. Experiment 4

2.6.1. Experiment 4 Methods

Participants

Sixteen students from the University of California, Berkeley (10 female) participated in the experiment for course credit. All had normal or corrected-to-normal vision. The experiment was approved by the University of California, Berkeley CPHS (#2004-3-35), and all participants gave informed consent before participating.

Stimuli

The Navon patterns used as primes were identical to those used in Experiments 1 and 2. There were two compound grating probe conditions: LOW and HIGH, referring to the absolute SF differences between the two grating probes. The LOW compound gratings were composed of a 0.9c/d (3cycle/image) grating (the relatively LSF component) and a 1.8c/d (6c/i) grating (the relatively HSF component) and the HIGH compound gratings were composed of a 1.8c/d grating (the relatively LSF component) and a 5.3c/d (18c/i) grating (the relatively HSF component). Seen from 1m the grating probes in both conditions subtended 3.4° of visual angle and were presented at fixation akin to Experiment 2. As in the previous two experiments, the relatively LSF component was oriented either at 45° (tilted to the right) or at 135° (tilted to the left) and the relatively HSF component was oriented in the opposite direction (Figure 9).

Procedure

The procedure was identical to Experiment 2, except that participants performed eight blocks of 60 trials. The same 4 blocks as in Experiments 1 and 2 (global/lower, global/higher, local/lower, local/higher) were performed once with the LOW grating probes and once with the HIGH grating probes.

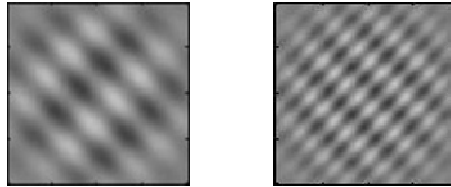


Figure 9. Examples of the absolute LOW (shown on the left) and absolute HIGH (shown on the right) grating probes. In both examples, the 3.5c/d grating is shown tilted to the left (not drawn to scale). It is the relatively higher SF of the set in the absolute LOW grating and the relatively lower SF of the set in the absolute HIGH grating.

2.6.2. Experiment 4 Results

Probe RTs

Similar to Experiments 1 and 2, probe-performance accuracy was at ceiling (96%) and therefore not analyzed further. RTs to incorrect responses, either to the prime or to the probe, and

those above or below two standard deviations of the mean were excluded (~16% of total trials; 9% for incorrect responses and 7% for outlier RTs).⁴ Eye movements were monitored but did not account for any of the excluded trials because participants had no trouble maintaining fixation. RTs to the grating probes were analyzed with a 2 x 2 x 2 ANOVA with repeated measures. The factors were primed level (global vs. local), absolute SF condition (LOW vs. HIGH) and relative SF attended in the probe (lower vs. higher) as factors. This analysis revealed a significant interaction between primed level and relative SF, [$F(1,15) = 6.6$, $MSe = 6999.2$, $p < .05$; partial $\eta^2 = 0.30$] and no other significant effects. Particularly noteworthy is that there was no main effect of the absolute SF and no interactions with this factor. Participants were faster reporting the relatively LSF orientation following global (555ms, SE = 22ms) than local (574ms, SE = 28ms) primes, and they were faster reporting relatively HSF orientation following local (530ms, SE= 31ms) than global (586ms, SE = 51ms) primes (Figure 10). In Figure 11, the probe RTs to relatively lower SF and relatively higher SF grating probes following global and local level primes are plotted separately for the absolute LOW condition and absolute HIGH condition. The second order interaction was not significant [$F(1,15)=1.2$]. As indicated by the lack of interaction with absolute SF, priming was contingent on relative SF despite the fact that the same 1.8c/d grating was the relatively higher SF in the absolute LOW condition and the relatively lower SF in the absolute HIGH condition.

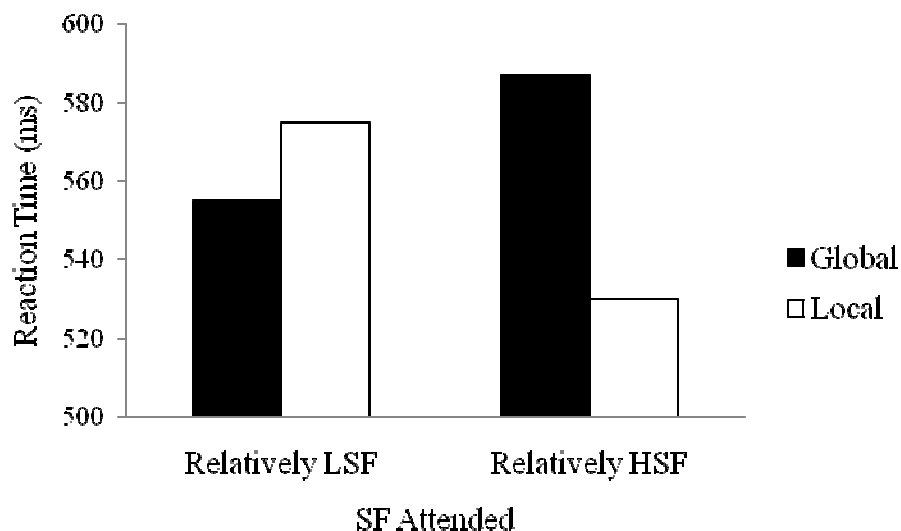


Figure 10. Average RTs to relatively LSF and relatively HSF targets (collapsed over absolute SF) in compound grating probes during the global and local attention blocks in Experiment 4.

I also analyzed mean RTs to the Navon patterns with a 2 x 2 x 2 ANOVA for repeated measures with absolute SF (LOW vs. HIGH), relative SF (lower vs. higher) and attended level (global vs. local) as factors. This analysis revealed a main effect of attended level [$F(1,15) =$

⁴ The same analysis performed without excluding trials showed a similar pattern. In the absolute LOW blocks, the mean RTs were: 569 ms and 579 ms following global and local processing, respectively, in the relative LSF blocks and 565 ms and 514 ms following global and local processing, respectively, in the relatively HSF block. In the absolute HIGH blocks, the mean RTs were: 528 ms and 572 ms following global and local processing, respectively, in the relative LSF blocks and 567 ms and 548 ms following global and local processing, respectively, in the relatively HSF block.

10.3, $MSe = 10359.7$, $p < .01$; partial $\eta^2 = 0.41$] indicating that, as in Experiments 1 and 2, participants were faster responding to global (635ms) than local (692ms) primes. There was also an interaction between relative SF and attended level [$F(1,15) = 5.5$, $MSe = 2833.8$, $p < .05$; partial $\eta^2 = 0.27$]. Participants were faster when attending to the global than local prime level in both relative SF conditions, but this difference was much greater in blocks when they were attending to the relatively lower SF (80ms difference) than the relatively higher SF (36ms difference) [$t(15) = 2.4$, $p < .05$; $d = .54$]. Importantly, like in the analysis of the probe RTs, there were no interactions with absolute SF and no other effects in the prime RT analyses.

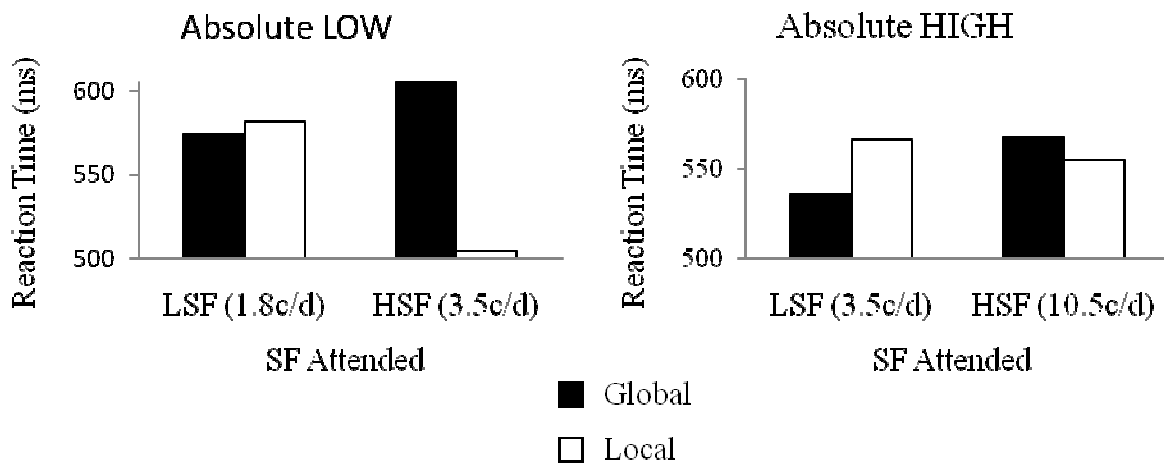


Figure 11. Average RTs to relatively LSF and relatively HSF targets in compound grating probes during local and global attention blocks in Experiment 4, shown separately for absolute LOW and absolute HIGH grating conditions.

Prime RTs

The analysis of prime accuracy revealed that, similar to Experiments 1 and 2, the main effect of attended level was qualified by a speed-accuracy tradeoff. That is, the 2 (absolute SF) x 2 (relative SF) x 2 (attended level) repeated measures ANOVA for prime accuracies revealed a main effect of attended level [$F(1,15) = 93.2$, $MSe = 7.4$, $p < .0001$; partial $\eta^2 = 0.86$], with more accurate responses to local (93%) than to global (88%) primes. There was also an interaction between relative SF and level [$F(1,15) = 8.0$, $MSe = 8.4$, $p < .05$; partial $\eta^2 = 0.35$], showing a greater difference between global and local primes in blocks when participants were attending to relatively lower SFs (6% difference) than higher SFs (3% difference) [$t(15) = 2.8$, $p < .05$; $d = 1.0$]. Similar to Experiments 1 and 2, the analysis of the primes in Experiment 4 using the combined measure (RT/proportion correct) revealed no statistically significant effects.

2.6.3. Experiment 4 Discussion

The results of Experiment 4 replicated the pattern of level priming that was found in Experiments 1 and 2, with RTs to relatively lower SFs in the probe faster following global than local attention, and RTs to relatively higher SFs in the probe faster following local than global attention. Importantly, this interaction was found for relative rather than absolute SFs as shown by the fact that the same 1.8c/d grating was relatively higher in half of the blocks and relatively lower in the other half of the blocks. That there were no effects or interactions with absolute SF is strong evidence that the priming effect is not merely due to lower level attentional tuning to SF *per se* but rather to a process that keeps the relatively global and local levels constant over large changes in stimulus location and SF content.

2.7. Discussion of Experiments 1-4

In four experiments I examined how same/different judgments about the local or global levels of information in pairs of hierarchical displays can affect subsequent allocation of attention to relatively high- and low- SFs in a compound grating. Although a direct link between the attended level in a hierarchical display (local versus global) and responses to simple sinusoidal gratings has long been known (Shulman et al., 1986, 1987), the mechanism by which attention to a given level affects the selection of SFs in an image has not been sufficiently characterized before. Using HSF and LSF compound gratings rather than simple sinusoidal gratings the present data indicate that attending to the local level facilitates the selection of the *relative* HSFs in the image while attending to global level facilitates the selection of the *relative* LSFs. I also showed that this pattern of facilitation cannot be explained by attention to size alone; large letters did not prime LSFs nor did small letters prime HSFs (Experiment 3).

Importantly, I found the interaction between attended level and SF selection both when the grating probes appeared at the same peripheral locations as the Navon patterns (Experiment 1) and when they appeared at fixation (Experiment 2), inconsistent with a simple spatial focus account of the results, and arguing against a simple early visual account for the priming effect (for example that given the different spatial resolution of the rods and the cones, images presented in the periphery would preferentially activate lower SF channels than images presented at fixation). In fact, previous studies suggested that 3c/d shows optimal contrast sensitivity at the fovea, whereas lower SFs of 0.6c/d to 1.2c/d show optimal contrast sensitivity at 1.7° eccentricity (Henriksson et al., 2008). Thus, in Experiment 1, the relatively LSFs in the compound grating (i.e., 0.7c/d at 1° eccentricity) were perceptually optimal whereas in Experiment 2, the relatively HSFs in the compound grating were perceptually optimal (i.e., 2.4c/d at fixation). The fact that I found the same pattern of results despite these early level differences across Experiments 1 and 2 is further evidence that this is a top down effect that influences selectivity to relative spatial scale.

More direct evidence for a selective attention effect was found in Experiment 4, where the selection of relative SFs interacted with attended prime level, and no effect of absolute SFs emerged. These findings strongly suggest that local vs. global attention involves a flexible mechanism by which attention selects relatively higher vs. relatively lower SFs, respectively. If the priming effects were due solely to the visual response to spectral information, I would have

found the same pattern of results for the 1.8c/d grating whether it was the relatively higher or relatively lower frequency in the probe. Instead, the priming effects did not interact with absolute SF but only with relative SF. This is not to say that absolute SFs are irrelevant. They may well set the spatial limits of what is visually available at any instant in time, but the selection of SFs can be modulated by top-down influences that link relative hierarchical levels across time and space.

Experiments 1-4 also demonstrate that the level of processing (local or global) in Navon stimuli can extend to a completely unrelated stimulus and task. Robertson (1996) suggested that when stimuli were similar in structure (multi-leveled), selecting a given level on one trial to make a certain type of response (identification) automatically primed the selection of that same level on the next trial to make a similar type of response whether the two stimuli were in the same or different locations. The current results extend the previous ones showing that the selected level in a Navon stimulus guides the selected “level” in the compound frequency probe even if the prime and the probe as well as the tasks are completely different. It is important to note that in the current study, the same broadband Navon displays and the same compound grating probes were presented in the local and global attention blocks. The only difference across the blocks was the attended level while processing the prime and the attended SF while processing the probe.

The present pattern of results is also consistent with the notion of flexible scale usage in face and scene processing posited by Schyns and colleagues (Gosselin & Schyns, 2001; Oliva & Schyns, 1997; Schyns & Oliva, 1999; Morrison & Schyns, 2001). According to this view, the visual system does not necessarily operate in a fixed processing order (from LSF to HSF) on incoming information, but instead can flexibly use its effective spatial scales in an order determined by the diagnostic features relevant to the current task. The present results strongly endorse this view by demonstrating that the attended level in Navon patterns determined subsequent SF selectivity.

Finally, although hemispheric asymmetry was not examined in the current study, much of the research on processing hierarchical displays was derived from studies of hemispheric laterality and, indeed, the present findings bear indirect relevance to that literature. Specifically, the current data are consistent with DFF theory (Ivry and Robertson, 1998). Central to DFF theory is the notion that the two cerebral hemispheres do not have an asymmetrical bias for the perceptual processing of SFs *per se*, but that they asymmetrically filter relatively high versus relatively low SF information after attention selects the task relevant frequency range. The fact that I found an interaction between attention to hierarchical level and SF selectivity using identical compound gratings that varied in peripheral and central presentation across experiments support this idea. Nonetheless, independent of the DFF theory, the present data clearly demonstrate a robust relationship between the attended level in a multi-level object and the order of selection of SFs in a subsequent image.

3. Unifying DFF and HI theories

3.1. Evidence for Hierarchical Integration (HI) theory

Recently, Hübner and Volberg (2005) called into question theories associating SF processing with hierarchical perception by challenging an implicit assumption of these theories; namely that the identity of a shape (e.g., a letter in a Navon display) and its level (local/global) are perceptually integrated *a priori* (e.g., Navon, 1977; Lamb & Yund, 1996; 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 considering the Navon displays used to study hierarchical perception (Figure 1); intuitively, the local and global levels in these displays seem unambiguous. However, when considering hierarchically structured objects in the natural environment, the traditional view seems wanting since 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. Moreover, the evidence that other features such as orientation and color are processed separately and only later integrated is quite compelling (Treisman & Gelade, 1980, Treisman & Schmidt, 1982, Treisman, 1996, Zeki, 1978).

In line with this challenge, Hübner and Volberg (2005) proposed a hierarchical “integration theory” in which 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 & Gelade 1980; Treisman, 1999). Evidence for FIT lies in the fact that deficits in spatial attention after brain injury lead to incorrect feature combinations in perception known as “illusory conjunctions” (e.g., mistakenly reporting a red X when presented with a blue X and a red T; Robertson et al., 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 binding shape and level (local/global), Hübner and Volberg (2005) interrupted processing of Navon displays by masking them after randomly flashing them in the left visual field (LVF) or right visual field (RVF), and asking participants to identify the letter at a directed level. Under these conditions, the rationale was that if shape and level are initially represented separately, then an interruption in processing should lead to instances in which binding fails, and illusory conjunctions of shape and level result (i.e., the letter at the unattended level should be seen as the letter at the attended level). Indeed, Hübner & Volberg (2005) 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 a visual field asymmetry in conjunction errors occurred consistent with evidence for functional hemispheric differences in hierarchical processing outlined in 2.1.1 (e.g.,

Delis, Robertson & Effron, 1986; Martin, 1979; Martinez et al., 1997; Robertson & Delis, 1986; Robertson, Lamb & Knight, 1988; Robertson, Lamb, M. R., & Zaidel, E., 1993; Weissman & Woldorff, 2005). Although some studies have not found this difference (Heinze et al., 1998; Fink et al., 1997; Polster & Rapcsak, 1994), a meta-analysis showed that overall there was strong evidence for a LH bias in local processing and a RH bias in global processing (Van Kleeck, 1989). This meta-analysis also showed that the hemispheric differences were more pronounced when the stimuli were incongruent (i.e., letter identity differed at the local and global levels), which would produce more illusory conjunctions in line with the integration theory. Hübner and Volberg (2005) found that participants made significantly more conjunction errors 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 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, followed by a binding stage, and that the rate of binding errors depends on the visual field in which the hierarchical displays are presented. In a follow-up experiment, Hübner and Volberg (2005) explicitly tested a multinomial model of their integration theory by asking participants to report both the local and the global letter. In so doing, they were able to include a “guessing” parameter in their model, and estimate the probability distribution of the responses while taking into account the fact that some correct responses will be correct guesses (Ashby et al., 1996; Prinzmetal, et al., 2002). Indeed, they found that the data still supported the integration model when participants were asked to report both letter identities, suggesting that the results were not due to a bias in guessing. This is also consistent with previous findings by Prinzmetal et al. (2002) demonstrating that participants do not guess a repeated feature if features do not reappear in the display.

However, although Hübner and Volberg (2005) provided strong evidence that shape and level are initially represented separately, the mechanism underlying shape-level binding is unknown. In FIT (Treisman & Gelade, 1980), features must be co-located (through spatial attention) to be properly bound. In contrast, the integration theory formulated by Hübner and Volberg (2005) does not offer a binding mechanism.

3.2. Aim of Experiment 5: SF selection as a possible mechanism underlying HI

The goal of Experiment 5 was to examine whether the medium of hierarchical binding is attentional selection of task-relevant SFs. This hypothesis is based on previous data (outlined in 2.1.2) suggesting that SFs cue the level of representation (Robertson, 1996) and that the relevant SFs in a stimulus can drive hemispheric differences in performance (Ivry & Robertson, 1998). Evidence that the LH is biased in selecting relatively HSFs while the RH is biased in selecting relatively LSFs has not only been demonstrated for discrimination of sinusoidal gratings (Christman, Kitterle & Hellige, 1991; Kitterle, Christman & Hellige, 1990) but also in the processing of letters, faces, scenes and objects (Idaka et al., 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 LSFs in the stimulus, whereas local perception relies more on the selection of relatively HSFs (Han et al.,

2003; Hughes, Fendrich & Reuter-Lorenz, 1990; Hughes, Nozawa & Kitterle, 1996; Jian & Han, 2005; Robertson, 1996; Shulman et al., 1986; Shulman & Wilson, 1987; Yoshida et al., 2007). Perhaps most importantly, SF processing is flexible and contingent both on bottom-up factors such as image information as well as on top-down factors such as attention and task constraints (Peyrin et al., 2006; Sowden & Schyns, 2006).

Given this evidence, my hypothesis is that SF is the medium for hierarchical binding, such that attentional selection of relatively HSFs facilitates shape-level binding by the LH, and attentional selection of relatively LSFs facilitates binding by the RH. To test this hypothesis, I used a priming paradigm designed to examine how directing attention to SF (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 higher SFs in a centrally presented compound grating (e.g., Olzak, 1986). A Navon display then flashed in the LVF or RVF and was masked. Participants indicated which of four possible letters appeared at the local or global level. Importantly, they were informed that each display would be constructed of two *different* letters, so if they only identified the letter at the unattended level, they should guess from the remaining three alternatives. Errors in which participants inadvertently reported the letter at the unattended level were considered to be shape-level “conjunction errors” and errors in which participants reported one of the two letters that were not presented at any level were considered to be “feature errors.”

If letters and levels are bound *a priori* (i.e., the traditional view), then there should be an even distribution of errors across conjunction and all possible feature errors (i.e., with 3 possible erroneous responses, conjunction errors should not exceed $\frac{1}{3}$ of the total errors). First, I replicated Hübner and Volberg’s (2005) findings, showing that participants made many more than $\frac{1}{3}$ conjunction errors, and that conjunction errors to local targets were greater when the stimulus was projected to the RH than to the LH, and conjunction errors to global targets were greater when they were projected to the LH than to the RH. More importantly, the attended SF in the prime task modulated the hemispheric asymmetry of conjunction errors such that attentional selection of HSFs reduced the hemispheric asymmetry in conjunction errors to local targets and attentional selection of LSFs reduced the hemispheric asymmetry in conjunction errors to global targets.

3.3. Experiment 5 Methods

Participants

Twenty-four undergraduates from the University of California, Berkeley participated in the experiment for course credit. Sixteen (twelve women) were tested in the primary experiment and eight (five women) in a subsidiary control experiment (see below). All were right handed and had normal or corrected-to-normal vision. The experiment was approved by the University of California, Berkeley CPHS (#2004-3-35), and all participants gave informed consent before participating.

Stimuli

The compound gratings were generated in MatlabTM (Mathworks, Natick, MA) with a sinusoid function for each SF. At 100% contrast, each compound grating subtended 6.6° of visual angle and was composed of a 3.6c/d grating (the relatively HSF component) and a 1.2c/d grating (the relatively LSF component). One SF component was oriented at +45° (tilted to the right) and the other was oriented at -45° (tilted to the left).

The Navon displays were black on a white background, and were made using Adobe PhotoshopTM. Seen from a distance of 57cm, each local letter subtended .9° of visual angle and was spatially arranged on a 5x5 grid to form a global letter that was 4.5° wide by 6° high. The letters used were squared 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), resulting in twelve distinct Navon displays. A mask was composed of local figure 8s arranged on the same grid to form a global figure 8, which overlapped with all possible letter combinations.

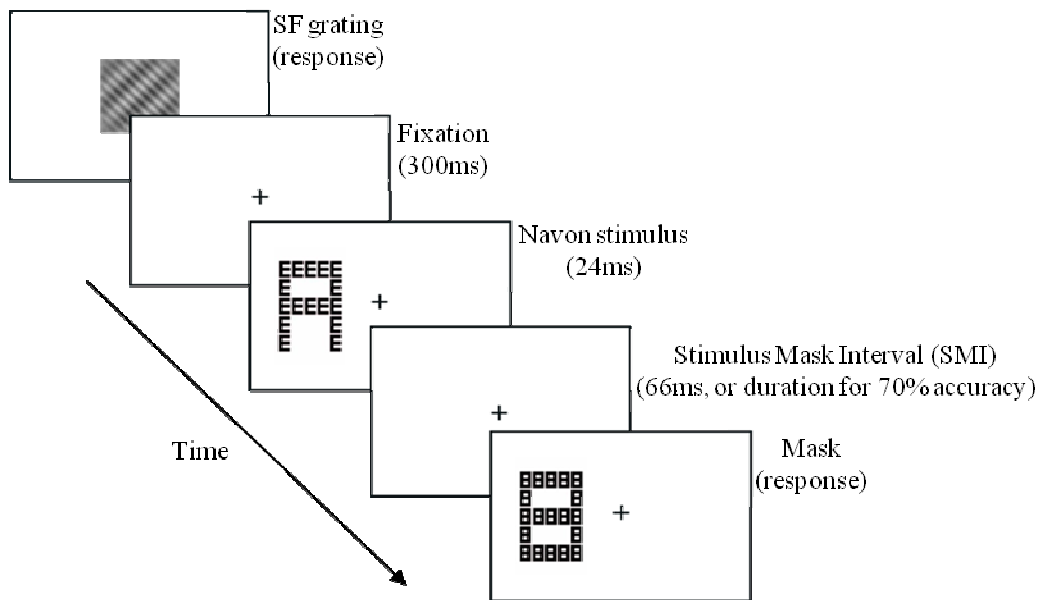


Figure 12. Example trial from (primary) Experiment 5. First, a compound SF grating appeared until response and participants reported the orientation (left or right) of the LSF or HSF component in separate blocks of trials. Next, a Navon stimulus flashed for 24ms to the left or right of fixation (randomly) and was replaced by a mask. Participants reported the identity of the global or local letter in separate blocks of trials by selecting among 4 alternatives. The stimulus-mask interval (SMI) started at 66ms and was gradually decreased when participants performed better than 70% accuracy in a given block. In the control experiment, there was no prime task; a trial began with the 300ms fixation cross.

Procedure

The stimuli were shown on a 17 inch color monitor with a vertical refresh rate of 60Hz at a resolution of 1024x768 pixels. Trial timing was controlled by PresentationTM (Neurobehavioral

Systems, Albany, CA) and is depicted in Figure 12. On each trial, a compound SF grating (prime) first appeared until response. In separate blocks of trials, participants reported the orientation of either the “thin bars” (HSFs) or “thick bars” (LSFs) quickly but accurately without moving their eyes over the grating. The grating was then replaced by a central, 300ms fixation cross, followed by a Navon display that flashed for 24ms with its medial edge 1° to the left or right of fixation and 3.25° from the midline. Visual field of presentation was randomized within each block. The mask then appeared in the same location as the Navon display and remained on the screen until response. In separate blocks of trials, participants were asked to indicate the identity of the local or global letter. The stimulus-mask interval (SMI) was initially 66ms (i.e., the mask appeared 66ms after the offset of the Navon stimulus) and was gradually decreased to maintain $\sim 70\%$ accuracy. The SMI was adjusted separately for local and global blocks. That is, if participants started in a local block condition, the SMI was adjusted accordingly for blocks in that condition and was reset to 66ms when they started the global block condition.

Importantly, participants were instructed to guess if they did not see the target letter. They were told that each Navon display would be composed of two different letters among the letters A, E, H and S, and if they did not see the letter at the target level, but did see the letter at the other, non-target level, not to report this letter but to guess from the remaining three alternatives. There were four blocks of 48 trials for each of the four prime (HSF versus LSF)/probe (local versus global) conditions, performed in sequential order while the order of conditions was counterbalanced across participants. I 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, and vice versa for the other eight. For the prime task, participants used the index and middle finger of the response hand; the left finger was used to indicate a “left” orientation of the target SF 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 make their response.

Prior to the main experiment, a control experiment was run (testing eight different participants from the same population) in order to assure that I could replicate Hübner and Volberg’s (2005) findings when blocking attended level (local/global) and using my stimuli. In the control experiment the same design was used as in the primary experiment except that there was no prime, resulting in only two blocked conditions, local and global. The control experiment was successful and will be presented at the end of the results section.

3.4. Experiment 5 Results

Main Experiment

Participants had no trouble performing the priming task, as average accuracy in reporting the orientation of the target SF was 98%. I was therefore confident that attention was directed to the relevant SF in each block.

I first established the separation of letter identity and hierarchical level as predicted by integration theory, by comparing the observed distribution of errors with that predicted by the

traditional view (Figure 13). The mean error rate across all conditions was 42%. Conjunction errors occurred in 21% of error trials, and feature errors occurred in the other 21%. As in Hübner and Volberg (2005), the distribution of errors was significantly different from that predicted by the traditional view, indicated statistically by the Model (traditional versus observed) x Error type (feature versus conjunction) interaction [$F(1,15)=56.2$, $MSe=13.0$, $p<.0001$; partial $\eta^2=.79$]. Follow-up t-tests (using Bonferroni correction) indicated that the rate of conjunction errors was significantly greater than that predicted by the traditional view [$t(15)=7.5$, $p<.0001$; $d=2.5$] and the rate of feature errors was significantly less than that predicted by the traditional view [$t(15) 7.5$, $p<.0001$; $d=1.0$]. An analysis comparing the observed pattern of errors with the pattern predicted by the traditional view for local and global blocks separately mirrored the overall analysis. For local blocks, the significant Model x Error type interaction [$F(1,15)=130.9$, $MSe=5.2$, $p<.0001$; partial $\eta^2=.89$] revealed significantly more conjunction errors (18%) than predicted by traditional view (13%; $t(15) 6.7$, $p<.0001$; $d=.93$) and significantly less feature

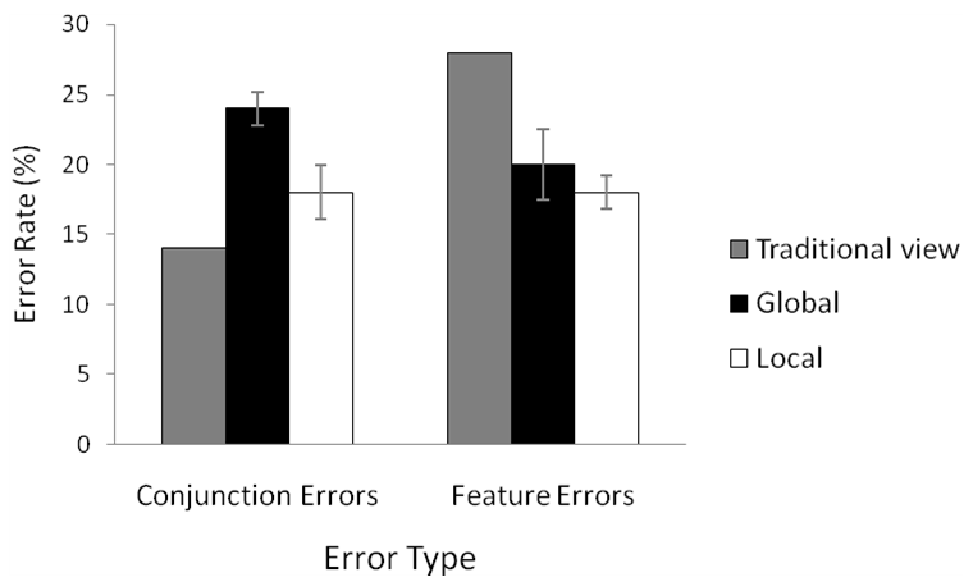


Figure 13. The percentage of conjunction and feature errors for global and local trials in Experiment 5, compared with those predicted by the traditional view. Error bars reflect standard errors of the mean.

errors (18%) than predicted by traditional view (26%; $t(15) 6.7$, $p<.0001$; $d=1.0$; both significant using Bonferroni correction). Likewise, for global blocks, the Model x Error type interaction [$F(1,15)=52.0$, $MSe=26.2$, $p<.0001$; partial $\eta^2=.78$] revealed significantly more conjunction errors (24%) than predicted by the standard view (16%; $t(15)=7.2$, $p<.0001$; $d=2.2$) and significantly less feature errors (20%) than predicted by the standard view (29%, $t(15)=7.2$, $p<.0001$; $d=1.1$; both significant using Bonferroni correction). These results replicate those found by 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 rather than a letter that was not present.

To examine my primary prediction that attentional selection of SFs would modulate the shape-level binding depending on the visual field of presentation, I conducted a 2x2x2 ANOVA of the conjunction errors, with attended SF in the prime (HSF versus LSF), attended target Level (local versus global), and Hemisphere (left versus right) as factors. This analysis revealed a

Level x Hemisphere interaction [$F(1,15)=9.3$, $MSe=52.8$, $p=.008$; partial $\eta^2=.38$], which is depicted in Figure 14. There were significantly more conjunction errors to local targets projected to the RH (19%) than to the LH (15%; $t(15)=2.5$, $p=.03$; $d=.73$) and significantly more conjunction errors to global targets projected to the LH (26%) than to the RH (22 %; $t(15)=2.4$, $p=.03$; $d=.65$; both significant using Bonferroni correction). There was no Level x Hemisphere interaction for feature errors, $F > 1$, and no other effects in the feature error analyses were close to significant levels.

Importantly, the analysis of the conjunction errors also revealed a SF x Level x Hemisphere second-order interaction [$F(1,15)=8.2$, $MSe=5.6$, $p=.01$; partial $\eta^2=.35$]. To examine this interaction, I conducted Level (local versus global) x Hemisphere (left versus right) ANOVAs for the LSF and HSF conditions separately, and these data are shown in Figure 15. For the LSF condition, there was a significant Level x Hemisphere interaction [$F(1,15)=5.1$, $MSe=24.4$, $p=.04$; partial $\eta^2=.25$]. As predicted, follow-up t-tests showed that following LSF selection, there were significantly more conjunction errors for local targets projected to the RH (20%) than the LH (17%; $t(15)=2.8$, $p=.01$; $d=.44$; significant using Bonferroni correction),

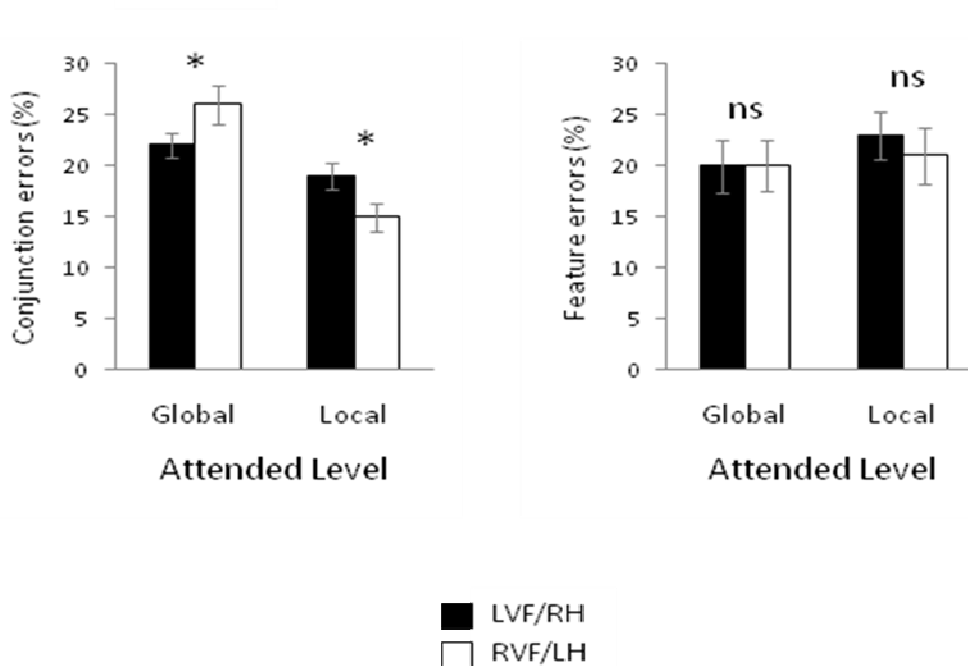


Figure 14. The Level x Hemisphere interaction for conjunction errors (significant) and feature errors (not significant) in Experiment 5. Errors bars reflect standard errors of the mean. LVF/RH: Navon display presented in the left visual field/ projected to the right hemisphere; RVF/LH: Navon display presented in the right visual field/ projected to the left hemisphere.

whereas there was no significant hemispheric difference global targets following LSF primes [$t(15)=1.3$, $p=.22$; $d=.30$]. The Level x Hemisphere ANOVA for the HSF condition also revealed a significant Level x Hemisphere interaction [$F(1,15)=12.0$, $MSe=34.9$, $p=.004$; partial $\eta^2=.44$]. As predicted, follow-up t-tests showed the opposite pattern than what was found for LSF primes. That is, following HSF primes, there were significantly more conjunction errors to global targets

projected to the LH (28%) than to the RH (21%, $t(15)=3.2$, $p=.006$; $d=.96$; significant using Bonferroni correction), whereas there was no statistically significant difference between the hemispheres for local targets following HSF primes [$t(15)=1.8$, $p=.09$; $d=.46$].

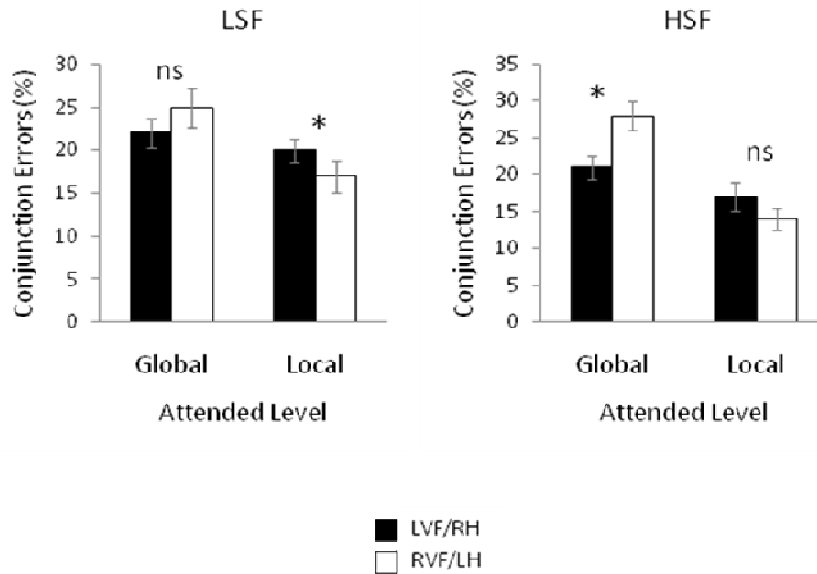


Figure 15. The Level \times Hemisphere interaction for conjunction errors modulated by the spatial frequency attended in the prime in Experiment 5. Following attention to low spatial frequencies (LSFs), there was an increased rate of conjunction errors to local targets presented in the left visual field (LRF)/right hemisphere (RH) and no reliable hemispheric difference in conjunction errors for global targets. Conversely, following attention to high spatial frequencies (HSFs), there was an increased rate of conjunction errors to global targets presented in the right visual field (RVT)/left hemisphere (LH) and no reliable hemispheric difference for local targets. Error bars reflect standard errors of the mean.

Control experiment

The results from the control experiment were similar to the results found for probes in the primary experiment collapsed over SF. The average overall error rate was 19%, 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%), indicated by a significant Model (traditional versus observed) \times Error type (feature versus conjunction) interaction [$F(1,15)=46.6$, $MSe=10.7$, $p<.0001$; partial $\eta^2=.87$]. Akin to the primary experiment, the rate of conjunction errors was significantly greater than that predicted by the traditional view [$t(15)=6.8$, $p<.0001$; $d=2.8$], and the rate of feature errors was significantly less than that predicted by the traditional view [$t(15)=6.8$, $p<.0001$; $d=1.8$; both significant using Bonferroni correction].

The attended Level (local versus global) \times Hemisphere (left versus right) ANOVA was also consistent with the results from the primary experiment, revealing a Level \times Hemisphere interaction [$F(1,7)=18.7$, $MSe=14.5$, $p=.003$; partial $\eta^2=.73$]. There were significantly more conjunction errors to local targets projected to the RH (18%) than to the LH (13%; $t(7)=2.7$, $p=.03$; $d=1.0$) and significantly more conjunction errors to global targets projected to the LH (28%) than to the RH (22%; $t(7)=4.3$, $p=.004$; $d=1.1$; both significant using Bonferroni

correction). There was no level x hemisphere interaction for feature errors, $F > 1$, and no other effects in the feature error analyses approached significant levels.

3.5. Experiment 5 Discussion

The results of Experiment 5 demonstrate that the selected SF in a previously presented stimulus facilitates shape-level binding in hierarchical displays. I 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 importantly, attentional selection of SF modulated shape-level binding in a manner consistent with hierarchical integration theory and the functional hemispheric literature. Attentional selection of relatively LSFs reduced the hemispheric asymmetry for global conjunction errors and facilitated binding by the RH of letters to global level. Conversely, selection of relatively HSFs reduced the hemispheric asymmetry for local conjunction errors and facilitated binding by the LH of letters to local level. This SF modulation occurred despite any habituation effects that may have occurred from presenting the same SF gratings throughout the experiment (albeit in different orientations).

These results are consistent with DFF theory, but with a new twist. The current data together with Hübner and Volberg's (2005) initial findings suggest that the asymmetry in selective tuning to SFs provides the basic features that segregate local and global levels, but when attention is overtaxed and biased toward one SF than another, the shapes are more likely to be perceptually bound incorrectly to the wrong level (as reflected by illusory shape-level conjunctions). That I did not find an interaction between SF and hemisphere is consistent with a higher-level mechanism underlying the asymmetrical SF filtering across the two hemispheres. That is, attention to relatively HSFs or LSFs did not generally facilitate processing by the LH or RH, respectively. Rather, attention to SF modulated specific, task-relevant processing in each hemisphere - namely, the binding of letter identity to hierarchical level. Thus, although HI theory was proposed as an alternative to DFF theory, the results from Experiment 5 suggest that the hemispheric asymmetries in local versus global perception can be explained by a combination of the two, and that selective attention to relative SF is the medium for shape-level binding.

4. Using SF scales to process face features and face configuration

4.1. Face perception: Relevant background

As explicated in 2.1, the use of Navon displays in studies of hierarchical perception has the advantage of isolating local versus global processes from other processes that occur during normal object and scene perception. On the other hand, to fully understand the neural and perceptual mechanisms involved in hierarchical perception, it is also important to examine hierarchical processing as it occurs in the natural environment. Experiment 6 approaches this question by examining the mechanisms involved in perceiving one of the most commonly viewed hierarchical objects, the face.

4.1.1. Perceptual processes involved in face perception

There are many computations involved in the detection and identification of a face, some of these shared with object perception generally, and some arguably more important for processing faces. Neurophysiological investigations have uncovered a network of regions in the brain that seem to be selective to the processing of faces, including the lateral fusiform gyrus (i.e., fusiform face area: “FFA”), lateral occipital gyrus and superior temporal sulcus (see Haxby, Hoffman, & Gobbini, 2000 for a review), though the precise role of each of these regions remains uncertain. Faces are a unique object category because, unlike most objects, we are experts at discriminating them as individual exemplars. Moreover, research has demonstrated that this subordinate level of categorization is the default entry point for faces, whereas we identify most objects at the basic level (Tanaka, 1997). Finally, since all faces share the same global organization of features (i.e., two eyes above a nose above a mouth), extended analysis of the inner face configuration as well as features has proven to be critical to normal face recognition (see Maurer, Le Grand, & Mondlock, 2002 for a review). These three factors (expertise, subordinate level classification and heavy reliance on configural analysis) are interrelated and might account for why faces are represented distinctly from other objects in the brain. The issue of whether faces are “special” is orthogonal to the current research, however. What is important is that, although there are many differences between faces and Navon displays, faces are commonly viewed hierarchical objects, and studies of face perception have revealed that normal recognition relies on the analysis of the basic global structure, the features, and their specific individual configuration.

Abundant research has revealed the importance of holistic processing of faces, that is, integrated processing of the features in conjunction. For example, a common finding that illustrates holistic processing is the “whole-part advantage” (Davidoff & Donnelly, 1990; Tanaka & Farah, 1993), that face parts are more easily recognized in the context of the whole face than when presented in isolation. Another well documented example of holistic face processing is the “composite face effect”, originally demonstrated by Young, Hellawell, & Hay (1987). In this paradigm, composite faces are generated by combining the top half of one face with the bottom half of a second face and the two halves are presented either aligned (i.e., sharing the same contour) or misaligned. Participants are asked to ignore the bottom half of the composites and indicate if the top halves are the same or different. When the bottom halves differ, participants are more likely to report that the top halves differ (even when they are the same) in the aligned

than in the misaligned condition. This suggests that when the faces are aligned participants process the features in an integrated fashion and are thus unable to ignore the bottom halves. The critical element of both the whole-part effect and the composite face effect is that perceptual processing of a single feature of a face is influenced by the other features. This stresses the importance of holistic processing of the global structure including the first order relationships between the features (i.e., two eyes above a nose above a mouth).

Research has also shown that face identification relies on computing spatial relations among inner face components, relative to each other and relative to the face contour. These computations have been termed second-order configural processing and are distinguished from the processing of the first-order configuration (Maurer et al., 2002). One of the most cited findings to support the importance of configural analysis for face identification is that faces are much more difficult to identify when they are inverted (i.e., upside down) than when they are upright (“face inversion effect”; Valentine & Bruce, 1988; Yin, 1969). Researchers have claimed that inverting a face breaks its spatial configuration, and it is therefore frequently used as a manipulation of configural processing (Leder and Bruce, 1998; 2000). For example, Leder and Bruce (2000) asked participants to make same/different judgments on pairs of faces that were either identical or differed on the basis of the second order configuration (e.g., spacing between the eyes). This task was much easier in the upright than inverted condition, suggesting that second order configural information is easily, and perhaps automatically, extracted from upright faces. Configural computations are more difficult to make with inverted faces, on the other hand, and consequently these stimuli may be processed with a piece-meal strategy, like other non-face objects (Moskivitch, Winocur, & Behrmann, 1997).

Although holistic and configural processing are considered vital to normal face recognition, research has also found local analysis of the individual features to be necessary. Cabeza and Kato (2000) explored the contributions of configural processing versus local feature analysis by examining recognition of face prototypes that were created either by combining the configurations of a set of faces (“configural prototypes”) or by merging their features (“featural prototypes”). Following an encoding phase, participants performed a recognition task in which they were presented with the prototypes, the original faces they had seen in the encoding phase and a set of new faces. They were asked to indicate which faces they had seen before, the assumption being that false recognition of either a configural or a featural prototype reflects the information that is stored in memory, thus implying what information is important for encoding the face. Participants falsely recognized both configural and featural prototypes, and this prototype effect was equal for the two, suggesting that both the configuration and individual features were encoded.

4.1.2. N170-effect: physiological marker of early face processing

The N170 component is an electrophysiological index of early face processing. While all visual stimuli elicit negative or negative-going ERPs during this epoch (N1), the N170 is larger (more negative) in response to faces than to other objects, a difference referred to as the “N170-effect” (Bentin et al., 1996; George et al., 1996; Itier and Taylor, 2004a). Given the existence of this physiological marker of early face perception, one question researchers have focused on to elucidate the mechanisms underlying the N170 effect has been whether it is more sensitive to

face features or to the face configuration. There is evidence that the N170-effect is at least as distinctive for isolated eyes as for full faces (Bentin et al., 1996; Itier et al., 2006), and it is not modulated by face identity (Bentin & Deouell, 2000), though there is also some evidence for its sensitivity to repetition of identical faces (Jacques & Rossion, 2006). Nonetheless, the N170-effect is insensitive to the configuration of the face features within or isolated from the face contour (Zion-Golombic & Bentin, 2007). That is, the N170-effect is equally large in response to faces with normally-configured and spatially-scrambled inner components, albeit slightly delayed in the latter condition. Hence, Bentin and colleagues have claimed that the N170-effect is associated with basic-level categorization (i.e., face detection) including the additional analysis of face features elicited by default when faces are detected. They have further argued that the N170 effect is dissociated from other neural events involving second-order configural processing that contributes to the structural encoding of a face (Bentin et al., 2006; Sagiv & Bentin, 2002; Zion-Golombic & Bentin., 2007).

4.1.3. Relation of face processing to general hierarchical perception

The RH dominance for processing relatively lower SFs is consistent with evidence showing enhanced activity in face-related cortical regions (e.g., the FFA) over the RH than the LH, since heavy reliance on global processing is characteristic of face perception. The N170-effect has also been reported to be greater over the RH than the LH, though this consistent trend has not always been significant. However, though faces have a hierarchical structure, it is important to note that the global and configural aspects of a face are contingent on the nature of the features. This differentiates faces from typical hierarchical displays, in which the global and local levels are independent. For example, to perceive a global “S” made up of local “Ts”, the spacing of the Ts is inconsequential (within certain limits). This is markedly different from the perception of a face, in which the spacing of the features is critical to the perception of the global structure. Thus, the relationship between global and local processing is presumably more integrated in face perception. Moreover, the distinction between global and configural analysis is important to face processing, whereas this is not relevant to the perception of typical hierarchical displays.

Despite the differences between face processing and hierarchical perception in other domains, it is clear that, for both faces and Navon displays, LSFs are more important for global/holistic processing and HSFs are more important for analyzing features. For faces, Goffaux and colleagues (2005) directly linked configural analysis with the use of LSFs and feature analysis with the use of HSFs in a face-matching task. In that study they manipulated either the spatial relations between the features of a face, or the features themselves, and found that frequencies below 1.86c/d (8c/i) were more important when faces differed on the basis of second-order configuration, while frequencies above 7.44c/d (32c/i) were more important when matching required processing the feature properties. In another study using the same SF filtering conditions, Goffaux and Rossion (2006) found that the whole-part advantage and composite face effect were both significantly larger for LSF faces than HSF faces, suggesting that holistic face processing (as demonstrated by these two paradigms) is largely supported by LSFs. These studies indicate that, indeed, the demand characteristics of the task could affect the SF used in a face image, supporting the idea of flexible usage of diagnostic information according to which

SF information usage is modulated by top-down factors (e.g., Schyns & Oliva, 1999; Sowden & Schyns, 2006).

4.1.4. SF scales relevant for the N170

If the N170 is associated with a face detection mechanism, reflecting base-level categorization as well as initial processing of face features, it should be relatively insensitive to frequency scale. This is because face detection may rely on analyzing the first-order (global) configuration (which preferentially relies on relatively LSFs) as well as processing the features (which is presumed to rely more on relatively HSFs). Hence, the difference between the N170 elicited by full-face and non-face objects could reflect either LSF information (supporting the global distinction) or HSF information (supporting the analysis of finer features). However, studies exploring the frequency scales that elicit the N170 effect have yielded mixed results.

Goffaux and colleagues (2003a) found that the N170-effect (face-car difference) was absent when SFs below 6.5c/d (32c/i) were filtered out of the images (i.e., high pass). However, the task in that study was orientation judgment, which may have encouraged participants to adopt a strategy that diverted their attention from the face features. Supporting this notion, the N170-effect was not enhanced by face inversion, as commonly found in N170 studies (e.g. Rossion et al., 1999). In a different paper, Goffaux et al. (2003b) found further evidence for the importance of task differences in determining the spatial scale eliciting the N170-effect. In a gender categorization task, they replicated their previous finding: the N170-effect was absent in high pass filtered images. However, in a familiarity task that required face recognition, they found similar N170 effects for low- and high-pass images. Another study examining processing of emotional faces also found no differential effects of frequency scale on the N170-effect (Holmes et al., 2005). Still another study using MEG found a reduction of the M170 only when the image was low-pass filtered (Hsiao et al., 2005). No similar decrease was found for mid-range or high-range.

Given that task demands modulate the use of SF scales, it is important to determine the SF scales used by default during visual processing level of faces. Assuming the N170-effect reflects a detection stage in face processing, one way to address this question is by determining the SF scales that elicit the N170-effect during a basic-level categorization task with minimum additional task constraints. In an attempt to address this question, Halit et al. (2006) used a face detection task in which participants viewed spatially filtered stimuli that either contained a famous face in noise or noise alone. The stimuli were presented at a brief exposure duration (120ms) and participants were asked to indicate the presence or absence of a face embedded in the noise. In addition to low-pass (i.e., LSF) and high-pass (i.e., HSF) spatially-filtered faces, they included two conditions that contained both low and high SFs: a “high-low face” condition that contained the frequencies in both the LSF and HSF conditions (i.e., omitting the mid-range frequencies), and a broadband face condition which contained all the SFs in the image. The “noise-only” condition was a “high-low” condition in that it always contained both the LSFs and HSFs, omitting the mid-range frequencies. Although the N170-effect was greater for LSF faces than HSF faces, the HSF faces elicited a significantly greater N170 than high-low noise, suggesting that HSFs, in addition to LSFs, are useful during basic-level categorization of faces, which is not surprising, assuming that basic-level categorizations are based on global shapes.

More importantly, the high-low face condition resulted in an even greater N170-effect than the LSF face condition, providing further evidence that HSFs are not redundant but important in eliciting the N170-effect. The N170 was greatest in response to broadband faces.

Although Halit et al. (2006) used a face detection task, the question of what SFs are used by default during face processing was not resolved in their study. Participants in their experiment were actively searching for faces in the stimuli, a task that proved to be more difficult in the HSF and high-low noise conditions than in the other conditions. Deciding if there is a face present in noise might engage different processes such as attention to face characteristics in the LSF range. Top-down mechanisms of this kind might not be used as extensively when faces are not masked. Consequently, the aim of Experiment 6 was to explore the SF scales used by default in early face processing when both faces and other objects can be ignored.

4.2. Aim of Experiment 6: SF scales used by default in eliciting the N170-effect

To examine the SF scales used in early face processing when both faces and objects are task irrelevant, I asked participants to detect infrequently presented flowers among a stream of other items. Thus, unlike previous studies, I did not impose task constraints on the faces that might recruit the use of certain SFs not otherwise employed during base level categorization of faces. In addition, I examined how the effects of different manipulations of face stimuli are modulated by SF scale. Assuming that face detection involves processing of some face features as well as the global structure, and that feature processing may rely more on HSF scales than configural processing, it is important to determine the relative use of LSFs and HSFs on processing face components. To this end, I presented participants with face stimuli that were canonical and intact, inverted and intact or without the global contour of the face. The perception of the inner features was enhanced by presenting them in isolation (while sparing the internal but not the overall configuration), and I hindered overall configural analysis by face inversion (Fig. 16). I compared the influence of low-pass and high-pass spatial filtering with broadband (BB) stimuli on the N170-effect across these different manipulations. Similar to Goffaux et al. (2003a,b) I equated overall spectral content across LSF and HSF conditions by adding a reciprocally filtered background texture to each filtered stimulus. That is, each LSF stimulus was combined with a HSF background texture and vice versa.

4.3. Experiment 6 Methods

Participants

Twenty five undergraduates from the Hebrew University in Jerusalem participated in the experiment. All had normal or corrected-to-normal vision and gave informed consent as approved by the University of California, Berkeley CPHS (#2004-6-25).

Stimuli

The original stimuli were photographs that were digitally scanned and transformed into grayscale. None of the faces had glasses or jewelry. 76 different stimuli were presented in each condition. The stimulus categories were: upright full faces, inverted faces, isolated inner face components (“inner components”), cars, and flowers.

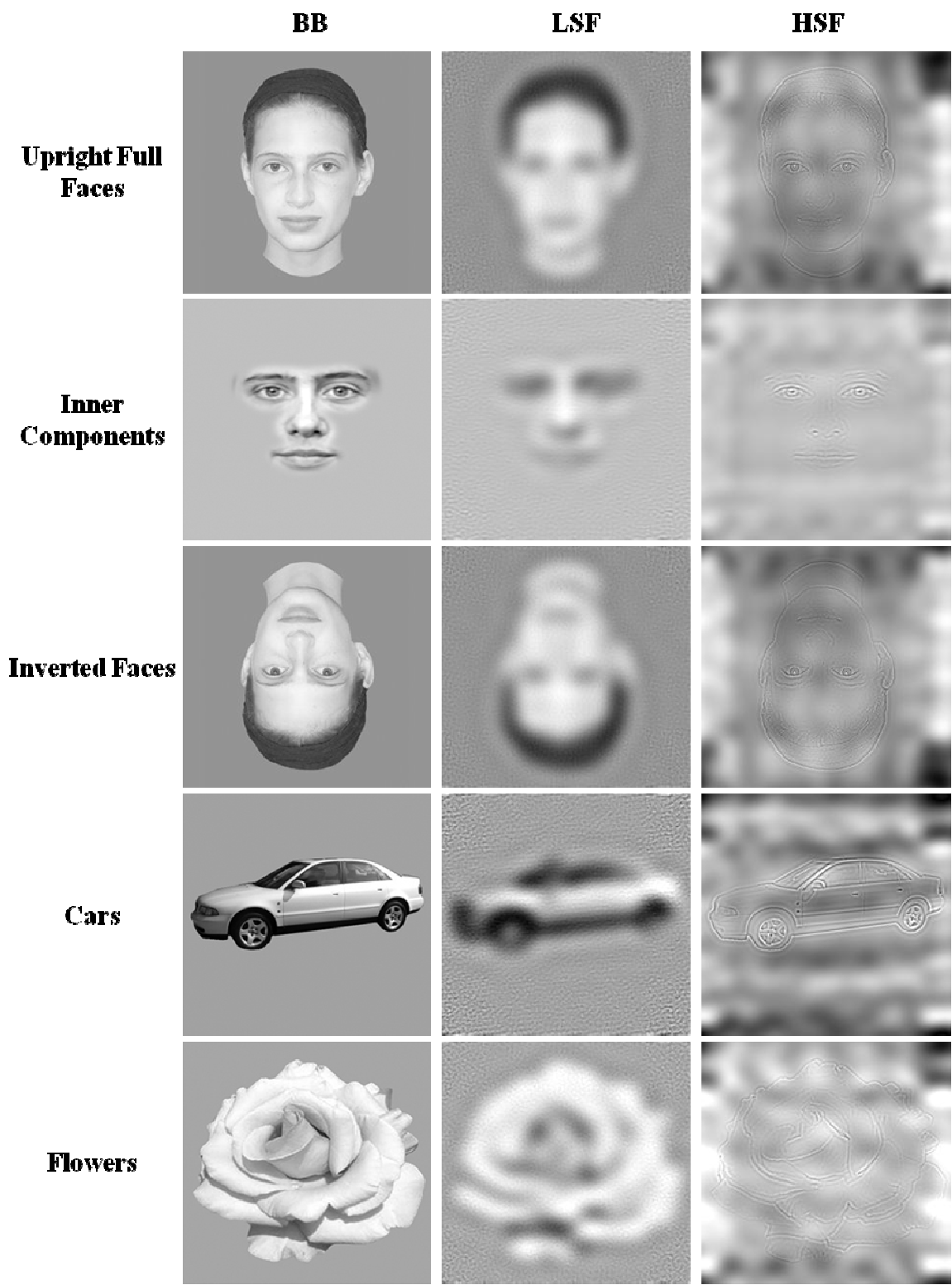


Figure 16. Examples of stimuli in Experiment 6. Participants passively viewed stimuli and pressed a button every time a flower appeared on the screen. BB: broadband stimuli; LSF: low-pass spatially filtered stimuli; HSF: high-pass spatially filtered stimuli.

There were three filter conditions; broadband (BB), low-pass filter (LSF) and high-pass filter (HSF). The pair of LSF and HSF filter cutoffs was determined so that the contrast sensitivity was equal within each cutoff SF. The low-pass cutoff was $0.9c/d$ and the high-pass cutoff was $5c/d$. Seen from a distance of 70 cm, these corresponded with $4c/i$ and $22c/i$ for the low and two high cutoffs, respectively. As in Goffaux et al. (2003a, b) each filtered image was combined with a reciprocally filtered background texture so that the resulting hybrids were equated for spectral content across LSF and HSF conditions. The broadband stimuli were presented as hybrids with the same background texture in its broadband version. The luminance of all stimuli across all three filter conditions was equated using a house-made Matlab algorithm.

Procedure

Following electrode montage, participants were seated in an electrically shielded and sound attenuated booth. They were instructed to maintain central fixation and press a button every time a flower appeared on the screen. Examples of LSF and HSF flowers were shown to familiarize participants with the nature of the stimuli. A short practice block preceded the experimental blocks, which was identical to the experimental blocks but half the length. All filtered stimuli were intermixed and presented in random order, at a rate of approximately 1 stimulus/second, in four filtered experimental blocks with short breaks between blocks. Stimulus exposure time was 350ms. The 4 filtered blocks were followed by a BB block, which was identical to the filtered blocks except that the stimuli were presented in their original BB versions.

EEG recording and analysis

The EEG analog signals were recorded continuously by 64 Ag-AgCl pin-type active electrodes mounted on an elastic cap (ECI) according to the extended 10-20 system, and from two additional electrodes placed at the right and left mastoids, all reference-free. Eye movements, as well as blinks, were monitored using bipolar horizontal and vertical EOG derivations via two pairs of electrodes, one pair attached to the external canthi, and the other to the infraorbital and supraorbital regions of the right eye. Both EEG and EOG were sampled at 250 Hz using a Biosemi Active II digital 24-bit amplification system with an active input range of -262 mV to +262 mV per bit without any filter at input. The digitized EEG was saved and processed off-line.

The ERPs were analyzed with Analyze-Brain Products, Inc. The data were referenced to the tip of the nose. Blink artifacts were corrected by a subtraction of VEOG components with ICA. Additional EOG and EEG artifacts were removed monitoring the bipolar EOG derivations and the posterior lateral EEG sites P8, P10, P08, right mastoid, and the homologous sites over the LH. A change in voltage of more than $50 \mu V$ during a 100 ms epoch in any of these channels was considered an artifact and the EEG recorded in the interval 200ms before and after the artifact was removed. Following this artifact removal procedure, more than 90% of the trials were preserved in each average. After removal of artifacts the EEG was digitally filtered between 0.8 and 17Hz (12dB), segmented and averaged separately for each stimulus type. An epoch of 100 ms prior to onset was used for baseline correction.

The peak latency and amplitude of the N170 component was extracted at the maximal negative amplitude between 150 and 220ms at 6 posterior lateral sites: P8, P10, P08 and the homologous sites over the LH. These sites were selected a priori based on previous studies. Additionally, the peak latency and amplitude of the P1 component was extracted at the maximal positive amplitude between 75 and 110 ms at the same sites. ANOVA with repeated measures and post hoc univariate contrasts were used to assess the statistical significance of the observed effects and, whenever necessary the degrees of freedom were adjusted using the Greenhouse-Geisser procedure.

4.4. Experiment 6 Results

The EEG data were processed and segmented individually for each stimulus type and experimental condition. Initial scrutiny of the waveforms showed a normal basic N170-effect across all SFs (Fig. 17A). It seems that the major effect of filtering on the N170-effect was a delay of the peak latency that was larger for the HSF than for the LSF conditions. However, note that the delay already started at P1, suggesting that it might reflect the influence of a visual process that is not specifically related to face processing (Fig. 18). Unlike the basic N170-effect (Fig. 17A), the effects of face inversion and isolating inner components were affected by filtering (Fig. 17B). Both effects were reduced for filtered stimuli relative to BB. Comparing low- and high-pass filtered stimuli, there was no obvious difference between the LSF and HSF conditions for inner components (i.e., faces without contour), while the inversion effect was completely eliminated in the HSF condition. Because the ERPs described above were elicited by a complex visual pattern that included a meaningful foreground image and a reciprocally filtered background texture, we sought to analyze these data after reducing the effect of the meaningless texture. This could be done with straightforward subtraction of the waveforms elicited by cars from those elicited by each face-related stimulus at each SF scale, with the residual being the net face-specific effects. However, such a subtraction is meaningless in the present set of data due to the high variation in latency across SF scales. We thus subtracted the peak N170 amplitudes elicited by cars from the peak N170 amplitudes elicited by the three face-related stimuli in each filter condition for each participant regardless of latencies and used this difference as our dependent variable in the statistical analyses. This subtraction also controlled for P1-related influences on the N170 (there was no main effect of filter on P1 amplitude [$F(2,48) < 1.00$]). These data are presented in Table 2 and Fig. 18.

The initial statistical evaluation of the N170-effects was based on a repeated-measures four-way ANOVA. The factors were Stimulus type (upright face, inverted face, inner components), Filter (BB, LSF, HSF), Hemisphere (LH, RH), and Site (P7/8, PO7/8, P9/10)⁵, followed where indicated by post hoc contrasts. Whenever necessary, the degrees of freedom were adjusted using the Greenhouse–Geisser correction. This analysis resulted in a significant main effect of Stimulus type [$F(2,48)=21.6$, $p < .001$], as well as of Filter [$F(2, 48)=11.1$, $p < .001$]. The effect of hemisphere only approached significance [$F(1,24)=3.5$, $p=.075$], with larger mean N170 amplitude effects over the RH ($-2.1 \mu\text{V}$) than the LH ($-1.3 \mu\text{V}$). The effect of site

⁵ These sites were selected a-priori on the basis of previous studies.

was also significant [$F(2,48)=3.7, p < .05$]. More revealing was the significant interaction between Stimulus type and Filter [$F(4,96)=9.0, p < .001$] that was qualified by a tendency for a three-way interaction between Stimulus Type, Filter and Site [$F(8,192)=2.4, p=.061$]. In addition, there was a significant interaction between Filter and Site [$F(4,96)=5.6, p < .005$]. No other effects were significant, albeit there was a tendency for Hemisphere to interact with both

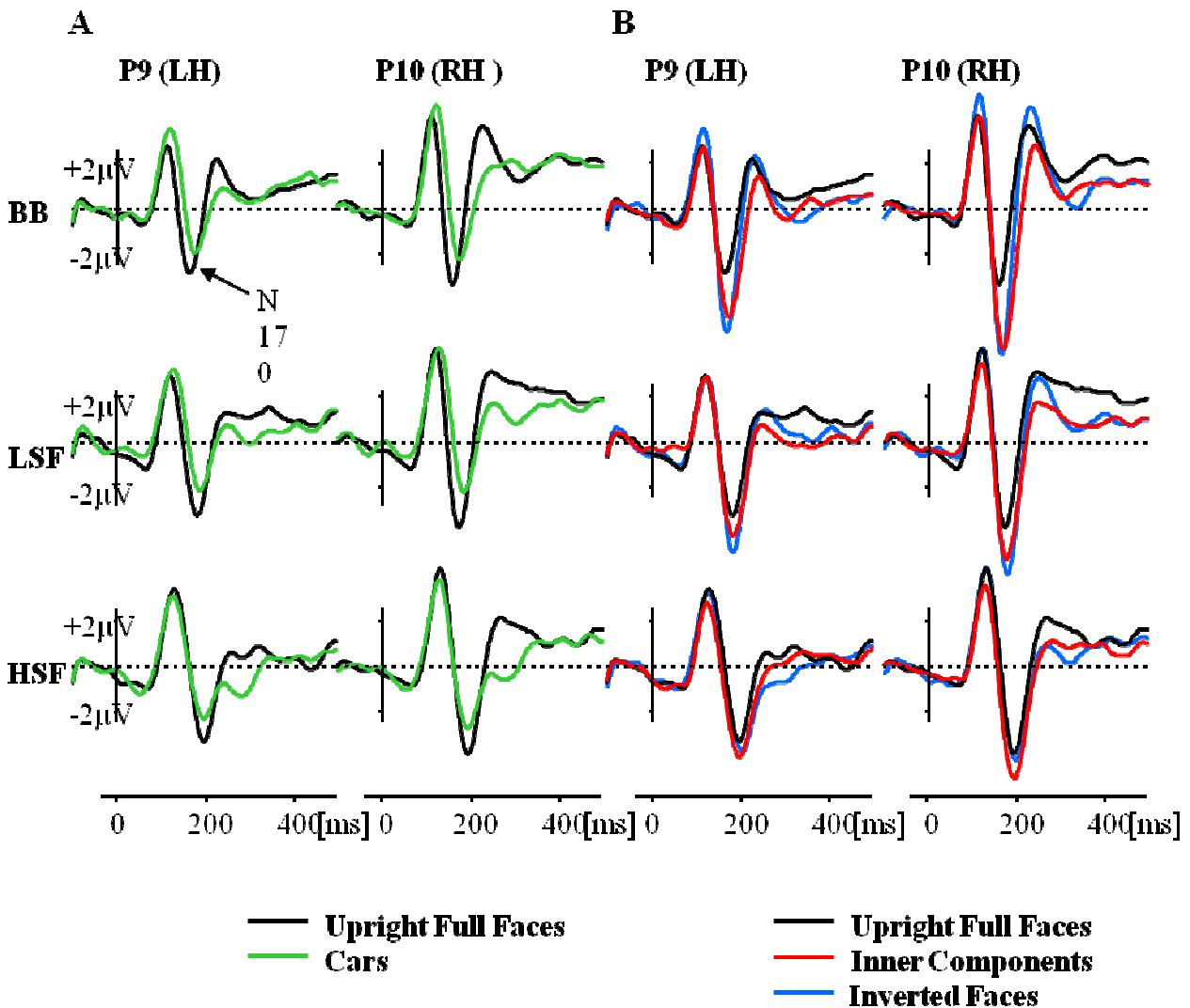


Figure 17. ERPs elicited by experimental stimuli in each filter condition in Experiment 6. Note that these ERPs reflect the response to both the experimental stimulus (foreground figure) and the reciprocally filtered background texture, so comparisons across frequency scale should be made cautiously. The effect of the background texture was diminished in the analyses by subtracting the peak N170 amplitude elicited by cars from the peak N170 amplitude elicited by each face-related stimulus within each filter condition. (A) The basic N170-effect (upright full faces vs. cars) is similar in each SF scale. (B) The enhancement of the N170 amplitude to isolated components is seen in all 3 spatial frequency scales, whereas the enhancement to inverted faces is only seen in BB and LSF conditions.

Filter [$F(2,48)=2.6, p=.08$] and Stimulus type [$F(2,48)=2.6, p=.09$]. Analyzing the three-way interaction first, I found that the two-way interaction between Stimulus type and Filter was significant at all sites, albeit more conspicuous at P9 and P10 than at other sites. Based on this similarity, as well as on the previously established posterior lateral distribution of the N170-effect, I continued analyses with a focus on P9 and P10 only.

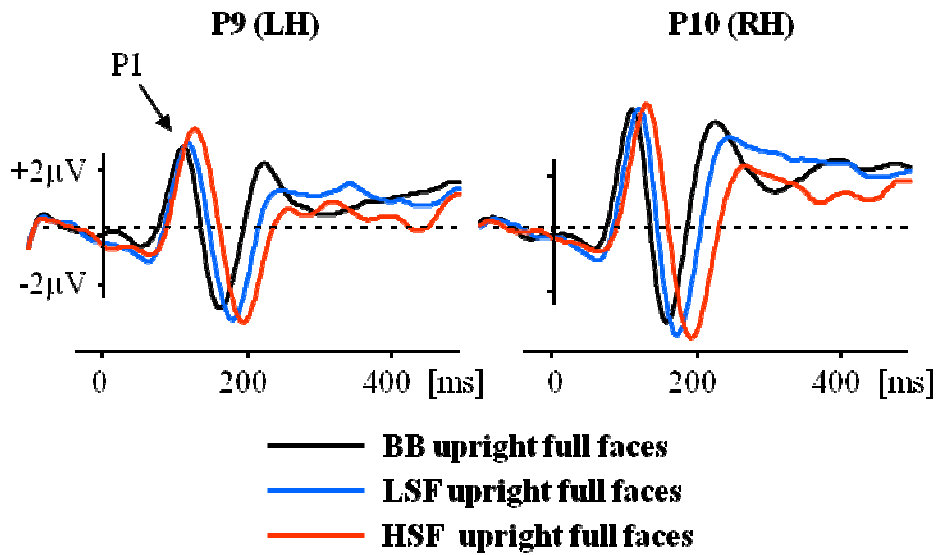


Figure 18. ERPs elicited by upright full faces in each frequency condition in Experiment 6. Note that the latency delay elicited by LSF and HSF stimuli relative to BB starts before the N170 at P1 (denoted by arrow).

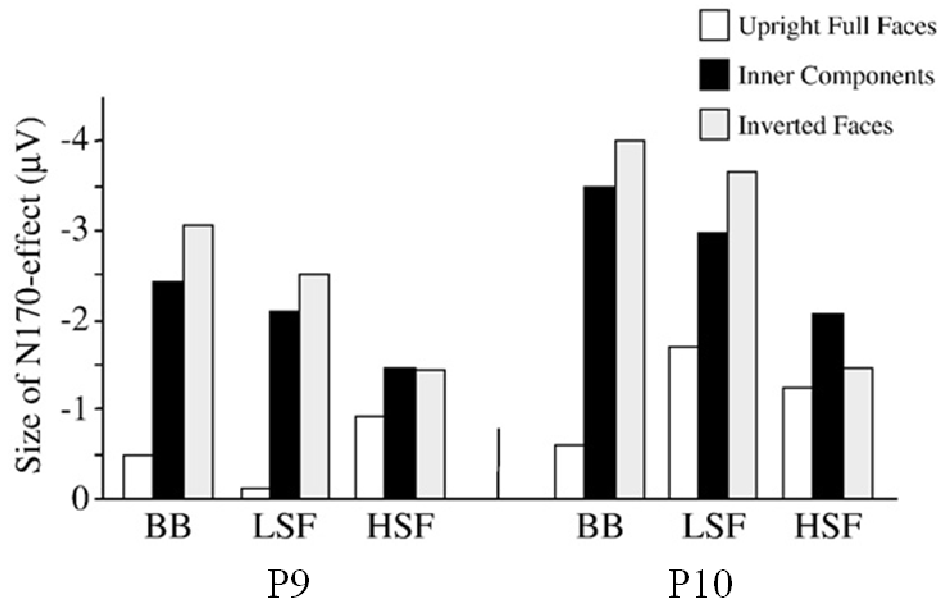


Figure 19. Mean amplitude difference between the N170 elicited by each face-related stimulus and that elicited by cars (N170-effect) in Experiment 6. Within each filter condition, comparison of the N170-effect for each face related stimulus. P9: LH electrode site; P10: RH electrode site.

The factorial analysis at P9 and P10 mirrored the 4-way analysis. There was a significant main effect of Stimulus Type [$F(2,48)=23.2$, $p<.001$]. Post hoc contrasts showed that across filters the amplitude of the N170-effect elicited by upright faces was smaller ($-1.0 \mu\text{V}$) than for that elicited by inner components and inverted faces [$-2.4 \mu\text{V}$ and $-2.7 \mu\text{V}$, respectively; $F(1,24)=52.1$, $p < .001$], with no significant differences between the latter two conditions. The main effect of Filter was also significant [$F(2,48)=5.4$, $p < .01$]. Post hoc contrasts showed no difference between the BB and LSF stimuli ($-1.9 \mu\text{V}$ and $-2.3 \mu\text{V}$, respectively), both producing a significantly larger N170-effect than the HSF stimuli [$-1.4 \mu\text{V}$; $F(1,24)=9.8$, $p < .01$]. The main effect of Hemisphere showed a tendency for significance [$F(1,24)=3.9$, $p=.06$]. The only significant interaction was between Stimulus type and Filter [$F(4, 96)=9.1$, $p < .001$]. To explore this interaction I analyzed the Filter effect separately for each Stimulus type with the N170-effect as the dependent variable.

Table 2. Mean amplitude difference (in μV) between the N170 elicited by each face-related stimulus and that elicited by cars in Experiment 6.

		LH Electrode Sites			RH Electrode Sites		
		P9	P7	P07	P10	P8	P08
Upright Full Faces	BB	-0.48	0.02	0.52	-0.62	-0.13	-0.18
	LSF	-0.12	-0.15	-0.81	-1.69	-1.84	-1.69
	HSF	-0.91	-0.06	0.11	-1.23	-0.40	-0.02
Inner Components	BB	-2.41	-1.21	-1.05	-3.49	-2.64	-2.55
	LSF	-2.10	-1.59	-1.90	-2.64	-3.02	-3.20
	HSF	-1.48	-1.07	-0.89	-2.55	-1.72	-0.90
Inverted Faces	BB	-3.06	-2.75	-2.79	-4.00	-3.90	-4.30
	LSF	-2.52	-2.99	-2.58	-3.66	-4.02	-3.73
	HSF	-1.44	-0.97	-0.27	-1.46	-0.77	0.09

For upright faces the N170-effect was similar across filters [$F(2,48)=1.7$, $p=.19$], and across hemispheres [$F(1,24)=1.0$, $p=.32$]. There was also no interaction between the two factors [$F(2,48) < 1.00$]. For inner components the main effect of Filter was significant [$F(2,48)=4.1$, $p < .05$]. Post hoc contrasts showed that the N170-effect for HSF stimuli was similar to LSF [$F(1,24) = 2.8$, $p=.11$], but smaller than the effect elicited by BB stimuli [$F(1,24)=10.0$, $p < .01$]. The Hemisphere effect was significant [$F(1,24)=7.8$, $p < .01$], showing that the N170-effect for inner components was larger at P10 ($-2.8 \mu\text{V}$) than at P9 ($-2.0 \mu\text{V}$), and there was no interaction between the two factors [$F(2,48) < 1.00$]. Finally, for inverted faces Filter had a significant main effect [$F(2,48)=19.7$, $p < .001$], while the Hemisphere effect was not significant [$F(1,24)=2.0$,

$p=.09$], and neither was there an interaction between the two factors [$F(2,48)=2.4$, $p=.10$]. Post hoc contrasts showed that there was no difference between the N170-effect elicited by inverted faces in the BB and LSF conditions [$F(1,24)=2.0$, $p=.17$], which were both significantly larger than the N170-effect elicited by inverted faces in HSF [$F(1,24)=31.2$, $p < .001$].

Analyses of the N170 peak latency differences were performed taking into account that these differences might have started earlier, at P1. Although the P1 amplitude was not affected by any of the independent variables, its latency was significantly affected by filter condition [$F(2,48)=44.3$, $p < .001$]. Moreover, as shown in Fig. 3, the sequence of P1 peaks in the different filter conditions was similar to the visible effect of filter on the N170 latency. Therefore, in order to isolate the experimental effects on the latency of the face-selective process reflected by the N170 I subtracted the P1 latency from the N170 latency. The ANOVA design for this analysis was similar to the one used for amplitude except that the Stimulus type factor included cars as one of 4 levels⁶ (Table 3).

Table 3. Mean latency difference (in ms) between the peak N170 latency and the peak P1 latency for each stimulus condition in Experiment 6.

		LH Electrode Sites			RH Electrode Sites		
		P9	P7	P07	P10	P8	P08
Cars	BB	57.5	59.3	54.1	56.8	56.7	55.0
	LSF	60.8	64.8	61.1	58.1	57.8	57.8
	HSF	69.1	66.9	66.2	61.4	60.6	58.8
Upright Full Faces	BB	50.4	55.8	53.9	47.3	49.7	50.0
	LSF	58.3	62.2	58.3	50.6	51.2	50.1
	HSF	65.6	63.9	61.7	62.2	57.2	57.2
Inner Components	BB	56.1	59.8	57.7	53.9	57.3	55.5
	LSF	60.1	60.3	58.3	53.9	59.2	56.6
	HSF	69.7	63.1	64.2	61.6	58.1	59.2
Inverted Faces	BB	53.9	61.2	57.8	50.3	53.6	52.3
	LSF	61.1	64.5	63.2	55.2	60.8	58.6
	HSF	74.5	73.8	69.8	65.8	61.9	63.1

⁶ I included cars in the analysis of latency to assess the filter effects that were face-specific and those that were not.

The 4-way ANOVA of the adjusted latencies revealed significant main effects of Stimulus type, Filter and Hemisphere [$F(3,72)=5.4$, $p < .01$; $F(2,48)=18.8$, $p < .001$; $F(1,24)=15.5$, $p < .001$, respectively]. The main effect of Site was not significant [$F(2,48)=1.5$, $p=.24$]. Post hoc contrasts showed that across filters the N170 elicited by cars peaked the latest but not significantly later than those elicited by inverted faces [$F(1,24)=1.0$], which peaked later than inner components [$F(1,24)=9.0$, $p < .01$], which in turn, were later than faces [$F(1,24)=10.2$, $p < .01$]. Post hoc analyses of the Filter effect showed that the N170 peaked earlier for BB than LSF stimuli [$F(1,24)=11.1$, $p < .01$], which in turn were earlier than for HSF stimuli [$F(1,24)=21.6$, $p < .001$]. Importantly, the interaction between Stimulus type and Filter was not significant [$F(6,144)=1.4$, $p=.22$], suggesting that the filter condition had similar effects on latency for all stimulus types. There was also no interaction between Stimulus Type, Filter and Site.

In summary, the results of Experiment 6 showed that the size of the basic N170-effect (faces relative to cars) was similar across BB, LSF, and HSF filter conditions, while its latency (after controlling for P1 effects) was delayed by both filters relative to BB, but more so by the HSF than the LSF. Similarly, while both filters reduced the N170-effect for inner components relative to BB, there was no difference between the LSF and HSF, conditions. Yet, the latency of the N170 peak was delayed for inner components as for faces. In contrast, the amplitude enhancement of the N170-effect by face inversion, while similar for BB and LSF conditions, was not present in the HSF condition. That is, for HSF stimuli there was no difference between faces and inverted faces. Again, the latencies were shortest for BB stimuli, followed by LSF stimuli, and longest for HSF stimuli.

4.5. Experiment 6 Discussion

The results of Experiment 6 support other recent evidence suggesting that both HSFs and LSFs are used during early stages of face processing. Early evidence reported by Goffaux et al. (2003a) found that LSFs were sufficient to produce the N170-effect for upright faces. Later, Halit et al. (2006) showed that HSFs are not redundant but provide important information in eliciting the N170-effect when faces are targets. The present results extend their findings to demonstrate that the SF effect is not limited to conditions when attention is directed to faces, but is also evident even when faces are part of the distracter set. Moreover, while Halit et al. found LSF faces elicited a greater N170-effect than HSF faces, the results from this study demonstrate that the two scales are equally important when faces are not the targets. Although target relevancy is the most obvious difference between the study by Halit et al. and the current study, there are also other differences that should be considered. For instance, Halit et al. used a higher high-pass filter (24c/i rather than the 22c/i in my experiment) and thus included less HSFs that might help the efficiency of face categorization. They also used a higher low-pass filter (8c/i rather than the 5c/i in the present experiment), thus including higher LSFs that may also increase efficiency of face categorization in their LSF condition. Whether or not these differences are substantial enough to account for the differences between my results and theirs, the present data demonstrate that the distinction between faces and cars, as reflected by the N170-effect, is as efficient when based on HSF channels (above 5c/d) as when it is based on LSF channels (below 0.9c/d). Relatively HSFs and LSFs were automatically accessed during early face categorization.

The results from Experiment 6 also extend those of Goffaux et al. (2003a), who found that the N170-effect was only present when LSFs were included in the stimuli. Participants in that were requested to determine the orientation of the stimuli (face and cars), again making faces task relevant. When faces are not task relevant, as was the case in the present study, both high and low SF information is extracted, at least for upright faces. Although it might be expected that the N170-effect would be robust to task differences, the evidence together demonstrates that its interaction with the SF spectrum is affected by top-down processes (Goffaux et al., 2003b). In the present study, I found no face inversion effects when the LSFs were excluded from the image. Again, there were differences between HSF filter cutoffs in mine and Goffaux et al's study. Specifically, in the HSF condition, they used a 32c/i cutoff, which is considerably higher than those used either by Halit et al. or by myself. Hence, it seems that excluding SFs below 22c/i (the present study) leaves face processing as indicated by the N170-effect intact. Excluding SFs below 24c/i (Halit et al's.2006 study) reduces the efficiency of the system to distinguish between faces and cars (as reflected by a reduced N170-effect), while excluding spatial frequencies below 32c/i (Goffaux et al.'s 2003a study) eliminates the N170-effect entirely, although faces can still be detected in this range. The differences between these studies underline the importance of a systematic investigation of the SFs that are necessary to obtain the N170-effect and how the range of these frequencies is modulated by task demands.

The present results also revealed new effects of SF filtering on the N170 response to different face-related stimuli. In the BB condition, both inner components and inverted faces elicited and increased N170 amplitude relative to upright full faces. This effect was seen across both spatial scales for inner components but only in the LSF stimuli for inverted faces. Although both of these manipulations in BB stimuli have been described as affecting “configural” processing, they do so in different ways. The present results demonstrate that they are also sensitive to different SF ranges, and these can be observed as early as the N170. Face inversion effects were driven entirely by the LSFs, while responses to inner components produced an increased N170 for BB, HSF and LSF stimuli. In other words the consequences of changing the face configuration by inversion and manipulating the salience of the inner components on passive face viewing are different.

It is particularly surprising that the inversion effect on the N170 was found in the LSF and not the HSF condition because it is commonly assumed that inversion breaks the face configuration and triggers part-based processing (e.g., Bartlett and Searcy, 1993; Carey, 1978; Carey and Diamond 1977; Rhodes, Brake, & Atkinson, 1993; Tanaka and Farah, 1993). For example, previous behavioral data have shown that while faces are recognizable as faces when blurred as well as when inverted, combining these two manipulations renders unrecognizable faces (Collishaw and Hole, 2000). This is presumably because blurring a face inhibits feature processing while inversion inhibits configural processing; while recognition was still possible when only one of these factors was present (i.e., blurring alone or inversion alone), it was not possible when both were present (i.e., blurring+inversion). If first-order configural processes that denote a potential face are inhibited when processing inverted faces, as has been argued, manipulations that change the ability to extract configural information should not be consequential. Specifically, the fact that HSFs disrupt configural processing, while LSFs do not, should not matter. In contrast, as previously reported (Goffaux et al., 2003a), the present results

suggest that face inversion effects are absent in HSF while present in LSF stimuli. This suggests that, although extraction of configural information is much more difficult in an inverted than upright face, it is nevertheless attempted.

The similar response to inner components across LSF and HSF conditions provides additional evidence that HSF scales are used by face-selective mechanisms associated with the N170-effect. As with BB stimuli, the N170-effect was larger for inner components than for upright faces in both SF scales, albeit peaking later in the HSF condition. Moreover, enhancement of the N170 elicited by inner components relative to full upright faces was equal in both the LSF and HSF conditions. As suggested by Bentin and colleagues in previous studies (e.g., Bentin et al., 2006) the enhancement of the N170 to inner components relative to the full face reflects particular sensitivity to features that produce the N170-effect. That is, removal of the face contour may enhance feature processing while reducing configural processing, leading to enhancement of the response. This enhancement was seen in both SF scales in the present study, suggesting that the common finding that inner components generate a greater N170 than full upright faces (in BB) seems to be carried by LSF and HSF information.

Finally, it is noteworthy that, unlike in many N170 studies, the manipulation of SF range (and possibly the interaction of this manipulation with factors affecting the N170) had significant effects on the P1 component that precedes the N170 where selectivity to faces is not consistently found (cf. Itier and Taylor, 2004a, b). These effects were found here for P1 amplitudes but primarily on peak latencies. Although I took steps to alleviate the confound suggested by the P1 modulation between face-related and image-related effects by subtracting the P1 latency from the N170 latency, the robust effects on the P1 latency could have extended beyond its peak, and therefore the interpretation of the SF-scale effects on the N170 latency should be considered cautiously. That said, it is apparent that, even after subtracting the P1 latency, the N170 latency was modulated by both stimulus type and SF scale. The effect of stimulus type on the N170 latency conformed to a delay of this component for inverted faces and isolated components relative to upright faces. While the interpretation of this effect is still under debate, this discussion is outside the scope of the current investigation. HSF delayed the N170 peak in all conditions, but it did not interact with inversion or components' isolation. The absence of this interaction makes it difficult to interpret these effects in terms of face processing mechanisms.

In conclusion, the results from Experiment 6 suggest that multiple processes associated with face detection are reflected in the N170-effect, and that they flexibly use both LSF and HSF channels even when the basic-categorization of the face⁷ is not task-relevant. Further research is required to clarify the nature of the difference between face inversion and other manipulations that may enhance feature processing (e.g., isolating the inner components). Yet, the current results indicate that these two manipulations are not simply two equivalent methods of decreasing the role of configural processing. Moreover, along with behavioral studies (e.g., Schyns and Oliva, 1999) the current findings point to a need for systematic investigations of interactions between the characteristic task demands and SF scales in ERPs as well as in psychophysical data.

⁷ Obviously, faces were categorized as “not flowers” but so were cars. Therefore, the base-level categorical distinction between faces and cars was incidental to the task.

5. Concluding Remarks

The present investigation examined the role of SF processing on hierarchical perception in general as well as in the context of face perception. Previous research has established an association between processing HSFs versus LSFs and local versus global perception, respectively, both for Navon displays and for more natural hierarchical objects like faces. The six experiments reported here expounded on that research, demonstrating that the association between SF processing and hierarchical perception involves a top-down attentional mechanism that interacts with low-level visual SF channels, therefore allowing for the flexible use of SF scales during local and global processing.

Experiments 1-4 revealed that attention to local and global aspects of a hierarchical stimulus biased the selection of *relatively* low and *relatively* high SFs during image processing of a subsequently presented compound SF stimulus. This bias occurred despite a change in the response dimension (from letter identification in the hierarchical stimulus to orientation discrimination in the grating), and despite a difference in retinal location of the hierarchical stimuli and the grating stimulus. Most importantly, the bias was determined by the relationship between the two SFs in the compound grating (i.e., their relative frequency) rather than the absolute SF values. The notion that attentional selection of relative rather than absolute SFs underlies local versus global perception is one of the main tenets of the DFF theory of hierarchical processing (Ivry & Robertson, 1998), but was not explicitly tested until now. That relative rather than absolute SF drove the priming effects in these experiments is clear evidence that SF selection in hierarchical processing is more than the mere low-level perceptual processing of SFs in the image.

Experiment 5 extended DFF theory to provide a possible mechanism for the integration of elements in hierarchical displays with the level at which they occur, by showing that attending to relative SF modulated the hemispheric asymmetry in element-level integration. Specifically, attentional selection of higher SFs facilitated binding by the LH of shapes to the local level and attentional selection of lower SFs facilitated binding by the RH of shapes to the global level. Consequently, the results from Experiment 5 unified two seemingly disparate theories of hierarchical processing, DFF and HI, into a single framework by suggesting that SF selection is the medium for hierarchical integration.

Finally, Experiment 6 examined the use of SF scales in early stages of face perception, as reflected in the early physiological marker of face categorization, the N170-effect. Importantly, by using hybrid images of spatially filtered foreground images (LSF or HSF) with reciprocally filtered background images, the spectral information in the displays were equated for all filtered conditions in Experiment 6, and thus the observed SF modulations on the N170-effect could not be due to low-level SF differences. Instead, these modulations reflect the diagnostic SFs that were important to process each stimulus category. The findings from Experiment 6 revealed that, though the N170-effect reflects a relatively early face-processing stage, both HSFs and LSFs contribute equally to the N170-effect found for upright BB faces, but that different configural manipulations may reflect separate processing mechanisms that rely on different SF channels.

Taken together, the results from the six experiments reported here reinforce the notion that neural mechanisms involved in higher-level visual processing flexibly use LSF and HSF channels depending on task demands and diagnostically-driven biases (Morrison & Schyns, 2001; Schyns & Oliva, 1999). This is not trivial, because during early stages of visual processing, LSF information is processed by the faster magnocellular pathway, whereas HSF information is processed by the slower parvocellular pathway. Thus, some researchers have proposed that scale selection may be fixed, following a coarse-to-fine progression (Breitmeyer, 1984; Fiorentini, Maffei, & Sandini, 1983; Sergent, 1982; Ginsburg, 1986; Parker et al., 1992). However, it is important to note that the flexible use of spatial scales for higher-level perceptual processing does not preclude an initial bias for coarse information. Neural mechanisms involved in higher-level perceptual processing may flexibly use LSF and HSF channels despite an initial advantage for LSF information. The current experiments provide strong evidence that the outputs of low-level visual SF channels are flexibly used for higher-level processing of local and global elements of hierarchical displays.

6. References

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