Journal of Experimental Psychology:
Human Perception and Performance
2006, Vol. 32, No. 4, 1023–1039

0096-1523/06/$12.00 DOI: 10.1037/0096-1523.32.4.1023

Faces Are “Spatial”—Holistic Face Perception Is Supported by Low Spatial Frequencies

Valérie Goffaux
University of Maastricht and Université Catholique de Louvain

Bruno Rossion
Université Catholique de Louvain

Faces are perceived holistically, a phenomenon best illustrated when the processing of a face feature is affected by the other features. Here, the authors tested the hypothesis that the holistic perception of a face mainly relies on its low spatial frequencies. Holistic face perception was tested in two classical paradigms: the whole-part advantage (Experiment 1) and the composite face effect (Experiments 2–4). Holistic effects were equally large or larger for low-pass filtered faces as compared to full-spectrum faces and significantly larger than for high-pass filtered faces. The disproportionate composite effect found for low-pass filtered faces was not observed when holistic perception was disrupted by inversion (Experiment 3). Experiment 4 showed that the composite face effect was enhanced only for low spatial frequencies, but not for intermediate spatial frequencies known be critical for face recognition. These findings indicate that holistic face perception is largely supported by low spatial frequencies. They also suggest that holistic processing precedes the analysis of local features during face perception.

Keywords: face perception, holistic processing, spatial frequencies, composite effect, whole-part advantage, inversion

A human face is a complex stimulus, composed of multiple internal and external features (e.g., eyes, nose, mouth, hair . . .). It is widely acknowledged that individual faces are discriminated and recognized on the basis of local features (i.e., the shape of the mouth, the color of the eyes . . .), but also on the relationships between these features, the so-called face configuration. The concept of configuration has received quite a lot of attention in the face-processing literature in the past 3 decades.

When one considers individual face discrimination or recognition, many investigators agree that the concept of face configuration encompasses at least two forms (see the reviews of Maurer, Le Grand, & Mondloch, 2002; Rossion & Gauthier, 2002). The first notion refers to the metric distances between facial features, or second-order relations. For example, this could be the interocular distance, or the nose-mouth distance. The second notion of face configuration refers to the fact that the face-processing system integrates the features into a gestalt, a so-called holistic representation. Whereas metric distances between facial features can be measured and manipulated on a face stimulus independently of an observer, the notion of *holistic* rather reflects a way of representing and processing the face stimulus.

The fact that faces are processed holistically was first put on record by Sir Francis Galton (1883), who suggested that “a face stimulus is perceived as whole, at a single glance, rather than as a collection of independent features,” and the concept has been developed in the face literature most notably by Young, Hellawell, and Hay (1987); Sergent (1984), as well as by Farah, Tanaka, and colleagues (e.g., Tanaka & Farah, 1993; Farah, Wilson, Drain & Tanaka, 1998).

Part of the confusion between holistic face processing and the ability to extract metric distances between features comes from the fact that presenting a face stimulus upside down affects both dramatically (Maurer, Le Grand, & Mondloch, 2002). Moreover, a so-called holistic face representation should, in principle, encompass both the local features and their metric distances. Yet, the two notions can be separated based on their sensitivity to experimental manipulations and their pattern of development. For instance, it has been shown that children as early as 6 (Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998) or perhaps 4 years old (Pellicano & Rhodes, 2003) process faces holistically, just like adults. Children of that age, however, are much less efficient than adults at processing differences among faces in the spacing among facial features (Mondloch, Geldart, Maurer, & Le Grand, 2003).

This article concerns holistic face processing, which we shall define here as the fact that facial features are integrated, rather than being represented and processed independently from one another (Sergent, 1984; Tanaka & Farah, 1993; Farah, Wilson, Drain, & Tanaka, 1998; Tanaka, Kay, Grinnell, Stansfield, & Szechter, 1998; Young, Hellawell, & Hay, 1987). Practically, this implies that the recognition of a face part is influenced (positively or negatively, depending on the context) by the processing of the other face parts.

Valérie Goffaux, Department of Neurocognition, University of Maastricht, The Netherlands, and Unité Cognition & Développement et Laboratoire de Neurophysiologie, Université Catholique de Louvain, Belgium; Bruno Rossion, Unité Cognition & Développement et Laboratoire de Neurophysiologie, Université Catholique de Louvain, Belgium

This research was supported by the Belgian National Scientific Research Foundation (FNRS). We are grateful to Quoc Vuong for his help during stimulus generation and to Barbara Hault, Nadège Dumont, and Fatima Ahmed for their help in data collection. We also would like to thank Glyn Humphreys, Philippe G. Schyns, and Frédéric Gosselin, for their comments on previous versions of the manuscript.

Correspondence concerning this article should be addressed to Valérie Goffaux, Department of Neurocognition, Faculty of Psychology, University of Maastricht, Universiteitssingel 40, P.O. Box 616, 6229 ER Maastricht, The Netherlands. E-mail: valerie.goffaux@psp.ucl.ac.be

Numerous phenomena exemplify the holistic processing of faces in real life situations or in the laboratory (Carey & Diamond, 1994; Davidoff & Donnelly, 1990; Endo, Masame, & Maruyama, 1989; Farah, Wilson, Drain, & Tanaka, 1998; Hole, 1994; Hole, George, & Dunsmore, 1999; Homa, Haver, & Schwartz, 1976; Le Grand, Mondloch, Maurer, & Brent, 2004; Sergent, 1984; Tanaka & Farah, 1993; Tanaka & Sengco, 1997; Young, Hellawell, & Hay, 1987; see Maurer, Le Grand, & Mondloch, 2002 for a review). Two experimental paradigms have been widely used to provide evidence for face holistic processing: the composite face paradigm (Young, Hellawell, & Hay, 1987) and the whole-part paradigm (Davidoff & Donnelly, 1990; Tanaka & Farah, 1993).

Holistic Effects in Face Perception

Young, Hellawell, and Hay (1987) created a composite stimulus by joining the top half of a familiar face (cut below the eyes) with the bottom half of another familiar face. Observers were slower to name the top half of a composite face when the top and bottom parts were vertically aligned than when the same top and bottom parts were offset laterally (i.e., misaligned). The slowing down in correct response times (RTs) was also found for the naming of bottom parts aligned with different top parts, but the effect was smaller. Since this original demonstration, the effect has been replicated and extended to unfamiliar faces during matching tasks, in several studies (Endo, Masame, & Maruyama, 1989; Hole, 1994; Hole, George, & Dunsmore, 1999; Le Grand, Mondloch, Maurer, & Brent, 2004). These findings provide compelling evidence that facial features, here the top and bottom parts of a face stimulus, are integrated into a holistic representation.

The advantage at processing features embedded in whole faces as compared to their presentation in isolation is another powerful illustration of the strong influence exerted by a facial gestalt on the processing of features (Davidoff & Donnelly, 1990; Farah, Wilson, Drain, & Tanaka, 1998; Leder & Carbon, 2005; Pellicano & Rhodes, 2003; Tanaka & Farah, 1993; Tanaka, Kiefer, & Bukach, 2004; Tanaka & Sengco, 1997). In a seminal study, Tanaka and Farah (1993) trained participants to name a series of upright faces, and showed that subjects later recognized face features (eyes, nose or mouth) better when these were embedded in the whole face stimulus than presented in isolation. This whole-part effect has also been found in matching tasks with unfamiliar stimuli (e.g., Farah, Wilson, Drain, & Tanaka, 1998; Pellicano & Rhodes, 2003), supporting the view that it occurs at a perceptual stage (although see Wenger & Ingvalson, 2002).

In both paradigms, the recognition of a face part is affected by the other face part(s). In the composite face paradigm, the recognition of the target face half is disrupted because the other half, irrelevant for the task, differs across target and test composite faces. In the whole-part paradigm, the recognition of one face feature (eyes, nose, or mouth) is facilitated when it is presented in the same face context at encoding and recognition stages. The holistic influence on part perception could be either positive or negative in both paradigms, however, depending on the conditions of presentation. For instance, Leder and Carbon (2005) recently showed that the whole-part effect could be manifested as a disadvantage for the "whole" condition if the encoding stimulus were an isolated part rather than a whole face. Whether it is manifested as a facilitation effect or an inhibition effect, the bottom line is that the recognition of a face part is affected by the other face part(s), a hallmark of holistic face processing.

Although these two effects illustrate the strength of holistic face processing, the performance of the subjects with single parts in these paradigms also show that individual features can be represented as such by the visual system. The effects strongly suggest, however, that the holistic representation of a face is extracted somewhat before the representation of isolated face parts is fully resolved. This reasoning assumes that the effects take place during the perceptual encoding of information (Farah, Wilson, Drain, & Tanaka, 1998; Hole, 1994; Le Grand, Mondloch, Maurer, & Brent, 2004) rather than taking place at a late decisional stage (Wenger & Ingvalson, 2002). This suggestion raises the question of the visual information upon which a holistic face representation is built, and can in turn, influence the extraction of facial features. Here, we aimed at clarifying this question by investigating the early visual information subtending holistic face perception.

Spatial Frequencies for Face Processing

The input to the visual system consists in complex luminance arrays rendering our visual environment. Early visual processes break down the variations of luminance intensities into discrete neural signals representing luminance over spatial regions of different size. Luminance variations at different scales, that is, spatial frequencies, convey different types of information for visual processing. Low spatial frequencies (LSF) represent the large-scale variations, that is, coarse visual information, whereas high spatial frequencies (HSF) represent tighter gradients of luminance changes, that is, fine visual information. In his influential model of visual processing, Marr (1982) postulated that the operation of SF channels is part of the initial bottom-up processing of the retinal image (i.e., primal sketch) and that information about SF content is not retained at higher levels of visual processing. In contrast, Ginsburg (1978, 1986) later relayed by Sergent (Sergent, 1986; Sergent & Hellige, 1986), postulated that different SF bands supply information for different high-level perceptual and cognitive functions, in particular for face processing. For example, HSF may convey information about detailed edges portraying the contours of features (e.g., eyes, mouth), whereas LSF could encode pigmentation and coarse shading cues (see also Morrison & Schyns, 2001; Schyns, Bonnar & Gosselin, 2002). Most interestingly for our purpose, Sergent (1986) suggested that processing a face as a gestalt versus analyzing its featural cues corresponded to processing distinct regions of spatial spectrum; whereas holistic face processing would depend mostly on LSF, the extraction of face parts would depend mostly on HSF. That is, high-level visual processes (holistic vs. analytic) dedicated to faces would be rooted in the early segregation of low-level visual information provided at different spatial scales in the stimulus.

Although a large number of studies have aimed at identifying the critical SF bands serving face recognition (e.g., Costen, Parker, & Craw, 1994, 1996; Fiorentini, Maffei, & Sandini, 1983; Gold, Bennett, & Sekuler, 1999; Hayes, Morrone, & Burr, 1986; Kornowski & Petersik, 2003; Liu, Collin, Rainville, & Chaudhuri, 2000; Näsänen, 1999; Parker & Costen, 1999; Tieger & Ganz, 1979), this hypothesis of a mapping between holistic/analytic processing of a face and the low/high extremes of the spatial frequency (SF) spectrum has neither been investigated directly by manipulating holistic processing nor systematically, that is, with spatially filtered faces. Indirect evidence that LSF may be critical for face holistic processing was provided by Collishaw and Hole (2000), who showed that blurred faces (i.e., preserving mostly LSF intensities) could still be recognized adequately unless they were presented upside down. Recent studies have tested (i.e., through Fourier-filtered stimuli) the respective role of LSF and HSF on the processing of metric distances between facial features (e.g., distance between two eyes; Boutet, Collin, & Faubert, 2003; Goffaux, Hault, Michel, Vuong, & Rossion, 2005), but the respective weight of LSF versus HSF for holistic face processing has never been tested directly.

Testing holistic face processing on spatially filtered face stimuli has several interests. First, this image processing can be applied on any kind of visual stimulus without any assumptions about what and where the relevant information is (Sergent & Hellige, 1986; Wenger & Townsend, 2000). SF filtering may thus turn out to be a valid means of objectively separating the cues subtending holistic and featural processing, and, as such, may become an invaluable tool to investigate high-level visual processing of faces. Second, spatial filtering is relevant for studying face categorization, because the processes supporting face categorization are highly sensitive to SF variations, as compared to object categorization processes (Biederman & Kalocsai, 1997; Collin, Liu, Troje, McMullen, & Chaudhuri, 2004). For example, several studies have shown that face recognition optimally relies on an intermediate band of SF, between 8 and 16 cycles per face image (e.g., Costen, Parker, & Craw, 1994, 1996; Gold, Bennett, & Sekuler, 1999; Näsänen, 1999). More recent studies have qualified this observation by showing that the critical factor for optimal performance in such experiments is the overlap of SF bands across face stimuli presented at encoding and recognition stages (Collin, Liu, Troje, McMullen, & Chaudhuri, 2004; Kornowski & Petersik, 2003; Liu, Collin, Rainville, & Chaudhuri 2000). Third and perhaps most interestingly, the use of spatially filtered faces may yield new insights about the respective time course of holistic and featural face processes. Hence, the visual system does not instantaneously extract the entire spectrum of luminance variations. Instead, visual perception develops over time, by progressively integrating the different ranges of spatial frequencies of a stimulus (Sergent, 1986). This temporal integration is thought to evolve from the early extraction of LSF to the later processing of HSF, for both the sensory processing of the scale information and its usage for face, object, and scene categorization (e.g., Fiorentini, Maffei, & Sandini, 1983; Flavell & Draguns, 1957; Ginsburg, 1978; Hugues, Nozawa, & Ketterle, 1996; Loftus & Harley, 2004; Parker & Costen, 1999; Schyns & Oliva, 1994; Sergent, 1986; Watt, 1987). Because of the initial availability of LSF, the early visual representation would be that of the global structure of a stimulus, this coarse frame being refined over time with the slower accumulation of higher spatial frequencies (for recent models of this coarse-to-fine visual recognition scheme, see Bar, 2004 and Hochstein & Ahissar, 2002).

The coarse-to-fine model leads to the following reasoning for face processing. If holistic processing of faces relies predominantly on LSF, as compared to HSF, as will be tested in this study, this will strongly suggest that the extraction of a holistic face representation precedes the analytical processing of facial features, as proposed first by Sergent (1986). In normal conditions, this temporal precedence of holistic processing may serve as a header to guide the extraction of detailed information on facial features, provided by HSF.

In the present study, we aimed at testing the hypothesis that holistic face processing relies mostly on LSF. To do so, the whole-part and composite face effects were tested on LSF, HSF, and unfiltered face stimuli. Because our hypothesis is that holistic processing of a face mostly depends on LSF, that is, on the extraction of a coarse representation, we expected to find larger whole-part advantages and composite face effects for LSF stimuli as compared to HSF stimuli. That is, the matching of a face part would be influenced by the other face parts more for LSF stimuli than for HSF stimuli. Alternatively, if holistic face processing is independent of spatial frequencies, the matching of a face part should be equally influenced by the other face parts for both LSF and HSF. In Experiment 1, we tested this hypothesis using the whole-part advantage paradigm, expecting a larger whole-part advantage for LSF. In Experiment 2, we used the composite face paradigm and hypothesized a larger interference of the bottom part on the matching of the top parts for LSF as compared to HSF stimuli. In Experiment 3, we tested the composite face effect with stimuli presented upside down. Because inversion disrupts holistic face processing (Tanaka & Farah, 1993), we predicted that any larger face composite effect for LSF stimuli would vanish with inverted pictures. Finally, in Experiment 4, we tested further the hypothesis of an LSF predominance in holistic processing by comparing the composite face effect for the lowest band of frequencies (i.e., 2–8 cycles/face) and the intermediate band of SF, supposedly optimal for face recognition (8–32 cycles/face).

Experiment 1

Method

Subjects. Thirty undergraduate students (mean age: 20.3 ± 2.6, six males, four left-handed) from the Department of Psychology (University of Louvain, Belgium) received course credit for participating in the experiment. They had normal or corrected-to-normal visual acuity.

Stimuli. We used 30 grayscale full-front pictures of unfamiliar faces posing with a neutral expression (half male, half female). Faces had neither facial hair nor glasses and the photos (approximate size was 190 pixels for width and 250 pixels for height) were trimmed to remove external features (neck and hairline). The pictures were fitted into a 256 × 256 pixel gray square (see Figure 1). Using Adobe Photoshop, we created 20 eye foils by swapping the eye region among the 20 original faces. The remaining 10 original faces were used to generate five nose foils and five mouth foils using the same feature-swapping procedure. Original and foil faces were Fourier transformed and multiplied by low-pass and high-pass Gaussian filters to preserve low (below 8 cycles per face width, cpf) and high SF (above 32 cpf), respectively (see Figure 1). We used Gaussian filters with $\sigma = 10$ pixels for LSF faces and $\sigma = 38$ pixels for HSF faces to prevent "ringing" artifacts in the filtered images. We then inverse-Fourier transformed the product and rescaled the values to the full 8-bit range (0.255). In order to test our hypothesis of a differential holistic processing for face low and high SF, we maximized the difference between LSF and HSF conditions by choosing cutoffs separated by two octaves. In line with previous works contrasting categorization performance in LSF and HSF stimuli (e.g., Goffaux, Gauthier, & Rossion, 2003; Goffaux, Hault, Michel, Vuong, & Rossion, 2005; Schyns & Oliva, 1999; Oliva & Schyns, 1997), LSF and HSF conditions excluded intermediate spatial frequencies (here 8–32 cpf). Because several studies have shown that SF overlap between pairs of faces to match was more important for face recognition than

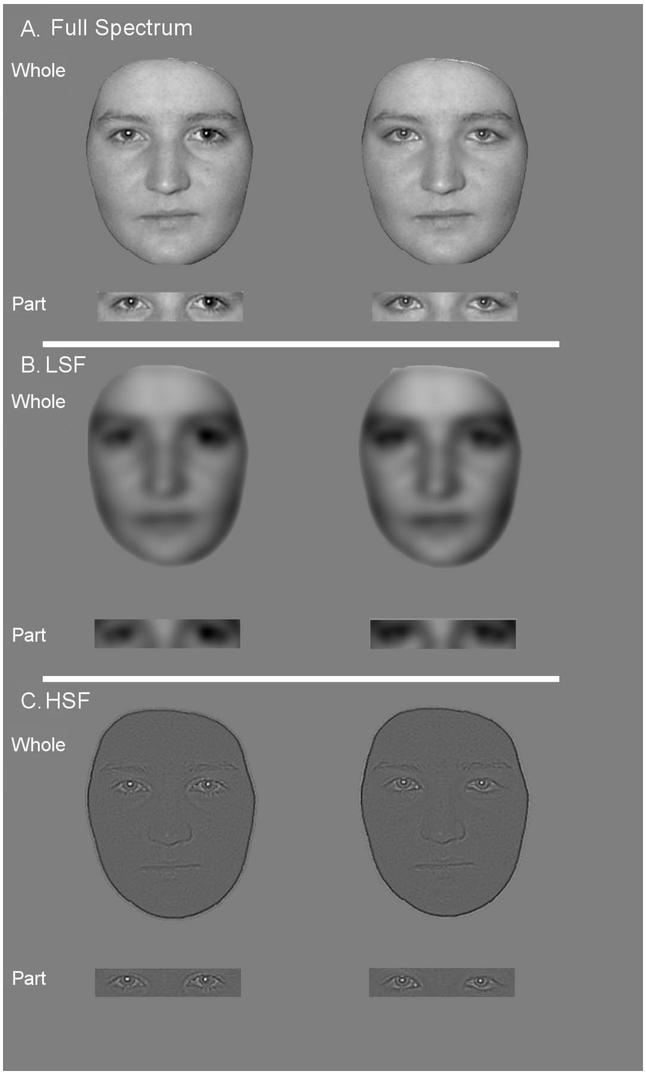

Figure 1. In Experiment 1, stimuli were presented in (A) full spectrum, (B) LSF, and (C) HSF as either whole or part displays. The foil stimuli (both wholes and parts) in the right column differ from those of the left column by only one feature (e.g., the eyes). LSF = low spatial frequency; HSF = high spatial frequency.

absolute SF content (Collin, Liu, Troje, McMullen, & Chaudhuri, 2004; Kornowski & Petersik, 2003; Liu, Collin, Rainville, & Chaudhuri, 2000), subjects were asked to match pairs of faces presented in congruent frequency bands (e.g., >32 cpf to >32 cpf; <8 cpf to <8 cpf).

Isolated features (eyes, nose, or mouth) were generated by cutting the relevant feature from filtered and full-spectrum versions of original and foil faces, resulting in a total of 60 feature stimuli for each SF version (LSF, HSF, and full spectrum, see Figure 1). Nose and mouth foil parts and faces were used as catch trials (one third of the trials) in the experiment to avoid that subjects focused exclusively on the eyes, but were not analyzed because of their lesser saliency (Pellicano & Rhodes, 2003; Tanaka & Farah, 1993; Wenger & Townsend, 2000).

Procedure. The task was a forced choice two-alternative identity matching. Trials began with a central fixation cross for 200 ms, followed by a 200-ms gray screen. A target face was then presented centrally during 2,000 ms. Following a blank of 300 ms, two probe stimuli appeared side by side and remained on the screen until a response was made. Subjects were instructed to select the probe that matched the target stimulus by pressing the key corresponding with probe location (right vs. left) on the screen. The next trial started 800 ms following response. The target stimulus was always an original face, either in full spectrum, LSF, or HSF version. In the whole display condition, the probes were whole faces, one of which was the target face, and the other one (i.e., foil) differed from the target by one feature only (eyes in experimental trials, nose or mouth in catch trials). In the part display condition, the probes depicted isolated face features (eyes in experimental trials, nose or mouth in catch trials). One of the probe features was identical to the target feature (as presented in the target face), the other probe was a foil feature. The experiment was a 3×2 within-subject design with SF (LSF, HSF, and full spectrum) and display (whole and part) as factors. There were 40 trials per experimental condition and 240 experimental trials in total. Target and probe stimuli appeared twice. The location of foil stimuli (right vs. left) was counterbalanced. One hundred twenty catch trials (mouth and nose whole and part foils) were added. Trial order was at random and varied for each participant.

Subjects were seated in a quiet and dark room at 110 cm from the 17-inch PC monitor (85 Hz refresh rate; 1024×768 pixel resolution). The viewing distance was held constant by a chin rest. Whole stimuli subtended $4.1° \times 4.1°$ of visual angle. Eyes feature stimuli were $0.5° \times 2.7°$ of visual angle, nose features were $1° \times 1°$, and mouth features were $0.72° \times 1.3°$. All stimuli were arranged on a gray background. The stimulus presentation was controlled using E-prime 1.1.

Analyses. After the rejection of outlier trials[1] (exceeding individual mean response time by more than two standard deviations), a two-way ANOVA for repeated measures was applied on correct RTs and rates, with display (whole or part) and SF (full spectrum, LSF, or HSF) as within-factors. Polynomial contrasts were used for post hoc comparisons.

Results

Figure 2 illustrates the mean accuracy rates and correct RTs (in ms, $n = 30$) for each experimental condition separately. A whole-part advantage, that is, superior recognition of a part when it is presented in the context of a whole face rather than isolated, was observed both in accuracy, $F(1, 29) = 37.15$, $p < .0001$ and correct RTs, $F(1, 29) = 15.33$, $p < .0005$. The main effect of SF was significant in accuracy, $F(2, 58) = 83.35$, $p < .0001$ and RTs, $F(2, 58) = 5.71$, $p < .005$. Accuracy was higher for full-spectrum faces compared to HSF faces, $p < .0001$, and higher for HSF faces compared to LSF faces, $p < .0001$. LSF and full-spectrum faces led to similar RTs, $p = .09$, but to significantly faster RTs than HSF faces, $p < .004$.

Of particular interest concerning the hypotheses, the interaction between these two factors was significant. The whole-part advantage was significantly modulated by SF content, both in accuracy, $F(2, 58) = 3.92$, $p < .02$ and for correct RTs, $F(2, 58) = 3.97$, $p < .024$. Although it was significant in each SF condition for accuracy, $ps < .008$, its magnitude for LSF faces was significantly larger (by a factor of two) than for HSF faces, $p < .012$, but only marginally larger than for full-spectrum faces, $p = .10$ (see Figure 2). For RTs, the whole-part advantage was significant for full-spectrum, $p < .0001$ and LSF faces, $p < .0001$, but not for HSF faces, $p = .09$. Its magnitude did not differ between LSF and full-spectrum conditions, $p < .44$.

[1] A maximum of 3 out of 240 experimental trials per subject were discarded.

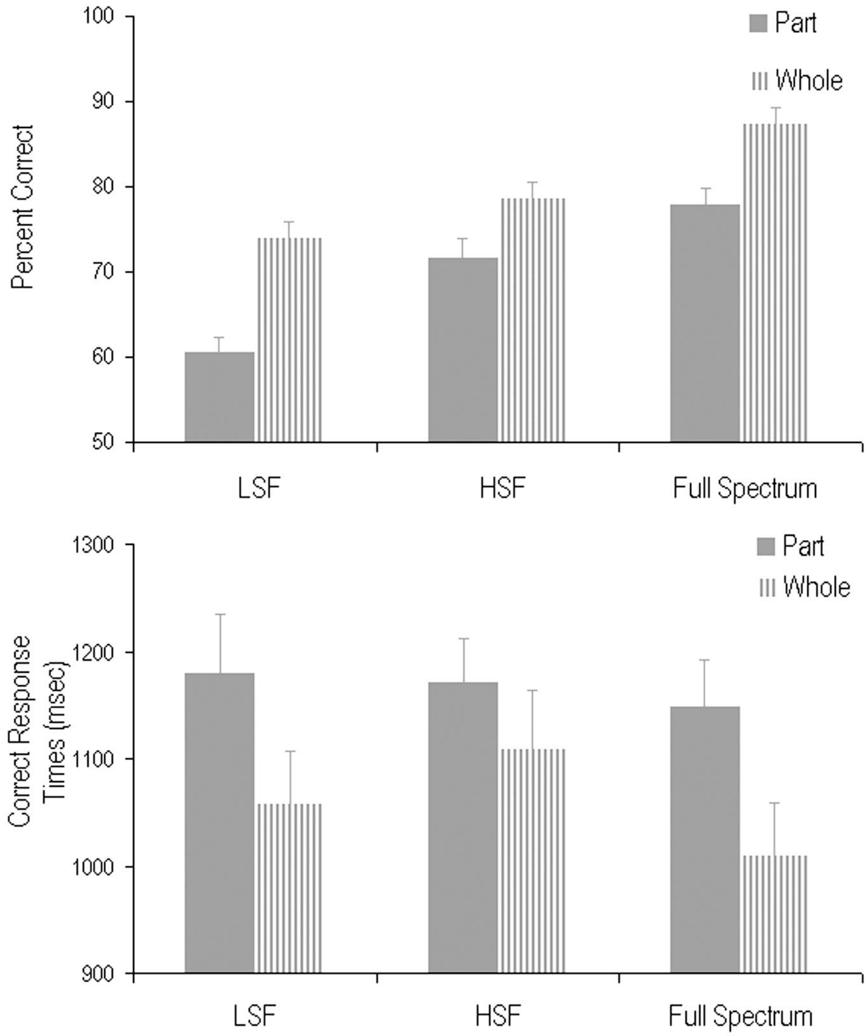

Figure 2. Mean accuracy and correct response times are shown as a function of display mode (whole vs. part) and spatial frequency content (full spectrum, LSF, and HSF). LSF = low spatial frequency; HSF = high spatial frequency.

Discussion

The whole-part advantage was twice as large in the LSF and full-spectrum conditions than in the HSF condition, both in accuracy and RTs. The fact that faces revealing only LSF gave rise to a whole-part advantage at least as large as full-spectrum faces confirms the hypothesis that holistic processes are supported mainly by the coarse scales of a face stimulus.

In general, LSF faces led to the lowest performance levels. Therefore, one might argue that the larger whole-part advantage observed for LSF faces as compared to HSF faces is due to the particularly poor performance observed for the isolated parts presented in LSF and that subjects were actually even better for HSF as compared to LSF in the "whole" condition (see Figure 2). This difference was small in accuracy, however, (only 4.5% difference in the "whole" condition), and subjects were 50 ms faster for LSF than HSF in "whole" condition. The accuracy decline for LSF faces could thus be due to a speed/accuracy trade-off in the "whole" condition. In any case, our hypotheses concerned the interaction between whole part and SF, which was obtained independently of any floor or ceiling effects. Moreover, whole faces were matched faster than isolated parts in all SF, but the effect was smaller for HSF faces (~50 ms) as compared to full-spectrum faces and LSF faces (~100 ms for both). Both accuracy and reaction time (RT) data concord to support the hypothesis that holistic processing mostly depends on LSF.

The lower performance in the "part" condition for LSF as compared to HSF stimuli and to full-spectrum faces may be explained by several factors. For instance, abrupt borders in part stimuli (see Figure 1) added artificial HSF noise to the images, which might possibly hamper the visibility of single parts in LSF stimuli more than in HSF stimuli. Because pairs of faces differed only by a single feature in both part and whole conditions, another possibility is that most subjects may have rapidly adopted an analytical strategy throughout the experiment, leading to an overall better performance with HSF than LSF faces (see Goffaux, Hault, Michel, Vuong, & Rossion 2005). This illustrates a limitation of the whole-part paradigm: Subjects have to match or discriminate individual faces without specific instructions about the strategy to apply (e.g., concentrate on one feature vs. encoding all features). This limitation is likely to add noise in the data by increasing intertrial and/or intersubject variability.

In the next experiments, we used the composite face paradigm. In this paradigm, subjects are explicitly told to match a part—the top half of the face—that is, to adopt an analytical strategy. Holistic processing is measured as the extent to which irrelevant bottom part automatically influences top part processing.

Experiment 2

In our second experiment, we explored the influence of SFs on the holistic processing of faces by means of the composite paradigm (Young, Hellawell, & Hay, 1987). Based on the assumption that LSFs predominantly convey global face cues, we again expected the strongest holistic effect to be observed for LSF faces.

Method

Subjects. Twenty-one undergraduate students (mean age: 19 ± 0.7, one male and three left-handed) from the Psychology Department (University of Louvain, Belgium) received course credit for participating in the experiment. They did not participate in Experiment 1 and had normal or corrected-to-normal visual acuity.

Stimuli. We used 20 grayscale egg-shaped full-front pictures of unfamiliar faces (neutral expression, half male, half female, no facial hair, no glasses, and no external features; see Figure 3). The photos were approximately 180 pixels wide and 250 pixels high and were fitted onto a 256 × 256 pixel gray background. Using the same procedure and cutoff frequencies as in Experiment 1, stimuli were Fourier transformed into frequency domain and multiplied by low-pass and high-pass filters to remove HSF (above 8 cpf) and LSF (below 32 cpf), respectively (see Figure 3). Using Adobe Photoshop, we separated the top and bottom parts of filtered and full-spectrum original faces by inserting a gap (3 mm height, or 0.15° of visual angle) just above the nostril upper limit; these faces constituted the same-aligned set ($n = 60$), as top and bottom parts belonged to the same original face. Same-aligned faces were then laterally offset (same-misaligned set, $n = 60$) by shifting the bottom part to the right, so that the middle of the nose (bottom part) was vertically aligned with the extreme right side of the top part. Sixty aligned and 60 misaligned stimuli were further generated by the combination of top and bottom parts of randomly selected original faces of corresponding gender. These sets constituted the different-aligned set and the different-misaligned set, respectively, because the top and bottom parts corresponded to different identities. These image transformations resulted in a total set of 240 faces (3 SF versions: LSF, HSF, and full spectrum, combined with 4 levels of alignment: same-aligned, same-misaligned, different-aligned, different-misaligned).

As in Experiment 1, the experimental room was quiet and dark. A chin rest maintained the subjects' distance from the PC monitor (17 in, 85-Hz refresh rate; 1,024 × 768 pixel resolution) at 110 cm. Aligned stimuli subtended 4.1° × 3.1° of visual angle, and misaligned stimuli were 4.1° × 4.7°. All stimuli were presented against a gray background. The stimulus presentation was controlled using E-prime 1.1.

Procedure. A trial consisted of the sequential presentation of face pairs. It began with a fixation cross at the center of the screen during 300 ms, followed by a 200-ms blank. The target face was then presented for 600 ms. After a 300-ms interstimulus interval, the sample face appeared for 800 ms. The target and sample faces appeared at slightly different screen locations, to avoid subjects comparing a specific location of the display to

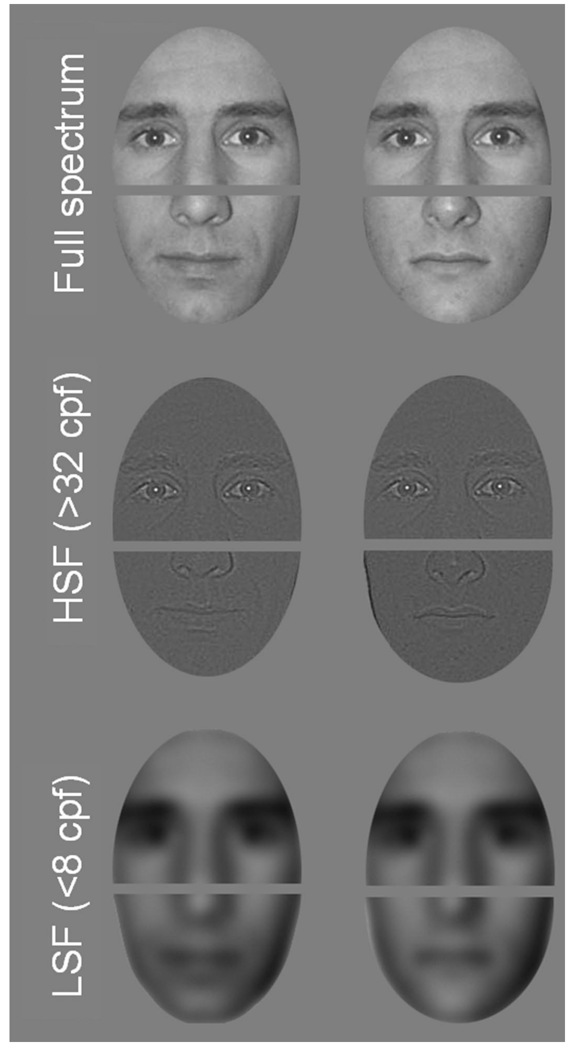

Figure 3. Composite faces combined identical top parts with different bottom parts. They were displayed in full spectrum, LSF, and HSF ranges in Experiments 2 and 3. In Experiment 3, all stimuli were turned upside down. LSF = low spatial frequency; HSF = high spatial frequency.

perform the matching task. The faces composing a trial pair always appeared in the same SF and alignment version. Subjects were instructed to attend only to top parts and had 1,000 ms to decide, as fast and accurately as possible, whether these were the same or different. The participants expressed their choice by pressing a left versus right key on a keyboard placed in front of them. Same-aligned and same-misaligned faces appeared twice as target faces: once in a "same" trial, once in a "different" trial. Target and sample faces always differed with regard to their bottom part. In half of the trials, the top parts were identical (demanding a "same" response). In the other half, both top and bottom parts differed ("different"). LSF, HSF, full-spectrum trials, as well as aligned and misaligned trials were randomly interleaved. The experiment comprised 240 experimental trials randomly mixed up across subjects. We expected to replicate Young, Hellawell, and Hay's (1987) results: poor performance in "same" aligned trials due to the processing of differing bottom parts.

Analyses. Two-way ANOVAs for repeated measures were applied on accuracy rates and correct RTs for "same" trials (i.e., hits and misses), with alignment (aligned or misaligned) and SF (full spectrum, LSF, or HSF) as within-subject factors. Polynomial contrasts were used for post hoc comparisons. In different trials, there was no difference in performance between misaligned and aligned conditions ($p > .08$ in accuracy and $p > .12$ in correct RTs). This absence of difference was expected given that both top and bottom parts differed between target and probe stimulus, providing a completely unequivocal stimulation to resolve.

Results

Subjects performed better and faster when face top and bottom parts were misaligned than aligned (accuracy: $F[1, 20] = 78.9$, $p < .0001$; RTs: $F[1, 20]) = 102.4$, $p < .0001$; Figure 4). Irrelevant bottom parts accordingly affected task performance on top parts. This indicates a composite effect, that is, that the holistic processing of aligned composite faces interfered with top part judgment. The main effect of SF was significant on response accuracy only ($F[2, 40] = 13.15$, $p < .0001$; for RTs, $p > .57$).

The main effects in response accuracy were qualified by a significant two-way interaction between stimulus alignment and SF ($F[2, 40]) = 9.4$, $p < .0001$; not significant for RTs: $p > .59$). When faces were misaligned, we did not observe any performance modulation across HSF, LSF, and full-spectrum face conditions, $p > .17$. Consequently, SF content only mattered for aligned faces, $F(2, 40) = 15.7$, $p < .0001$. Aligned LSF faces produced the lowest performance relative to aligned HSF and full-spectrum faces, *ps* <.002. Aligned HSF faces led to a marginal performance advantage over aligned full-spectrum faces, $p = .053$.

The composite effect (computed for each participant and each SF condition as the difference in accuracy between aligned and misaligned conditions) was the largest for LSF faces as compared to HSF, $p < .001$ and full-spectrum faces, $p < .04$. The smallest composite effect was observed in HSF condition, significantly lower than in the full-spectrum condition, $p < .01$.

Discussion

Subjects had to ignore the bottom parts of composite faces, but they nevertheless influenced their matching judgments of top parts. Given that the holistic interference arises despite the specific instruction to concentrate on a face part, this paradigm probably measures automatic holistic face processing better than the whole-part paradigm (see also Michel, Rossion, Han, Chung, & Caldara, 2006).

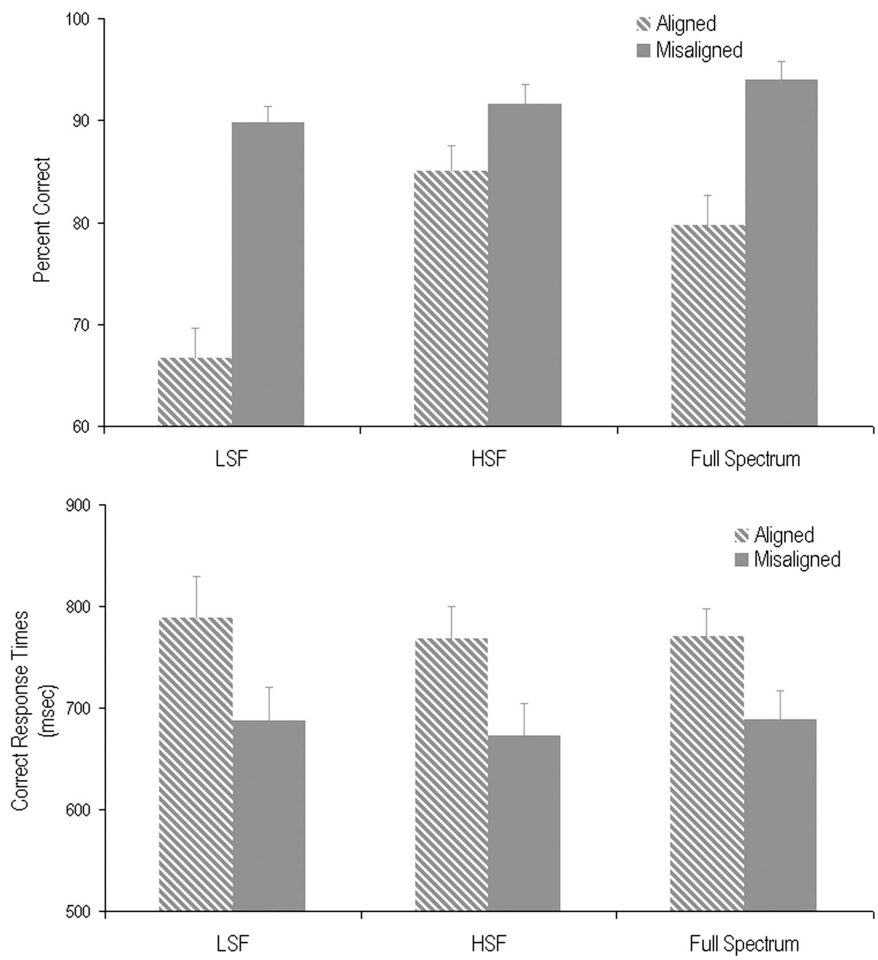

Figure 4. Mean accuracy (hit rate) and correct response times are shown for "same" trials in Experiment 2 as a function of alignment (aligned vs. misaligned) and spatial frequency (full spectrum, LSF, and HSF). LSF = low spatial frequency; HSF = high spatial frequency.

SF filtering dramatically modulated the degree to which global face properties were processed in the composite faces. The extent of face holistic perception, as measured classically by the composite effect with full-spectrum faces, was reduced by the removal of LSF (in HSF faces) and increased when only LSFs were available. When face stimuli were misaligned, SF had no effect on top part matching performance (see Figure 4). This indicates that, taken in isolation, top parts displayed in LSF and in HSF conveyed sufficient information to be discriminated. Once top and bottom parts were aligned, however, performance decreased mostly with LSF faces, as compared to HSF faces and full-spectrum faces (by 25.7%, 7% and 15%, respectively). In coarse scales, face features were integrated so strongly that identical top halves were perceived as being different. This finding shows that holistic processes predominated in face LSF.

Holistic processing was not exclusively related to LSF and full-spectrum faces. The composite effect, although dramatically reduced, was still significant for HSF faces. This demonstrates that face HSF also provided cues for holistic processes. The integration of facial features could be partly recovered from detailed local information that HSF conveys about face features, but the reduced composite effect in HSF condition indicates that the integration of facial features from LSF is much more effective than from HSF.

Experiment 3

In this experiment, we investigated whether the large holistic interference obtained in Experiment 2 for LSF composite stimuli reflects genuine holistic processes dedicated to faces. Therefore, the disproportionate composite effect found in the LSF condition of Experiment 2 might stem from a general masking effect occurring when blurred regions are in spatial vicinity (e.g., top and bottom parts of a LSF composite face).

To rule out this alternative explanation, we repeated Experiment 2 with all stimuli presented upside down. Because inversion is thought to disrupt holistic face processing (e.g., Farah, Wilson, Drain, & Tanaka, 1998; Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987; Maurer, Le Grand, & Mondloch, 2002), it should eliminate, or at least substantially reduce the composite face effect in all stimulus conditions. If the large composite effect found in LSF (Experiment 2) was due to a general factor such as masking, however, it should still be disproportionately increased for inverted LSF composites.

Method

Subjects. Twenty-one undergraduate students (mean age: 24 ± 4.3, five were males, and two were left-handed) were recruited on the University of Louvain campus and were remunerated (5) for participating in the experiment. They did not participate in Experiments 1 or 2 and had normal or corrected-to-normal visual acuity.

Stimuli. The stimuli were the same as in Experiment 2, except that they were inverted in the picture plane (using vertical flip in Adobe Photoshop; see Figure 3 with the sheet turned upside down). As in previous experiments, the experimental room was quiet and dark. A chin rest maintained the subjects' distance from the PC monitor (17 in, 85-Hz refresh rate; $1{,}024 \times 768$ pixel resolution) at 110 cm, and the stimulus presentation was controlled using E-prime 1.1.

Procedure. Experiment 3's procedure was strictly identical to that of Experiment 2.

Analyses. As in Experiment 2, two-way ANOVAs for repeated measures were applied on accuracy rates and correct RTs for "same" trials (i.e., hits and misses) with alignment (aligned or misaligned) and SF (full-spectrum, LSF, or HSF) as within-subject factors. Polynomial contrasts were used for post hoc comparisons. For different trials, which were not of interest in this paradigm, subjects ranked slightly lower in performance (by 4%) in misaligned compared with aligned conditions $F(1, 20) = 6.41$, $p < .02$ (RTs, $p > .6$), and there was no interaction between alignment and SF ($p > .6$).

Results

Figure 5 illustrates the mean accuracy and RTs observed in Experiment 3. There was a significant effect of alignment in accuracy, $F(1, 20) = 19.3$, $p < .0003$ and in RTs, $F(1, 20) = 21.72$, $p < .0002$, indicating a composite effect for faces presented upside down. The main effect of SF was also significant in accuracy, $F(2, 40) = 29.97$, $p < .0001$ and in RTs, $F(2, 40) = 5.014$, $p < .0114$. Subjects were less accurate with LSF faces as compared to HSF ($p < .01$) and full-spectrum faces ($p < .01$). They were faster with LSF faces as compared to HSF faces ($p < .01$).

The main effects were qualified by a significant SF $\times$ alignment interaction in accuracy, $F(2, 40) = 3.55$, $p < .038$ but not in RTs ($p > .64$). Significant composite effects in accuracy were observed in full-spectrum and LSF conditions ($p < .0002$ and $p < .05$, respectively) but not in HSF conditions ($p > .34$). The magnitude

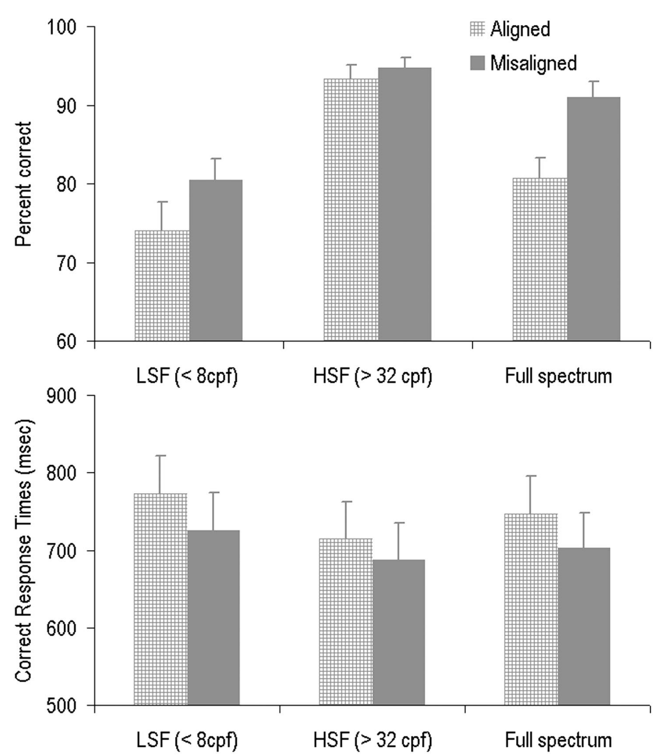

Figure 5. In Experiment 3, all stimuli were displayed turned upside down. This figure shows mean accuracy and correct response times ("same" trials) as a function of alignment (aligned vs. misaligned) and spatial frequency (full spectrum, LSF, and HSF). LSF = low spatial frequency; HSF = high spatial frequency.

of the effect was larger for full-spectrum than HSF faces ($p <$ .003), but unlike Experiment 2, did not differ significantly between LSF and HSF faces ($p >$ .22) and between LSF and full-spectrum faces ($p >$ .32). Thus, with inverted stimuli, the composite effect was reduced in all conditions (i.e., compare Figures 4 and 5), but most strikingly for LSF faces.

To assess more directly the influence of inversion on composite effect, we ran a three-way ANOVA on accuracy in Experiment 2 and Experiment 3, with orientation (upright vs. inverted) as a between-subjects factor and alignment and SF as within-subject factors. In the following, we only report those effects or interactions that implied the factor of orientation. There was an interaction of orientation and alignment, $F(1, 40) = 16.2$, $p < .0002$ because inversion significantly decreased the magnitude of the composite effect. There was also a significant interaction between orientation and SF, $F(2, 80) = 3.3$, $p < .044$. These interactions were qualified by a significant three-way interaction between orientation, SF, and alignment, $F(2, 80) = 3.82$, $p < .026$. For LSF faces, the composite effect was larger when composite faces were presented upright than when they were shown upside down (25.7% vs. 6%, $p < .001$). For HSF faces, inversion also significantly reduced the composite effect (6% reduction, $p < .05$). For full-spectrum faces, the reduction of composite effect was not significant ($p = .22$).

For RTs, there was a significant interaction between orientation and SF, $F(2, 80) = 19.51$, $p < .0001$. Inverting composite faces increased RTs in full-spectrum and LSF conditions, but decreased RTs in HSF conditions. There was also a marginal interaction between orientation and alignment, $F(1, 40) = 3.8$, $p = .059$ because inversion significantly decreased the magnitude of composite effect (compare Figures 4 and 5). Although the triple interaction orientation $\times$ SF $\times$ alignment was not significant for RTs ($p = .6$), we compared the magnitude of the composite effect in RT for upright and inverted faces for each SF condition. Inversion marginally decreased the composite effect only for LSF faces, $p <$ .06 (full-spectrum and HSF faces: ps$>$ .43).

Discussion

Together with Experiment 2, the results of Experiment 3 favor the view that holistic processing is supported by LSF. As expected, stimulus inversion dramatically reduced composite effects in all conditions, both in accuracy rates and correct RTs. Composite effects were weak (1%, 6% and 10% in HSF, LSF, and full-spectrum conditions, respectively) compared to Experiment 2 (7%, 25.7%, and 15% in HSF, LSF, and full-spectrum conditions, respectively).

We found it important that Experiment 3 was designed to test whether the particularly large composite effect found for upright LSF faces in Experiment 2 was due to a general form of masking, rather than being related to the holistic integration of facial features. If so, it should have remained very large for LSF faces presented upside down. In contrast, it was for LSF faces that the magnitude of the composite effect decreased the most (compare Figures 4 and 5), and it became lower than for full-spectrum faces. This information clearly indicates that the larger composite effect found for LSF faces as compared to HSF faces is related to upright holistic face processing.

In addition to this observation, two findings are worth discussing in Experiment 3. First, there was still a substantial composite effect for faces presented upside down. That is, inversion did not disrupt holistic processing completely, but to a large extent. This is an interesting result, which is in line with previous observations with other methods (Endo, 1986; Moscovitch & Moscovitch, 2000; Murray, 2004).

The second finding was that inversion caused a reduction of the composite effect for LSF both by increasing the performance on aligned trials and by decreasing the performance on misaligned trials. On the one hand, an increase of performance on aligned trials with inversion was expected, given that inversion reduces holistic interference in this condition, as for HSF stimuli. On the other hand, the performance decrease in misaligned trials for an LSF condition indicates that the combination of both inversion and misalignment effectively reduced the processing of a face to its local information. When this local information is reduced further by low-pass filtering, performance dropped significantly, in line with previous evidence (Collishaw & Hole, 2000).

In short, Experiment 3 was effective in dissociating between alternative accounts raised for the disproportionate composite effect found for the LSF condition in Experiment 2. Holistic interference observed in the LSF condition was substantially reduced as compared to Experiment 2 and no greater than in the full-spectrum condition. From these results, it can be concluded that the alignment $\times$ SF interaction observed for upright faces in Experiment 2 emanated from genuine holistic processes dedicated to upright faces and not from general masking effects.

Experiment 4

In our three experiments, holistic face processing was investigated in low, HSF, compared to full-spectrum stimulation. Previous studies, however, showed that important information for recognizing faces is comprised in a middle spatial frequency range (MSF), situated at around 8–16 cpf (e.g., Costen, Parker, & Craw, 1994, 1996; Gold, Bennett, & Sekuler, 1999; Näsänen, 1999). This article mainly addressed the hypothesis of a mapping between holistic/analytic and LSF/HSF continua and gathered consistent evidence for LSF range as providing diagnostic cues for holistic integration of face stimuli. In agreement with previous studies (Goffaux, Gauthier, & Rossion, 2003 and Goffaux, Hault, Michel, Vuong, & Rossion, 2005), we deliberately chose to contrast our conditions maximally and to present extremes of the SF continuum.

Experiment 4 aimed at replicating Experiment 2, but provided a direct comparison of the role of low, medium, and HSF in supporting holistic face processing. In line with our hypotheses and the findings of our previous experiments, we predicted smaller composite effects in MSF range than in LSF and full-spectrum conditions, since MSFs are thought to provide detailed information more useful for face identification than LSFs.

Method

Subjects. Twenty-one subjects (mean age: 21 $\pm$ 3.3, four males, and two left-handed) from the University of Louvain received either course credit, or remuneration (5) for participating in the experiment. They did not participate in any of the previous experiments and had normal or corrected-to-normal visual acuity.

Stimuli. LSF, MSF, and HSF stimuli were Fourier transformed and multiplied by two-octave wide bandpass filters. The SF ranges in LSF, MSF, and HSF were of 2–8 cpf, 8–32 cpf, and 32–128 cpf, respectively (Figures 3 and 6). To strictly match the range of SF contained in LSF, MSF, and HSF conditions, the stimuli from the full-spectrum condition contained luminance variations between 2 and 128 cpf. Although they did not comprise the 0–2 cpf range, we maintained the term "full spectrum" in Experiment 4 for sake of clarity. The luminance was equalized between LSF, HSF, MSF, and full-spectrum stimuli. The same procedure as in Experiment 2 was followed to combine top and bottom parts. The total composite set comprised 160 faces (4 SF versions: LSF, MSF, HSF and full spectrum, combined with 2 levels of alignment: aligned and misaligned).

Procedure. The trial sequence and general procedure were the same as in Experiments 2 and 3, except that the present experiment consisted of 320 trials instead of 240 (Experiments 2 and 3), because there was one more stimulus condition (MSF).

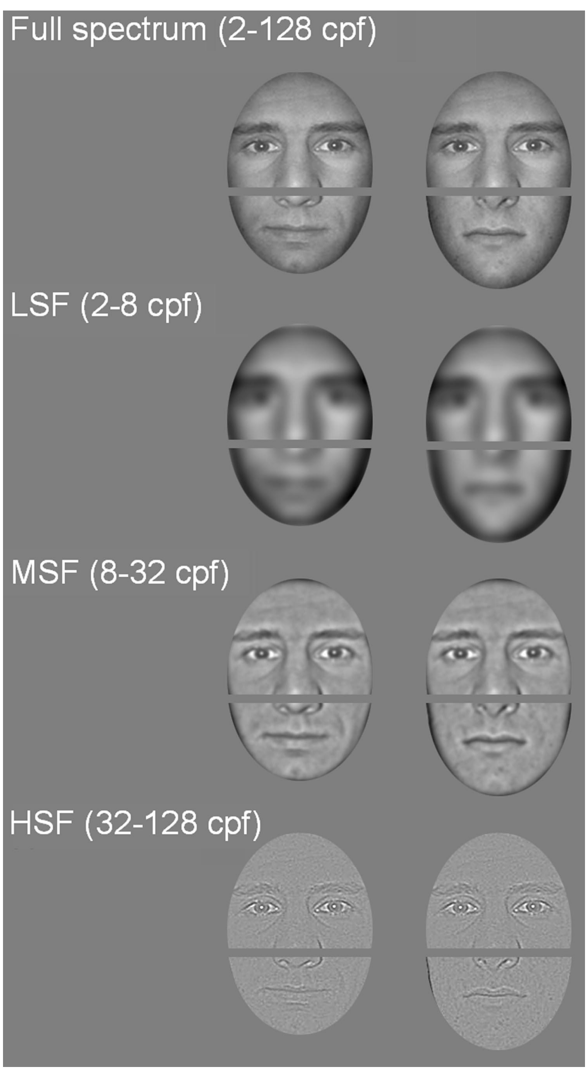

Figure 6. This figure illustrates the stimulus conditions tested in Experiment 4. LSF, HSF, MSF, and full spectrum stimuli were of same global luminance. LSF = low spatial frequency; HSF = high spatial frequency; MSF = middle spatial frequency.

Analyses. Two-way ANOVAs for repeated measures were applied on accuracy rates and correct RTs for "same" trials (i.e., hits and misses) with alignment (aligned or misaligned) and SF (full-spectrum, LSF, MSF, or HSF) were used as within-subject factors. Polynomial contrasts were used for post hoc comparisons. As expected, there was no composite effect in "different" trials neither on accuracy ($p > .5$), nor on correct RTs ($p > .6$). The following statistical analyses were carried on "same" trials, which disclosed the composite effect of interest.

Results

The difference in performance between aligned and misaligned conditions was significant both in accuracy, $F(1, 20) = 32.64$, $p < .00001$ and RTs ($F[1, 20] = 44.55$, $p < .00001$; see Figure 7). The main effect of SF was significant in accuracy only, ($F[3, 60]) = 8.445$, $p < .0001$; RTs: $p > .5$). The main effects obtained in accuracy were qualified by a significant two-way interaction between alignment and SF ($F[3, 60]) = 7.1$, $p < .0004$; no interaction in RTs: $p > .36$[2]). Similarly to Experiment 2, performance in the misaligned condition was constant across SF, $p > .36$; it was only when bottom parts were aligned with top parts that significant differences between SF conditions emerged, $F(3, 60) = 9.8$, $p < .0001$. The composite effect was significant in all conditions, but it was maximal for LSF faces (25% accuracy decline from misaligned to aligned condition) as compared to full-spectrum (16% accuracy decline, $p < .02$) HSF (8% accuracy decline, $p < .0001$) and MSF (12% accuracy decline, $p < .005$) conditions (LSF vs. all other SF conditions: $p < .0002$). Larger composite effects were also obtained in full-spectrum condition as opposed to HSF condition, $p < .021$. The effect obtained in MSF was of intermediate magnitude compared to full-spectrum and HSF conditions and did not differ significantly from these two conditions, all ps$> .28$.

Discussion

The results of Experiment 4 replicated the holistic effects observed in Experiment 2 for LSF, HSF, and full-spectrum conditions. In fact, the percentages of accuracy decline related to composite illusion in LSF, HSF, and full-spectrum conditions strikingly matched those obtained in Experiment 2 (compare Figures 4 and 6). Composite effects were prominent with LSF faces as compared to full-spectrum faces, whereas HSF composites led to the weakest holistic interference. These observations support the view that the holistic integration of face cues mostly relies on LSF cues.

Here we also monitored holistic processing in a medium range of SF (MSF condition, 8–32 cpf) that was adjacent with both LSF and HSF bands. We expected reduced composite effects relative to LSF because the MSF range provides fine-grained information useful for face identification and likely conveys enough local

[2] Despite the absence of interaction between conditions and for RTs, the magnitude of the composite effect was slightly larger (10 msec on average) for MSF faces than for LSF faces ($p < .023$) compared directly. Compared to the large difference in accuracy between the two conditions of interest (13% larger for LSF, $p < .005$), however, this RT difference between MSF and LSF conditions appears marginal. Furthermore, the differences in RTs and accuracy were uncorrelated in MSF conditions ($r = -.191$; $p > .41$), ruling out the contribution of a trade-off to these results.

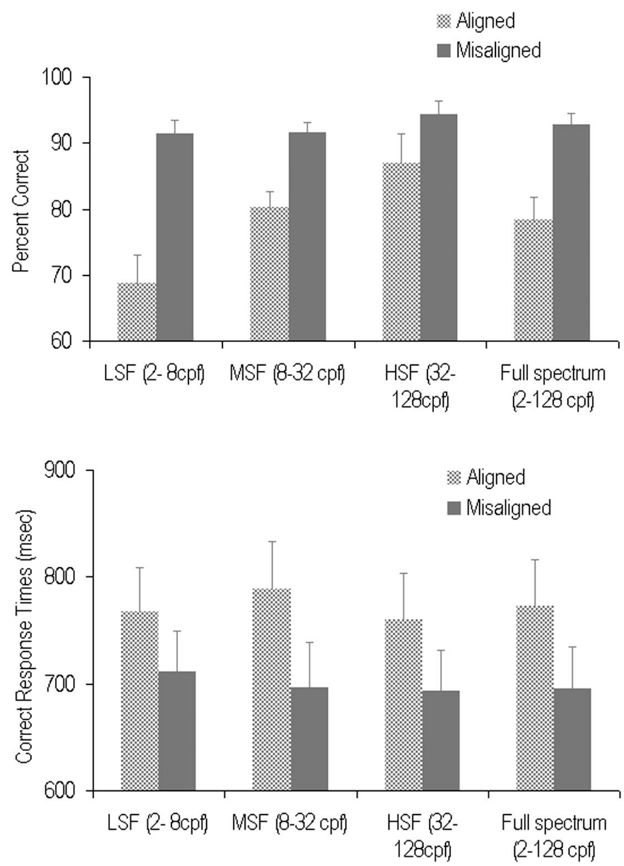

Figure 7. Mean accuracy (hit rate) and correct response times ("same" trials) in Experiment 4 as a function of alignment (aligned vs. misaligned) and spatial frequency (full spectrum, LSF, MSF, and HSF). LSF = low spatial frequency; HSF = high spatial frequency; MSF = middle spatial frequency.

information to attenuate the reliance on holistic cues to perform top part matching. This is exactly what was observed.

An interesting aspect of this experiment was that the stimulus conditions were strictly controlled for SF bandwidth and global luminance. This allows circumscribing the range for holistic face processing in the 2–8 cpf range and further indicates that the disproportionate composite effect in the LSF condition does not stem from the naturally highest energy values contained in this SF range.

Although our experiments do not inform directly about how the different scales interact during full-spectrum stimulation, the results of both Experiments 2 and 4 provide an indication on how subjects used LSF and HSF cues present in full-spectrum stimulation. Larger composite effects occurred when LSFs were isolated, as compared to when LSFs were combined with higher SFs, that is, in full-spectrum faces. This information suggests that subjects relied to a certain extent on fine-grained cues present in full-spectrum conditions to attenuate the holistic interference. The results of Experiments 2 and 4 point to a striking systematicity in the magnitude of composite effect in the full-spectrum condition, which appears to correspond to the average of the effects observed for the distinct SF bands.

General Discussion

In four experiments, we aimed at characterizing the contribution of low-level visual information to holistic face processing. Based on earlier proposals (Sergent, 1986; see also Morrison & Schyns, 2001), we hypothesized that the integration of face cues into a holistic representation mainly operates on information contained in LSFs. We tracked two holistic effects on face processing: first, a facilitation effect, in which a feature is recognized better if it is embedded in its complete face context (whole-part advantage) and second, an interference effect, in which identical top parts of faces are erroneously considered as different if they are perceptually bound with distinct bottom parts (composite effect). We replicated the results of previous studies using these two paradigms, showing that subjects processed the face stimuli holistically. This holistic representation influenced—positively in the whole-part experiment and negatively in the composite experiment—the processing of a given face part.

The whole-part and composite paradigms differ in many aspects (e.g., instructions given and stimulus displays). Nevertheless, filtering the stimuli in the spatial domain modulated holistic face perception in a similar way in the two paradigms (Experiments 1, 2, and 4). Both the whole-part and the composite effects were significantly larger with LSF faces as compared to HSF faces. Small but significant whole-part and composite effects were observed for high-pass filtered stimuli, suggesting that HSF cues can be integrated at least partially into a holistic representation.

These results support the view that holistic processing—as opposed to local, featural processing—is largely supported by coarse information, as provided by LSF (Sergent, 1986). This holistic predominance in LSF conditions is due to the genuine processing of face global structure and not to general masking effects in LSF because it does not resist stimulus inversion (Experiment 3), that is, a manipulation known to disrupt holistic face processes (Tanaka & Farah, 1993; Young, Hellawell, & Hay, 1987). Furthermore, the holistic predominance appears to be circumscribed to LSF since it was not found for intermediate SF ranging from 8 to 32 cpf (Experiment 4).

We conclude that holistic face perception is rooted in coarse visual cues transmitted by early SF filters. This observation has several theoretical and practical consequences for our understanding of normal and pathological face processing.

The Role of Holistic Processing During Face Recognition

In everyday vision, faces and objects are embedded in cluttered environments and appear degraded due to occlusions, illumination variations, cast shadows, eccentricity, and distance. These visual conditions entail that faces and objects initially appear to us with a poor resolution (see Loftus & Harley, 2005). This coarse representation is sufficient to help the detection of faces and objects, however, and to guide ocular foveation for the extraction of finer-grained cues (Lewis & Edmonds, 2003; Oliva & Schyns, 2000; Torralba, 2003). Our finding that holistic face representations can be built from low-resolution face photographs suggests that holistic processing may help detecting and segmenting the face stimulus by linking internal and external facial features together against the background scene.

Beyond segmentation, the ability to perceive faces holistically may be critical for the extraction of an individual 3-D representation, as evidenced by neuropsychological and developmental studies on human face recognition. For instance, Sergent and Villemure (1989) reported a brain-damaged patient suffering from face recognition impairments (“prosopagnosia,” Bodamer, 1947) who, as in other cases of prosopagnosia (e.g., Sergent & Signoret, 1992), presented with difficulties in recognizing faces across viewpoint changes, a task selectively indexing 3-D derivation abilities. We found it interesting that this patient showed a marked impairment at processing face LSF (see also Davidoff, Matthews & Newcombe, 1986) with an inability to process faces holistically (Sergent & Villemure, 1989).

Developmental studies further support the view that the inability to process faces holistically from LSF is related to impairment in deriving face 3-D structure. Due to the poor visual acuity and contrast sensitivity at birth, the input to the visual system in the first months of life is limited to LSF information (Maurer & Lewis, 2001). Infants born with bilateral congenital cataracts are deprived of this early input and present with permanent visual deficits even when the cataracts are surgically removed at 2 months of age. Recent studies have shown that such patients tested in adulthood perform in the normal range for matching facial local features but do not process faces holistically in the composite paradigm (Le Grand, Mondloch, Maurer, & Brent, 2004). This observation suggests that early LSF visual input is essential for the normal development of holistic face processing. The same patients are also strikingly impaired on matching individual faces across different viewpoints, despite normal performance in eye gaze and facial expression processing, as well as lip reading (Geldart, Mondloch, Maurer, de Schonen, & Brent, 2002). Altogether, these data point to a fundamental role of the ability to extract coarse holistic face representations to recover a face 3-D structure. In line with this proposal, psychophysical studies showed that face recognition and/or 3-D extraction is partially based on shading cues (see Liu, Collin, & Chaudhuri, 2000 for a review), which were almost exclusively depicted in the LSF stimuli in our experiments.

Holistic representations of faces appear to proceed from coarse stimulations, in the absence of detailed information about edges, contours, and textures. Thus, they may be a necessary first step during the building of long-term (3-D) individual facial representations, but certainly not a sufficient one. As a matter of fact, some prosopagnosic patients do not present with difficulties at processing LSF, but they are still unable to match faces across viewpoint changes (Barton, Cherkasova, Press, Intriligator, & O’Connor, 2004; Rizzo, Corbett, Thompson, & Damasio, 1986). The fact that information in the intermediate SF, situated between 8 and 16 cpf, is optimal in face long-term recognition tasks (Gold, Bennett, & Sekuler, 1999; Näsänen, 1999) further suggests that a holistic face representation must be refined by higher SF visual cues to form the robust memory trace of an individual face.

Spatial Frequencies for Holistic Face Processing Versus Part-Based Stimulations

In the introduction, we outlined the significance of spatial frequencies in understanding high-level visual processes dedicated to faces. The present results fully support this claim because filtering spatial frequencies proved highly effective in ruling the holistic/analytic balance for face processing. Similarly, for nonface stimuli, it has been shown that when subjects must process hierarchical items (e.g., Navon, 1977; Pomerantz, 1983) at the global scale, they rely on lower SF bands than when they process them at the local scale (Shulman, Sullivan, Gish, & Sakoda, 1986).

Our observations suggest that the SF filtering technique provides a means to reduce, or enhance, holistic processing of faces. To reduce holistic encoding, for instance, one may ask subjects to encode faces by concentrating on specific features, while using HSF face stimuli. Alternatively, asking subjects to encode faces presented only in LSF would favor a robust holistic encoding strategy. Another way to probe holistic or featural processing on the same full-spectrum face stimulus would be to prime this target stimulus with either nonface (e.g., gratings) LSF or HSF primes (see Sanocki, 2001). In general, combining task instructions and available SF bands may allow manipulating holistic and analytic face processes more objectively.

Although SF filtering of full faces is not a panacea, it has the advantage to be a natural dimension of visual perception and to preserve the face structure even at severe cutoff frequencies. More systematic stimulation techniques have been developed to derive face cues relevant for face perception. The general principle of these techniques is to confront observers on each trial with visual information randomly sampled in the stimulus. The stimulus samples leading to optimal performance are monitored trial per trial, and the face cues that are relevant to resolve a given task can be identified. The early demonstration was put forward by Haig (1985), who presented faces to observers through a varied number of randomly positioned apertures (Haig, 1985; for reviews see Shepherd, Davies, & Ellis, 1981; Valentine, 1988). By computing the percentage of correct recognition for each separate aperture, Haig (1985) was able to highlight the facial features that were diagnostic to recognize the faces. This kind of approach has recently been reintroduced using more elaborated computational methods and referred to as “Bubbles” (e.g., Gosselin & Schyns, 2001), or *reverse correlation* (Ahumada, 2002; Sekuler, Gaspar, Gold, & Bennett, 2004). The strengths of these methods is that they allow one to search any specified image space in an entirely unbiased way, thus enabling the participant to locate the face cues that are diagnostic for a given task in the image plane (e.g., Gosselin & Schyns, 2001, Experiment 1; Sekuler, Gaspar, Gold, & Bennett 2004), across SF (e.g., McCotter, Gosselin, Sowden, & Schyns, 2005), across time (e.g., Neri & Heeger, 2002; Vinette, Gosselin, & Schyns, 2004), or across a combination of some of these search spaces (e.g., Gosselin & Schyns, 2001, Experiment 2). The choice of a particular search space can bias participants’ strategies to a certain extent. As already noted by several authors in the mid-1980s (Endo, 1986; Shepherd et al., 1981; Valentine, 1988), for example, searching only the image plane (e.g., through apertures in Endo, 1986; Haig, 1985; Schyns, Bonnar, & Gosselin, 2002; or through noise-free areas such as in Sekuler, Gaspar, Gold, & Bennett, 2004) can restrict the processing of a face to its local cues. Given that subjects are largely prevented from using holistic processes during perception, it is not surprising that part-based stimulation methods disrupt core face-processing abilities such as face recognition (Endo, 1982, 1986; Inui & Miyamoto, 1984; Saida & Ikeda, 1979) or the disproportionate inversion effect for faces (Endo, 1986; Sekuler, Gaspar, Gold, & Bennett, 2004).

Holistic Processing and Metric Distances Between Features

In the introduction section, we mentioned that the notion of holistic processing is conceptually dissociated in the literature from the metric distances between facial features or second-order relations, such as the interocular distance, or the nose-mouth distance, for instance. Both holistic processing and the ability to extract metric distances between features are considered as forming the face configuration (Maurer, Le Grand, & Mondloch, 2002). In this article, we showed that holistic processing as measured in the composite face and whole-part paradigms largely depends on LSF.

Although the ability to extract metric distances and holistic processing can be separated based on their sensitivity to experimental manipulations and their development pattern (Maurer, Le Grand, & Mondloch, 2002), holistic processing of faces observed in the whole part and composite face paradigms may also be related to the perception of metric distances between features (e.g., eyes/mouth distance). The issue of whether processing metric distances between features also depends on LSF was addressed in a previous experiment (Goffaux, Hault, Michel, Vuong, & Rossion, 2005). In that study, we showed that the processing of metric distances in a face (interocular distance and eye height) was favored in LSF as compared to the processing of featural information. The opposite was true for HSF (advantage of featural processing over relational processing). The mapping between LSF/HSF and featural/relational was much less robust than in the present experiments, however, and we limited our manipulations to local distances between features. The much stronger results observed here suggest that LSFs are mostly recruited for processing holistic cues, that is, in a larger extent than for the processing of local metric distances between features, although this issue should be investigated in further studies.

Neural Correlates of SF and Holistic Processing

The primary interest of our findings is in supporting the view that the early SF filtering of visual information forms a basis for higher-level operations, such as the holistic processing of an individual face. The relationship between the neural systems underlying early SF filtering and high-level holistic processing of faces is also suggested by neural evidence. The mammal (e.g., cat, monkey, and human) visual system decomposes retinal stimulation in terms of spatial frequencies. Different SF ranges are processed by different cells in the retina, lateral geniculate nuclei, and primary visual cortices (Enroth-Cugell & Robson, 1966; Hubel & Wiesel, 1977; Issa, Trepel, & Stryker, 2000; Tootell, Silverman, Hamilton, Switkes, & De Valois, 1988; for a review see De Valois & De Valois, 1988). They project onto dissociable neural streams: LSF information is relayed through the magnocellular pathway, while HSF information is relayed through both the magno- and parvocellular pathways. In light of the present findings, it is particularly interesting that these low-level visual distinctions are preserved, at least to a certain extent, in high-level visual areas involved in face processing. Pollen, Nagler, Daugman, Kronauer, and Cavanagh (1984) showed that a proportion of face-selective cells (e.g., Desimone, Albright, Gross, & Bruce, 1984; Gross & Sergent, 1992; Perrett, Rolls, & Caan, 1982) in the monkey inferotemporal (IT) cortex were preferentially sensitive to one SF band over the entire extent of their receptive field and that input from many striate cells sensitive to a common SF band fed into a single IT neuron. More recently, face-sensitive extrastriate regions in the human visual cortex have been shown to be differentially sensitive to the LSF versus HSF component of face pictures, even though the results of these neuroimaging studies are somewhat difficult to reconcile with each other (Eger, Schyns, & Kleinschmidt, 2004; Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Vuilleumier, Armony, Driver, & Dolan, 2003).

As for the neural underpinnings of holistic face processing, several sources of evidence also point to high-level visual areas in the ventral stream, supporting the perceptual locus of these processes. For example, a large proportion of face-selective cells in the IT respond to the whole face stimulus, but they do not discharge if parts of the face are removed (Tanaka, 1996; Wang, Tanaka, & Tanifuji, 1996) or if all face parts are present but scrambled (Desimone, Albright, Gross, & Bruce, 1984). In humans, neuroimaging studies indicate a predominant role of the anterior part of the lateral fusiform gyrus (BA37) over posterior face-sensitive areas in processing faces as a whole, with a right hemispheric advantage (Rossion, de Gelder, et al., 2000). Finally, the N170, an early event-related potential maximally recorded at occipitotemporal scalp electrodes in response to faces, is sensitive to the holistic/analytic dichotomy, being delayed when face parts are removed or when faces are presented upside down (e.g., Bentin, Allison, Puce, Perez & McCarthy, 1996; Rossion, Gauthier, et al., 2000). We found it interesting that filtering out face LSF abolishes the N170 delay caused by face inversion (Goffaux, Gauthier, & Rossion, 2003).

In sum, both functional and neural evidence point to LSF as supporting the extraction of holistic facial representations, in line with the direct behavioral evidence reported in this article.

Clues to the Microgenesis of Face Perception

Because the neurofunctional streams sensitive to LSF and HSF have dissociable time scales (Enroth-Cugell & Robson, 1966; Marrocco, 1976; Maunsell et al., 1999; Nowak, Munk, Girard, & Bullier, 1995; Schmolesky et al., 1998; for a review, see Bullier, 2001), our findings may help explain how holistic and analytic cues integrate over time to develop a face representation. Neurons in the primary visual cortex have recently been found to dedicate their first transient responses to the processing of large-scale visual information (i.e., LSF sinusoidal gratings) and to later shift their tuning curve to finer information (i.e., HSF sinusoidal gratings; Bredfeldt & Ringach, 2002). In humans, the latency of visual-evoked potentials is known to increase with SF gratings (Mihaylova, Stomonyakov & Vassilev, 1999; Musselwhite & Jeffreys, 1985). These early temporal differences are reflected in human behavioral performance. Psychophysical evidence indicates that LSF gratings are resolved faster than their HSF analogs (Gish, Shulman, Sheehy, & Leibowitz, 1986; Parker & Dutch, 1987). The question of how such early temporal dynamics of information integration affect the recognition of complex visual stimuli is still a matter of debate (see Loftus & Harley, 2004; Morrison & Schyns, 2001). It has been argued that the identification of natural scenes presented centrally may proceed flexibly from LSF to HSF or from HSF to LSF (Oliva & Schyns, 1997; Parker, Lishman, &

Hughes, 1992; Schyns & Oliva, 1994; see Peyrin, Chauvin, Chokron, & Marendaz, 2003, for differential precedence effects when scenes are presented laterally). In contrast, object identification is found to proceed from large-scale to fine-scale cues (defined by size; Sanocki, 2001; or by SF: Loftus & Harley, 2004). As for faces, it has been argued that spatial scales can be used flexibly (i.e., depending on the task) rather than following a coarse-to-fine scheme (Schyns & Oliva, 1999), but these results may simply indicate that HSF can be dominant for certain tasks requiring a detailed analysis of the stimulus, not that these scales are processed faster than LSF during such tasks. Other studies suggest that LSF are processed faster than HSF (Coin, Versace & Tiberghien, 1992; Parker, Lishman, & Hughes, 1997).

Taken together, the well-documented temporal precedence of LSF processing over HSF processing and the present observations that holistic perception of faces is predominantly supported by LSF, suggest that the holistic integration of face information may be an early stage in face processing. Such initial LSF-derived holistic representation may be based on the earliest visual inputs to high-level face-selective areas. In the monkey IT cortex, face-selective cells start discharging at about 100–120 ms (Bullier, 2001; Oram & Perrett, 1992). In humans, scalp event-related potentials showing a selective response to faces start at about 130 ms (e.g., Jeffreys, 1989; Rossion, Gauthier, et al., 2000; Rousselet, Mace, & Fabre-Thorpe, 2004). Evidence from single-cell recordings in IT and information analyses suggest that these initial responses to faces are based on a coarse input and that high-resolution representations necessary for making fine discriminations are built in the same neuronal populations, at a longer time scale (Sugase, Yamane, Ueno, & Kawano, 1999). In normal viewing conditions, an early holistic representation, inherently coarse, may serve as a header to refine the percept progressively, perhaps through feedback to lower-level cortical visual processes and may accumulate converging evidence for categorization decisions.

Based on the present findings, we speculate that holistic processing of a face may be a first step in the generation of a robust individual face representation, preceding the extraction of detailed features (i.e., the whole before the parts). Yet, with behavioral methods alone and relatively late RTs (about 800 ms in all our experiments), one cannot completely rule out that holistic processing effects also take place at later stages of processing (see Wenger & Ingvalson, 2002). Testing the hypothesis of the temporal precedence of holistic face processing further will most likely require high temporal resolution methods such as event-related potential recordings during the presentation of spatially filtered stimuli.

Conclusions

In two classical face paradigms measuring the whole-part and composite effects, we monitored the holistic interference on the perception of face parts with spatially filtered stimuli. Our findings of larger interference effects with LSF face stimuli demonstrate that holistic processes mostly operate on coarse facial cues, selectively delivered by LSF. High-level visual face processing is constrained by the operation of low-level SF filters. These findings open new perspectives on the microgenesis of face perception, that is, how the various sources of face information dynamically integrate over processing time to form face percepts, suggesting that the initial representation of a face is inherently coarse and holistic.

References

Ahumada, A. J., Jr. (2002). Classification image weights and internal noise level estimation. *Journal of Vision, 2,* 121–131.

Bar, M. (2004). Visual objects in context. *Nature Reviews Neuroscience, 5,* 617–629.

Barton, J. J., Cherkasova, M. V., Press, D. Z., Intriligator, J. M., & O'Connor, M. (2004). Perceptual functions in prosopagnosia. *Perception, 33,* 939–956.

Bentin, S., Allison, A., Puce, A., Perez, T., & McCarthy, G. (1996). Electro-physiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8,* 551–565.

Biederman, I., & Kalocsai, P. (1997). Neurocomputational bases of object and face recognition. *Philosophical Transactions of the Royal Society of London, 29,* 1203–1219.

Bodamer, J. B. (1947). Die prosop-agnosie. (Die Agnosie des Physiognomieerkennens). *Archhiv für Psychiatrie und Zeitschrift für Nervenkrankheiten, 179,* 6–54.

Boutet, I., Collin, C., & Faubert, J. (2003). Configural face encoding and spatial frequency information. *Perception & Psychophysics, 65,* 1078–1093.

Bredfeldt, C. E., & Ringach, D. L. (2002). Dynamics of spatial frequency tuning in macaque V1. *Journal of Neuroscience, 22,* 1976–1984.

Bullier, J. (2001). Integrated model of visual processing. *Brain Research Brain Research Reviews, 36,* 96–107.

Carey, S., & Diamond, R. (1994). Are faces perceived as configurations more by adults than by children? *Visual Cognition, 1,* 253–274.

Coin, C., Versace, R., & Tiberghien, G. (1992). Role of spatial frequencies and exposure duration in face processing: Potential consequences on the memory format of facial representations. *European Bulletin of Cognitive Psychology, 12,* 79–98.

Collin, C. A., Liu, C. H., Troje, N. F., McMullen, P. A., & Chaudhuri, A. (2004). Face recognition is affected by similarity in spatial frequency range to a greater degree than within-category object recognition. *Journal of Experimental Psychology Human Perception and Performance, 30,* 975–987.

Collishaw, S. M., & Hole, G. J. (2000). Featural and configurational processes in the recognition of faces of different familiarity. *Perception, 29,* 893–909.

Costen, N. P., Parker, D. M., & Craw, I. (1994). Spatial content and spatial quantisation effects in face recognition. *Perception, 23,* 129–146.

Costen, N. P., Parker, D. M., & Craw, I. (1996). Effects of high-pass and low-pass spatial filtering on face identification. *Perception & Psychophysics, 58,* 602–612.

Davidoff, J., & Donnelly, N. (1990). Object superiority: A comparison of complete and part probes. *Acta Psychologica, 73,* 225–243.

Davidoff, J., Matthews, B., & Newcombe, F. (1986). Observations on a case of prosopagnosia. In H. Ellis, M. Jeeves, F. Newcombe, & A. Young (Eds.), *Aspects of face processing* (pp. 279–290). Dordrecht: Martinus Nijhoff.

Desimone, R., Albright, T. D., Gross, C. G., & Bruce, C. (1984). Stimulus-selective properties of inferior temporal neurons in the macaque. *Journal of Neuroscience, 4,* 2051–2062.

De Valois, R. L., & De Valois, K. K. (1988). *Spatial vision.* New York: Oxford University Press.

Eger, E., Schyns, P. G., & Kleinschmidt, A. (2004). Scale invariant adaptation in fusiform face-responsive regions. *NeuroImage, 22,* 232–242.

Endo, M. (1982). Cue saliency in upside-down faces. *Tohoku Psychologica Folia, 41,* 116–122.

Endo, M. (1986). Perception of upside-down faces: An analysis from the viewpoint of cue saliency. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. Young (Eds.), *Aspects of face processing* (pp. 53–58). Dordrecht: Martinus Nijhoff.

Endo, M., Masame, K., & Maruyama, K. (1989). Interference from configuration of a schematic face onto the recognition of its constituent parts. *Tohoku Psychologica Folia, 48,* 97–106.

Enroth-Cugell, C., & Robson, J. D. (1966). The contrast sensitivity of retinal ganglion cells of the cat. *Journal of Physiology, 187,* 517–522.

Farah, M. J., Wilson, K. D., Drain, M., & Tanaka, J. N. (1998). What is "special" about face perception? *Psychological Review, 105,* 482–498.

Fiorentini, A., Maffei, L., & Sandini, G. (1983). The role of high spatial frequencies in face perception. *Perception, 12,* 195–201.

Flavell, J. H., & Draguns, J. (1957). A microgenetic approach to perception and thought. *Psychological Bulletin, 54,* 197–217.

Galton, F. (1883). *Inquiries into human faculty and its development.* London: Macmillan.

Geldart, S., Mondloch, C., Maurer, D., de Schonen, S., & Brent, H. (2002). The effects of early visual deprivation on the development of face processing. *Developmental Science, 5,* 490–501.

Ginsburg, A. P. (1978). *Visual information processing based on spatial filters constrained by biological data.* Unpublished doctoral dissertation, Cambridge University, Cambridge, England.

Ginsburg, A. P. (1986). Spatial filtering and visual form perception. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), *Handbook of perception and human performance* (Vol. 2, pp. 34-1–34-44). New York: Wiley.

Gish, K., Shulman, G. L., Sheehy, J. B., & Leibowitz, H. W. (1986). Reaction times to different spatial frequencies as a function of detectability. *Vision Research, 26,* 745–747.

Goffaux, V., Gauthier, I., & Rossion, B. (2003). Spatial scale contribution to early visual differences between face and object processing. *Cognitive Brain Research, 16,* 416–424.

Goffaux, V., Hault, B., Michel, C., Vuong, Q. C., & Rossion, B. (2005). The respective role of low and high spatial frequencies in supporting configural and featural processing of faces. *Perception, 34,* 77–86.

Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Identification of band-pass filtered letters and faces by human and ideal observers. *Vision Research, 39,* 3537–3560.

Gosselin, F., & Schyns, P. G. (2001). Bubbles: A technique to reveal the use of information in recognition tasks. *Vision Research, 41,* 2261–2271.

Gross, C. G., & Sergent, J. (1992). Face recognition. *Current Opinion in Neurobiology, 2,* 156–161.

Haig, N. D. (1985). How faces differ—A new comparative technique. *Perception, 14,* 601–615.

Hayes, A., Morrone, M. C., & Burr, D. C. (1986). Recognition of positive and negative band-pass filtered images. *Perception, 15,* 595–602.

Hochstein, S., & Ahissar, M. (2002). View from the top: Hierarchies and reverse hierarchies in the visual system. *Neuron, 36,* 791–804.

Hole, G. J. (1994). Configural factors in the perception of unfamiliar faces. *Perception, 23,* 65–74.

Hole, G. J., George, P. A., & Dunsmore, V. (1999). Evidence for holistic processing of faces viewed as photographic negatives. *Perception, 28,* 341–359.

Homa, D., Haver, B., & Schwartz, T. (1976). Perceptibility of schematic face stimuli: Evidence for a perceptual Gestalt. *Memory & Cognition, 4,* 176–185.

Hubel, D. H., & Wiesel, T. N. (1977). Ferrier lecture: Functional architecture of macaque monkey visual cortex. *Proceedings of the Royal Society of London, 198,* 1–59.

Hugues, H. C., Nozawa, G., & Ketterle, F. (1996). Global precedence, spatial frequency channels and the statistics of natural images. *Journal of Cognitive Neuroscience, 8,* 197–230.

Iidaka, T., Yamashita, K., Kashikura, K., & Yonekura, Y. (2004). Spatial frequency of visual image modulates neural responses in the temporo-occipital lobe: An investigation with event-related fMRI. *Cognitive Brain Research, 18,* 196–204.

Inui, T., & Miyamoto, K. (1984). The effect of changes in visible area on facial recognition. *Perception, 13,* 49–56.

Issa, N. P., Trepel, C., & Stryker, M. P. (2000). Spatial frequency maps in cat visual cortex. *Journal of Neuroscience, 20,* 8504–8514.

Jeffreys, D. A. (1989). A face-responsive potential recorded from the human scalp. *Experimental Brain Research, 78,* 193–202.

Kornowski, J. A., & Petersik, J. T. (2003). Effects on face recognition of spatial-frequency information contained in inspection and test stimuli. *Journal of General Psychology, 130,* 229–244.

Leder, H., & Carbon, C. C. (2005). When context hinders: Learn-test-compatibility in face recognition. *Quarterly Journal of Experimental Psychology, 58,* 235–250.

Le Grand, R., Mondloch, C. J., Maurer, D., & Brent, H. P. (2004). Impairment in holistic face processing following early visual deprivation. *Psychological Science, 15,* 762–768.

Lewis, M. B., & Edmonds, A. J. (2003). Face detection: Mapping human performance. *Perception, 32,* 903–920.

Liu, C. H., Collin, C. A., & Chaudhuri, A. (2000). Does face recognition rely on encoding of 3-D surface? Examining the role of shape-from-shading and shape-from-stereo. *Perception, 29,* 729–743.

Liu, C. H., Collin, C. A., Rainville, S. J., & Chaudhuri, A. (2000). The effects of spatial frequency overlap on face recognition. *Journal of Experimental Psychology Human Perception and Performance, 26,* 956–979.

Loftus, G. R., & Harley, E. M. (2004). How different spatial-frequency components contribute to visual information acquisition. *Journal of Experimental Psychology Human Perception and Performance, 30,* 104–118.

Loftus, G. R., & Harley, E. M. (2005). Why is it easier to identify someone closer than far away? *Psychonomic Bulletin & Review, 12*, 43–65.

Marr, D. (1982). *Vision: A computational investigation into the human representation and processing of visual information.* San Francisco: Freeman.

Marrocco, R. T. (1976). Sustained and transient cells in monkey lateral geniculate nucleus: Conduction velocites and response properties. *Journal of Neurophysiology, 39,* 340–353.

Maunsell, J. H., Ghose, G. M., Assad, J. A., McAdams, C. J., Boudreau, C. E., & Noerager, B. D. (1999). Visual response latencies of magnocellular and parvocellular LGN neurons in macaque monkeys. *Visual Neuroscience, 16,* 1–14.

Maurer, D., Le Grand, R., & Mondloch, C. J. (2002). The many faces of configural processing. *Trends in Cognitive Sciences, 6,* 255–260.

Maurer, D., & Lewis, T. L. (2001). Visual acuity: The role of visual input in inducing postnatal change. *Clinical Neuroscience Research,* 239–247.

McCotter, M., Gosselin, F., Sowden, P., & Schyns, P. G. (2005). The use of visual information in natural scenes categorization. *Visual Cognition, 12,* 938–953.

Michel, C., Rossion, B., Han, J., Chung, C.-S., Caldara, R. (2006). (in press). Holistic processing is finely tuned for faces of our own race. *Psychological Science*

Mihaylova, M., Stomonyakov, V., & Vassilev, A. (1999). Peripheral and central delay in processing high spatial frequencies: Reaction time and VEP latency studies. *Vision Research, 39,* 699–705.

Mondloch, C. J., Geldart, S., Maurer, D., & Le Grand, R. (2003). Developmental changes in face processing skills. *Journal of Experimental Child Psychology, 86,* 67–84.

Morrison, D. J., & Schyns, P. G. (2001). Usage of spatial scales for the categorization of faces, objects, and scenes. *Psychonomic Bulletin & Review, 8,* 454–469.

Moscovitch, M., & Moscovitch, D. A. (2000). Super face-inversion effects for isolated internal or external features and for fractured faces. *Cognitive Neuropsychology, 18,* 201–220.

Murray, J. E. (2004). The ups and downs of face perception: Evidence for holistic encoding of upright and inverted faces. *Perception, 33,* 387–398.

Musselwhite, M. J., & Jeffreys, D. A. (1985). The influence of spatial frequency on the reaction times and evoked potentials recorded to grating pattern stimuli. *Vision Research, 25,* 1545–1555.

Näsänen, R. (1999). Spatial frequency bandwidth used in the recognition of facial images. *Vision Research, 39,* 3824–3833.

Navon, D. (1977). Forest before trees: The precedence of global features in visual perception. *Cognitive Psychology, 9,* 353–383.

Neri, P., & Heeger, D. J. (2002). Spatiotemporal mechanisms for detecting and identifying image features in human vision. *Nature Neuroscience, 5,* 812–816.

Nowak, L. G., Munk, M. H., Girard, P., & Bullier, J. (1995). Visual latencies in areas V1 and V2 of the macaque monkey. *Visual Neuroscience, 12,* 371–384.

Oliva, A., & Schyns, P. G. (1997). Coarse blobs or fine edges? Evidence that information diagnosticity changes the perception of complex visual stimuli. *Cognitive Psychology, 34,* 72–107.

Oliva, A., & Schyns, P. G. (2000). Diagnostic colors mediate scene recognition. *Cognitive Psychology, 41,* 176–210.

Oram, M. W., & Perrett, D. I. (1992). Time course of neural responses discriminating different views of the face and head. *Journal of Neurophysiology, 68,* 70–84.

Parker, D. M., & Costen, N. P. (1999). One extreme or the other or perhaps the golden mean? Issues of spatial resolution in face processing. *Current Psychology: Developmental, Learning, Personality, 18,* 118–127.

Parker, D. M., & Dutch, S. (1987). Perceptual latency and spatial frequency. *Vision Research, 27,* 1279–1283.

Parker, D. M., Lishman, J. R., & Hughes, J. (1992). Temporal integration of spatially filtered visual images. *Perception, 21,* 147–160.

Parker, D. M., Lishman, J. R., & Hughes, J. (1997). Evidence for the view that temporospatial integration in vision is temporally anisotropic. *Perception, 26,* 1169–1180.

Pellicano, E., & Rhodes, G. (2003). Holistic processing of faces in preschool children and adults. *Psychological Science, 14,* 618–622.

Perrett, D. I., Rolls, E. T., & Caan, W. (1982). Visual neurones responsive to faces in the monkey temporal cortex. *Experimental Brain Research, 47,* 329–342.

Peyrin, C., Chauvin, A., Chokron, S., & Marendaz, C. (2003). Hemispheric specialization for spatial frequency processing in the analysis of natural scenes. *Brain & Cognition, 53,* 278–282.

Pollen, D. A., Nagler, M., Daugman, J., Kronauer, R., & Cavanagh, P. (1984). Use of Gabor elementary functions to probe receptive field substructure of posterior inferotemporal neurons in the owl monkey. *Vision Research, 24,* 233–241.

Pomerantz, J. R. (1983). Global and local precedence: Selective attention in form and motion perception. *Journal of Experimental Psychology General, 112,* 516–540.

Rizzo, M., Corbett, J. J., Thompson, H. S., & Damasio, A. R. (1986). Spatial contrast sensitivity in facial recognition. *Neurology, 36,* 1254–1256.

Rossion, B., de Gelder, B., Dricot, L., Zoontjes, R., De Volder, A., Bodart, J.-M., & Crommelinck, M. (2000). Hemispheric asymmetries for whole-based and part-based face processing in the human fusiform gyrus. *Journal of Cognitive Neuroscience, 12,* 793–802.

Rossion, B., & Gauthier, I. (2002). How does the brain process upright and inverted faces? *Behavioral and Cognitive Neuroscience Reviews, 1,* 63–75.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., & Crommelinck, M. (2000). The N170 occipito-temporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in the human brain. *Neuroreport, 11,* 69–74.

Rousselet, G. A., Mace, M. J., & Fabre-Thorpe, M. (2004). Spatiotemporal analyses of the N170 for human faces, animal faces and objects in natural scenes. *Neuroreport, 15,* 2607–2611.

Saida, S., & Ikeda, M. (1979). Useful visual field size for pattern perception. *Perception & Psychophysics, 25,* 119–125.

Sanocki, T. (2001). Interaction of scale and time during object identification. *Journal of Experimental Psychology Human Perception and Performance, 27,* 290–302.

Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, et al. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology, 79,* 3272–3278.

Schyns, P. G., Bonnar, L., & Gosselin, F. (2002). Show me the features! Understanding recognition from the use of visual information. *Psychological Science, 13,* 402–409.

Schyns, P. G., & Oliva, A. (1994). From blobs to boundary edges: Evidence for time and spatial scale dependent scene recognition. *Psychological Science, 5,* 195–200.

Schyns, P. G., & Oliva, A. (1999). Dr. Angry and Mr. Smile: When categorization flexibly modifies the perception of faces in rapid visual presentations. *Cognition, 69,* 243–265.

Sekuler, A. B., Gaspar, C. M., Gold, J. M., & Bennett, P. J. (2004). Inversion leads to quantitative, not qualitative, changes in face processing. *Current Biology, 14,* 391–396.

Sergent, J. (1984). An investigation into component and configural processes underlying face perception. *British Journal of Psychology, 75,* 221–242.

Sergent, J. (1986). Microgenesis of face perception. In H. D. Ellis, M. A. Jeeves, F. Newcombe, & A. M. Young (Eds.), *Aspects of face processing* (pp. 17–33). Dordrecht: Martinus Nijhoff.

Sergent, J., & Hellige, J. B. (1986). Role of input factors in visual-field asymmetries. *Brain & Cognition, 5,* 174–199.

Sergent, J., & Signoret, J. L. (1992). Varieties of functional deficits in prosopagnosia. *Cerebral Cortex, 2,* 375–388.

Sergent, J., & Villemure, J. G. (1989). Prosopagnosia in a right hemispherectomized patient. *Brain, 112,* 975–995.

Shepherd, J., Davies, G., & Ellis. H. (1981). Studies of cue saliency. In G. Davies, H. Ellis, & J. Shepherd (Eds.), *Perceiving and remembering faces* (105–131). New York: Academic Press.

Shulman, G. L., Sullivan, M. A., Gish, K., & Sakoda, W. J. (1986). The role of spatial-frequency channels in the perception of local and global structure. *Perception, 15,* 259–273.

Sugase, Y., Yamane, S., Ueno, S., & Kawano, K. (1999). Global and fine information coded by single neurons in the temporal visual cortex. *Nature, 400,* 869–873.

Tanaka, J. W., & Farah, M. J. (1993). Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology, 46,* 225–245.

Tanaka, J. W., Kay, J. B., Grinnell, E., Stansfield, B., & Szechter, L. (1998). Face recognition in young children: When the whole is greater than the sum of its parts. *Visual Cognition, 5,* 479–496.

Tanaka, J. W., Kiefer, M., & Bukach, C. M. (2004). A holistic account of the own-race effect in face recognition: Evidence from a cross-cultural study. *Cognition, 93,* B1–9.

Tanaka, J. W., & Sengco, J. A. (1997). Features and their configuration in face recognition. *Memory & Cognition, 25,* 583–592.

Tanaka, K. (1996). Inferotemporal cortex and object vision. *Annual Review of Neuroscience, 19,* 109–139.

Tieger, T., & Ganz, L. (1979). Recognition of faces in the presence of two-dimensional sinusoidal masks. *Perception & Psychophysics, 26,* 163–167.

Tootell, R. B., Silverman, M. S., Hamilton, S. L., Switkes, E., & De Valois, R. L. (1988). Functional anatomy of macaque striate cortex. V. Spatial frequency. *Journal of Neuroscience, 8,* 1610–1624.

Torralba, A. (2003). Contextual priming for object detection. *International Journal of Computer Vision, 53,* 169–191.

Valentine, T. (1988). Upside down faces: A review of the effect of inversion upon face recognition. *British Journal of Psychology, 79,* 471–491.

Vinette, C., Gosselin, F., & Schyns, P. G. (2004). Spatio-temporal dynamics of face recognition in a flash: It's in the eyes! *Cognitive Science, 28,* 289–301.

Vuilleumier, P., Armony, J. L., Driver, J., & Dolan, R. J. (2003). Distinct spatial frequency sensitivities for processing faces and emotional expressions. *Nature Neuroscience, 6,* 624–631.

Wang, G., Tanaka, K., & Tanifuji, M. (1996). Optical imaging of functional organization in the monkey inferotemporal cortex. *Science, 272,* 1665–1668.

Watt, R. J. (1987). Scanning from coarse to fine sptial scales in the human visual system after the onset of a stimulus. *Journal of the Optical Society of America, 4,* 2006–2021.

Wenger, M. J., & Ingvalson, E. M. (2002). A decisional component of holistic encoding. *Journal of Experimental Psychology Learning, Memory, and Cognition, 28,* 872–892.

Wenger, M. J., & Townsend, J. T. (2000). Spatial frequencies in short-term memory for faces: A test of three frequency-dependent hypotheses. *Memory & Cognition, 28,* 125–142.

Young, A. W., Hellawell, D., & Hay, D. C. (1987). Configurational information in face perception. *Perception, 16,* 747–759.

Received January 26, 2005
Revision received January 18, 2006
Accepted January 22, 2006 ■