Research Article

Psychological Science
21(1) 58–66

DOI: 10.1177/0956797609354064
http://pss.sagepub.com

How Spatial Frequencies and Visual Awareness Interact During Face Processing

Vincent de Gardelle and Sid Kouider
Laboratoire des Sciences Cognitives et Psycholinguistique, CNRS/EHESS/DEC-ENS, Paris, France

Abstract

In vision, high and low spatial frequencies have been dissociated at the cognitive and neural levels. Usually, high spatial frequency (HSF) is associated with slow analysis along the ventral cortical stream, and low spatial frequency (LSF) is associated with fast and automatic processing. These findings suggest a specific relation between spatial-frequency processing and visual awareness. We investigated this issue using masked-face priming with hybrid prime images of variable visibility. We found subliminal priming for both LSF and HSF information, along with a strong interaction between spatial frequency and visibility: HSF-related priming increased with stimulus visibility, whereas LSF influences remained unchanged. We argue that the results limit the validity of the coarse-to-fine model of vision and of models equating ventral-stream activity with perceptual awareness. Interpreting our results in light of the diagnostic approach suggests a close relation between awareness and diagnosticity.

Keywords

face processing, spatial frequencies, priming, ventral stream, unconscious perception, implicit memory

Received 1/21/09; Revision accepted 3/25/09

The limits of unconscious cognition and, more generally, the relation between perceptual processes and awareness are deep and fascinating issues. In the visual domain, high and low spatial frequencies have been well dissociated. In the case of a face image, for instance, low-spatial-frequency (LSF) information corresponds to the global shape, whereas high-spatial-frequency (HSF) information represents mainly inner details. These two types of information have been associated with separate neural pathways (Livingstone & Hubel, 1988) and distinct functional roles (e.g., Bar et al., 2006; Hughes, Nozawa, & Kitterle, 1996; Vuilleumier, Armony, Driver, & Dolan, 2003); additional evidence suggests a close relation between spatial-frequency processing and whether the stimulus is perceived consciously or unconsciously. Yet no study to date has demonstrated an interaction between spatial frequency and awareness. We addressed this issue by studying the influences of HSF and LSF information as a function of participants' awareness of this information.

Two types of evidence suggest that HSF information and LSF information are differentially related to visual awareness: One is related to the temporal dynamics of spatial-frequency processing, whereas the other concerns the cortical structures associated with HSF and LSF information.

First, regarding temporal considerations, behavioral studies have provided support for a coarse-to-fine model of vision in which a fast, global, and rough analysis based on LSF information leads to the categorization of a visual stimulus and the details of the image conveyed by HSF information are extracted only later. Thus, the "natural" temporal order of visual processing appears to proceed from LSF to HSF information (Parker, Lishman, & Hughes, 1992, 1996; Schyns & Oliva, 1994). Early physiological investigations of the visual system also support the temporal precedence of LSF over HSF information. In particular, researchers have described two parallel anatomical pathways that convey HSF and LSF information separately from the retina to the primary visual cortex (Livingstone & Hubel, 1988). The relatively rapid magnocellular pathway, which comprises large (*magno*) cells that exhibit fast responses over large receptive fields, preferentially conveys LSF information. The slower parvocellular pathway, which comprises smaller cells with slower responses over small receptive fields, carries HSF information. As most theories of consciousness contend that subliminal processing precedes conscious processing (e.g., Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Lamme, 2003), the facts that LSF information is processed quickly and that HSF information is associated with a slow analysis that dominates the

Corresponding Author:
Vincent de Gardelle, Ecole Normale Supérieure, 29 rue d'Ulm, 75005 Paris, France
E-mail: gardelle@ens.fr

conscious percept strongly suggest that LSF and HSF processing may be dissociated along the subliminal/conscious dichotomy.

Second, HSF information and LSF information are associated with distinct cortical regions, some of which have been specifically linked to visual awareness. In particular, HSF information is specifically associated with occipito-temporal regions. Indeed, the segregation of information along the subcortical parvocellular and magnocellular pathways has been shown to continue beyond V1 toward ventral (i.e., occipito-temporal) and dorsal (i.e., occipito-parietal) pathways of the visual cortex (Livingstone & Hubbel, 1988; Merigan & Maunsell, 1993). More precisely, the dorsal stream preferentially processes magnocellular inputs (thus, LSF information), whereas the ventral stream receives both parvocellular and magnocellular inputs (thus, both HSF and LSF information; Ferrera, Nealey, & Maunsell, 1994; Merigan & Maunsell, 1993). Evidence that HSF information is processed solely in the ventral stream has been provided by several functional magnetic resonance imaging studies showing that processing of HSF information from faces specifically involves several ventral areas, such as the inferior occipital and temporal gyri (Eger, Schyns, & Kleinschmidt, 2004; Rotshtein, Vuilleumier, Winston, Driver, & Dolan, 2007) and the fusiform gyrus (Iidaka, Yamashita, Kashikura, & Yonekura, 2004; Vuilleumier et al., 2003).

The dissociation between ventral and dorsal visual pathways has also been described in terms of "vision for perception" versus "vision for action" in the influential duplex vision theory put forward by Milner and Goodale (1995). The duplex vision theory suggests that ventral-stream activity is slower and sustained because it involves a recognition process in which the visual stimulus is compared with perceptual attributes stored in memory; in contrast, the dorsal stream triggers rapid actions through a fast and automatic process that does not necessitate storage of visuomotor attributes. Going one step further, the theory postulates that the dorsal and ventral visual pathways might be specifically linked to unconscious processing and conscious perception, respectively (Milner & Goodale, 1995; see Kouider, in press, for a review).

In sum, several lines of evidence converge in suggesting that coarse LSF information can be extracted without awareness, whereas HSF information requires a precise, slow, and conscious analysis in the ventral stream, and may not be available unconsciously. However, the diagnostic approach (Oliva & Schyns, 1997; Schyns, 1998; Schyns & Oliva, 1999; Sowden & Schyns, 2006) suggests that the extraction of spatial frequencies might not be as rigid as proposed by coarse-to-fine models. That is, when task requirements favor reliance on a specific frequency range, this "diagnostic" information may be amplified early on. Thus, the diagnostic approach allows for the possibility that HSF information might be extracted during the early and unconscious stages of processing under some task-specific conditions favoring HSF processing. For example, in face identification, which is driven by HSF information (e.g., Costen, Parker, & Craw, 1996; Fiorentini, Maffei, & Sandini, 1983; Liu, Collin, Rainville, & Chaudhuri, 2000), one might expect this diagnostic HSF information to be available unconsciously.

In the present study, we investigated this issue by combining the masked-face priming paradigm (Kouider, Eger, Dolan, & Henson, 2009) with the hybrid-image manipulation introduced by Schyns and Oliva (1994). Participants performed a fame judgment task (which implied identification of faces on the basis of primarily HSF information) on normal target faces preceded by primes that were hybrid faces (i.e., mixtures of LSF information from one face and HSF information from another face). Stimulus awareness was manipulated by gradually increasing the prime duration (from 43 ms to 300 ms), thereby increasing visibility (i.e., from subliminal to fully visible presentations). This method allowed us to assess the influence of LSF, HSF, or full-band information as a function of awareness (see Fig. 1).

Method

Participants

The participants were 110 college students (age range = 18–35 years) from Paris. All reported normal or corrected vision, and they were paid for their participation. Each participant was assigned to one of four groups, which corresponded to the four prime durations we used in this study (43 ms, 86 ms, 129 ms, and 300 ms). Nine participants were excluded because of low accuracy in the fame judgment task (below 70% for either famous or unknown people), and 1 was excluded because of extremely slow reaction times (RTs). The four groups comprised 45, 21, 22, and 22 participants, respectively, before outlier exclusion and 40, 20, 20, and 20 participants in the final analysis. We included more participants in the condition with the shortest prime duration because small subliminal effects usually require more data to be detected.

Stimuli

The images used in this study were 90 gray-scale photographs of faces (45 famous faces, 45 unknown faces; two thirds male and one third female), cropped to show only the face on a black background, and then matched for size (115 pixels wide   170 pixels high) and for global luminance. Target images were full-frequency-band images; prime images were created by reducing the size of the images to 80%, then applying a frequency filter, and finally overlaying one LSF-filtered image and one HSF-filtered image. The filters used were low-pass and high-pass finite-impulse-response filters (implemented in a MATLAB code adapted from van Diepen, 2002); their cutoff frequency was 3 cycles per degree, which corresponds to about 12 cycles per face width

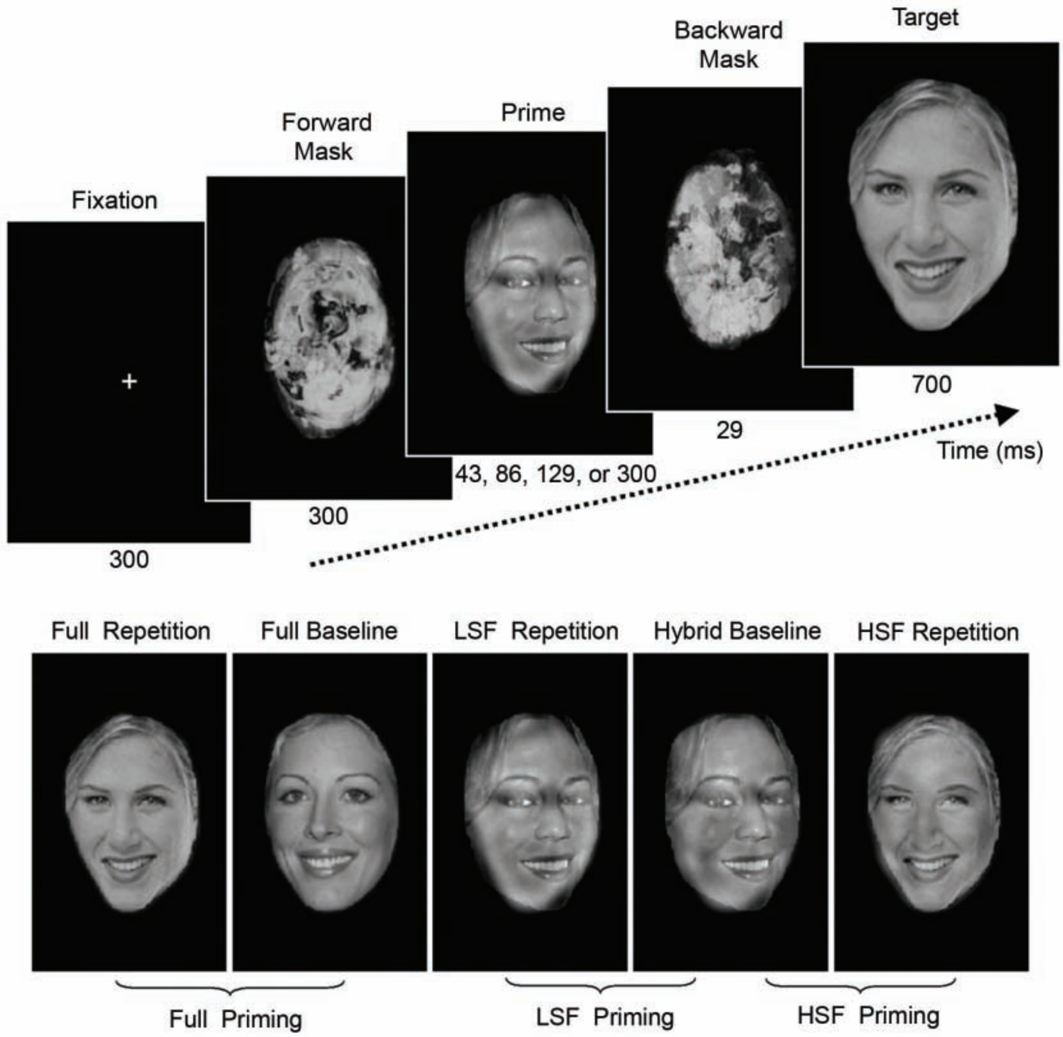

Fig. 1. Illustration of the trial sequence (top row) and examples of prime pictures in the five conditions (bottom row). The brackets indicate the conditions that were compared to measure each type of priming. HSF = high spatial frequency; LSF = low spatial frequency.

and 18 cycles per face height. The information in an LSF-filtered image and the information in the corresponding HSF-filtered image were complementary; that is, the two filters used the same cutoff frequency, and the sum of an LSF-filtered image and the corresponding HSF-filtered image was the original image. Masks were created using Adobe Photoshop to superpose 6 images from the original database; special features of this software were applied in order to match the perceptual quality of the masks with the face images. The global luminance of primes and masks was set to be 80% of the targets' global luminance.

To create the primes, we grouped our targets in bins of three faces (A, B, and C) of the same familiarity. Then, from each bin, we took one face as a target and created five prime images to be used with this target. For instance, if A was taken as the target face, then the five primes were the following: The *full-band repetition* was A (i.e., the same face as the target), the *full-band baseline* was B, the *HSF repetition prime* combined HSF information from A and LSF information from B, the *LSF repetition prime* combined HSF information from C and LSF information from A, and the *hybrid baseline* combined HSF information from C and LSF information from B (so that the same baseline was used to compute LSF and HSF priming). After applying this procedure with A as the target, we applied the same procedure to create primes for the images B and C taken as targets.

Procedure and design

The experimental session included the masked priming experiment and a visibility test. The tasks were presented using Cogent 2000 (Laboratory of Neurobiology, Functional

Imaging Laboratory, and Institute of Cognitive Neuroscience, University College London; http://www.vislab.ucl.ac.uk/cogent_2000.php). Participants sat at a normal viewing distance (about 60 cm) from a 17-in. CRT screen, so that they were comfortable, and they were asked to keep the viewing distance constant during the entire procedure. Under these conditions, both LSF information and HSF information were visible when there was no time pressure (e.g., if faces were presented for a few seconds).

During the masked priming experiment (see Fig. 1), all trials included the following sequence of visual events, presented centrally: a fixation cross (300 ms), a forward mask (300 ms), the prime (43, 86, 129, or 300 ms), a backward mask (29 ms), and the target face (700 ms). Participants were asked to decide as quickly as possible, and before the target disappeared, whether the face they saw belonged to a famous person or not, and to ignore other visual events. All participants started with a training block followed by five experimental blocks of 90 trials each. There were five conditions, corresponding to the five prime types. The two full-band conditions allowed us to assess full-band priming (full-band repetition vs. full-band baseline), and the three hybrid conditions allowed us to assess HSF priming (HSF repetition vs. hybrid baseline) and LSF priming (LSF repetition vs. hybrid baseline; see Fig. 1). For each participant, the five conditions were counterbalanced by arranging blocks and items as a Latin square. Hence, each participant received each target item in each condition. Prime duration was controlled as a between-participants factor.

After the priming experiment, participants were informed about the presence of the primes and were asked to perform a visibility test with 90 trials. Each trial comprised the same sequence of masks and stimuli as in the priming experiment, and then, after the target disappeared, two faces were presented simultaneously, one on each side of fixation. One of the faces always corresponded to the prime, and the other was a distractor. The prime was equally likely to appear on the left or right side. Participants were asked to determine which of the two faces corresponded to the preceding prime, and to press the button on the corresponding side to indicate their choice. They were told that only accuracy, not response speed, was important.

Because we wanted to measure separately observers' ability to consciously perceive HSF and LSF information in the primes, the distractor face that was presented along with the prime could differ on LSF or HSF information, or both. To assess HSF visibility, for instance, we used trials in which the target was a face A, the hybrid prime was made of LSF information from A and HSF information from C, and the hybrid distractor combined LSF information from A and HSF information from B. Under these conditions, the prime and the distractor differed only on HSF information, and to respond correctly, participants had to catch this critical information. To assess LSF visibility, we applied the same logic, having the prime and distractor differ only on LSF information. On other trials, the prime and distractor differed on both HSF and LSF information: In trials corresponding to full-band repetition and full-band baseline trials in the priming experiment, the alternatives were always the full-band repeated and the full-band baseline primes, and in trials corresponding to hybrid-baseline trials in the priming experiment, the alternatives were the prime and an unrelated hybrid image. On these trials, any type of information was sufficient to respond correctly.

Table 1. Discrimination (d') Scores in the Prime Visibility Test

Information condition	Prime duration (ms)				Mean
	43	86	129	300	
Full band	−0.009	0.254**	1.327***	2.093***	0.731***
High spatial frequency	−0.010	0.193*	0.724***	2.001***	0.580***
Low spatial frequency	0.008	0.141	0.207*	0.443***	0.161***
Mean	−0.004	0.196***	0.752***	1.512***	

Note: Asterisks indicate the results of planned *t* tests assessing whether the d' scores were significantly greater than 0.
*$p < .05$. **$p < .01$. ***$p < .001$.

Results

Prime visibility

We computed a d' discrimination score for each participant in each condition of the visibility test (full-band, LSF, and HSF information). An analysis of variance (ANOVA) on these values revealed a main effect of prime duration, $F(3, 96) = 112.8$, $p < .001$; visibility increased as a function of duration. There was also a main effect of condition, $F(2, 192) = 32.9$, $p < .001$; discrimination was globally better in the full-band condition than in the HSF condition, $t(99) = 2.3$, $p < .05$, and discrimination in the HSF condition was, in turn, better than discrimination in the LSF condition, $t(99) = 4.7$, $p < .001$. Finally, an interaction between duration and condition, $F(6, 192) = 16.9$, $p < .001$, reflected the fact that increased prime duration benefited visibility more in the full-band and HSF conditions than in the LSF condition (see Table 1). Planned *t* tests assessing the reliability of these visibility measures revealed that participants were unable to detect any information when the shortest prime duration (43 ms) was used.

Priming effects

To analyze priming effects, we excluded trials with incorrect responses and trials on which the response came after target offset (9% of the correct trials). We then computed the amount of each type of priming (full band, LSF, and HSF), separately for each participant and familiarity condition. An ANOVA on

Table 2. Response Times and Priming Effects in the Fame Judgment Task

Face type and prime duration	Response time (ms)					Priming effect (ms)		
	Full repetition	Full baseline	LSF repetition	HSF repetition	Hybrid baseline	Full	LSF	HSF
Famous faces								
43-ms prime	514	528	521	521	527	14***	6**	6**
86-ms prime	496	544	534	520	542	48***	8**	22***
129-ms prime	455	524	523	501	526	70***	3	25***
300-ms prime	362	440	480	442	491	78***	11*	49***
Unknown faces								
43-ms prime	557	561	563	561	560	4*	−2	−1
86-ms prime	546	564	562	560	565	18***	3	1*
129-ms prime	519	552	544	540	552	33***	7*	11**
300-ms prime	420	481	485	471	494	61***	8*	23***

Note: Asterisks indicate the results of planned *t* tests assessing whether the priming effects were significantly greater than 0. HSF = high spatial frequency; LSF = low spatial frequency.
$^{*}p < .05$. $^{**}p < .01$. $^{***}p < .001$.

these priming effects revealed a main effect of prime duration, $F(3, 96) = 53.9$, $p < .001$; priming increased with prime duration. Familiarity also had a main effect, $F(1, 96) = 64.2$, $p < .001$; priming was greater for famous faces than for unknown faces. Finally, priming type also had a main effect, $F(2, 192) = 150.2$, $p < .001$, with priming being greatest in the LSF condition, intermediate for the HSF condition, and smallest for the full-band condition. In addition, we found interactions between priming type and duration, $F(6, 192) = 24.4$ $p < .001$, and between priming type and familiarity, $F(2, 192) = 15.5$ $p < .001$, as well as a triple interaction of priming type, familiarity, and duration, $F(6, 192) = 5.4$ $p < .001$.

Planned *t* tests revealed that priming effects were weak for unknown faces, especially under subliminal conditions (see Table 2). This finding is consistent with previous work on masked priming using words versus nonwords (Forster & Davis, 1984; Kouider & Dupoux, 2005) and using familiar versus unfamiliar faces, as in the current study (Henson, Mouchlianitis, Matthews, & Kouider, 2008; Kouider et al., 2009). The locus of this interaction remains unclear. It may be that familiar stimuli have an advantage because in this case masked priming involves preexisting representations (as proposed by Forster, 1998). Alternatively, unfamiliar stimuli may also induce perceptual repetition and facilitation, an effect that could be considered a familiarity bias due to repetition, but this effect might be erased at the decision level as participants choose the “unfamiliar” response in these trials (as described in Kouider et al., 2009). We therefore restricted further analysis to famous faces, as in previous studies. Except for LSF priming with 129-ms primes, priming was always significant, even in the case of HSF information presented subliminally. Further analyses revealed that both full-band priming, $F(3, 96) = 36.1$, $p < .001$, and HSF priming, $F(3, 96) = 19.9$, $p < .001$, benefited from longer prime durations, but LSF priming did not ($F = 0.99$, $p = .4$).

Relation between priming and prime visibility

The previous analyses of famous-face trials show that, unlike processing of HSF and full-band information, processing of LSF information is not influenced by prime duration. Does this mean that processing of LSF information is independent of LSF visibility? To analyze further the relation between priming and prime visibility, we regressed priming effects on d' values across participants (see Fig. 2 and Table 3). We observed that the intercepts, corresponding to the priming effects extrapolated to conditions in which participants performed at chance on the relevant prime-visibility task (null d'), were always significantly positive. This result shows that for famous faces, full-band, LSF, and HSF information all induce priming under genuinely subliminal conditions. In addition, the slopes of the regressions revealed that for HSF and full-band information, but not for LSF information, priming effects correlated with conscious accessibility of the prime (i.e., d' scores). An additional regression revealed a significant interaction between spatial frequency (HSF vs. LSF) and prime awareness, $F(3, 196) = 21.91$, $p < .001$, such that priming increased as a function of prime awareness with HSF priming but not LSF priming.

Discussion

In this study, we used a masked-face priming paradigm with hybrid primes to investigate the relation between spatial-frequency processing and visual awareness. In a fame judgment task, priming effects for famous faces revealed two main results. First, we found subliminal priming for both LSF and HSF information. Thus, both frequency bands can contribute to unconscious perception. Second, when we analyzed the relation between priming and visibility, we observed that effects of HSF and full-band information correlated with

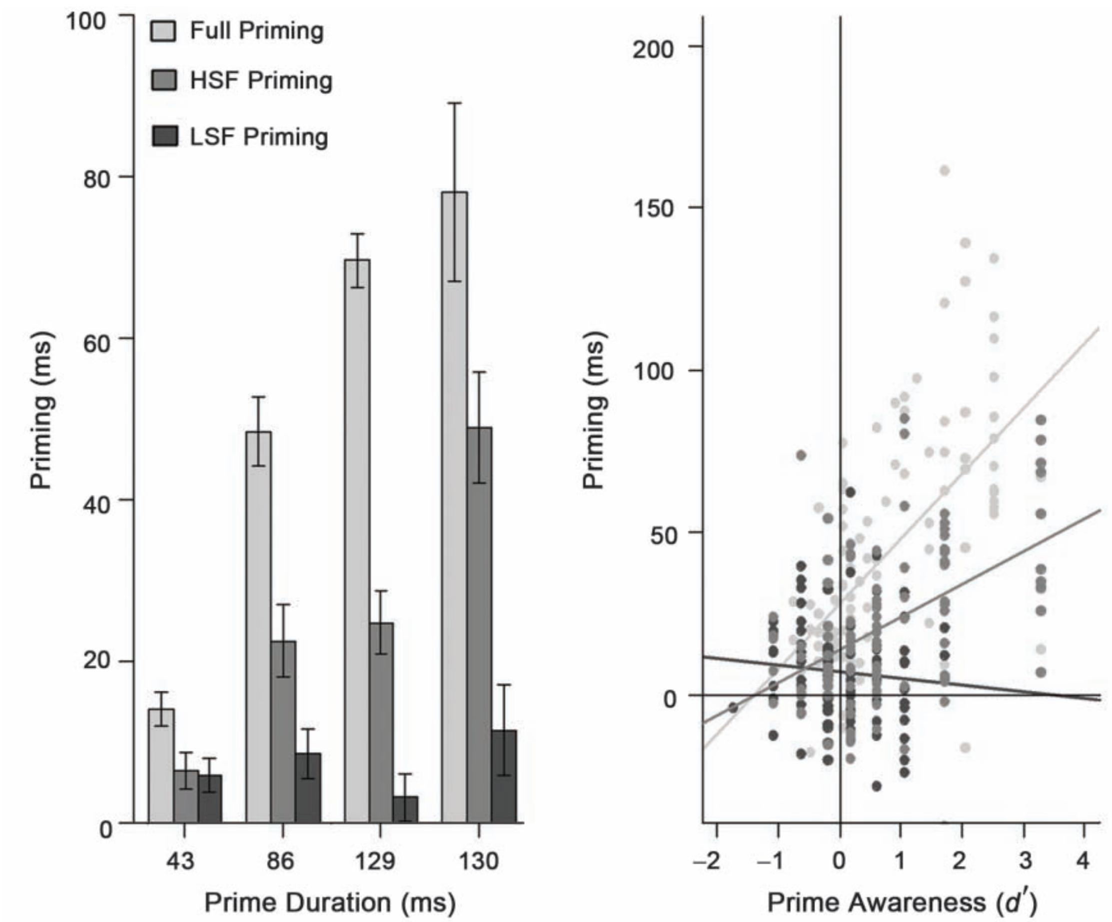

Fig. 2. Results for famous faces: mean magnitude of priming as a function of prime duration (left panel) and regression of the priming effect on prime visibility (awareness, or d'), across participants (right panel). Error bars represent ±1 *SE*. Results are shown separately for full-band, high-spatial-frequency (HSF), and low-spatial-frequency (LSF) information.

participants' awareness of this information, whereas influences of LSF information were independent of awareness.

When hybrid images are exposed consciously for a duration sufficient to allow precise identification, HSF components usually dominate conscious perception (Schyns & Oliva, 1994; Parker et al., 1992, 1996). In our visibility test, we consistently found that HSF information was more available for conscious report than LSF information, especially for longer durations. These psychological results, along with additional neurobiological evidence (e.g., Livingstone & Hubel, 1988) for faster transmission of LSF cues in the magnocellular than in the parvocellular pathway, provide support for the influential coarse-to-fine model of face, object, and scene recognition (for reviews, see Ruiz-Soler & Beltran, 2006, and Hegdé, 2008). A similar model (Bar et al., 2006) has also proposed that LSF information is projected quickly and automatically to the orbitofrontal cortex, from where it triggers top-down modulation of the slow-and-conscious bottom-up analysis of HSF information. The fact that LSF information was found to be processed independently of awareness in the present study is also in agreement with these theories, as well as with brain-imaging studies (Vuilleumier et al., 2003; Winston, Vuilleumier, & Dolan, 2003) showing that emotional LSF cues conveyed to the amygdala can influence behavior and neural activity in the fusiform cortex (usually assumed to underlie face recognition) even

Table 3. Summary of the Regression Analysis of the Relation Between Priming Effects and Prime Discrimination Scores (d') for Famous Faces

	Intercept		Slope	
Type of priming	Estimate	t	Estimate	t
Full band	28.4***	7.4	20.0***	7.2
High spatial frequency	14.1***	5.2	10.1***	5.2
Low spatial frequency	7.1***	4.3	−2.0	−0.9

Note: Asterisks indicate the results of planned t tests assessing whether estimate values were significantly different from 0.
***$p < .001$.

when the observer consciously reports the content of HSF information.

However, one main result in the present study might limit the validity of a fixed coarse-to-fine model. We observed that HSF information in masked prime images can be processed under stringent subliminal conditions (i.e., presentation for only 43 ms). This result is in complete agreement with the first experiment of Oliva and Schyns (1997), in which participants processed both LSF and HSF information in very short (30-ms), masked presentations of natural scenes. That study provided evidence for parallel extraction of LSF and HSF information under low-awareness conditions. Here, we found that this result extends to another class of stimuli and, crucially, to stringent subliminal conditions (as determined by a visibility test). As we discuss next, our results challenge both coarse-to-fine models of vision and theories of consciousness in which ventral-stream activity is mandatorily linked with conscious awareness.

One can interpret our findings in light of the diagnostic model (Schyns, 1998), an alternative to the fixed coarse-to-fine view. According to the diagnostic framework, the use of spatial-frequency scales is not fixed but flexible, and may be modulated by the requirements of the visual task and stimulus properties. This view has received support from studies showing that the particular categorization task at hand can affect the balance between HSF and LSF contributions to the conscious perception of a hybrid image (for recent reviews, see Ruiz-Soler & Beltran, 2006, and Sowden & Schyns, 2006). What was the diagnostic information in the present study? There is evidence that when the identification of a face is required, as in our fame judgment task, HSF cues are more informative than LSF cues (e.g., Costen et al., 1996; Fiorentini et al., 1983; Liu et al., 2000).[1] The advantage of HSF over LSF information in the visibility test also supports the idea that HSF information was diagnostic. An alternative possibility is that the HSF dominance reflects instead a bias in our stimuli that favored HSF repetition over LSF repetition. To rule out this possible confound, we calculated a post hoc measure of visual similarity for each prime-target pair; this measure revealed that, if anything, similarity at the pixel level was in fact greater for LSF than for HSF information. Neither can our results be explained by an advantage related to decision processes or predictability of the target, as HSF and LSF information in the prime were of the same fame status, and thus predicted the same response. Finally, if HSF information was diagnostic, this would predict an amplification of early processing by HSF detectors, and hence larger priming effects for HSF than for LSF information, as we observed.

Thus, it seems that diagnosticity of HSF information, in the context of face identification, is the critical factor, explaining enhanced HSF priming and the correlation between HSF priming and HSF visibility.[2] Oliva and Schyns (1997) have shown that categorizing hybrid scene stimuli containing meaningful information in only one domain (e.g., stimuli with LSF structured information and HSF noise) leads subjects to ignore the information in the other domain, even when, unbeknownst to the subjects, it becomes meaningful in following trials. To explain their results, these researchers introduced the notion of scale-directed attention driven by diagnosticity. Attentional selection and amplification have been shown to create favorable conditions for observing subliminal priming effects. Although this notion of flexible use of spatial scales can be seen as a contradiction to the cognitive impenetrability of early modules postulated by Fodor (1983), it has received additional support in a recent brain-imaging study demonstrating similar task-driven modulations of subliminal priming in the language-processing network (Nakamura, Dehaene, Jobert, Le Bihan, & Kouider, 2007). In that study, the authors demonstrated a dissociation between two tasks: a semantic categorization task that elicited neural priming in the left middle temporal gyrus, which is associated with lexico-semantic processing, and a naming task that produced neural priming in the left inferior parietal lobe, which is associated with print-to-sound conversion. In our study, diagnosticity-driven attention to the HSF scale might also have created a favorable condition for observing HSF-induced subliminal priming effects.

Yet, although HSF information was diagnostic, LSF information was not totally suppressed and still influenced processing of the target. This result corroborates previous work (Oliva & Schyns, 1997, Experiments 3 and 4) showing that when the LSF information is diagnostic, subjects still process the HSF information implicitly, and that this unreported information primes the perception of the next LSF scene. Here, we extended Oliva and Schyns's results by showing that nondiagnostic processing (LSF information in the present case) has only a small influence that is independent of visibility, which suggests that it is probably restricted to unconscious processing; in contrast, the influences from diagnostic information (HSF information in the present case) are larger and increase with visibility. This strongly suggests a close relation between awareness and diagnosticity. Such a relation would be consistent with the notion of scale-directed attention driven by diagnosticity (Oliva & Schyns, 1997), as well as with theories of consciousness postulating that the impact of specific information on the cognitive system, which is roughly equivalent to its diagnosticity, determines its availability to conscious awareness (e.g., Baars, 1988; Dehaene & Naccache, 2001).

The observed subliminal effect of HSF information, which is associated with ventral-stream processing (see the introduction), is consistent with brain-imaging studies showing unconscious ventral-stream activity in binocular fusion (Moutoussis & Zeki, 2002) or masking (Kouider et al., 2009) paradigms, though in these studies it was unclear whether these activations corresponded to the subliminal processing of HSF or LSF information. These results constrain the original duplex vision theory, which associates ventral-stream activity with perceptual awareness (Milner & Goodale, 1995), though the "vision for perception" that the ventral stream contributes can be extended to include unconscious perception (see Milner & Goodale, 2008), for instance, by introducing a threshold mechanism whereby awareness is induced only if ventral-stream activity exceeds a certain level (see Kouider, in press, for more details).

Alternatively, the evidence also is consistent with theories of consciousness that allow for both conscious and unconscious processing within the ventral stream. For instance, several models associate the conscious/unconscious dichotomy not with two distinct cerebral substrates (e.g., dorsal/ventral or subcortical/cortical), but rather with two different modes of processing (e.g., Dehaene et al., 2006; Lamme, 2003). In these models, subliminal processing is purely feedforward and fades rapidly, which is why it is often restricted to sensory areas in the brain (including the ventral stream; see Kouider & Dehaene, 2007, for a review), whereas conscious processing involves recurrent loops within sensory regions (Lamme, 2003) or between ventral and fronto-parietal "workspace" regions (Dehaene et al., 2006). In these models, any visual attributes, including HSF information, can be processed subliminally in the ventral stream.

In sum, we found that both LSF information and HSF information can be extracted from subliminal face stimuli. In addition, only the influences from HSF information, which was diagnostic in our paradigm, correlated with conscious awareness, a result suggesting a special relation between awareness and diagnosticity. One testable prediction suggested by our results is that by using a task in which the LSF information is diagnostic (e.g., discriminating emotional expressions in faces, as in Schyns & Oliva, 1999), one could enhance LSF and attenuate HSF effects (possibly eliminating HSF subliminal effects), and also make LSF, rather than HSF, influences correlate with conscious awareness. Further development of informational measures of diagnosticity and awareness might help researchers to investigate more generally the relation between these two key concepts in cognition.

Acknowledgments

The authors thank Philippe Schyns and two anonymous reviewers for their useful comments, and Managing Editor Michele Nathan for copyediting of the article.

Declaration of Conflicting Interests

The authors declared that they had no conflicts of interests with respect to their authorship and/or the publication of this article.

Notes

1. As one of the reviewers pointed out, the medium-spatial-frequency (MSF) range has also been put forward as critical for face recognition (Costen et al., 1996), and in our stimuli, that range was contained in the HSF information. Thus, it is possible that the HSF effects we found were instead driven by MSF information. In any case, our data still support a dissociation between lower and higher spatial-frequency ranges as a function of visibility.

2. We would like to emphasize that diagnostic cues can in fact be distributed over a range of spatial-frequency bands and are not limited by the dichotomy between HSF and LSF information, as demonstrated by the Bubbles method (Gosselin & Schyns, 2001).

References

Baars, B.J. (1988). *A cognitive theory of consciousness*. New York: Cambridge University Press.

Bar, M., Kassam, K.S., Ghuman, A.S., Boshyan, J., Schmid, A.M., Dale, A.M., et al. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences, USA*, *103*, 449–454.

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.

Dehaene, S., Changeux, J.-P., Naccache, L., Sackur, J., & Sergent, C. (2006). Conscious, preconscious, and subliminal processing: A testable taxonomy. *Trends in Cognitive Sciences*, *10*, 204–211.

Dehaene, S., & Naccache, L. (2001). Towards a cognitive neuroscience of consciousness: Basic evidence and a workspace framework. *Cognition*, *79*, 1–37.

Eger, E., Schyns, P., & Kleinschmidt, A. (2004). Differential sensitivity to facial identity across spatial scales in fusiform and occipital face responsive regions. *NeuroImage*, *22*, 232–242.

Ferrera, V.P., Nealey, T.A., & Maunsell, J.H.R. (1994). Responses in macaque visual area V4 following inactivation of the parvocellular and magnocellular LGN pathways. *Journal of Neuroscience*, *14*, 2080–2088.

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

Fodor, J.A. (1983). *The modularity of mind*. Cambridge, MA: MIT Press.

Forster, K.I. (1998). The pros and cons of masked priming. *Journal of Psycholinguistic Research*, *27*, 203–233.

Forster, K.I., & Davis, C. (1984). Repetition priming and frequency attenuation in lexical access. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *10*, 680–698.

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

Hegdé, J., (2008). Time course of visual perception: Coarse-to-fine processing and beyond. *Progress in Neurobiology*, *84*, 405–439.

Henson, R.N., Mouchlianitis, E., Matthews, W.J., & Kouider, S. (2008). Electrophysiological correlates of masked face priming. *NeuroImage*, *40*, 884–895.

Hughes, H.C., Nozawa, G., & Kitterle, 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.

Kouider, S. (in press). Neurobiological theories of consciousness. In W. Banks (Ed.), *Encyclopedia of consciousness*. New York: Elsevier.

Kouider, S., & Dehaene, S. (2007). Levels of processing during non-conscious perception: A critical review of visual masking. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*, 857–875.

Kouider, S., & Dupoux, E. (2005). Subliminal speech priming. *Psychological Science*, *16*, 617–625.

Kouider, S., Eger, E., Dolan, R.J., & Henson, R.N. (2009). Activity in face-responsive brain regions is modulated by invisible, attended faces: Evidence from masked priming. *Cerebral Cortex*, *19*, 13–23.

Lamme, V.A. (2003). Why visual attention and awareness are different. *Trends in Cognitive Sciences*, *7*, 12–18.

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.

Livingstone, M., & Hubel, D. (1988). Segregation of form, color, movement, and depth: Anatomy, physiology, and perception. *Science*, *240*, 740–749.

Merigan, W.H., & Maunsell, J.H.R. (1993). How parallel are the primate visual pathways? *Annual Review of Neuroscience*, *16*, 369–402.

Milner, A.D., & Goodale, M.A. (1995). *The visual brain in action*. New York: Oxford University Press.

Milner, A.D., & Goodale, M.A. (2008). Two visual systems reviewed. *Neuropsychologia*, *46*, 774–785.

Moutoussis, K., & Zeki, S. (2002). The relationship between cortical activation and perception investigated with invisible stimuli. *Proceedings of the National Academy of Sciences, USA*, *99*, 9527–9532.

Nakamura, K., Dehaene, S., Jobert, M., Le Bihan, D., & Kouider, S. (2007). Task-specific change of unconscious neural priming in the cerebral language network. *Proceedings of the National Academy of Sciences, USA*, *104*, 19643–19648.

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.

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. (1996). Evidence for the view that temporospatial integration in vision is temporally anisotropic. *Perception*, *26*, 1169–1180.

Rotshtein, P., Vuilleumier, P., Winston, J., Driver, J., & Dolan, R. (2007). Distinct and convergent visual processing of high and low spatial frequency information in faces. *Cerebral Cortex*, *17*, 2713–2724.

Ruiz-Soler, M., & Beltran, F.S. (2006). Face perception: An integrative review of the role of spatial frequencies. *Psychological Research*, *70*, 273–292.

Schyns, P.G. (1998). Diagnostic recognition: Task constraints, object information and their interactions. *Cognition*, *67*, 147–179.

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.

Sowden, P.T., & Schyns, P. (2006). Channel surfing in the visual brain. *Trends in Cognitive Sciences*, *10*, 538–545.

van Diepen, P.M.J. (2002). *Matlab filter program for full color images*. Retrieved November 2007 from http://psy.van-diepen.com/pvdmatl.html

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.

Winston, J.S., Vuilleumier, P., & Dolan, R.J. (2003). Effects of low-spatial frequency components of fearful faces on fusiform cortex activity. *Current Biology*, *13*, 1824–1829.