

# Multi-feature objects elicit nonconscious priming despite crowding

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The conscious representation we build from the visual environment appears jumbled in the periphery, reflecting a phenomenon known as crowding. Yet, it remains possible that object-level representations (i.e., resulting from the binding of the stimulus' different features) are preserved even if they are not consciously accessible. With a paradigm involving gaze-contingent substitution, which allows us to ensure the constant absence of peripheral stimulus discrimination, we show that, despite their jumbled appearance, multi-feature crowded objects, such as faces and directional symbols, are encoded in a nonconscious manner and can influence subsequent behavior. Furthermore, we show that the encoding of complex crowded contents is modulated by attention in the absence of consciousness. These results, in addition to bringing new insights concerning the fate of crowded information, illustrate the potential of the Gaze-Contingent Crowding (GCC) approach for probing nonconscious cognition.

Keywords: crowding, face processing, action priming, nonconscious cognition

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## Introduction

When we are immersed in a complex environment, objects in the periphery appear jumbled and become hardly discriminable. This phenomenon, known as crowding, is a breakdown in the process leading to the identification of peripheral objects when they are surrounded by similar neighbors (Levi, 2008). As opposed to visual masking, in which even detection can be abolished, crowding reflects a situation where a stimulus can be detected but not discriminated (Pelli, Palomares, & Majaj, 2004). Due to the correct detection capabilities, it is commonly accepted that crowding occurs after featural detection, arguably during the integration of the features into one unified object (e.g., the integration of different elementary shapes forming a more complex pictograph). However, there is no general consensus regarding the specific mechanisms underlying crowding, and theories largely diverge on the origins of this phenomenon.

According to neuronal, or bottom-up accounts, crowding occurs when both the object and its neighbors overlap within the same receptive field, which is also called integration field (Pelli, 2008). In peripheral vision, as the size of the integration fields widens with eccentricity, the probability with which several features from different adjacent stimuli are integrated into the same field becomes higher, correlating with the eccentricity dependence of crowding (Bouma, 1970). This correlation is alternatively explained by higher level or top-down accounts of

crowding in which the overlap is not attributed to hard-wired limitations in the visual cortex but rather to a coarsening of the resolution of spatial attention in the periphery (Intriligator & Cavanagh, 2001). Along this line, recent physiological evidence shows that crowded perception is associated with a spread spatial distribution of attention around the target stimulus and its neighbors (Fang & He, 2008). The attentional account is also supported by crowding asymmetry (i.e., crowding is stronger in the upper than in the lower visual field, as demonstrated with several attentional effects; see He, Cavanagh, & Intriligator, 1996). It is also supported by crowding temporal resolution (i.e., around 6–8 Hz, similar to that of attention; see Chakravarthi & Cavanagh, 2007) and by the attentional dependence of the encoding of crowded contents (Montaser-Kouhsari & Rajimehr, 2005). Other accounts, noting that spatial uncertainty is high in the periphery (Pelli, 1985), assert that the jumbled aspect of crowded objects arises from a loss of position information. This lack could potentially induce the integration of mislocalized features from different stimuli into the same object (Poppel & Levi, 2005). These different operationalizations of crowding are not mutually exclusive, as illustrated by a recent computational approach relying on classification image techniques (i.e., without preassumptions regarding the origin of crowding). This computational account, in fact, supports both inappropriate feature integration and feature mislocalization as contributors to crowding (Nandy & Tjan, 2007). Finally, supported by both empirical data and computational

models, some accounts state that the information available during crowding is textural and consists of summary statistics that comprise distributions of feature values rather than of localized feature maps (Balas, Nakano, & Rosenholtz, 2009; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001).

Here, we studied the nonconscious processing of crowded multi-feature stimuli, defined as the processing of their informational content in the absence of a corresponding conscious experience. Despite the subjective feeling of uninformative contents, previous findings show that low-level information such as tilt orientation is properly encoded even when crowded by adjacent vertical flankers (He et al., 1996). This study used visual adaptation as an index of nonconscious orientation processing, a situation in which the perceptual threshold of a target is increased when preceded by a crowded adaptor sharing the same orientation.

The present study tested whether nonconscious processing of crowded stimuli extends beyond single feature information (e.g., line orientations) to higher levels of processing involved in processes such as face recognition and directional symbol processing. For this purpose, we combined crowding, in order to impede the discrimination of a multi-feature stimulus, with a priming paradigm in order to measure its influences on behavior. Nonconscious priming occurs when the processing of a highly visible target is facilitated by a preceding related prime stimulus, which is maintained under the threshold of consciousness by techniques such as visual masking (Kouider & Dehaene, 2007). By manipulating the prime–target relation, one can investigate which levels of processing influence behavior (e.g., priming for semantic associates such as “nurse–doctor” implies nonconscious processing of the meaning of the prime). In order to control for prime discriminability, we use a method termed gaze-contingent crowding (GCC). This technique ensures perception without discrimination of long-lasting peripheral objects through high-resolution eye tracking. Specifically, it allows for the relevant crowded prime to be substituted by noninformative content as soon as the participant attempts to move their gaze from a fixation position, thus preventing foveal access to the prime stimulus.

In a first experiment, we studied the influence of peripheral faces subject to crowding (rendered nondiscriminable by GCC) on a fame categorization task. In a second experiment, we studied the influences of crowded symbols (pointing arrows). In addition, we assessed the role played by spatial attention on the encoding of crowded stimuli. We found that both types of information can prime behaviors in a nonconscious manner, revealing that the dissociation between perceptual consciousness (jumbled, uninformative) and perceptual processing (distinct, informative) extends to higher level objects such as faces and symbols. In addition, we observed that the impact of crowded information on sensorimotor pathways

is modulated by the allocation of spatial attention. These results and their implications are discussed in the light of both the partial awareness framework (Kouider, de Gardelle, Sackur, & Dupoux, 2010) and top-down accounts of the crowding phenomenon.

## Experiment 1

The mechanisms underlying nonconscious face perception are now well documented, both at behavioral and neural levels. Recent evidences have shown that subliminal and supraliminal faces are processed differently depending on their frequency spectrum (de Gardelle & Kouider, 2010), while they elicit neural activity in common cortical areas (e.g., in the fusiform face area; see Kouider, Eger, Dolan, & Henson, 2009). Yet, as this issue has been mainly addressed through visual masking, little is known about the nonconscious processing of faces during crowding. For this purpose, we adapted a face repetition priming paradigm to GCC (see Figure 1a). Face crowding can occur both between features within a face (i.e., featural or self-crowding; see Martelli, Majaj, & Pelli, 2005) and between the configurational representation of different adjacent faces (i.e., holistic or configurational crowding; see Farzin, Rivera, & Whitney, 2009; Louie, Bressler, & Whitney, 2007). We established the encoding quality of peripheral faces subject to self-crowding by measuring their ability to elicit repetition priming effects in a fame categorization task while remaining nondiscriminable, as demonstrated by a 2-alternative forced-choice measure of consciousness.

## Methods

### Subjects

Eighteen university students (age range = 18–35) participated in Experiment 1. All participants were recruited in function of their media exposure (to ensure that famous faces were familiar to them), reported normal or corrected vision, and were paid for their participation.

### Stimuli

Target stimuli were  $3^\circ \times 3.5^\circ$  grayscale photographs of 40 famous and 40 unknown faces selected from a previously used set (de Gardelle & Kouider, 2010). Half were male; half were female. All pictures were matched for image size and luminance and cropped to show only the face. Distractors were 40 different  $3^\circ \times 3.5^\circ$  meaningless patterns created by blending 6 randomly chosen images from 3 different categories (2 nonfamous faces from a different stimulus set, 2 watches, 2 flowers). The

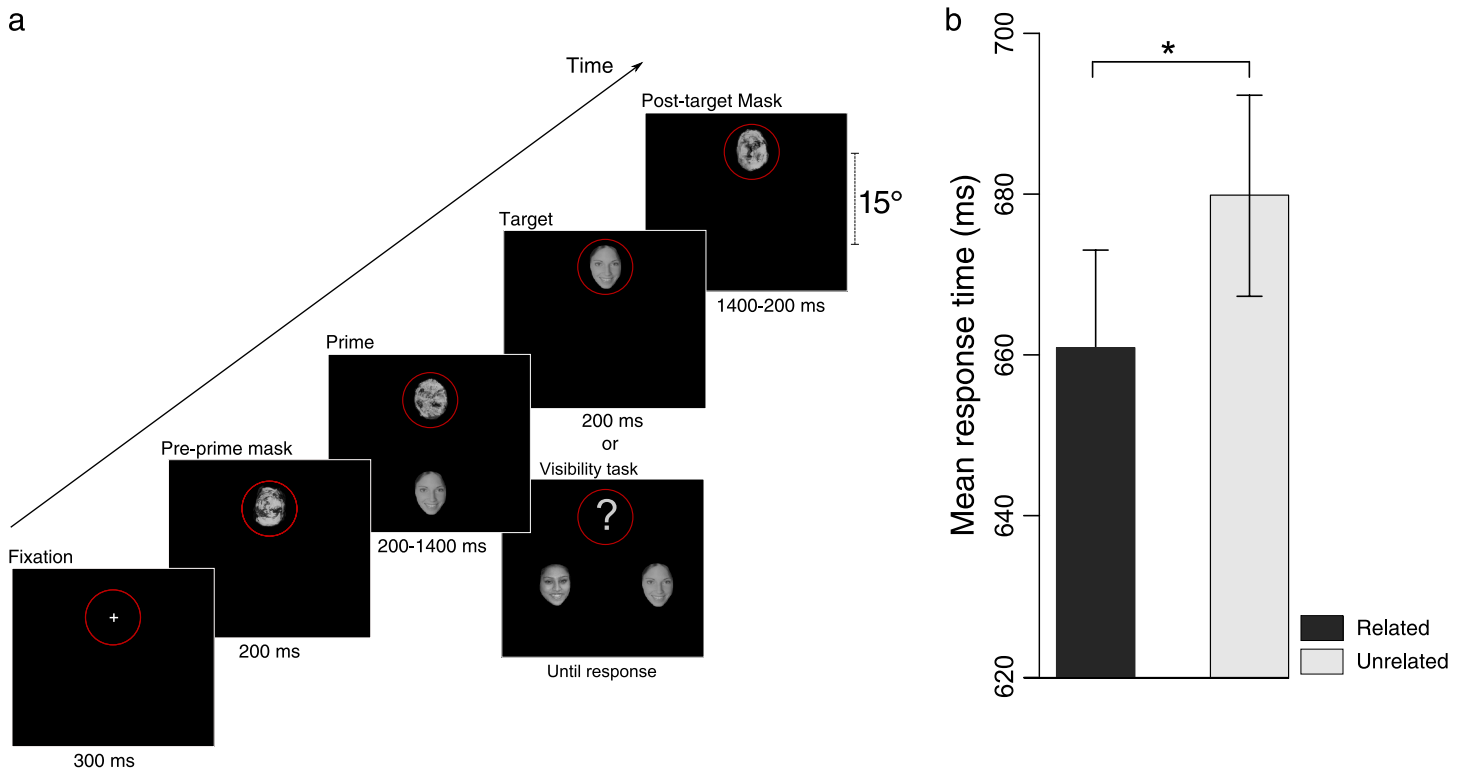


Figure 1. (a) Face priming paradigm. Each trial started with the presentation of a fixation cross, followed by a mask presented at fixation location and a peripheral preprime mask presented at the bottom. This was followed by a stream of alternating masks at fixation position until the target display, while a prime face appeared downward. The target appeared on the top of the screen after an unpredictable time and consisted either of a face on which participants judged whether it belonged to a famous or unknown person (priming trials), or in a question mark between two faces, among which participants had to choose the prime face (prime discrimination trials). Priming trials were “related” when the prime and the target were identical faces and “unrelated” when they were different faces belonging to the same category (both famous or both nonfamous). Priming trials ended with a final display of post-target masks, while prime discrimination trials ended with the participant’s response. (b) Famous face priming results. Averaged reaction times on the fame categorization task for famous faces in related (black) and unrelated (gray) trials. Error bars denote one standard error; \* $p$ -value < 0.05.

average luminance, contrast, and shape of the distractors were set to be similar to those of the faces.

### Procedure and design

Eccentricity between prime and target was  $15^\circ$ , with target location centered at the quarter top of the screen and prime location at the bottom. Each trial started with the appearance of a fixation cross for 300 ms and a  $6^\circ$  diameter red circle at the target location, which remained on the screen until the end of a trial. Following the fixation cross, two different distractors appeared simultaneously for 200 ms, one at target location and the other at prime location (preprime mask). Then, subjects were presented with either 1, 3, 5, or 7 distractors, each for 200 ms at the target location, while the primes appeared at the bottom of the screen for the same duration (e.g., 200 ms, 600 ms, 1000 ms, or 1400 ms). These events were immediately followed by the target face while another distractor replaced the prime, both for 200 ms. Finally, the target was followed by 7, 5, 3, or 1 post-target

mask(s), in inverse proportion to the preceding distractors. Participants were instructed to keep track of the target location until the target face appeared. Importantly, as soon as a participant ceased to gaze at a  $5^\circ$  by  $5^\circ$  area surrounding the target location, the prime was substituted by a pattern during the next refresh cycle of the monitor screen, guaranteeing that the prime was never accessed foveally.

Participants’ main task was to decide, as fast as possible, whether each target face belonged to famous or unknown person, with their right or left index finger, respectively. Within a trial, the prime and the target could either be the same faces (repetition trials) or different faces (unrelated trials). In the latter case, the two prime–target counterparts always belonged to the same category (as well as to the same gender and same approximate age), assuring that the unrelated and related conditions referred to the same motor response. This was designed in order to avoid confounding response congruency with perceptual priming (Abrams, Klinger, & Greenwald, 2002; Damian, 2001; Kouider & Dehaene, 2009). In addition to the main

task, a prime discrimination task was randomly administered to the participants in 1 out of 5 trials. In this case, a question mark appeared instead of the target, simultaneously with the two alternatives (i.e., the prime and its counterpart) appearing at  $7.5^\circ$  on the left or  $7.5^\circ$  on the right side of the screen. While the two alternatives were accessible foveally, the participant's task was to decide in a two-alternative forced-choice task (2-afc) whether the left or right face corresponded to the prime, by pressing the corresponding left or right button. This control was preferred to applying the same fame decision task to the primes, because it allows ruling out eventual situations where participants have a partial consciousness (i.e., access to some of the featural information), which would be insufficient to extract the fame of the prime face but which is sufficient to speed up the processing of the subsequent identical target face (see Kouider, Dehaene, Jobert, & Le Bihan, 2007; Kouider & Dupoux, 2004). Participants received a total of 80 prime discrimination trials randomly intermixed with 320 priming trials.

Stimuli were displayed against a black background by a 22-in. Iiyama Vision master pro 510 monitor (frame rate of 85 Hz, resolution of  $1024 \times 768$  pixels) on a computer running Matlab with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997). The participant sat 57 cm from the screen in a dimly lit room. A chin rest and a headrest were used. Eye movements were recorded monocularly with a video-based tower mounted eye tracker (Eyelink 1000 System, SR Research, Ontario, Canada) controlled with the Eyelink Toolbox (sampling rate 1000 Hz; spatial resolution  $1^\circ$  or above).

## Results and discussion

Trials in which the gaze position was maintained outside the target area for more than 50 ms were rejected (see Methods section), leading to a removal of 8.7% ( $SD = 7.8$ ) of the total trials. Famous target faces were correctly recognized with a rate of 84.7% ( $SD = 10.8$ ), and nonfamous faces were categorized as nonfamous with a rate of 82.8% ( $SD = 12.8$ ). Only correct responses were included in the analyses. We performed an ANOVA on reaction time, with participants as a random variable and relation and prime duration as main factors. Because masked repetition priming for unknown faces is usually nonsignificant unless faces are visible, we analyzed famous and unknown faces separately (see de Gardelle & Kouider, 2010; Henson, Mouchlianitis, Matthews, & Kouider, 2008; Kouider et al., 2009). Here, with crowded faces, we found significant priming for famous faces [19 ms;  $F(1,17) = 5.79$ ;  $p < 0.05$ ] but not for unknown faces ( $F < 1$ ; see Figure 1b). Further analyses restricted to famous faces revealed neither effect of prime duration nor an interaction between priming and prime duration ( $F_s < 1$ ). One could argue that some residual information whose access is not impeded by crowding (e.g., in the edge of the

face, which might be less subject to crowding) could drive the priming effect. However, faces were cropped such as the more eccentric discriminatory facial features, like the ears, were not presented. Crucially, if any other uncontrolled peripheral features (which are only poorly discriminatory) were at the origin of the priming effect, these very same features would have led participants to discriminate above chance between the two faces during the prime discrimination trials. Debriefing the participants after the experiment revealed, however, that none of them could identify the prime faces even when they were told about their presence. A 2-afc on the prime confirmed that our method rendered the stimuli nondiscriminable, as performance was at chance for both famous (mean  $d' = 0.07$ ;  $SD = 0.47$ ;  $p = 0.54$ ) and nonfamous faces (mean  $d' = -0.22$ ;  $SD = 0.77$ ;  $p = 0.25$ ). In sum, Experiment 1 revealed that stimulus information is maintained even for peripheral faces subject to self-crowding and that this information facilitates foveal face recognition.

## Experiment 2

Nonconscious symbolic action priming reflects the facilitation of a motor response on a directional target stimulus, when it is preceded by the same directional

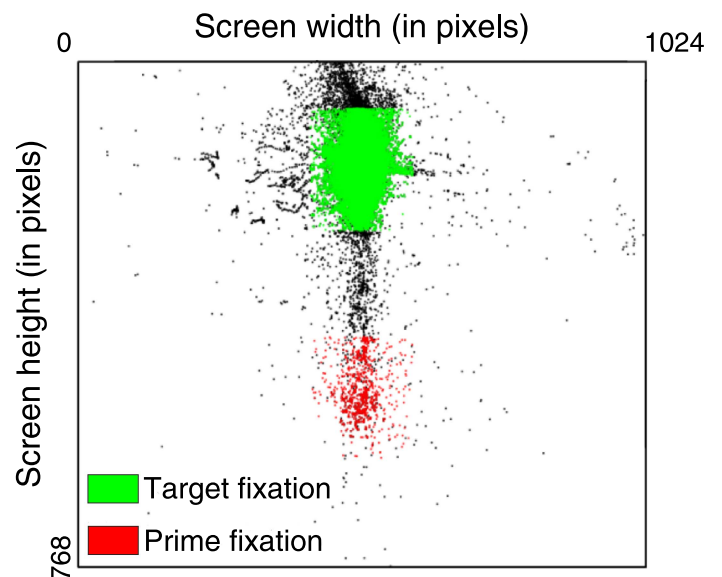


Figure 2. Averaged fixation positions during Experiment 2 (collapsed across 2A and 2B). Each dot stands for a gaze position measured at 1000 Hz. Green dots correspond to target position fixation (compliantly to the instructions). Red dots represent attempts to stare at the peripheral prime, despite the instructions, homogeneously spread across a session. Participants tried to look at the prime while it was displayed on 9.3% ( $SD = 13.2$ ) of the trials, representing 0.5% ( $SD = 0.7$ ) of total looking time.

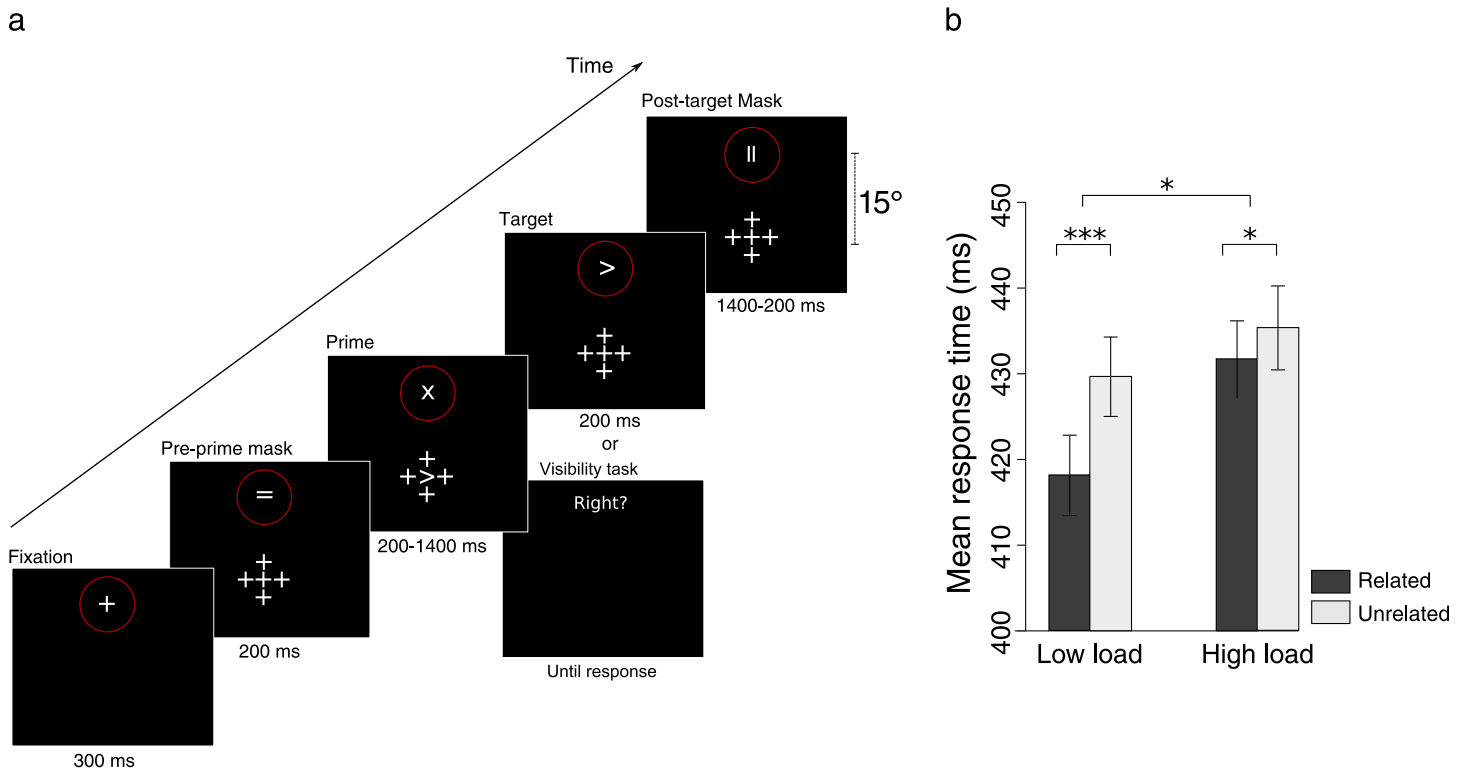


Figure 3. (a) Action priming paradigm. Each trial started with the presentation of a fixation cross. At the bottom of the screen, this was followed by the apparition of four flanker crosses surrounding first a central cross (preprime mask) and then the prime arrow for variable durations. Afterward, the target appeared at the top of the screen among a sequence of geometrical distractors. The target was either an arrow on which participants had to indicate its orientation (priming trials) or a question about the orientation to which participants were forced to answer (yes or no) before continuing (prime discrimination trials). Priming trials ended with a final display of post-target masks, while prime discrimination trials ended with the participant's response. This figure illustrates the high attentional load condition. In the low attentional load condition, the exact same procedure was used, except that instead of the sequence of geometrical distractors, a fixation cross was presented for the duration of each trial. (b) Action priming results. Averaged reaction times on the target orientation task for low attentional load and high attentional load conditions, in related (black) and unrelated (gray) trials. Error bars denote one standard error; \* $p$ -value < 0.05, \*\*\* $p$ -value < 0.001.

prime presented below the threshold of consciousness (e.g., Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003). So far, these nonconscious sensorimotor effects have only been established using visual masking and it remains unclear whether they can be induced by crowded stimuli. Here, we measured the action priming effects induced by crowded chevron arrows (i.e., < or >, see Figure 2a), while manipulating the allocation of spatial attention devoted to the encoding of crowded stimuli. This latter aspect allowed us to test whether attention plays a role in crowded perception, as postulated by top-down accounts (Figure 3).

## Methods

### Subjects

A new group of 39 university students (age range = 18–35) participated in Experiment 2, separated into two subgroups for Experiments 2A ( $N = 19$ ) and 2B ( $N = 20$ ).

All subjects reported normal or corrected vision and were paid for their participation.

### Stimuli

Arrow stimuli were  $1.2^\circ \times 1.2^\circ$  chevrons. Flankers were four  $1.2^\circ \times 1.2^\circ$  + signs. Distractors were 5 types of  $1.2^\circ \times 1.2^\circ$  geometrical forms (+, =, ×, ||, #). All stimuli were presented in gray against a black background.

### Procedure and design

A similar procedure and design to Experiment 1 was used in Experiments 2A and 2B, except with the following main aspects: (a) Target arrows were either identical or opposite to the prime arrows. (b) The prime arrows were now surrounded by flankers with a center-to-center spacing of  $1.4^\circ$ . During the prime discrimination task, subjects received the words “left?” or “right?” and were

asked to indicate whether or not this indicated the prime direction (yes with right index finger, no with left index finger). The critical difference between Experiments 2A and 2B was the presence of either a constant and single + sign at the target location in Experiment 2A (low attentional load) or a stream of nine alternating distractors chosen randomly (while excluding contiguous presentations) in Experiment 2B (high attentional load). As in Experiment 1, as soon as participants' gaze diverged from a  $5^\circ$  by  $5^\circ$  area surrounding the target location, the prime was substituted by a + sign in order to prevent foveal access of the prime (see Figure 2).

## Results and discussion

As in Experiment 1, only trials for which gaze position was outside the target area less than 50 ms were conserved for analysis. This corresponded to the removal of 4.6% of total trials ( $SD = 6.9$ ) in Experiment 2A and 10.6% ( $SD = 8.1$ ) in Experiment 2B. Only correct responses were analyzed, corresponding to a removal of 6.6% of responses ( $SD = 6.5$ ) in Experiment 2A and 4.9% of responses ( $SD = 5.0$ ) in Experiment 2B. An ANOVA on reaction time was performed, with participants as a random variable and relation, attentional load, and prime duration as main factors. We found a main effect of relation showing that participants were faster for

congruent compared to incongruent trials [7 ms;  $F(1,37) = 19.48$ ;  $p < 0.0001$ ]. Crucially, we also found an interaction between relation and perceptual load [ $F(1,37) = 5.38$ ;  $p < 0.03$ ], reflecting the fact that the magnitude of priming was larger under low attentional load [11.5 ms;  $t(18) = 3.8$ ;  $p < 0.001$ ] compared to high attentional load condition [4 ms;  $t(19) = 2.25$ ;  $p < 0.05$ ] (see Figure 2b). Although there was a main effect of prime duration [ $F(1,37) = 20.95$ ;  $p < 0.0001$ ] reflecting averaged reaction times decreasing with prime duration, this factor did not interact with relation ( $F < 1$ ). This latter aspect suggests that, as for Experiment 1, the magnitude of priming was not affected by the amount of sensory evidence in the prime stimulus. With regard to prime consciousness, while participants were informed that oriented arrows were presented in their peripheral visual field, none of them declared being able to discern their orientations during the post-experiment debriefing. The objective prime discrimination measure interleaved within the priming measure confirmed this subjective report by revealing chance-level performance under both low (mean  $d' = 0.17$ ;  $SD = 0.62$ ;  $p = 0.24$ ) and high attention load conditions (mean  $d' = -0.01$ ;  $SD = 0.57$ ;  $p = 0.95$ ). In addition, there was no significant difference in prime discrimination as a function of attentional load ( $p = 0.35$ ). Finally, we verified that crowding was the limiting factor impeding prime discrimination by conducting an additional control experiment with five new participants. While they were exposed to the same display as in Experiment 2B (i.e., with prime

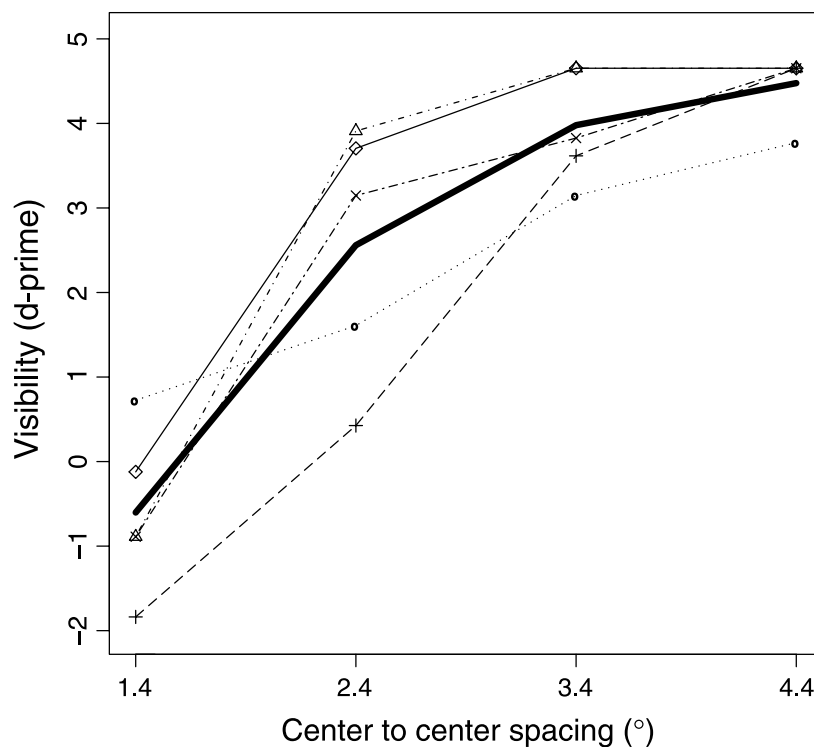


Figure 4. Visibility as a function of center-to-center spacing of the prime and flankers. Each symbol is the average of prime discrimination as computed by a measure of  $d'$ -prime for one participant. The thick line represents the prime discrimination averaged across all participants.

presented for 200 ms, 600 ms, 1000 ms, or 1400 ms), we manipulated the center-to-center spacing between the prime arrow and the flankers (i.e., they were presented randomly with a spacing of 1.4°, 2.4°, 3.4°, or 4.4°). We performed an ANOVA on correct response rate, with prime duration and spacing as main factors. We did not observe a significant effect of prime duration ( $F < 1$ ), in coherence with the fact that crowding is insensitive to stimulus duration (Kooi, Toet, Tripathy, & Levi, 1994). Importantly, we found a main effect of spacing ( $F(1,4) = 55.7$ ;  $p < 0.01$ ), with prime discrimination increasing when flankers were pulled aside, revealing the critical role of flanker position in prime discrimination. Furthermore, plotting of the discrimination performance against the prime-to-flankers distance revealed a horizontal ceiling at greater spacing, followed by a falling slope, a shape proposed by Pelli et al. (2004) as a criterion for crowding (see Figure 4).

## General discussion

This study examined the dissociation between our subjective experience and our processing of crowded contents. For this purpose, we combined gaze-contingent crowding, a novel approach for preventing perceptual discrimination of peripheral stimuli, with a repetition priming paradigm that served as an index of nonconscious perceptual processing. By observing priming effects elicited by peripheral faces subject to self-crowding (Experiment 1) and crowded visual symbols (Experiment 2), we show that although crowded features are integrated into a subjectively jumbled texture, they are nonetheless preserved and used for subsequent processes including those underlying face recognition and directional symbol processing. The two major priming effects reported here have been previously observed with visual masking, posing GCC as one of its legitimate alternative. With regard to face priming, the effect of amplitude measured with GCC is similar to the one previously reported (Henson et al., 2008; Kouider et al., 2009). Similarly, we also found that only famous faces elicit nonconscious priming, suggesting that this effect arises when the subliminal prime triggers some preexisting target face representations. Alternatively, the absence of priming effect with nonfamous faces could be a consequence of the specific fame judgment task we used. Indeed, subjects' preexposure to the nonfamous prime might induce a feeling of familiarity of the target in related trials only (for which the target is the same as the prime), thus interfering with the fame judgment (see Jacoby, Kelley, Brown, & Jasechko, 1989). Concerning symbolic action priming, while the effects we report are highly significant, it is of note that their amplitude is globally smaller than

what is usually observed using meta-contrast masking (Vorberg et al., 2003).

Altogether, the present results extend previous findings that single feature informational contents are processed during crowding (e.g., line orientation; see He et al., 1996). Indeed, they reveal the correct capabilities of multi-feature integration during crowding (e.g., in Experiment 2, only the correct building of a symbolic arrow from the binding of two opposite oriented lines can account for the priming effects we measured). Consequently, these results question the two-step model explaining the origins of crowding (Levi, 2008) and suggest that crowding arise from an impaired access to the integrated content rather than from an impaired featural integration per se. The fact that long-lasting crowded information is processed without consciousness at higher levels (i.e., multi-featural, involving face recognition and directional symbol processing) might reflect the obvious ecological relevance of peripheral vision. Indeed, contrary to masking, peripheral vision is omnipresent during perceptual life and probably results from evolutionary processes whereby visual pathways might have been tuned to efficiently process crowded contents. Thus, when facing a complex visual scene, the nonconscious processing of peripheral faces or sensorimotor cues might improve social interactions and spatial navigation, respectively. Furthermore, because it allows for the visual display of long-lasting complex objects, GCC might represent a suitable approach for a fine-grained probing of these visual pathways and allow for the study of phenomena such as sustained covert attention and temporal integration. Previous research has shown that when the peripheral prime is presented briefly, nonconscious repetition priming disappears above 4° of eccentricity when the prime and target appear at different locations (6° when both appear at the same location; Marzouki & Grainger, 2008), suggesting that brief peripheral stimuli have restricted impact on the cognitive system. Thus, increasing the strength (e.g., duration) of crowded stimuli seems to constitute a relevant, empirically based motivation. Along this line, it is important to stress that gaze-contingent substitution appears to be crucial since participants consistently tried to stare at the long-lasting prime in both experiments, despite the instructions to stare continuously at the target location and the automatic substitution rendering their attempts useless (see Figure 2). Further analyses revealed the efficiency of the gaze-contingent substitution. First, we found no significant difference regarding the prime visibility between trials in which participants stared continuously at the target location and trials in which they stared outside the target location (Welch's  $t$ -test with  $p = 0.91$  in Experiment 1;  $p = 0.34$  in Experiment 2). Furthermore, for the trials in which participants stared outside the target location, we found no correlation between prime visibility and the total looking time outside the target location (slope =  $1.2e - 04$ ,  $p = 0.43$

in [Experiment 1](#); slope =  $-6.8e - 05$ ,  $p = 0.60$  in [Experiment 2](#); see [Figure 5](#)).

It is important to stress that the locus of the priming effects observed in this study cannot result from low-level overlap: despite the congruent physical identity of the prime and targets, they were displayed at different, far apart locations on the screen. It remains unclear, however, whether these effects arise from cortical activity induced by striate and extrastriate routes or rather from direct subcortical pathways. Previous studies relying on nonconscious priming through visual masking have shown that both masked faces and masked arrows induce cortical responses, respectively, in the occipitotemporal cortex for face priming (Kouider et al., 2009) and from visual to motor cortical areas for action priming (Sack, van der Mark, Schuhmann, Schwarzbach, & Goebel, 2009). Investigating the neural correlates of the priming effects observed in this study would improve our comprehension of the origins of crowding. On one hand, there is evidence for the occurrence of featural integration as early as V1 (Neri & Levi, 2006; Pelli, 2008), although these accounts do not predict the existence of informative extrastriate cortical activity during crowding. On the other hand, top-down accounts postulate a causal role for spatial attention occurring between V1 and the lateral occipital complex (Chakravarthi & Cavanagh, 2009). In our study, we found

that decreasing the allocation of covert attention to the crowded prime (by increasing the attentional load of the task) roughly halved the magnitude of action priming. This suggests a two-step model in which the integration of the prime and flankers' features occurs beyond V1 along the visual pathways (downstream integration), allowing for early nonconscious processing (upstream multi-featural processing). In this view, the different adjacent stimuli are processed independently as “uncrowded” by upstream neural systems and reach consciousness once integrated, via downstream neural activity, into a jumbled, texture-like appearance (Balas et al., 2009; Parkes et al., 2001). Thus, crowding might refer to a typical situation of partial consciousness (Kouider et al., 2010) in which the stimulus is perceived as a jumbled object because restricted levels of processing are consciously accessed, while most others remain below the threshold of consciousness.

This finding also has important implication in the current debate concerning the dissociation between attention and consciousness (Koch & Tsuchiya, 2007), bringing additional evidence for attention without consciousness, which is the capacity to attend to something nondiscriminable. We show that nonconscious priming is modulated by spatial attention in addition to temporal attention (Naccache, Blandin, & Dehaene, 2002). This is in line with a previous study showing a similar attentional

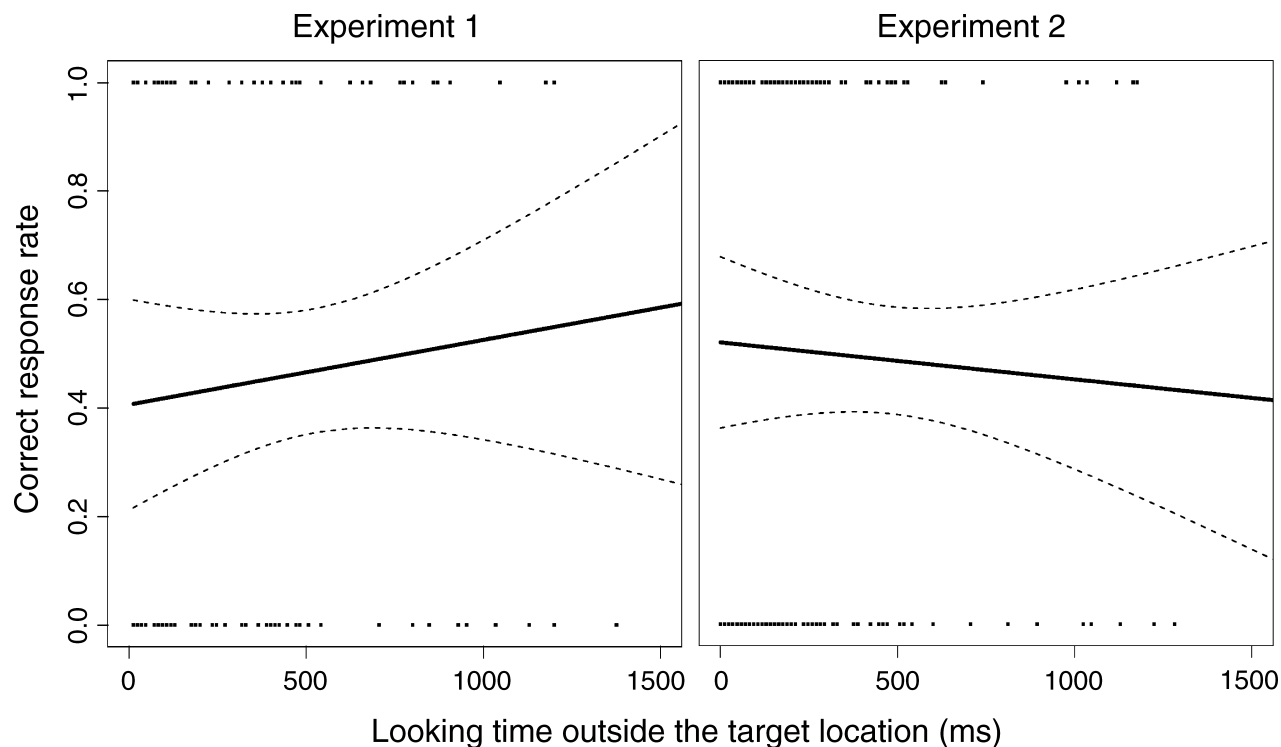


Figure 5. Linear regression between prime visibility and looking time outside the target location (i.e., triggering a gaze-contingent substitution) in [Experiments 1](#) and [2](#). Each black dot stands for one prime discrimination trial, the position on the horizontal axis being defined by the looking time outside the target location, the position on the vertical axis being 1 in case of a correct response or 0 in case of an incorrect response on the prime visibility task. The continuous line represents the linear regression between the looking time and correct response rate. The dashed lines represent the intervals of confidence at 95%.

dependence for the processing of crowded stimuli, restricted though to lower level visual adaptation measures (Montaser-Kouhsari & Rajimehr, 2005). Taken together, higher level priming effects and attentional modulation tend to support top-down accounts, according to which crowded information is not lost but rather not accessed due to an attentional deficit in the periphery. According to this perspective, attention modulates the widening of the integration window (Intriligator & Cavanagh, 2001). However, instead of attributing a causal role to spatial attention in crowding, our results suggest that, at the least, attention modulates upstream multi-features processing in a nonconscious manner prior to integration. Consequently, we propose that the impact of top-down attention actually rests on the amplification of crowded sensory signals by increasing the signal-to-noise ratio (i.e., between prime and flankers) and thus increasing the probability of escaping crowding. Whether attention impacts both the nonconscious encoding of crowded information and the widening of the integration window remains an open question for future research.

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