

Increased sensory evidence reverses nonconscious priming during crowding

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Sensory adaptation reflects the fact that the responsiveness of a perceptual system changes after the processing of a specific stimulus. Two manifestations of this property have been used in order to infer the mechanisms underlying vision: priming, in which the processing of a target is facilitated by prior exposure to a related adaptor, and habituation, in which this processing is hurt by overexposure to an adaptor. In the present study, we investigated the link between priming and habituation by measuring how sensory evidence (short vs. long adaptor exposure) and perceptual awareness (discriminable vs. undiscriminable adaptor stimulus) affects the adaptive response on a related target. Relying on gaze-contingent crowding, we manipulated independently adaptor discriminability and adaptor duration and inferred sensory adaptation from reaction times on the discrimination of a subsequent oriented target. When adaptor orientation was undiscriminable, we found that increasing its duration reversed priming into habituation. When adaptor orientation was discriminable, priming effects were larger after short exposure, but increasing adaptor duration led to a decrease of priming instead of a reverse into habituation. We discuss our results as reflecting changes in the temporal dynamics of angular orientation processing, depending on the mechanisms associated with perceptual awareness and attentional amplification.

Keywords: sensory adaptation, crowding, priming, perceptual awareness

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Introduction

Sensory adaptation is a general property of perceptual systems in which a change of responsiveness follows the processing of a specific stimulus (Webster, 2011). At the behavioral level, sensory adaptation is responsible for two phenomena with opposite consequences. The first one is a positive effect classically referred to as priming and reflects a facilitation when processing a target preceded by an adaptor stimulus sharing some physical (e.g., angular orientation) or conceptual (e.g., semantic) properties. The second one is referred to as sensory habituation (although it is often termed by using the generic term sensory adaptation in the psychophysics literature) and reflects, on the contrary, an inhibitory effect whereby overexposure to an adaptor hurts the processing of a related target. These two effects have been extensively used for probing the neural and cognitive processes underlying perception, by following the assumption that a given stimulus property is indeed processed whenever the system shows adaptive responses on a subsequent target sharing this property. Furthermore, this logic can be extended to the domain of nonconscious perception, as priming and habituation can be observed even when participants are not able to report the presence (chance-level detection) or the nature (chance-level discrimination)

of the adaptor (see Kouider & Dehaene, 2007, for nonconscious priming during masking; see Lin & He, 2009, for nonconscious habituation during binocular rivalry).

When stimuli are consciously visible, sensory adaptation occurs on multiple timescales, ranging from milliseconds to minutes, or even hours (see Kohn, 2007, for a review). Depending on the timescale, sensory adaptation may involve different mechanisms (Grill-Spector, Henson, & Martin, 2006). For instance, the facilitation model states that an adaptor facilitates the identification of a subsequent related target (i.e., priming effect) by improving the coding of the stimulus' features, notably through an increase in synaptic efficacy (i.e., synaptic potentiation). Another account suggests that instead of improving the coding of all stimulus' features, longer adaptor exposure induces the selection of diagnostic features only, while neurons coding features that are nonessential for its recognition stop responding (Desimone, 1996; Wiggs & Martin, 1998). The mechanism underlying this selection, or sharpening, may involve mechanisms such as lateral inhibition, whereby the neurons with the strongest initial response inhibit the rest of the population. Therefore, increasing adaptor exposure decreases the number of adaptor encoded features, which leads to a decrease of overlapping features between the adaptor and the target and, consequently, to a decrease of priming effects.

Behavioral and neural evidences of priming seem to support the coexistence of both the facilitation and the selection accounts, by showing a “rise-and-fall” pattern, with a first period (i.e., following 40 to 250 ms of adaptor exposure) in which priming increases and a second period (i.e., following 350 to 1900 ms of adaptor exposure) in which it decreases (Zago, Fenske, Aminoff, & Bar, 2005). Thus, long adaptor exposure may first facilitate the information coding and then induce a selection of its key features for sustained representation. Paradoxically, after overexposure to the adaptor, the mechanisms involved in priming may become too extreme and, together with neural fatigue, impair the processing of the related target and finally give rise to habituation (Gotts, 2003). Thus, the dynamic change in responsiveness supported by distinct mechanisms is supposed to induce a shift from priming to habituation.

However, deciphering the dynamics of sensory adaptation with visible stimuli might lead to potential confounds. Indeed, theories of consciousness state that perceptual awareness is associated with mechanisms responsible for sustaining perceptual information over time, for instance, through neural broadcasting (Dehaene & Naccache, 2001) or through neural reentrance (Lamme & Roelfsema, 2000). Consequently, the rise-and-fall pattern previously observed might diverge from the substantial properties of sensory adaptation, the decay due to habituation being counteracted by the top-down amplification mechanisms associated with perceptual awareness. Thus, we predicted that preventing perceptual awareness would lead to stronger habituation and actually lead to a switch from a facilitatory to an inhibitory effect when adaptor exposure is increased, in a kind of “rise-and-reverse” pattern of sensory adaptation.

In this study, we focused on the link between priming and habituation, by studying how the strength of sensory signals (i.e., oriented gratings with short vs. long stimulus duration) affects conscious and nonconscious sensory adaptation. We relied on visual crowding, a perceptual caveat in peripheral vision that impairs the discrimination of a peripheral stimulus when it is surrounded by similar flankers (Levi, 2008). This approach offers two main advantages for addressing this issue. First, as long as foveal access to the adaptor is prevented, the strength of crowding does not depend on stimulus duration (Kooi, Toet, Tripathy, & Levi, 1994), which allows for the presentation of long-lasting stimuli remaining undiscriminable. In order to control for participants’ oculomotor behavior, we relied on gaze-contingent crowding, which consists of monitoring gaze position with an eye tracker and substituting the peripheral adaptor by an irrelevant content as soon as participants stare outside a fixation position defined by instructions. Second, while a crowded stimulus appears as jumbled and its informative content remains inaccessible to conscious reports, it still induces sensory adaptation, both at the level of single feature stimuli (e.g., habituation for line orientations; see He,

Cavanagh, & Intriligator, 1996) and multi-feature stimuli (e.g., priming for directional arrows and faces; see Favre & Kouider, 2011; Kouider, Berthet, & Favre, 2011). Using gaze-contingent crowding with both discriminable and undiscriminable stimuli, we assessed how stimulus duration modulated the conscious and nonconscious processing of line orientations. When perceptual awareness was prevented by crowding, we found that being exposed with short-lasting oriented adaptors (i.e., 200 ms) had facilitatory effects on the processing of subsequent related targets (priming), while longer exposure (i.e., 1000 ms) reflected, instead, inhibitory effects (habituation). Restoring perceptual awareness through psychophysical manipulations had a large facilitatory effect on target processing, as it increased priming and canceled habituation. Thus, while our results are similar to the rise-and-fall pattern previously observed during conscious priming, they suggest a reverse of priming into habituation under situations of perceptual unawareness. These results are discussed in light of neural and behavioral correlates of sensory adaptation and perceptual awareness.

General methods

Participants

All observers were university students between 18 and 35 years old. They reported normal or corrected vision and were paid for their participation. Thirteen observers participated in [Experiment 1a](#), 12 in [Experiment 1b](#), 11 in [Experiment 2](#), 16 in [Experiment 3](#), and 15 in [Experiment 4](#).

Stimuli

All stimuli consisted in $1.2^\circ \times 1.2^\circ$ Gabor patches (0.45 Michelson contrast; 2 cycles per degree). Six flanker patches were organized on a circular array surrounding the adaptor patch (center-to-center spacing: 1.3° between two flankers; 2.4° between one flanker and the adaptor). Adaptor and target patches were tilted either 5° to the right or left from vertical. In [Experiment 1a](#), adaptor and target patches shared the same contrast phase. In all the other experiments, adaptor and target patches were presented in contrast counterphase.

Procedure and design

Threshold evaluation

Eccentricity between the adaptor and fixation location was fixed individually prior to the priming experiment with a Quest staircase procedure (Watson & Pelli, 1983), such as participant performed at chance level on the

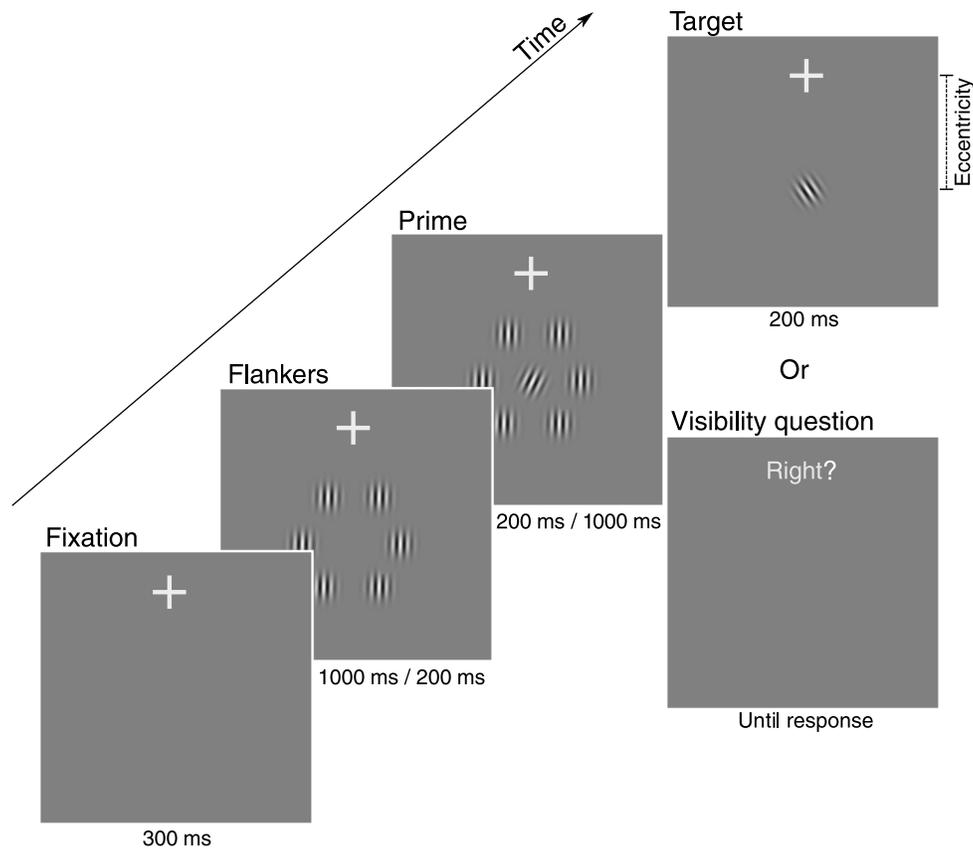


Figure 1. Paradigm used in [Experiment 1](#). Each trial started with the presentation of a fixation cross at the quarter top of the screen. At the bottom of the screen, with an eccentricity fixed individually, this was followed by the apparition of six flanker patches during 1000 ms or 200 ms. Afterward, the adaptor patch appeared in the middle of the flankers, respectively, for 200 ms (short duration condition) or 1000 ms (long duration condition). Following an interstimulus interval of 100 ms, participants were then presented either with a peripheral target on which they had to indicate the orientation or with a question about the adaptor orientation to which they were forced to answer (visibility question). In [Experiment 1a](#), adaptor and target patches shared the same contrast phase. In [Experiment 1b](#), adaptor and target patches were presented in contrast counterphase.

adaptor discrimination task (except in [Experiment 3](#) in which eccentricity was fixed such as participants performed on the adaptor discrimination task with an accuracy of 60%). While participants gazed continuously at a fixation cross situated at the quarter top of the screen, they were first presented with a peripheral circular array of flanker patches for 200 ms. While the flanker patches remained on screen, the adaptor appeared in the middle of the array for 1000 ms. Then, both the flankers and the adaptor patches disappeared, while a question at fixation position relative to the adaptor orientation appeared (i.e., “Left?” or “Right?”). Participants were instructed to answer the question by yes or no, by pressing, respectively, a button with their right or left finger. The question remained on screen until a response was provided. The staircase determined after 70 trials the eccentricity value at which observers performed at chance level. All staircases were inspected, and a staircase was discarded and repeated if it had not properly converged within the maximum number of trials. Importantly, as soon as a participant ceased to gaze at a 5° by 5° area surrounding

the fixation location, the tilted adaptor patch was substituted by a vertical patch during the next refresh cycle of the monitor screen. This gaze-contingent substitution procedure guaranteed that the tilt orientation information was never processed foveally.

Priming experiment

As in the threshold evaluation phase, participants were instructed to stare continuously at the fixation location materialized by the fixation cross. Each trial started by the apparition of the flanker patches at the predetermined eccentricity for 1000 ms or 200 ms, which remained on screen while the adaptor patch appeared, respectively, for 200 ms (short duration condition) or 1000 ms (long duration condition). Thus, taken as a whole, each trial had a constant duration, no matter adaptor duration. Following an interstimulus interval of 100 ms, a target patch appeared for 200 ms at the location previously occupied by the adaptor patch, and participants had to indicate, as fast as possible, whether it was tilted to the right (right

button press) or to the left (left button press) from vertical. By contrast to the adaptor, the target was not surrounded by flankers and, thus, was clearly discriminable (see [Figure 1](#)). The long duration and short duration priming trials were intermixed randomly. In addition to the main task, an adaptor discrimination task similar to the one used for threshold evaluation was randomly administered to the participants in 1 out of 3 trials. In this case, instead of the target, a question relative to the adaptor orientation appeared at fixation position (i.e., “Left” or “Right”). The participant’s task was to decide whether the answer was yes (right button press) or no (left button press). Participants received a total of 60 adaptor discrimination trials randomly intermixed with 120 priming trials. Measuring visibility in alternation with priming presents two advantages. First, the visibility measure is consequently sensitive to potential changes in perceptual thresholds occurring during the experiment (e.g., training or fatigue effects). Second, as participants never know which of the two tasks they will encounter, they must attend to the peripheral adaptor at each trial in case a visibility task occurs. This attentional amplification has been shown to maximize priming effects (Favre & Kouider, 2011; Naccache, Blandin, & Dehaene, 2002). The gaze-contingent substitution was applied as for the threshold evaluation phase. Only trials for which gaze position was correct during 90% of total adaptor duration were analyzed (i.e., 180 ms in the short duration condition and 900 ms in the long duration condition).

Apparatus

Stimuli were displayed against a gray background by a 22-in. Iiyama Vision master pro 510 monitor (luminance of 15.7 cd/m²; frame rate of 85 Hz; resolution of 1024 × 768 pixels) with 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. Chin and headrests were used. Eye movements were recorded monocularly with a tower-mounted eye tracker (Eyelink 1000 System, SR Research, Ontario, Canada) controlled with the Eyelink toolbox (resolution: temporal 500 Hz; spatial > 1°).

Results

Experiment 1

In [Experiment 1](#), we relied on the independence between stimulus duration and stimulus discriminability under crowding (Kooi et al., 1994), in order to measure the influence of adaptor duration on nonconscious sensory adaptation. Participants exposed to short- and long-lasting

oriented adaptors that remained undiscriminable were asked to indicate the orientation of subsequent target stimuli. Comparison of reaction times in related trials (i.e., in which adaptors and targets shared the same orientation) and unrelated trials (i.e., in which adaptors and targets had an opposite orientation) served as an index of sensory adaptation. In [Experiment 1a](#), adaptors and targets shared the same contrast phase. In [Experiment 1b](#), adaptors and targets were presented in contrast counterphase. Since adaptors and targets appeared at the same location on the screen, we wanted to control with [Experiment 1b](#) that adaptation effects do not arise before any cortical processing, for instance, from adaptation to local luminance changes at the level of the retina. [Experiments 1a](#) and [1b](#) are analyzed together, with contrast similarity (i.e., phasic stimuli in [Experiment 1a](#) and counterphasic stimuli in [Experiment 1b](#)) as a between-subject factor.

Results and discussion

First, we determined with the threshold evaluation phase the eccentricity value at which observers performed at chance level (mean eccentricity = 17.38°, *SD* = 3.95). Then, in the priming experiment, data cleaning based on oculomotor behavior during adaptor exposure conserved 91.44% of total trials (see [General methods](#) section). Participants responded correctly on 82.70% of the remaining trials (*SD* = 12.51). Only correct responses were included in the reaction time analyses. We performed an ANOVA on reaction time, with participants as a random variable, relation and adaptor duration as main factors, and contrast similarity as a between-subject factor. We found a main effect of adaptor duration [$F(1,23) = 11.63$, $p < 0.005$], reflecting the fact that participants were faster to answer in the short duration compared to the long duration condition (28 ms, *SD* = 39.79). Importantly, we found an interaction between relation and adaptor duration [$F(1,23) = 63.31$, $p < 0.0001$]. This signed the existence of a priming effect at short duration (i.e., participants were faster to indicate the target orientation when it was preceded by a related vs. unrelated adaptor, mean priming effect = 52 ms, $t(24) = 5.26$, $p < 0.0001$) and a habituation effect at long duration (participants were slower in related vs. unrelated trials, mean habituation effect = -37 ms, $t(24) = -3.81$, $p < 0.001$; see [Figure 2](#)). No significant interaction with contrast similarity was found ($p > 0.1$).

Debriefing the participants after the experiment revealed that none of them declared being able to identify the adaptors. However, while the adaptor discrimination task confirmed that performance was at chance level in the long duration condition (mean $d' = 0.09$, $t(24) = 0.56$, $p = 0.58$), it differed slightly from chance level in the short duration condition (mean $d' = 0.35$, $t(24) = 2.62$, $p < 0.05$). This could indicate that in some trials, some participants might have been able to discriminate the orientation of short-lasting adaptors. In order to address this possibility, we relied on Greenwald’s regression method (Greenwald,

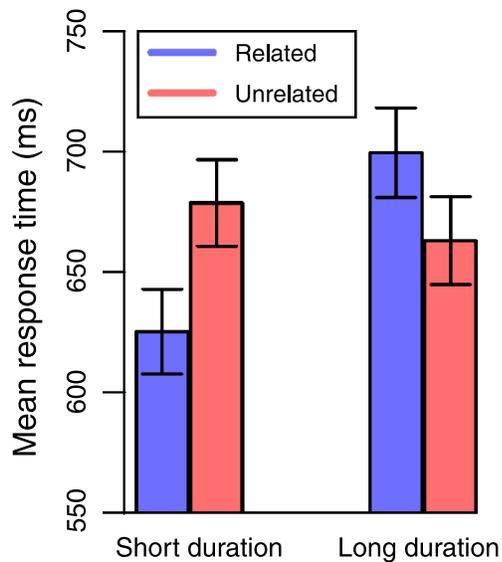


Figure 2. Bar plots of mean reaction times in [Experiments 1a](#) and [1b](#), in related trials in blue (i.e., same orientation shared by the adaptor and the target) versus unrelated trials in red (i.e., opposite orientation shared by the adaptor and the target). Error bars indicate the standard error of the mean.

Klinger, & Schuh, 1995), which revealed that priming extrapolated to null visibility was still significantly above chance (intercept = 44 ms, $p < 0.001$). Furthermore, post-hoc comparisons revealed that the positive priming effect was significant both in [Experiment 1a](#) (31 ms, $t(12) = 3.29$, $p < 0.01$), while adaptor discriminability was at chance (mean $d' = 0.32$, $t(12) = 1.28$, $p = 0.23$), and in [Experiment 1b](#) (74 ms, $t(11) = 4.71$, $p < 0.001$), while visibility was above chance (mean $d' = 0.38$, $t(11) = 4.80$, $p = 0.001$). The higher visibility in [Experiment 1b](#) may explain the larger priming effect (74 ms vs. 31 ms). We come back to this issue in the discussion.

Experiment 2

We aimed at assessing with [Experiment 2](#) that the pieces of evidence we accumulated regarding the reverse of priming into habituation was specific to nonconscious sensory adaptation. We designed this new experiment as an exact replicate of [Experiment 1](#), with the exception that flanker patches were now presented with a horizontal orientation. Thus, the similarity between the peripheral adaptor (tilted $\pm 5^\circ$ from vertical) and flankers was greatly diminished, and crowding was virtually absent (Andriessen & Bouma, 1976). According to the rise-and-fall pattern of conscious adaptation reported by Zago et al. (2005), we postulated that abolishing crowding would preserve the priming effects induced by short adaptor exposure, while it would decrease or cancel the habituation effects induced by long adaptor exposure.

Results and discussion

First, eccentricity threshold was evaluated such as each participant performed at chance level on the adaptor discrimination trial (mean eccentricity = 14.09° , $SD = 3.67$). Importantly, the eccentricity threshold was evaluated with vertical flankers, since the use of horizontal flankers would have led to greater eccentricity values and, thus, to a confound between perceptual awareness and stimulus strength. In the priming experiment, data cleaning based on oculomotor behavior during adaptor exposure preserved 97.12% of total trials (see [General methods](#) section). Participants mean accuracy was 90.21% ($SD = 8.97$). We performed an ANOVA with participants as a random variable and adaptor–target relation and adaptor duration as main factors. As expected, we found an interaction between relation and duration [$F(1,10) = 12.10$, $p < 0.01$], revealing priming effect in the short duration condition (65 ms, $t(10) = 4.29$, $p < 0.01$), while no effect was found in the long duration condition (-6 ms, $t(10) = -0.32$, $p = 0.76$, compared to the significant negative effect of -37 ms found in [Experiment 1](#); see [Figure 3](#)). Here, as we diminished the strength of crowding, adaptor visibility increased both in the short duration (mean $d' = 1.81$, $t(10) = 4.14$, $p < 0.01$) and the long duration condition (mean $d' = 2.22$, $t(10) = 5.04$, $p < 0.001$), without any difference between the two ($p = 0.51$).

Experiment 3

Results from [Experiment 1](#) revealed that the duration of adaptor exposure could determine the direction of

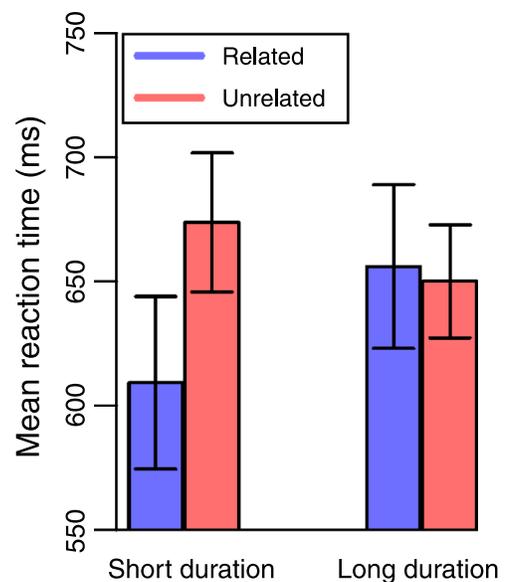


Figure 3. Bar plot of reaction times in related (in blue) versus unrelated trials (in red). In [Experiment 2](#), flanker patches were oriented horizontally, such that crowding was significantly reduced. Error bars indicate the standard error of the mean.

nonconscious sensory adaptation (i.e., priming or habituation), resulting in a reverse pattern in which priming transforms into habituation. Yet, accordingly to other studies (Zago et al., 2005), we did not find such a reversal during conscious priming. In [Experiment 3](#), we aimed at confirming this dissociation in a within-subject design, by contrasting conscious and nonconscious adaptation at constant stimulation. For this purpose, visual crowding offers an interesting perceptual phenomenon for assessing how stimulus awareness impacts on the switch from priming to habituation without any confound with signal strength. Indeed, on a trial-by-trial basis, perceptual awareness (i.e., stimulus discriminability) can vary, while the strength of the visual signal remains equal. Thus, we measured sensory adaptation induced by short- vs. long-lasting adaptors on each trial depending on a subjective adaptor discriminability rating provided by participants. This procedure insured a manipulation of perceptual awareness with a constant stimulation around the discrimination threshold.

Procedure and design

Threshold evaluation

The eccentricity between fixation and adaptor position was set such as participants performed on the adaptor discrimination task with an accuracy of 60% (mean eccentricity = 14.56° , $SD = 3.30$). This performance level allowed us to obtain different visibility levels on a trial-by-trial basis, while stimulation remained constant (see below).

Priming experiment

Each trial started with the apparition of the peripheral flanker patches for 200 ms or 1000 ms, to which was added the adaptor patch, respectively, for 1000 ms (long duration condition) or 200 ms (short duration condition). The gaze-contingent substitution was applied as in [Experiments 1](#) and [2](#). After an interstimulus interval of 100 ms, the target appeared at the location previously occupied by the adaptor. Participants had to indicate as fast as possible whether the target patch was tilted on the right (right button press) or on the left (left button press), within a delay of 1500 ms. Then, they were asked to indicate their subjective level of visibility of the adaptor patch only, on a scale appearing at fixation location ($32^\circ \times 0.12^\circ$ horizontal bar). The scale comprised 20 grades, labeled “rien vu” (i.e., nothing seen) below the leftmost grade and “visibilité maximale” (i.e., maximal visibility) below the rightmost grade. Participants moved a cursor on the scale with the left and right button presses and validated their response with a space bar.

Pilot experiment

As a validation of the subjective visibility rating procedure we used in the priming experiment, we ran a pilot experiment with seven naive participants. For each

of them, the 60% accuracy threshold was evaluated (mean eccentricity = 15.14° , $SD = 2.48$). Then, after being exposed to the crowded adaptor for 1000 ms, they were first asked to answer to the visibility question related to the adaptor orientation (i.e., “Left” or “Right?”). This measure estimated objectively the adaptor discriminability. Then, they had to indicate their subjective level of visibility using the visibility scale. A strong correlation between the objective and subjective discriminability measures [adjusted R -squared = 0.76, $p < 10e - 6$] confirmed that participants used the visibility scale accordingly to their objective performance. In order to analyze reaction times in the priming experiment, we binned trials in function of individual subjective visibility ratings into three different groups (de Gardelle, Kouider, & Sackur, 2010). The low visibility group comprised the 15% of total trials for which the individual visibility ratings were the lowest. Objective discriminability measures in this group did not differ from zero (mean $d' = -0.051$, $t(6) = -0.18$, $p = 0.86$). The high visibility group comprised the 15% of total trials for which the individual visibility ratings were the highest. Objective discriminability measures in this group was high (mean $d' = 3.6$, $t(6) = 7.02$, $p < 0.001$). Finally, the medium visibility group comprised all the other trials (mean $d' = 2.21$, $t(6) = 5.92$, $p < 0.01$). The same classification was used in the priming experiment.

Results and discussion

Based on the validation provided by the pilot experiment, we binned trials individually for each participant in a low visibility group (comprising the 15% trials with the lowest visibility ratings), a high visibility group (comprising the 15% trials with the highest visibility ratings), and a medium visibility group (comprising all the other trials; see [Figure 4](#)).

After the data cleaning based on oculomotor behavior, 84.56% of total trials were analyzed (see [General methods](#) section). Participants responded correctly on 86.68% of the remaining trials ($SD = 6.65$). Only correct responses were included in reaction time analyses. We performed an ANOVA with participants as a random variable and adaptor–target relation and adaptor duration as main factors. We found a main effect of relation, with shorter reaction times in related vs. unrelated trials [21 ms, $F(1,15) = 10.19$, $p < 0.01$], as well as a main effect of adaptor duration, with shorter reaction times in the short vs. the long duration condition [26 ms, $F(1,15) = 17.41$, $p < 0.001$]. Again, we found an interaction between relation and duration [$F(1,15) = 20.63$, $p < 0.001$], showing a priming effect in the short duration condition (53 ms, $t(15) = 4.89$, $p < 0.01$), while the habituation effect for long duration condition did not reach significance (-11 ms, $p > 0.1$). Analyzing effects of sensory adaptation depending on adaptor visibility revealed that in the short duration condition, the priming effect increased

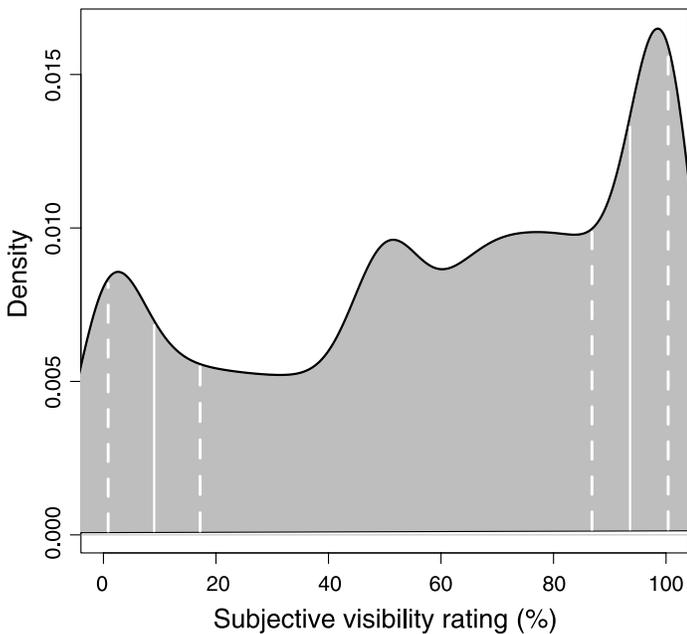


Figure 4. Density estimate of subjective visibility rating in [Experiment 3](#). Full white line represents the boundaries between low, medium, and high visibility groups averaged across all participants (dashed lines represent two standard deviations around the mean).

with adaptor visibility, while in the long duration condition, the habituation effect was significant at low visibility and was abolished as soon as the adaptor became visible (see [Figure 5](#) and [Table 1](#)). Finally, regarding subjective discriminability, an ANOVA with participants as random variable revealed that neither adaptor–target relation nor adaptor duration influenced adaptor discriminability (both $p > 0.1$). To sum up, relying on subjective measures of discriminability with constant stimulation and a within-subject design, [Experiment 3](#) confirmed that the directionality of sensory adaptation (i.e., priming or habituation) depended both on perceptual awareness and adaptor duration. When perceptual awareness was absent, we found evidences for the reverse of priming into habituation, although the priming effect induced by short-lasting stimuli did not reach significance. In comparison to the other experiments, each trial here requested the participant to realize one task on the target followed by another task on the adaptor. This combination might have changed the participants’ strategy and, therefore, disrupted the priming effect. Nonetheless, the effect amplitude (i.e., 26 ms) was similar to what we found in the other experiments, and it remains possible that the analysis we performed based on subjective visibility grouping simply lacked statistical power. Finally, when perceptual awareness was present, the decay of priming we found is similar to the rise-and-fall pattern previously observed during object priming (Zago et al., 2005). Mechanistic interpretation of this pattern supports the

succession of facilitation and selection. First, the processing of all stimulus features is facilitated, which explains the origin of priming effects. After longer exposure, only diagnostic features of the adaptor stimulus remain encoded, which decreases the similarity between the adaptor and the target and induces the decay of priming effects (Wiggs & Martin, 1998).

Experiment 4

In [Experiment 1](#), we found that short- and long-lasting adaptors, respectively, gave rise to priming (i.e., shortening of related target processing) and habituation (i.e., slowing of related target processing). However, short and long exposures differed not only regarding stimulus duration but also regarding stimulus onset asynchrony (SOA) between adaptors and targets. Indeed, in the long duration condition, the SOA was 1100 ms (i.e., 1000 ms of adaptor exposure and 100 ms of interstimulus interval), while the SOA in the short duration condition was 300 ms (i.e., 200 ms of adaptor exposure and 100 ms of interstimulus interval). In order to control that the SOA difference was not at the origin of the reverse pattern of nonconscious sensory adaptation we found so far, we designed [Experiment 4](#), in which participants were exposed with a short-lasting adaptor (200 ms) preceding the target either with a short (300 ms) or long SOA (1100 ms).

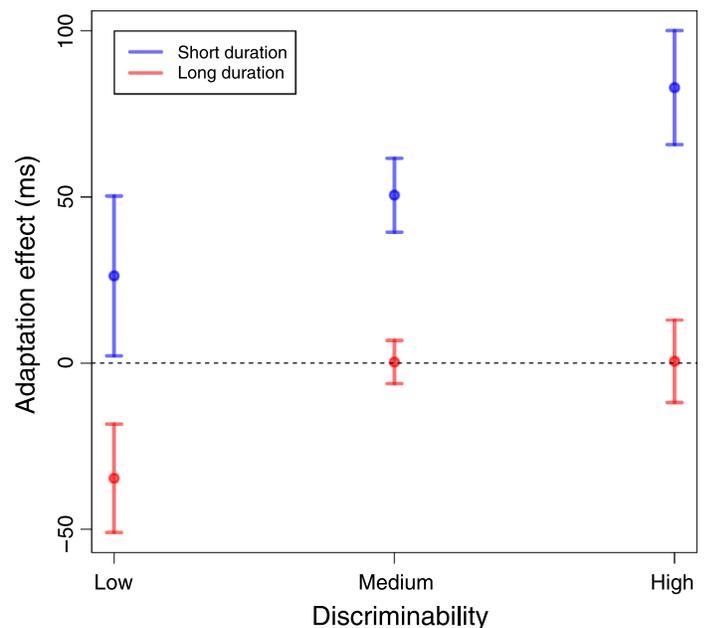


Figure 5. Mean adaptation effects in [Experiment 3](#), depending on adaptor duration (short duration in blue and long duration in red) and adaptor discriminability (low, medium, and high discriminability). Error bars indicate the standard error of the mean.

	Low visibility	Medium visibility	High visibility
Short duration	26 ($p = 0.29$)	51 ($p < 0.001$)	83 ($p < 0.001$)
Long duration	-35 ($p < 0.05$)	0 ($p = 0.96$)	1 ($p = 0.96$)

Table 1. Priming effects (ms) depending on adaptor duration and adaptor visibility.

Procedure and design

Priming experiment

On each trial, flanker patches were presented peripherally during 1200 ms. In the short SOA condition, the adaptor patch appeared 1000 ms after the flankers' onset (i.e., 300 ms before the target). Thus, this condition respected the exact same timing than the short duration condition in [Experiment 1](#). In the long SOA condition, the adaptor patch appeared 200 ms after the flankers' onset (i.e., 1100 ms before the target). The short and long SOA conditions were intermixed randomly. Participants received a total of 60 adaptor discrimination trials randomly intermixed with 120 priming trials. The gaze-contingent substitution was applied as in [Experiment 1](#).

Results and discussion

First, as in [Experiment 1](#), eccentricity threshold was evaluated such as each participant performed at chance level on the adaptor discrimination trial (mean eccentricity = 16.2° , $SD = 3.93$). After gaze-contingent control, 92.00% of total trials were analyzed. Participants performed correctly on 86.98% ($SD = 8.68$). The ANOVA analysis revealed a main effect of relation [$F(1,14) = 8.36$, $p < 0.05$] and only a marginal interaction between relation and SOA [$F(1,14) = 3.19$, $p < 0.1$]. This revealed a priming

effect in the short SOA condition (45 ms, $t(14) = 3.06$, $p < 0.01$) and no effect in the long SOA condition (12 ms, $t(14) < 1$; see [Figure 6](#)). One can note that, if anything, there is a trend for positive rather than negative priming in the long SOA condition. The fact that nonconscious priming decreases very rapidly across time is coherent with the literature on nonconscious priming (Dupoux, de Gardelle, & Kouider, 2008; Ferrand, 1996). Here, what is crucial is that long SOA is not a factor explaining the habituation effect we found with long adaptor exposure in [Experiment 1](#). Regarding now adaptor discriminability, we found chance-level performance both in the short SOA condition (mean $d' = 0.21$, $t(14) = 1.48$, $p = 0.16$) and in the long SOA condition (mean $d' = -0.004$, $t(14) = -0.02$, $p = 0.98$), without any difference between the two conditions ($t(14) = 1.26$, $p = 0.23$). Thus, this result consists in a good replication of the priming effect we found in [Experiment 1](#), this time with both counterphase stimuli and null visibility.

General discussion

So far, the majority of studies on conscious and nonconscious perception have relied on inferences from priming and habituation taken separately. Consequently, little is known regarding the links between these two phenomena. By manipulating independently stimulus duration and stimulus discriminability through crowding, the four experiments presented in this study bring new insights regarding the influences of sensory evidence and perceptual awareness on sensory adaptation.

Nonconscious sensory adaptation

We found that despite being undiscriminable, short-lasting adaptors induced facilitatory effects, both when adaptors and targets shared the same contrast phase ([Experiment 1a](#)) and when they were presented in contrast counterphase ([Experiments 1b](#) and [4](#) in short SOA condition). These typical priming effects reflect that line orientation is processed during crowding, a phenomenon that is now well described (He et al., 1996; Montaser-Kouhsari & Rajimehr, 2005; Parkes, Lund, Angelucci, Solomon, & Morgan, 2001). The reaction time measure we used here to unveil this phenomenon is interesting as it extends the perceptual threshold measures usually employed. Now regarding long adaptor exposures, we

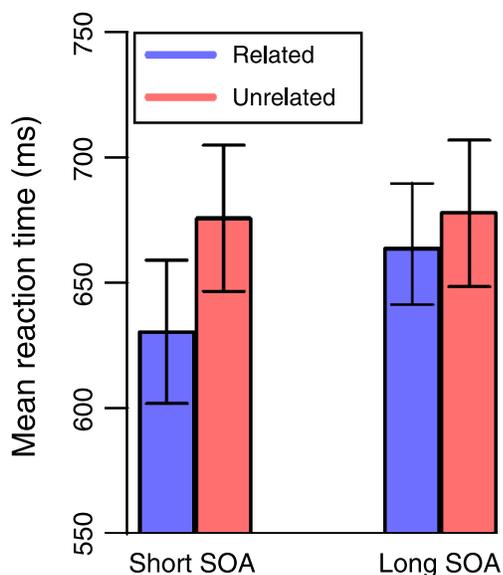


Figure 6. Bar plot of mean reaction times in related (in blue) versus unrelated trials (in red) in [Experiment 4](#). Error bars indicate the standard error of the mean.

found habituation effects, here also both when adaptors and targets shared the same contrast phase ([Experiment 1a](#)) and when they were presented in counter phase ([Experiment 1b](#)). In [Experiment 4](#), we controlled that the long SOA resulting from long adaptor exposure was not at the origin of habituation, as short adaptor exposure with long SOA did not give rise to any trend toward a habituation effect. Thus, it seems that overstimulating the system in the absence of perceptual awareness has a cost in terms of responsiveness, as revealed by sensory habituation.

Taken together, priming after short adaptor exposure and habituation after long adaptor exposure suggest a facilitation–suppression pattern during nonconscious sensory adaptation. This finding is supported by two other studies probing different levels of nonconscious visual processing through different techniques. The first one relied on visual masking, whereby a very short-lasting stimulus preceded and followed by mask patterns remains impossible to detect (see Kouider & Dehaene, 2007, for a review). It has been shown that increasing the repetition number of a masked adaptor word, and thus its cumulated duration, induced a switch from positive to negative influences during semantic priming (Wentura & Frings, 2005). The second one is a recent study from our group relying on continuous flash suppression, a variant of binocular rivalry in which conscious perception of the stimulus in one eye is suppressed when the other eye receives dynamic contour-rich flashes (Barbot & Kouider, [in press](#)). Relying on a face repetition priming paradigm in which participants had to indicate whether a target face was familiar or unknown, this study revealed that face processing was facilitated by prior exposure to short-lasting adaptors (i.e., reaction times decreased), while it was hurt by overexposure to long-lasting adaptors (i.e., reaction times increased). Here, each pair of adaptor and target was either constituted by identical faces or different faces belonging to the same fame category (i.e., they were both famous or both unknown). Thus, as the task involved a fame judgment, the motor responses triggered by the adaptor and the target mapped onto the same hand response in related and unrelated trials. Consequently, the differences in terms of priming or habituation observed when comparing related and unrelated trials cannot arise from motor facilitation and motor inhibition (see Eimer & Schlaghecken, 2003, for a review). In our study however, related trials involved congruent motor activations (e.g., a left-oriented adaptor followed by a left-oriented target), while unrelated trials involved incongruent sequences (e.g., a left-oriented adaptor followed by a right-oriented target). Thus, replicating our findings with estimations of perceptual threshold instead of motor responses (i.e., reaction times) would discard a potential motor origin of the nonconscious overstimulation cost.

Altogether, these results comfort the existence of a nonconscious overstimulation cost, independently of the hierarchical level of processing (i.e., semantic, facial identity, or line orientation in our case) and regardless of

the technique employed to prevent perceptual awareness (i.e., visual masking, binocular rivalry, or gaze-contingent crowding in our case). In consequence, stimulus duration seems to be a property that influences neural responsiveness when perceptual awareness is prevented. This comforts the idea that nonconscious cognition is not limited to a sum of “snapshots,” which are independent from each other, but is able to integrate over time informative signals present in the optic flow (VanRullen & Koch, 2003). Further parametric experiments with higher temporal resolution would be necessary in order to describe more accurately this pattern.

Conscious sensory adaptation

Gaze-contingent crowding allowed for the modulation of adaptor discriminability while maintaining stimulus strength unchanged. Consequently, we were able to make post-hoc comparisons regarding the amplitude of conscious and nonconscious sensory adaptation. In order to increase statistical power, we merged together results obtained from similar conditions across several experiments. First regarding nonconscious priming, we merged results from [Experiment 1a](#) (in which short-lasting adaptor discriminability was at chance) with results from the lowest visibility group of [Experiment 3](#) (in which participants rated the short-lasting adaptor as not perceived). Regarding conscious priming, we merged results from [Experiment 2](#) (in which short-lasting adaptor discriminability was above chance due to the presence of horizontal flankers) with results from the highest visibility group of [Experiment 3](#) (in which participants rated the short-lasting adaptor as perceived). Comparing these two sets of data, we found that priming effects were significantly larger in the conscious compared to the nonconscious situation (74 ms versus 29 ms, $t = 2.38$, $p < 0.02$). Note, however, that within an experiment, no correlation between priming and adaptor visibility was found. Furthermore, in [Experiment 1b](#), in which adaptor discriminability happened to be slightly above chance, we observed the same priming effect amplification in comparison to [Experiment 1a](#) (74 ms versus 31 ms, $t = 2.33$, $p < 0.05$). This argues for the idea that perceptual awareness is associated with an amplification of priming, a phenomenon that was previously reported both at the behavioral (Kouider & Dehaene, 2009) and neural levels (Kouider, Dehaene, Jobert, & Le Bihan, 2007). Along this line, the fact that crowding decreases the amplitude of orientation priming implies that it decreases the coding efficiency of angular orientation. Thus, at the neural level, it suggests that crowding arises at the site where angular orientation is encoded, starting from the primary visual cortex up to area V4 (see Bi, Cai, Zhou, & Fang, 2009; Fang, Murray, Kersten, & He, 2005; Gardner et al., 2005).

Another factor that might explain the lower amplitude of orientation priming in the presence of crowding is the

participants' ability to deploy covertly spatial attention on the peripheral adaptor. Indeed, it has been proposed that crowding reflects a coarsening of spatial attentional resolution in the periphery of the visual field (Intriligator & Cavanagh, 2001). Thus, crowding may reduce the capacity to amplify attentionally the signal from the adaptor and, consequently, decrease its priming influence. Fitting with this view, previous results using gaze-contingent crowding showed that reducing attentional amplification to crowded symbols (i.e., undiscriminable arrows) by exerting an attentional load decreases their priming influences (Favre & Kouider, 2011).

Regarding now the condition with long adaptor exposure, we compared nonconscious and conscious habituation following the same post-hoc analysis strategy. First, regarding nonconscious habituation, we merged results from [Experiment 1a](#) (in which long-lasting adaptor discriminability was at chance) with results from the lowest visibility group of [Experiment 3](#) (in which participants rated the long-lasting adaptor as not perceived). Regarding conscious habituation, we merged results from [Experiment 2](#) (in which long-lasting adaptor discriminability was above chance due to the presence of horizontal flankers) with results from the highest visibility group of [Experiment 3](#) (in which participants rated the long-lasting adaptor as perceived). We found that restoring perceptual awareness canceled the habituation effect we obtained in the nonconscious situation (i.e., -39 ms versus -2 ms, $t = 2.59$, $p < 0.02$). This suggests a negative relationship between sensory habituation and perceptual awareness, since the amplitude of habituation effects decreases with adaptor discriminability.

The results we report concerning the influence of crowding on sensory habituation come within the scope of a recent debate. On the one hand, one study reported that long-lasting adaptors surrounded by high-contrast flanker patches induced less habituation than when surrounded by low-contrast flanker patches (Blake, Tadin, Sobel, Raissian, & Chong, 2006). This result suggests that crowding weakens the influence of long-lasting stimuli on orientation habituation. On the other hand, other studies using long-lasting adaptors in the presence or in the absence of flanker patches reported that crowding has no impact on the amplitude of orientation habituation (Bi et al., 2009; He et al., 1996). These results are at odd with the ones we report, since we found that habituation was present only when perceptual awareness was prevented by crowding. Several differences between our study and the others cited might explain such a discrepancy. First, the studies by Bi et al. (2009), Blake et al. (2006), and He et al. (1996) measured habituation through estimations of perceptual thresholds, while we relied on reaction time measures. Second, all these studies compared the influence of crowding on sensory habituation while manipulating the signal strength (i.e., contrast or presence of flankers), whereas, in our case, the comparisons between nonconscious (i.e., crowded) and conscious habituation (i.e., less

or not crowded) was realized at constant stimulation. Furthermore, in the study by Blake et al., the adaptor was presented during 5 s, while it flickered in counterphase with the flankers at 1 Hz in order to prevent Troxler's fading. In the study by Bi et al., the adaptor was presented during 3 s, while it flickered in counterphase with the flankers at 2 Hz. In our case, no flickering was applied since no Troxler's fading occurred at the exposure duration we used (1000 ms). The roles of stimulus constancy and stimulus duration during sensory habituation remain to be tested. Finally, it is of note that all the studies we referred to relied on long-lasting stimulation and, thus, reported habituation without considering priming effects.

A possible mechanism for the anti-correlation between sensory habituation and perceptual awareness is that when the adaptor becomes visible, participants are able to compensate for any influence that is perceived to be distracting or detrimental to task performance. Typically, this is the case in unrelated trials, in which the adaptor is orthogonal to the target. A prediction made by this account is that increasing the proportion of related compared to unrelated trials should restore the conscious habituation effects, as participants would not repress the influences from highly predictive adaptors. Using fMRI, a recent study showed that repetition suppression was reduced when stimulus repetitions were improbable, suggesting the involvement of top-down strategies during sensory adaptation (Kaliukhovich & Vogels, 2011; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). We could argue that the repression of short-lasting visible adaptors should also disrupt the priming effects they induce. Yet, with a duration of only 200 ms, the time necessary to develop intentionally this strategy might be insufficient, explaining why no repression occurs.

Another explanation for our results on priming and habituation is, as stated in the [Introduction](#) section, the change of neural regime depending on perceptual awareness. Indeed, several theoretical arguments suggest that the processing of angular orientation leading to priming and habituation might have two different time courses depending on the adaptor discriminability. First, compared to nonconscious perception that primarily involves feed-forward activity sweeping from the sensory cortex up to higher regions, perceptual awareness involves feedback activity from frontoparietal regions down to the sensory cortex (Dehaene et al., 2006; Lamme & Roelfsema, 2000). Reentrance has been shown to modify many neural sensory processes, among which neural tuning (Ringach, Hawken, & Shapley, 1997). According to the tuning account of priming (Desimone, 1996), sharpening stimulus encoding by reentrance is likely to increase priming effects. Second, it is known that perceptual awareness is associated to a maintenance of information through top-down amplification, once the neural inputs enter into a global workspace consisting of distributed long-distance brain networks linking visual cortex to frontoparietal regions (Dehaene & Naccache, 2001). On the one hand,

this maintenance is likely to preserve the positive influence of short-lasting stimuli on related targets even in condition of long SOA. On the other hand, this maintenance is likely to counteract or delay the occurrence of sensory habituation arising from long-lasting stimuli. Furthermore, as for perceptual awareness, attentional amplification is a plausible mechanism counteracting the occurrence of sensory habituation, as it decreases the strength of afterimages induced by prolonged stimulus exposure (Suzuki & Grabowecky, 2003). One prediction arising from this hypothesis is that an experimental condition using long-lasting visible stimuli under a strong attentional load should restore the negative effects we found with invisible stimuli. However, attentional load is also known to reduce the level of habituation induced by indiscriminable stimuli (Bahrami, Carmel, Walsh, Rees, & Lavie, 2008; Montaser-Kouhsari & Rajimehr, 2005). Experiments manipulating both the discriminability and the attentional amplification of long-lasting stimuli will be necessary to disentangle the interaction of perceptual awareness and attention during sensory habituation. Additionally, one limitation of the current study is that we focused on the comparison of two data points only (relatively short vs. long duration), which does not allow for an interpretation of the dynamics behind the reversal from a positive effect of priming to a negative effect of habituation. Further experiments with a finer range of stimulation duration will be necessary in order to assess whether our results reflect a change in the properties of sensory adaptation or, more generally, a shift in the temporal dynamics of conscious and nonconscious processing.

Conclusion

Relying on gaze-contingent crowding, we measured sensory adaptation induced by short- vs. long-lasting stimuli. When perceptual awareness was prevented, we found an increase in visual responsiveness after brief stimulus exposure (priming), which reversed into a decrease in visual responsiveness after longer stimulus exposure (habituation). In the presence of perceptual awareness, priming associated with brief stimulus exposure was amplified, while habituation associated with longer stimulus exposure was canceled. We proposed that the mechanisms associated with perceptual awareness and attentional amplification are at the origin of the amplification of priming and the prevention of sensory habituation.

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