Current Biology 23, 150–155, January 21, 2013 http://dx.doi.org/10.1016/j.cub.2012.11.047

Report

Cueing Attention after the Stimulus Is Gone Can Retrospectively Trigger Conscious Perception

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Summary

Is our perceptual experience of a stimulus entirely determined during the early buildup of the sensory representation, within 100 to 150 ms following stimulation [1, 2]? Or can later influences, such as sensory reactivation, still determine whether we become conscious of a stimulus [3, 4]? Late visual reactivation can be experimentally induced by postcueing attention after visual stimulus offset [5]. In a contrary approach from previous work on postcued attention and visual short-term memory, which used multiple item displays [6, 7], we tested the influence of postcued attention on perception, using a single visual stimulus (Gabor patch) at threshold contrast. We showed that attracting attention to the stimulus location 100 to 400 ms after presentation still drastically improved the viewers' objective capacity to detect its presence and to discriminate its orientation, along with drastic increase in subjective visibility. This retroperception effect demonstrates that postcued attention can retrospectively trigger the conscious perception of a stimulus that would otherwise have escaped consciousness. It was known that poststimulus events could either suppress consciousness, as in masking, or alter conscious content, as in the flash-lag illusion. Our results show that conscious perception can also be triggered by an external event several hundred ms after stimulus offset, underlining unsuspected temporal flexibility in conscious perception.

Results

Experiment 1

We tested the hypothesis that late sensory reactivation, as can be induced by orienting attention after stimulus offset [5, 8, 9], can trigger conscious perception of a stimulus that would otherwise pass unseen. Previously, robust effects of postcued attention have only been found in contexts that challenged visual short-term memory, with four or more clearly visible items [5–7, 10]. Postcued attention was found to improve the selective transfer of sensory information into visual short-term memory. However, whether postcued attention retrospectively affects perceptual experience itself remains unknown [11–13]. Studies interested in the effect of attention on perception actually postulate that postcued attention cannot affect perception per se and exclusively used postcues as a control for nonperceptual decision biases [14–20].

In contrast, here we assessed whether postcued attention could influence the perception of a single stimulus at threshold in an exogenous attention paradigm [21] where the attentional cue provided no information on stimulus location, thus minimizing its influence on decision. The target stimulus was a single low-contrast Gabor patch of random orientation, which could be flashed randomly within one of two circles to the left or right of central fixation (Figure 1A). Participants had to report the target's orientation. Target contrast was determined individually, in the absence of cueing, to reach 80% accuracy. During the actual experiment, attention was randomly cued to the left, right, or both sides by a brief dimming of one or both circles. Importantly, dimming prevented masking of the target, which could result from more usual attentional cues, such as thickening or abrupt onset of a shape near the target's location. This cue appeared either before or after the target. At the end of each trial, a response cue (thickening of one side of the fixation circle) indicated the target's side, thus eliminating location uncertainty [14]. Eighteen volunteers were included in this experiment. Accuracy here was immune to response biases, and similar patterns of results were obtained on *d'* (see Figure S1 available online). It should be noted that even if the participants had a response bias for some response options (e.g., left-tilted options or the most vertical or horizontal options), such bias averaged out in the calculation of accuracy. Furthermore, participants judged stimulus orientation, a dimension that was orthogonal to its location. When the cue preceded the target, our results replicated the typical time course of precued exogenous attention (Figure 1B): congruent cues—same side as target—improved orientation accuracy relative to incongruent cues—opposite side [ANOVA with factors congruency (2) × precue stimulus onset asynchrony (SOA) (3); congruency: $F(1,17) = 8.78$, $p < 0.01$]. As expected, this effect was strong for cues presented 200 or 100 ms before target and absent earlier [congruency × SOA: $F(1.6,27.6) = 8.3$; $p < 0.005$]. Critically, congruent cues presented after the target also substantially improved orientation discrimination (Figure 1B) [ANOVA for postcues; congruency: $F(1,17) = 37$; $p < 0.0001$]. This strong effect was maintained 400 ms after the target. It was mainly due to a benefit of congruent cueing, which improved performance compared to 80% accuracy in the absence of cueing. Reaction times here are less informative because participants waited for the response screen. However, the fact that acceleration in reaction time paralleled the effects observed on performance confirmed the absence of a speed-accuracy tradeoff (Figure S1).

These results contrast with previous studies, which assumed that postcues can only act at a nonperceptual

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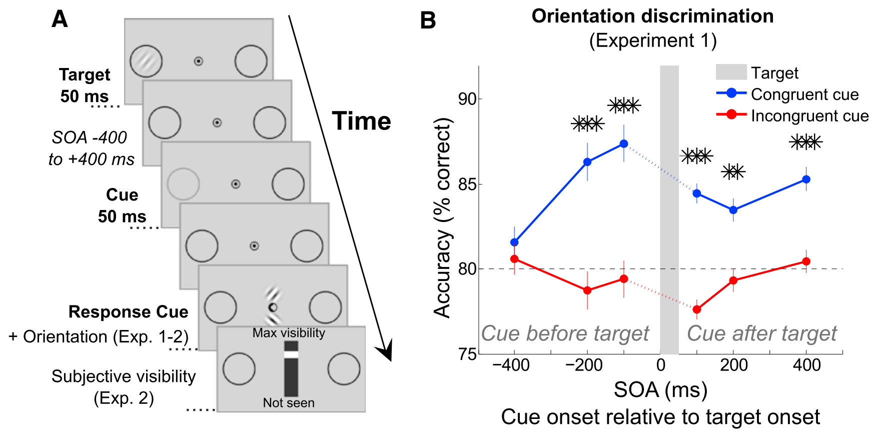

Figure 1. General Experimental Protocol and Results of Experiment 1

(A) Experimental protocol. Each trial began with the onset of a dot at the center of the fixation circle. Following a random delay (500 to 900 ms), a target—Gabor patch with random orientation—was presented for 50 ms within one of the circles to the left or right of fixation. Target contrast was determined for each subject following a staircase. A cue could appear before or after the target. It consisted in a brief dimming of one of the circles, either on the same side as the target (congruent cue, illustrated here) or on the opposite side (incongruent cue). A response screen appeared 500 to 900 ms after target offset, with a response cue accurately indicating the target's side (thickening on one side of the central fixation circle). Participants reported the target's orientation by choosing between two response options, above or below fixation, representing the matching orientation and the orthogonal orientation. In experiment 2, a second response screen followed, with a scale on which participants rated the subjective visibility of the target using a cursor.

(B) Results from experiment 1. Congruent cues improved participants capacity to correctly report the target's orientation, even when presented after the target's offset. Post hoc paired t test for cues presented 400 ms after the target: t (17) = 3.33; $p < 0.005$. Baseline accuracy in the absence of cueing was 80% (set during the staircase procedure). Error bars represent standard error of the mean effect size. Significance: *$p < 0.05$; **$p < 0.01$; ***$p < 0.005$. See also Figures S1 and S2.

decisional stage [15–20]. These studies found either no effect or a disruptive effect of postcueing on sensitivity, except for one study reporting that informative postcues that reduced location uncertainty on the target improved sensitivity by biasing the weigh of the target versus the distracters in the decision. This subtle decision bias was found in only two subjects out of three [19]. In contrast, here we observed strong and robust postcueing effects, despite an experimental design that minimized decisional effects. This suggests that, contrary to a commonly held assumption, postcueing can influence perception itself.

The bilateral cueing condition—dimming on both sides—provided further details about the spatial properties of this effect. Bilateral cues improved orientation discrimination with a similar time course to congruent cueing, except at the latest SOA, where the bilateral cueing effect was abolished (Figure 2A) [ANOVA with factors congruency (bilateral versus incongruent) × SOA (6 levels); congruency: $F(1,17) = 13$, $p < 0.005$; congruency × SOA: $F(3.2,54.5) = 3.29$, $p < 0.05$]. This result is consistent with previous studies showing that exogenous precues can enhance sensitivity at multiple locations simultaneously [22, 23] and confirms that postcueing can affect sensitivity even when the cue cannot possibly bias decision. The bilateral cueing effect was slightly smaller than the congruent cueing effect (Figure 2B) [ANOVA for postcue; congruent versus bilateral cues: $F(1,17) = 4.70$, $p < 0.05$], a difference that was even clearer on sensitivity (Figure S1C). However, the similarity of these two conditions between −200 ms and +200 ms suggests that, at these SOAs, cueing involved more than a single spatial focus of attention. Cueing probably reinstantiated the placeholders as important spatial indexes for the task [23]. Such a mechanism can be efficient unilaterally or bilaterally. At these SOAs, cueing probably also involved low-level interactions: the transient dimming of the cue might produce local sensory effects similar to a luminance context effect [24]. Finally, congruent cues still produced a robust improvement in orientation discrimination 400 ms after target onset, whereas the effect of bilateral cues was abolished (post hoc t test at +400 ms: t (17) = 4.47, $p < 0.001$). Because low-level interactions around the target position are identical in the congruent and bilateral cueing condition, this suggests that, at this SOA, low-level interactions ceased to play a role.

To further assess the role of low-level sensory interactions, we performed a control experiment (21 participants) in which the low-level properties of the cue were modified. If local sensory interactions fully accounted for the cueing effects, important physical changes should alter the effects [25]. The new cues (Figure S2A) were noise-textured annuli with a transient texture-contrast modulation (i.e., a second-order transient with no change in mean luminance) and were 1.5 times larger than in experiments 1 and 2. Both pre- and postcueing effects were maintained [congruency for precues: $F(1,20) = 14.1$, $p < 0.005$; congruency for postcues: $F(1,20) = 27.1$, $p < 0.0001$] (Figure S2B). The retroperception effect is therefore unlikely to rely on low-level mechanisms only.

In conclusion, these results show that when a single stimulus is presented, attracting attention toward its location after its offset can still have a very substantial effect on our capacity to report a simple feature of this stimulus, such as orientation. Because the stimulus was presented alone, sensitivity improvements probably directly reflected improved perception. However, this effect could still reflect a form of "blindsight" [26]: good objective performance in the absence of conscious visual experience. Indeed, previous studies have shown that attention can improve processing even when the stimulus remains unconscious [27–29]. To precisely assess how this effect relates to conscious perception, we performed a similar experiment measuring both objective report and subjective visibility.

Experiment 2

This second experiment, including 18 new volunteers, was similar to the previous one except that participants also reported the subjective visibility of the target on a scale [30, 31] (Figure 1A). Results on the objective orientation discrimination task replicated the results of the first experiment (Figure 3A) [congruency: $F(1,17) = 34$, $p < 0.0001$].

We could determine participants' detection sensitivity (Figure 3B) by comparing visibility ratings for "target present" versus "target absent" (Supplemental Experimental Procedures). When no target was presented, the response cue

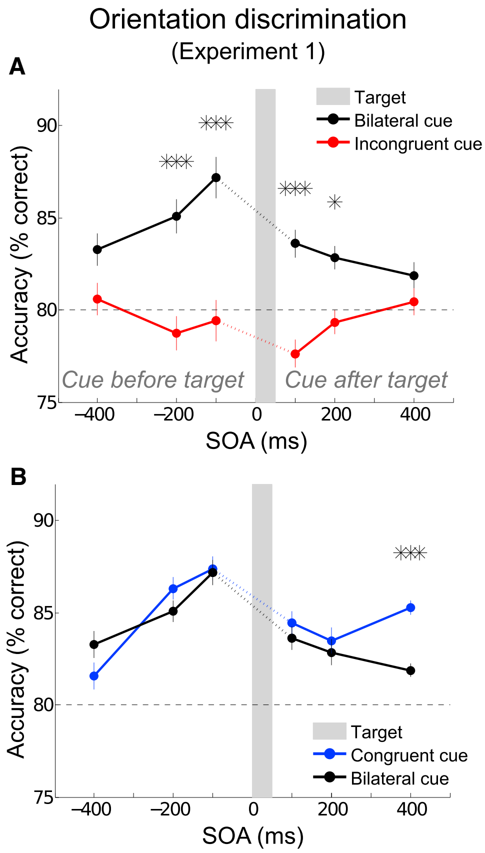

Figure 2. Experiment 1: Comparison with the Bilateral Cueing Control

(A) Bilateral cues (simultaneous dimming on both sides) also improved accuracy for orientation judgment compared to incongruent cues, both when presented before or after the target.

(B) This effect closely followed the beneficial effect of congruent cues, except 400 ms after target's presentation, where a benefit of cueing was observed only for congruent cues. Conventions are as in Figure 1.

randomly instructed the participants to indicate what they saw on the same side as the preceding attentional cue (congruent) or on the opposite side (incongruent). Therefore, we could assess the response bias introduced by the attentional cue: in the absence of a target, participants still reported slightly higher visibilities on the cued side than on the opposite side (Figure 4B). The effects we describe next are corrected for this bias. Detection sensitivity (Figure 3B) was significantly improved by congruent cues relative to incongruent cues, both before and after the target [congruency: $F(1,17) = 23$, $p < 0.0001$; congruency restricted to postcues: $F(1,17) = 15$, $p < 0.001$]. In other words, postcued attention improved participants' capacity to detect the presence of the target.

The correspondence between subjective visibility and objective performance on orientation discrimination confirmed that participants accurately used the scale to rate fine variations in target visibility (Figure 3C). This tight correspondence was unchanged across all experimental conditions (Figure S3). Detailed analysis of visibility ratings (Figure 4) showed that the observed improvement in detection sensitivity for congruent versus incongruent cues was explained by a decrease in the proportion of trials where subjects claimed they did not see the target at all (visibility 0%) and an increase in the proportion of trials where they used high visibility ratings, with no significant changes for intermediate visibilities (Figure 4A). This suggests that attention did not induce a simple unimodal shift in subjective visibility [30] and associated objective performance. Instead, it seems that attention influenced the balance between two types of trials: (1) trials where participants did not perceive the stimulus consciously and thus rated its visibility as if it were absent (Figure 4B), corresponding to near-chance performance on the objective task (Figure 3C), and (2) trials where participants did perceive the stimulus consciously, in which case both subjective visibility and objective performance were high. This interpretation was supported by modeling the distribution of subjective visibility ratings in each condition as a mixture of two unimodal distributions present in the experiment (Figures 4C and 4D): the visibility ratings obtained when the target was present and "seen" (congruent precueing with correct report of target's orientation) versus when the target was absent. This model, applied to each participant individually, significantly fitted the data in every experimental condition for 16 out of 18 participants ($p < 0.05$, average $r^2 = 0.94 \pm 0.06$; Figure S4 and Table S1). The proportion of "seen" trials estimated through this model (β) was strongly influenced by both pre- and postcued attention and could account for the effect observed on detection sensitivity (compare Figures 4E and 3B). Following this estimation, congruent cues presented 100 and 400 ms after the target increased the proportion of "seen" trials by 16% and 9%, respectively. This analysis suggests that both pre- and postcued attention induced the crossing of a threshold between the absence of conscious access and conscious perception [30]. This sensitive measure of visibility also reveals that the effect probably starts to decline at 400 ms, consistent with a decay of the sensory memory trace at long latencies. Future experiments will be needed to probe the temporal extent of retroperception.

In conclusion, experiment 2 replicated the results of experiment 1 and its associated control experiment and additionally showed that the improvement in objective perceptual report induced by postcues was paralleled by drastic improvements in subjective visibility, thus discarding the interpretation of the results in terms of blindsight. These results demonstrate that postcued attention had a direct and drastic impact on the conscious perceptual experience of the target.

Discussion

Retroperception

The present study demonstrates that attracting attention several hundred ms after a single near-threshold stimulus can produce robust enhancement of the visual experience associated with this stimulus. This validates our initial prediction and supports the hypothesis that late sensory reactivation, beyond the initial construction of a sensory representation, plays a causal role in conscious perception. Postcueing induced drastic improvements both in objective report and in subjective judgment of visual experience. These enhancements could reflect two possible mechanisms: either the postcue directly triggered a new percept, by giving conscious access to a previously unconscious memory trace, or the postcue improved memory for an already conscious percept. The present data rather favor a perceptual interpretation. Indeed, postcueing's major effect was to reduce the number of trials where participants claimed they did not see any target at all, using 0% visibility, which was the visibility they also used to rate absent targets. Participants were explicitly instructed to

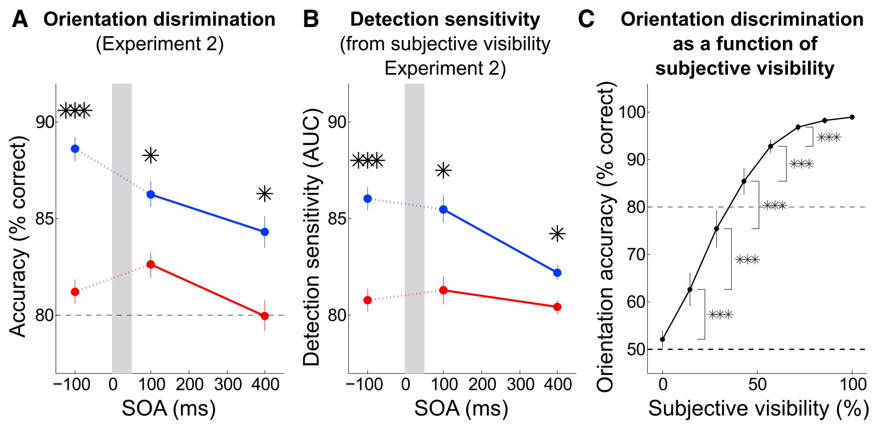

Figure 3. Results from Experiment 2 Replicated and Extended Results from Experiment 1

(A) Results for the orientation discrimination task replicated the results of experiment 1.

(B) Participants' detection sensitivity, derived from subjective visibility ratings for present and absent targets (see Supplemental Experimental Procedures), was also improved by congruent cues both before and after target presentation.

(C) Objective performance on orientation discrimination for the eight possible subjective visibility ratings between 0% ("not seen") and 100% ("maximal visibility"). When participants rated subjective visibility as 0% ("not seen"), corresponding performance on orientation was not significantly different from chance. With each increment in subjective visibility, associated orientation accuracy showed a significant increase, except for the three highest visibilities, where orientation performance reached a plateau. Chance level is 50%; the baseline average performance is 80% in the absence of cueing. See also Figure S3.

use visibilities above 0% as soon as they had a vague impression of having seen a stimulus. So if postcueing only improved the memory of an already conscious percept, one would expect participants to shift their ratings from low, but still above 0%, visibilities toward higher visibilities, but not to change their claim of having seen the target at all. Thus, although future studies will be needed to specify how postcues operate in this new protocol, present evidence already favors the interpretation that postcueing retroactively induced the conscious perception of stimuli that would otherwise not have been seen. This new phenomenon could thus be termed "retroperception."

Relationship with Previous Studies on Postcueing

The present study invites us to amend the commonly held assumption that postcued attention cannot influence perception itself [15–20]. In studies using postcued attention in multiple-item displays [5–7, 10], the limited capacity to report these items need not reflect the full content of conscious perceptual experience, because detailed report of individual items is limited by the capacity of visual short-term memory [32, 33]. George Sperling's seminal work on iconic memory [6] and more recent developments on longer lasting "fragile visual short-term memory" [7] have demonstrated that this limitation to report can be indirectly bypassed by using postcues to probe report of only a subset of items. However, one cannot conclude about the conscious or unconscious nature of the information that is not probed by the postcue: Is it conscious but not reported because it overflows the limitations of visual short-term memory [1, 11]? Or is it unconscious and remains so because it is not selected by attention [34, 35]? Thus, one cannot decide whether the postcue directly acts on perception or whether it only acts on consolidation in visual short-term memory.

In the present work, we alleviated constraints on visual short-term memory by using a single stimulus defined by only one major feature: orientation [32, 33]. Consequently, we observed no dissociation between the ability to report stimulus orientation and the subjective visual experience of this stimulus, which contrasts with iconic memory experiments [6]. Furthermore, we could directly compare conscious perception of the stimulus when it was cued or not cued. This provided direct proof that, contrary to what was previously assumed [15–20], postcued attention can trigger the conscious perception of a stimulus that would otherwise have remained unconscious. Although it is true that late postcues cannot influence the initial formation of a sensory representation, the present results demonstrate that they can, however, have a major impact on perceptual experience by triggering conscious access to this representation.

Relationship with Other "Postdictive" Effects

Previous studies have described intriguing "postdictive" effects [36], in which the perception of a stimulus is influenced by another perceptual event occurring shortly after its offset. Such phenomena include backward masking [37], apparent motion, and the flash-lag effect [36]. The present retroperception phenomenon provides a further example that conscious perception can deviate from the strict timing of external events. It also extends this observation in several important ways. It was known that a poststimulus event could either alter conscious content, as in the flash-lag illusion, or impair perceptual experience, as in backward masking. The present study demonstrates that a poststimulus event can also drastically improve perception. Furthermore, although masking or other postdictive phenomena are no longer effective beyond 100 to 150 ms poststimulus, retroperception can happen as late as 400 ms poststimulus, suggesting previously unsuspected temporal flexibility in conscious perception.

Putative Neural Mechanisms

Many studies have shown that the brain can retain a very rich sensory trace for a second or more after stimulus offset [5–7], even for low-contrast stimuli [38]. We propose that as long as this sensory trace remains active within sensory areas [39], conscious access to this trace—be it iconic memory or another form of sensory memory—can be induced by a subsequent external event, even if the initial processing of the stimulus was too weak to produce a conscious percept in the first place. Recent neuroimaging studies have shown that postcued attention can indeed reestablish neural activations in sensory areas [5, 8, 9] and even in the primary visual cortex [5]. In the present case, this postcued reactivation probably involved both low-level sensory interactions and higher-level top-down influences on sensory areas, and future neuroimaging studies will be needed to investigate the neural basis of the present retroperception phenomenon. We tentatively propose that, in the present experiments, this reactivation of the sensory trace provoked the ignition of

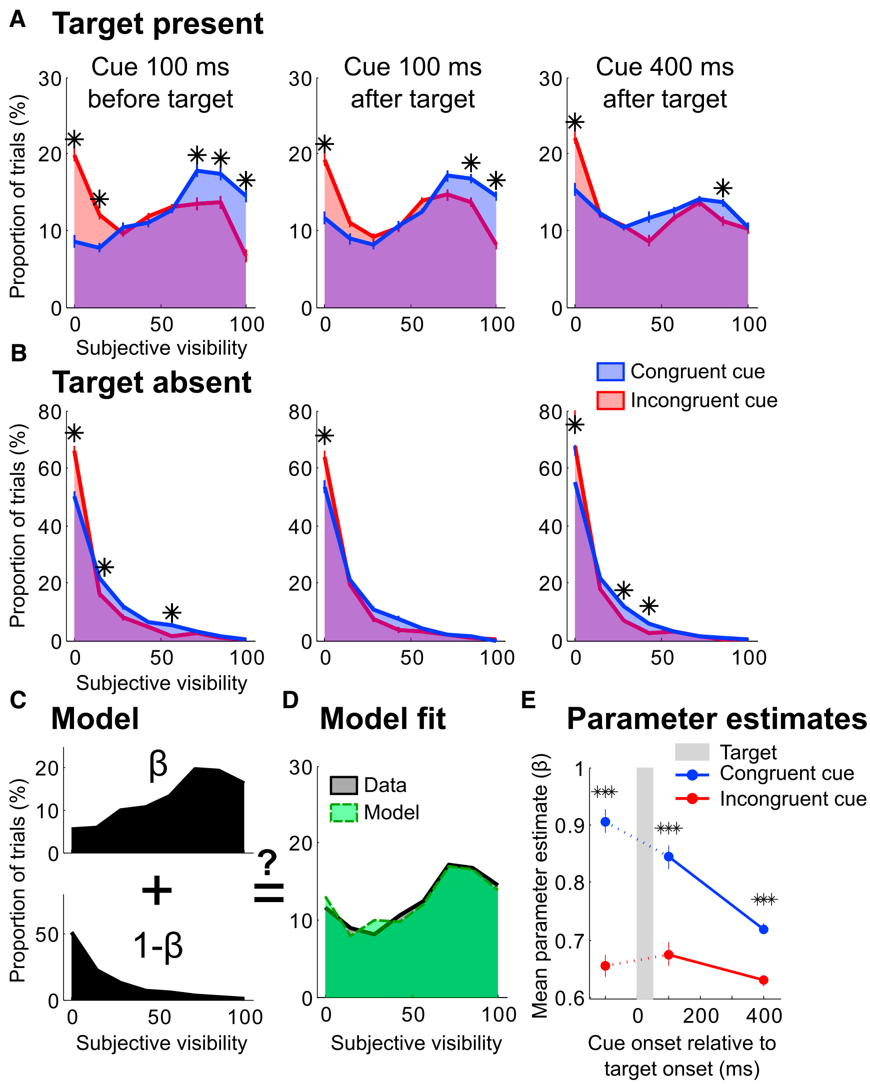

Figure 4. Response Distributions on the Subjective Visibility Scale in Experiment 2

(A) Response distributions on the subjective visibility scale (0% is "not seen"; 100% is "maximal visibility") when the target was present for congruent versus incongruent cues at the three tested stimulus onset asynchronies (SOAs) (in columns). Distributions for congruent cues are transparent blue areas; distributions for incongruent cues are transparent red areas. The area is purple where the two distributions overlap.
(B) Response distributions in the same experimental conditions when the target was absent. Congruent and incongruent cueing conditions can still be distinguished in that case, thanks to the use of a response cue.
(C–E) Modeling of the response distributions.
(C) Schematic representation of the model. For each subject, we modeled the visibility distributions in each experimental condition as a balance between the distributions obtained—for this subject—when the target was absent (bottom row) and when the target was present with a good visibility (top row; precued targets with a correct response on orientation; see Supplemental Experimental Procedures). Shown here is the average of these two template distributions across all participants. The model was tested using a simple regression with one parameter: β.
(D) Illustration of the model fit for one experimental condition. In black is the averaged distribution across participants for congruent postcue at SOA = +100 ms (reproduced from A, second column). In green is the average of the modeled distribution across participants for this condition.
(E) Parameter estimates. The average β value across participants, which estimates the contribution of the "seen" trials as modeled in (C) top row, was significantly increased for congruent versus incongruent cues, both before and after target presentation. See also Figure S4 and Table S1.

a more global network of areas. Within this global workspace, this specific sensory representation would be shared with higher-level areas, thus allowing conscious access to this representation [4]. The observed jump in subjective visibilities already suggests such nonlinear mechanisms of late global ignition.

Conclusion

In conclusion, the present study demonstrates that conscious perception can be triggered by an event that is independent of the stimulus itself, even beyond 100 to 150 ms after stimulus offset, i.e., beyond the establishment of local recurrent loops in visual cortex [1, 2]. This observation challenges the view that such early interactions are sufficient to yield conscious experience of the stimulus [1]. It rather suggests that the initial sensory processing associated with a stimulus can occur preconsciously [4], because its conscious or nonconscious fate can change drastically beyond this phase. Conscious perception would thus relate to the secondary amplification of preconscious information held in sensory areas [4]. Our results further bring a notable and interesting amendment to that view: this secondary amplification does not have to be a direct consequence of the initial processing of the stimulus itself but can be triggered by a subsequent and independent external event.

Supplemental Information

Supplemental Information includes four figures, one table, and Supplemental Experimental Procedures and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2012.11.047.

Acknowledgments

We thank Patrick Cavanagh for very useful comments on the manuscript. This study was supported by a Marie Curie Reintegration Grant from the European Community (to C.S.), by a grant from the Fyssen Foundation (to V.W.), and by the Fondation pour la Recherche Médicale ("Equipe FRM 2010" grant to L.N.).

Received: June 26, 2012
Revised: October 12, 2012
Accepted: November 23, 2012
Published: December 13, 2012

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