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(Citation)

Journal of Vision, 16(7):3-3

(Issue Date)

2016-05

(Resource Type)

journal article

(Version)

Version of Record

(Rights)

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(URL)

<https://hdl.handle.net/20.500.14094/90003487>



Retrospective triggering of conscious perception by an interstimulus interaction

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Attention facilitates conscious perception of a visual stimulus at an attended location. Interestingly, a recent study (using the Posner spatial-cueing task) reported that attention facilitated conscious perception even when it was cued after a stimulus was gone (postcued-attention or retroperception effect). Here, we show that this effect can be induced without any contribution of attention. Contrary to previous situations, we fixed a position of a target (Gabor patch) and cue (luminance change of a circle encompassing the target) across trials so that subjects always could allocate their full attention to the target position. The cue (luminance change) improved objective and subjective visibility of the nearby target even when it was given ~200 ms after the target's offset. This retrospective improvement was diminished when a shape of the cue was changed from a circle to a dot pattern, suggesting that the improvement emerged from a visual interaction (combinations of shapes) between the circular cue and target. Those results indicated that a local visual interaction between the target and cue is sufficient to trigger consciousness of the target, revealing a new type of retroperception effect mediated by sensory (nonattentional) mechanisms.

Introduction

When two visual stimuli are presented in a rapid temporal succession, conscious perception of the first stimulus is disrupted by the second one, even when viewers pay full attention to the first stimulus (Breitmeyer & Ganz, 1976; Kahneman, 1968). This is called the backward masking and known to be a typical example for a retrospective cancelling of perceptual consciousness. It represents a temporal flexibility in conscious perception and has provided an important

insight into mechanisms through which the brain produces conscious representations of visual stimuli (Dehaene, Changeux, Naccache, Sackur, & Sergent, 2006; Lamme, 2006; Tononi & Koch, 2008). In contrast to a number of studies on the backward masking; however, little attention has been assigned to an opposite effect of backward interaction; the second stimulus facilitates (rather than inhibits) conscious perception of the first. Investigating this possibility of “backward facilitation (or a retrospective triggering of consciousness)” would directly contribute to understanding how neural responses to a stimulus are converted into a conscious representation in the brain.

Recently, a study by Sergent et al. (2013) reported that attention played a key role to induce the retrospective triggering of consciousness (Sergent et al., 2013). Using the Posner spatial-cueing task (Posner, 1980), they tested whether attention that was cued after an offset of a target stimulus (postcued attention) facilitated conscious perception of the target. The target was a Gabor patch with a threshold contrast (duration: 50 ms) presented at one of two (left or right) peripheral locations demarcated by black circles (rings). Attention was cued by a short dimming (luminance change) of the ring, although a position of the target was determined independently of a cue position. The authors found that performance in an orientation judgment task (and scores of visibility ratings) on the target was improved when it appeared at a cued location (congruent trials) compared to a noncued location (incongruent trials), even though the cue was presented 100–400 ms after the target offset (the retroperception effect).

The study aforementioned strongly indicated that postcued attention can facilitate conscious perception of a preceding stimulus. It is known, however, that attention is a cognitive function that is closely related

Citation: Xia, Y., Morimoto, Y., & Noguchi, Y. (2016). Retrospective triggering of conscious perception by an interstimulus interaction. *Journal of Vision*, 16(7):3, 1–8, doi:10.1167/16.7.3.

doi: 10.1167/16.7.3

Received October 10, 2015; published May 3, 2016

ISSN 1534-7362

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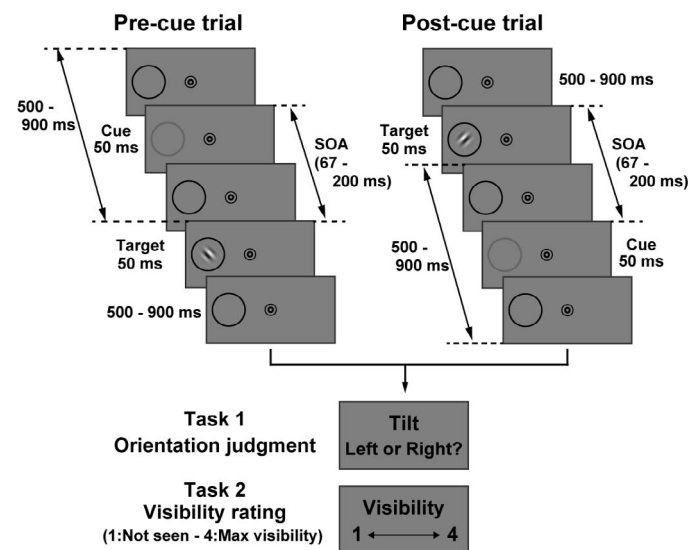


Figure 1. Structures of trials. A target stimulus was a Gabor patch (tilted either leftward or rightward by 45° , 50 ms in duration) presented at 9° away from the fixation point (at the left visual field in this Figure). A position of the target was demarcated by black circle (ring) and fixed throughout an experimental session so that subjects could attend to the target's position in every trial. In most trials, the black ring changed its luminance into dark gray for 50 ms (called the “dimming” or “cue,” conforming to a previous study). A stimulus-onset asynchrony (SOA) between the cue and target was variable across trials from -200 to 200 ms (negative SOAs denote precue trials where the cue preceded the target). Subject answered an orientation (leftward or rightward, task 1) and subjective visibility (using a four-point scale, task 2) of the target, neglecting the cue.

to perceptual consciousness (Cohen, Cavanagh, Chun, & Nakayama, 2012; Koch & Tsuchiya, 2012), sometimes playing a decisive role to determine whether the same stimulus is consciously recognized or not (e.g., inattention blindness; Mack & Rock, 1998). The backward facilitation (retroperception) described previously thus might be achieved by this power of attention that strongly modulates consciousness (Sergent et al., 2013). In other words, no study has investigated whether the backward consciousness can be triggered solely based on a sensory interaction between the cue and target (as the backward masking), not requiring any contribution of attention.

A purpose of the present study is to explore this possibility of the “sensory-level (nonattentional)” retroperception effect. Specifically, we tested a situation where positions of cue and target were fixed across trials. While there were two possible locations for a target previously (Sergent et al., 2013), the target in our study was always presented at a left visual field throughout an experimental session (and at a right visual field in another session). Subjects could predict a

position of a target and thus could allocate their full attention continuously to the target position in every trial. If a dimming of a black ring after the target (cue in a previous study) improved a visibility of the target in the present study, this would reflect a local sensory (visual) interaction between the dimming and target, not a modulation by postcued attention.

Experiment 1

Methods

Participants

Twenty-eight healthy subjects (13 females, age: 19–57) participated in Experiment 1. All subjects had normal or corrected-to-normal vision. Informed consent was received from each subject after the nature of the study had been explained. All procedures in this study conformed to The Declaration of Helsinki. All experiments were carried out in accordance with guidelines and regulations approved by the ethics committee of Kobe University, Japan.

Stimuli and task

All visual stimuli were generated using Matlab Psychophysics Toolbox (Brainard, 1997; Pelli, 1997), and were presented on a screen of a CRT monitor (resolution: 1024×768 pixels, viewing distance: 57 cm; NEC Tokyo, Japan) at a refresh rate of 60 Hz. Basic structures of stimuli are shown in Figure 1. Two black circles (0.01 cd/m^2) were continuously presented on a gray background (13 cd/m^2). One was small (0.63° in diameter) and located at the center of a screen. Another was large (2.44° in diameter) and located at 9.3° eccentricity either to the left or right of the central point. The large circle (ring) indicated a position where a target (Gabor patch, see the following material) would appear. Its location was fixed (left or right) throughout an experimental session so that subjects could predict the target position.

Each trial began with a presentation of a black circle (fixation point, 0.31° in diameter) within the central small circle. After a random delay of 500–900 ms, a Gabor patch (target, size: 2° in diameter, spatial frequency: 1 c/°) appeared for 50 ms at a position demarcated by the ring. The target was tilted either into rightward or leftward by 45° (variable across trials). A luminance contrast of the target was determined for each subject to produce an accuracy of 60%–70% in an orientation-judgment task (see the following material). After another (posttarget) delay of 500–900 ms, task screens were presented to prompt subjects to perform two tasks sequentially. In the first task, subjects

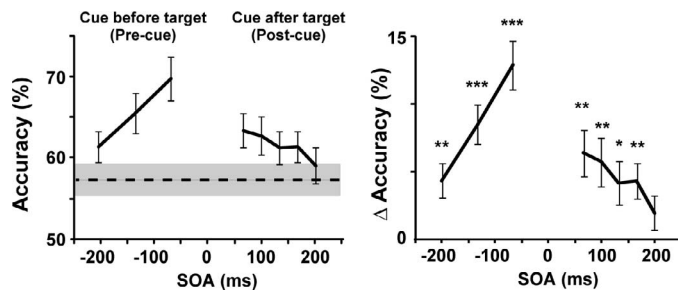


Figure 2. Accuracies in the orientation judgment task (chance level: 50%) averaged across all subjects. Results in LVF (left visual field) and RVF (right visual field) were combined. A dotted horizontal line indicates a mean accuracy in a control (no-cue) condition with the SE (across subjects) shown by the background shading. Accuracies in the cue-present trials were higher than that in the no-cue trials both when the cue preceded (precue trials) and followed (postcue trials) the target. A differential accuracy between the no-cue trials and each of the cue-present trials was shown in the right panel. Asterisks indicated significant differences from the no-cue trials (uncorrected p values of one-group t tests at each SOA, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).

answered an orientation of the target (leftward or rightward) by pressing one of two buttons (orientation judgment task). In the second task (visibility rating task), they reported subjective visibility of a target using a four-point scale (Koivisto, Mantyla, & Silvan-to, 2010) from one (not seen) to four (maximum visibility). No time limitation was imposed on either task.

We instructed subjects to maintain the fixation throughout the trial. Changes in their eye positions were monitored and recorded at 1000 Hz using the EyeLink CL system (SR Research, Ontario, Canada) and the EyeLink Toolbox on Matlab (Cornelissen, Peters, & Palmer, 2002). If subjects broke the fixation during a trial, data in that trial were discarded and the same trial was repeated later.

Procedures

In Experiment 1, we investigated how a dimming of a ring (cue) affected objective and subjective visibility of a nearby target. In the cue-present trials, the ring changed its luminance from black (0.01 cd/m^2) to dark gray (5.8 cd/m^2) for 50 ms. A stimulus-onset asynchrony (SOA) between the cue and target was chosen from -200 , -133 , -67 , 67 , 100 , 133 , 167 , and 200 ms. Negative SOAs (-200 , -133 , and -67 ms) indicate the precue trials in which the cue preceded the target (Figure 1, left), while positive SOAs (67 , 100 , 133 , 167 , and 200 ms) denote the post-cue trials where the cue followed the target (Figure 1, right). No-cue trials were also conducted as a control condition. Subjects

performed six sessions of 90 trials in which trials of those nine conditions (eight cue-present conditions and the no-cue condition, 10 trials for each) were randomly intermixed. In half of the six sessions, all stimuli (target and cue) were presented at the left visual field (LVF) whereas those were shown at the right visual field (RVF) in the other half. An order of the LVF and RVF sessions were counterbalanced across subjects.

Before going to main experimental sessions previously mentioned, subjects conducted a practice session of 30 trials. A luminance contrast of a Gabor patch that would produce the 60%–70% accuracy was estimated for each subject based on performances of the practice session. The Michelson contrast of the Gabor patch for the main sessions ranged from 0.045–0.068.

Results and discussion

Figure 2 show accuracies (% correct) of the orientation judgment task averaged across all subjects. Accuracies in the cue-present trials (pre-cue trials: 61.65–70.2%, postcue trials: 59.3%–63.7%) were generally higher than that of the no-cue condition (57.3%, indicated by a horizontal dotted line). We measured an effect of the cue on task performances by computing differential accuracy (Δ accuracy) between the no-cue condition and each of eight cue-present conditions (right panel of Figure 2). The cue effect was statistically evaluated by a one-group t test applied to each condition. Since we repeated the t test for eight times (SOAs of -200 to 200 ms), the p values were corrected for multiple comparisons by a factor of eight (the Bonferroni methods). In the precue conditions, significant increases in task accuracy (compared with the no-cue trials) were observed at all three SOAs, -200 ms: $t(27) = 3.44$, corrected $p = 0.015$; -133 ms: $t(27) = 5.78$, $p < 0.001$; and -67 ms: $t(27) = 7.20$, $p < 0.001$. Accuracies in the postcue trials also showed significant increase at SOAs of 67 ms, $t(27) = 3.68$, corrected $p = 0.008$; 100 ms, $t(27) = 3.18$, corrected $p = 0.03$; and 167 ms, $t(27) = 3.27$, corrected $p = 0.024$. The Δ accuracies at 133 ms and 200 ms did not reach significance, 133 ms: $t(27) = 2.59$, corrected $p = 0.12$, 200 ms: $t(27) = 1.51$, $p = 1$. Those results showed that a dimming of a black ring facilitated an identification of a target not only when the dimming took place before the target but also when it was given after an offset of the target.

We also analyzed visibility scores (1: not seen to 4: maximum visibility) in the second task. Similar to the task accuracies, subjects reported higher visibility of a target in the cue-present than no-cue trials. Means and SEs across subjects were 1.36 ± 0.07 (no-cue), 1.96 ± 0.12 (SOA: -200 ms), 2.04 ± 0.11 (-133 ms), 2.09 ± 0.12 (-67 ms), 2.04 ± 0.12 (67 ms), 2.04 ± 0.12 (100 ms), 2.04 ± 0.12 (133 ms), 2.04 ± 0.12 (167 ms), and

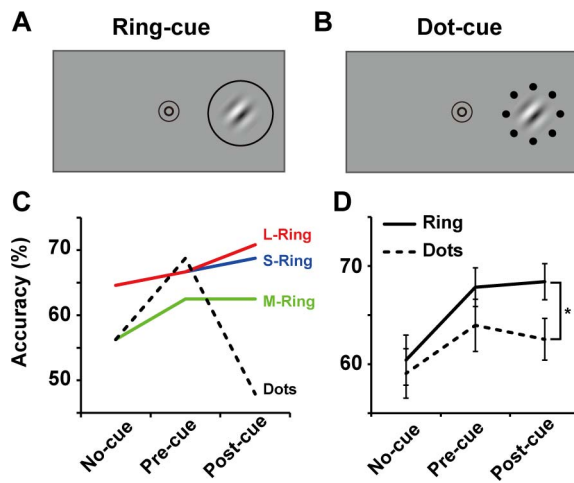


Figure 3. Experiment 2. (A) Ring cue. As with Experiment 1, the black ring changed its luminance into dark gray for 50 ms (called “dimming” or “cue”). (B) Dot cue. Eight black dots (0.19° in diameter) were placed around a target (Gabor patch) region. The center-to-center distance from the target to each dot was 1.22° . In the cue-present trials, those eight dots simultaneously increased their luminance into dark gray for 50 ms. (C) Accuracy of the orientation judgment task in a representative subject. The SOAs between the target and cue were -100 ms in the precue and 100 ms in the postcue conditions. The baseline accuracy (accuracy in the no-cue trials) of the dot-cue condition was comparable to that of the M-ring condition (green) in this subject (see text for details). (D) Task accuracy averaged across all 12 subjects. The postcuing effect by the ring cue (Experiment 1) was successfully replicated in Experiment 2 (solid line), although changing a shape of cue (from a ring to dots) significantly diminished the effect (dotted line). Error bars denote SE across subjects. $*p < 0.05$, paired t tests corrected for multiple comparisons.

2.03 ± 0.11 (200 ms). One-group t tests applied to differential scores yielded significant increases at all eight SOAs, $t(27) > 6.49$, $p < 0.001$ for all. These scores, however, were poorly correlated with an objective measure (task accuracy) in both precue ($r = 0.20$, $p = 0.065$) and postcue ($r = 0.03$, $p = 0.69$) conditions. The scores therefore might reflect a perceptual bias (or a response bias) in which the presentation of a clear supraliminal stimulus (cue) caused subjects to report higher visibility of a threshold stimulus (target).

Experiment 2

Results in Experiment 1 suggested that a local sensory (visual) interaction between the dimming and target was sufficient to induce the retroperception effect. One might argue, however, that the retroper-

ception effect in Experiment 1 can be explained by allocation of temporal (rather than spatial) attention. For example, when the black ring dimmed at 100 ms later than the target (100-ms SOA trials), subjects could guess an approximate time at which the target was presented. This attentional cuing in the temporal domain might enable recognition of the target that would otherwise have been omitted, resulting in higher task accuracies in the cue-present than no-cue trials (Figure 2). In Experiment 2, we examined this possibility by changing experimental procedures in the following two points. First, while a delay from the fixation point to the target (Gabor patch) had been variable across trials (500–900 ms) in Experiment 1, it was fixed at 400 ms in Experiment 2 so that subjects could easily predict a time at which the target appeared on the screen. If the retroperception in Experiment 1 reflected an allocation of temporal attention, such attentional effect would be induced in all trials in Experiment 2 (because subjects knew when they should pay attention to a target position). We thus expect no difference in accuracy between the cue-present and no-cue conditions. Second, we tested the postcuing effect caused by another type of cue (a dot pattern in Figure 3B). If temporal attention was critical, the retroperception effect (if any) would be equally observed in the ring-cue (Figure 3A, same as Experiment 1) and dot-cue trials, because both types of cues work as a temporal marker for an onset of the target (that would trigger an allocation of temporal attention). If the retroperception effect reflected a sensory interaction between the cue and target, however, changing a shape of the cue (from a ring to dot pattern) would cast some influences on a magnitude of the effect. Given a spatial sparseness of dot elements, one might predict a diminishment of the postcuing effect in the dot-cue compared to ring-cue trials.

Methods

Subjects

Twelve subjects (four females, age: 20–36) participated in Experiment 2. Other details were identical to Experiment 1.

Procedures for main experimental sessions

As described previously, we compared two types of cues (ring vs. dots) in Experiment 2. Different shapes of cues, however, involved different spatial configurations of the target and cue regions (compare Figure 3A and B). This difference in visual configurations might greatly influence a visibility of the target through, for example, the visual crowding effect (Whitney & Levi, 2011). To make a fair comparison

between the ring-cue and dot-cue conditions, task accuracy in the baseline (no-cue) trials therefore should be matched between the two conditions. We dealt with this issue by testing three types of ring-cue conditions with different sizes: S-ring (2.44° in diameter), M-ring (3.75°), and L-ring (5°). For each subject, task accuracy of the baseline trials in those three (S, M, and L) ring-cue conditions were compared with that in the dot-cue conditions (Figure 3C). A ring-cue condition with baseline accuracy closest to the dot-cue condition was identified and used for a comparison of the ring-cue versus dot-cue conditions. As shown in Figure 3D, this procedure achieved a matched task accuracy in the baseline (no-cue) trials between two cues (ring vs. dots).

Structures in one trial were identical to Experiment 1 except for the following two points. First, a delay from the fixation to target was kept constant (400 ms). Second, subjects performed the orientation judgment task only (they did not perform the visibility rating in Experiment 2). In addition to the baseline (no-cue) trials, we tested a precue condition (SOA: -100 ms) and postcue condition (SOA: 100 ms) for each shape of cue. Crossing four types of cue shapes (S-ring, M-ring, L-ring, and dot pattern) with those three conditions (no-cue, -100 ms, and 100 ms) produced 12 conditions. Each subject performed six sessions (three for the LVF and three for the RVF) of 96 trials in which trials in those 12 conditions were randomly intermixed. Other details (monitoring of eye movements, etc.) were identical to Experiment 1.

Procedures for supplementary sessions

Apart from the main sessions previously mentioned, we conducted supplementary sessions using the same group of 12 subjects. Although a stimulus sequence in those supplementary sessions was identical to the main sessions in Experiment 2, subjects attended to a cue region (black ring or dots, not Gabor patch) and monitored an onset of cue (luminance increase) in that region. They were asked to hit a key as quickly as possible when the ring (or dots) changed its luminance from black (0.01 cd/m²) to dark gray (5.8 cd/m²). No response was necessary when they saw no dimming. Each session comprised 16 cue-present trials (four trials each for S-ring, M-ring, L-ring, and dot pattern) randomly intermixed with eight no-cue trials. Subjects performed two sessions, one for the LVF and another for the RVF. We analyzed hit and false-alarm rates as well as reaction times to each type of cue. The hit and false-alarm rates were then converted into a sensitivity measure (d') in the signal detection theory. Those data were used to check whether visual salience of a cue (luminance increase) was balanced between the

ring-cue and dot-cue conditions (see the following material).

Results and discussion

Accuracy in the orientation discrimination task (main sessions in Experiment 2) is shown in Figure 3D. We first examined whether a fixed delay from the fixation to target (400 ms) eliminated the postcueing effect in the ring-cue trials (by enabling an allocation of temporal attention to the target in every trial). A one-way analysis of variance (ANOVA) over the three conditions (no-cue, precue, and postcue) in the ring-cue trials (solid line in Figure 3D) yielded a significant main effect, $F(2, 22) = 7.37$, $p = 0.004$, $\eta^2 = 0.40$, and post-hoc comparisons with the Bonferroni correction indicated significant differences in the no-cue versus pre-cue (corrected $p = 0.028$) and the no-cue versus post cue (corrected $p = 0.025$) conditions. These results replicated findings in Experiment 1 and did not support the possibility of temporal attention. We then analyzed the postcueing effect induced by a dot pattern (dotted line in Figure 3D). No significant main effect was observed in the one-way ANOVA over the three (no-cue, precue, and postcue) conditions, $F(2, 22) = 1.68$, $p = 0.21$, $\eta^2 = 0.13$. Furthermore, direct comparisons between the ring-cue and dot-cue trials using t tests (corrected for multiple comparisons by a factor of three) revealed a significant difference only in the postcue conditions (mean \pm SE: $68.4 \pm 1.8\%$ for the ring-cue and $62.5 \pm 2.1\%$ for the dot-cue, $t(11) = 3.47$, corrected $p = 0.016$). Those results indicated the postcueing effect selectively induced by the ring-cue (not the dot-cue) trials, which did not support an account by temporal attention.

We also analyzed the d' (sensitivity) and reaction time to each type of cue (luminance increase) in the supplementary sessions. The d' (mean \pm SE across 12 subjects) was 2.84 ± 0.14 for the ring cue and 2.63 ± 0.2 for the dot cue. The reaction times were 425.4 ± 24.8 ms for the ring cue and 433.1 ± 25.1 ms for the dot cue. No significant difference between the ring and dot cues was observed in the d' , $t(11) = 1.79$, $p = 0.10$, and reaction time, $t(11) = 1.22$, $p = 0.25$, suggesting that visual salience of the dimming (that might trigger an allocation of temporal attention) was balanced between the two types of cues.

Those results in the main and supplementary sessions of Experiment 2 indicated that changing a shape of a cue from a ring to a dot pattern significantly attenuated the postcueing effect. This attenuation might be explained by the same mechanism as the meta-contrast masking in previous studies. Unlike a normal type of masking where

target and mask are presented at a spatially-overlapping position (the pattern masking), the metacontrast masking occurs when a mask is shown at an adjacent but nonoverlapping position to a target (Breitmeyer, 1984). Since a masking shape needs to closely fit contours of a target, the metacontrast masking is thought to emerge from local interactions (e.g., lateral inhibition) between neurons encoding contours of the target and mask (Enns & Di Lollo, 2000). If the postcueing effect in the present study depends on such local interaction among visual neurons, a use of the dot cue would substantially reduce contour-to-contour interactions between the cue and target (because of a spatial sparseness or discontinuity of dot elements), resulting in the diminishment of the postcueing effect as shown in Figure 3D.

General discussion

In the present study, we investigated how a dimming of circular place holder (cue) affected perception of a target stimulus (near-threshold Gabor patch). The dimming increased both accuracies of the orientation judgment not only when it was given before the target but also when it occurred after the target was gone (Experiment 1). This effect of retrospective facilitation was difficult to be explained by temporal attention (Experiment 2), indicating that a part of the facilitatory effect reflected a local sensory interaction between the cue and target.

The present results indicate that there were at least two types of retrospective perception (Sergent et al., 2013), one emerging from sensory (visual) interaction and another from allocation of postcue attention. This distinction between sensory-based and attention-based retroperception has remained unclear in the previous study. As described in the Introduction, Sergent et al. (2013) used the Posner spatial-cueing task and showed that a presentation of postcue elevated task accuracy in the congruent compared to incongruent conditions. Importantly, they also tested the third condition in which circular place holders (rings) in the left and right visual fields dimmed simultaneously (bilateral condition). They found that the bilateral postcue at SOAs of 100–200 ms facilitated recognition of the target as the congruent postcue did. Those results suggested that the retroperception effect actually emerged from a local sensory interaction between cue and target (rather than postcued spatial attention). Another interpretation, however, was that this improvement resulted from more than a single spatial focus of attention guided by the bilateral cue (Sergent et al., 2013). It is known that one can divide a spotlight of spatial

attention into multiple separate locations (McMains & Somers, 2005; Muller, Malinowski, Gruber, & Hillyard, 2003) and that exogenous precues of attention can enhance sensitivity of visual processing at multiple locations simultaneously (Solomon, 2004; Wright, 1994). The increased task accuracy in the bilateral condition, therefore, can be explained by *postcued divided attention*. In summary, it has remained unclear whether the retroperception effect at SOAs of 0–200 ms reflected the attention-based mechanism or sensory interaction. Our present study demonstrated the sensory-based retroperception effect by controlling spatial (Experiment 1) and temporal (Experiment 2) attention.

When a target is followed by a second stimulus at adjacent positions, the second stimulus normally disrupts conscious perception of the target (metacontrast masking and object-substitution masking; Enns & Di Lollo, 2000). Why did the dimming of a black ring in the present study facilitate (not inhibit) conscious perception of a preceding target stimulus? One possibility would be the visible persistence or iconic memory for the target stimulus (Coltheart, 1980). It is generally known that a visual representation of a brief stimulus could persist after a physical offset of that stimulus. The dimming of a black ring thus somehow might interact with an iconic memory of the target, enabling its conscious perception in a retrospective manner.

Another possibility that can explain the present effect would be that the dimming worked as a visual transient to activate weak information in the brain (Kawabe, Yamada, & Miura, 2007). This effect of visual transient can be typically seen in motion-induced blindness (Bonneh, Cooperman, & Sagi, 2001), an illusion in which a static target (e.g., yellow disc) on a continuously rotating background (e.g., a grid pattern of blue lines) disappears and reappears from awareness periodically. When another stimulus (visual transient) was presented during a period of perceptual suppression, it triggered a reappearance of the suppressed target (Kawabe et al., 2007). This restoration of conscious percepts by visual transients was also reported in other types of perceptual suppression such as binocular rivalry (Wu, Busch, Fabre-Thorpe, & VanRullen, 2009) and continuous flash suppression (Noguchi, Kimijima, & Kakigi, 2015). Thus, a dimming of a black ring in the present study might play a role as a visual transient to activate weak information in the brain, triggering conscious perception of a target that would otherwise have been omitted.

In conclusion, our present study showed that a sensory-level interaction between cue and target was strong enough to induce the retroperception effect. This point should be recognized by future studies investi-

gating an effect of postcued attention. Our results also show a unique case of interaction between two visual stimuli in which the second stimulus facilitates (not inhibits) conscious perception of the first stimulus. Further research using, for example, neuroimaging techniques might reveal neural mechanisms underlying this intriguing effect.

Keywords: backward masking, temporal flexibility, postdiction, invisible

Acknowledgments

This work was supported by KAKENHI Grants (22680022 and 26700011) from the Japan Society for the Promotion of Science (JSPS).

Commercial relationships: none.

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