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Yamada, Yuki Kyushu University | NTT Communication Science Laboratories

Kawabe, Takahiro Kyushu University | NTT Communication Science Laboratories

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# Illusory line motion and transformational apparent motion during

# continuous flash suppression

Yuki Yamada (Kyushu University)

Takahiro Kawabe (NTT Communication Science Laboratories)

## Abstract

A static bar is perceived to dynamically extend from a peripheral cue (illusory line motion, ILM) or from a part of another figure presented in the previous frame (transformational apparent motion, TAM). We examined whether visibility for the cue stimuli affected these transformational motions. Continuous flash suppression, one kind of dynamic interocular masking, was used to reduce the visibility for the cue stimuli. Both ILM and TAM significantly occurred when the *d'* for cue stimuli was zero (Experiment 1) and when the cue stimuli were presented at subthreshold levels (Experiment 2). We discuss that higher-order motion processing underlying TAM and ILM can be weakly but significantly activated by invisible visual information.

#### Introduction

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Correspondence to: Yuki Yamada, Faculty of Human-Environment Studies, Kyushu University, 6-19-1 Hakozaki Higashi-ku, Fukuoka 812-8581, Japan yamadayuk@gmail.com

A static bar is often perceived to extend from a pre-cued location. This phenomenon is called illusory line motion (ILM; Hikosaka, Miyauchi, & Shimojo, 1993a, 1993b). Previous studies have shown that ILM occurs due to a presentation of visual. auditory and somatosensory cues (Bavelier, Schneider, & Monacelli, 2002; Chica, Charras, & Lupiáñez, 2008; Ghorashi, Jefferies, Kawahara, & Watanabe, 2008; Hikosaka et al., 1993a, 1993b; Hikosaka, Miyauchi, & Shimojo, 1996; Ishigami, Klein, & Christie, 2009; Kawahara, 2002; Shimojo, Miyauchi, & Hikosaka, 1997; Yamada, Miura, & Kawabe, 2008). The cue stimuli may be necessary in order for the apparent motion mechanism to take part in the processing for ILM (Kawahara, Yokosawa, Nishida, & Sato, 1997; von Grünau, Dubé, & Kwas, 1996; Kawahara & Yokosawa, 2001).



Fig. 1. Examples of stimuli and percept of illusory line motion (left) and transformational apparent motion (right). The arrow on the horizontal bars represents perceived motion direction.

A static bar is perceived to extend from the side of a preceding cue that has geometrical properties that are concordant with the static bar. This second kind of illusory motion is known as 'transformational apparent motion' (TAM; Tse, Cavanagh, & Nakayama, 1998). TAM occurs as a result of parsing and matching of objects within a frame or across frames. Several geometrical properties, such as concavity/convexity of edges (Hoffman & Richards, 1984; Singh, Seyranian, & Hoffman, 1999) and the smooth arrangement of Gabor orientation (Field, Hayes, & Hess, 1993), strongly contribute to the formation of visual objects in a static scene. These properties are also the determinants of the transformation between visual objects in a dynamic scene, TAM (Tse et al., 1998). A recent study demonstrated that three-dimensional form analysis also contributes to TAM (Tse & Logothetis, 2002); hence, TAM is considered to be one kind of high-level motion perception that is not simply accounted for by means of outputs from spatiotemporally oriented motion detectors (Fracasso, Caramazza, & Melcher, 2010; Tse, 2006; Tse & Caplovitz, 2006).

Between ILM and TAM, different kinds of processing likely cause the similar illusory motion of a static bar. In ILM, the cue and the trailing bar are processed in a pre-attentive, apparent motion mechanism (Kawahara et al., 1997). A recent study has shown that ILM was induced by a cue that was subjectively invisible due to object substitution masking (Blanco & Soto, 2009), suggesting that ILM occurs without a visible cue. The results of Blanco and Soto are consistent with the finding that apparent motion also occurs without awareness of the previous frame (Blake, Ahström, & Alais, 2000). In TAM the geometric relationship between cue and the trailing bar is analyzed in higher-level visual processing (Tse & Logothetis, 2002). However, no studies have made an attempt to clarify whether TAM occurs without a visible cue.

The present study aimed at investigating whether ILM and TAM occurred when visibility for cue stimuli was controlled by continuous flash suppression. In Blanco and Soto (2009), object-substitution masking was utilized to render the cue for ILM (i.e. ILM cue) invisible. In object substitution masking, four-dot maskers and a maskee should have common onsets while the maskee should disappear earlier than the maskers. Hence, in object-substitution masking it is hard to render the cue for TAM (i.e. the TAM cue) invisible because the TAM cue should physically exist during and simultaneously disappear with the presentation of the trailing bar. Therefore, to reduce visibility of the TAM cue, we employed a dynamic interocular masking technique called 'continuous flash suppression' (Tsuchiya & Koch, 2005) in which static (or non-salient dynamic) stimuli exposed to one eye are rendered invisible because of the periodical swapping of salient colorful squares exposed to the other eye.

It was predicted that ILM would occur under continuous flash suppression if an invisible cue was enough to cause ILM, as shown in Blanco and Soto (2009). In addition, we predicted that TAM would also occur under continuous flash suppression if the spatiotemporal analysis of visual forms, which was necessary for TAM, occurred independently of the cue visibility.

In Experiment 1, to precisely learn the relationship between cue visibility and ILM/TAM, we first measured detection thresholds for the ILM and TAM cues separately by controlling the luminance contrast of continuous flashes. Second, using the cue stimuli above and below detection thresholds, we further examined the effect of the visibility of cue stimuli on ILM and TAM. The visibility of cue stimuli was assayed by perceptual sensitivity, d', based on signal detection theory (Green & Swets, 1966). Then in Experiment 2, we reexamined the effect of the visibility of the cue stimuli on ILM and TAM under conditions in which the cue stimuli were presented at subthreshold levels.

## Experiment 1

#### Method

*Observers* Ten observers including the two authors participated in Experiment 1. They reported that they had normal or corrected-to-normal visual acuity. Apart from the authors, the observers were naive as to the purpose of the experiment.

Stimuli were presented on a *Apparatus* 19-inch CRT monitor (RDF193H, Mitsubishi, Japan). The resolution of the monitor was  $1024 \times$ 768 pixels, and the refresh rate was 100 Hz. The presentation of stimuli and collection of data were computer-controlled (Mac Pro; Apple). Using a photometer (3298F; Yokogawa, Japan), we performed a correction for the luminance emitted from the monitor. Observers viewed stimuli through а mirror stereoscope (Screenscope; Stereoaids, Australia).

Stimuli Stimuli were generated by MATLAB (Mathworks Inc.) with the Psychtoolbox extension (Brainard, 1997; Pelli, 1997). Stimuli consisted of two fixation crosses, two square outlines, continuous flashes, and transformational motion figures (ILM and TAM; Fig. 1) displayed on a gray background (45.8  $cd/m^2$ ). To ensure binocular fusion, we presented a square outline to each eye. The square outlines had a side of 14.2 deg, and a border width of 0.2 deg. The luminance of the border was  $66.5 \text{ cd/m}^2$ . Continuous flashes were achromatic mesh grids  $(15 \times 9 \text{ cell})$  in which the luminance of each cell was randomly selected from 0 to 45.8  $cd/m^2$  at 8.3 Hz. The center of the mesh grids was set at 4.5 deg left and right of the center of a square outline and at 2.6 deg above the fixation. The side length of each cell was 0.5 deg. The ILM figure comprised a cue square (ILM cue; 0.5  $\times$ 0.9 deg) and a horizontal bar  $(0.5 \times 7.6 \text{ deg})$ , and was positioned 4.0 deg above the fixation cross. The ILM cue was presented 3.3 deg to the left or right of the fixation cross; the horizontal position of the bar was always at the center. The TAM figure comprised an H-shaped figure with two stalks (3.8  $\times$  0.9 deg) and a small part of a horizontal bar (TAM cue;  $0.5 \times 0.5$  deg), and an additional horizontal bar to complete the horizontal bar  $(0.5 \times 6.6 \text{ deg})$ . The luminance of ILM and TAM figures was 39.4 cd/m2. The fixation and the square outline were dichoptically presented to both eyes without binocular disparity. Each of the transformational motion figures was presented to one eye while continuous flashes were presented to the other eye.

*Procedure* Observers were individually tested in a dark room and viewed stimuli by means of a mirror stereoscope. The viewing distance was 40 cm. The square outlines and fixation crosses were presented throughout the experiment.

To measure a 75% detection threshold of the cue stimuli in each observer, we controlled the

luminance contrast of continuous flashes with a one-up/ one-down staircase method with setting the ratio of up/down step sizes to 3 (Kaernbach, 1991). Observers pressed the space bar to start each experimental block and each trial automatically started after observers' previous response. After a blank interval of 300 ms, the presentation of continuous flashes was started. In the ILM condition, 500 ms after the start of a trial, the ILM cue was presented to the left or right of the central fixation for 20 ms. Then, the horizontal bar was presented with an exposure duration of 100 ms. The inter-stimulus interval between the ILM cue and horizontal bar was kept at 140 ms. In the TAM condition, 500 ms after the start of a trial, the TAM cue was presented (to the left or right side) for 300 ms, and the horizontal bar immediately followed the cue and lasted for 100 ms<sup>1</sup>. The cue stimuli were presented in half of the trials. Two hundred ms after stimulus presentation, observers indicated whether the cue stimulus existed regardless of location of the cue. They reported this by pressing assigned keys and were informed of the appearance of cue stimuli in advance. Each staircase was ended after 20 reversals of a staircase. No explicit feedback for the correctness of responses was provided. An experimental block which contained a single staircase was successively repeated twice, and the final 5 reversal points in each of the staircases (10 reversal points in total) were averaged to calculate the 75% detection threshold for the cue stimuli of each of the ILM and TAM conditions in each observer. The luminance of each cell in continuous flashes was selected from a range





between certain maximum and minimum luminance values. We defined the luminance contrast as the Michelson contrast calculated on the basis of the maximum and minimum luminance values, and in accordance with the observers' responses, these values varied. The luminance contrast of the mask stimuli increased after a correct response (i.e. 0.02 log unit of luminance contrast); correspondingly, the maximum luminance values decreased while the minimum luminance value increased. Furthermore, the luminance contrast decreased after an error (i.e. 0.06 log unit of luminance contrast); correspondingly, the maximum luminance values increased while the minimum luminance value decreased.

After the determination of the threshold contrast of continuous flashes. observers performed blocks with motion direction judgment and cue detection tasks. Observers pressed the space bar to start each trial. The observers viewed the same stimulus presentation as one used in the detection threshold measurement. Observers were asked to judge motion direction and presence/absence of a cue in each trial. The judgments were made using a 2-alternative forced-choice method ('leftward' or 'rightward' for motion direction judgment; 'present' or 'absent' for cue detection) by pressing assigned keys. The luminance contrast of the mask stimuli was varied at five levels from 50% to 400% of a 75% threshold, but fixed within a single block. Each observer performed 800 trials with four experimental blocks including two motion conditions (ILM and TAM)  $\times$  five mask strength conditions (50, 100, 200, 300, and 400% of a 75% threshold), and two conditions for cue location (left and right)  $\times$  40 replications. In half of the trials, the cue stimuli were not presented. In each block, the trial order was randomized. The order of the blocks was counterbalanced across observers. It took about two hours for each observer to complete the experiment.

#### Results

The mean 75% detection threshold averaged across observers in the ILM and TAM conditions were .48 and .15 Michelson contrast, respectively.

For each observer, visibility of the cue stimuli was calculated as d' on the basis of the cue detection data obtained from the cue detection test. Moreover, using data from the cue-present

<sup>&</sup>lt;sup>1</sup> These temporal properties were determined so as to obtain optimal motion sensation in each transformational motion based on preliminary observations.

trials, we calculated the proportions of trials in which the observers reported the illusory motion of the bar from the cue side in the ILM and TAM conditions. Fig. 3a illustrates the relationship between d' and proportions of illusory motion from the cue side. The regression intercept was considered as an indirect measure of ILM and TAM with zero perceptual sensitivity of the cue stimuli (e.g., Abrams & Greenwald, 2000; Draine & Greenwald, 1998; Greenwald, Klinger, & Schuh, 1995). We fitted a cumulative Gaussian function (Finney, 1971) to the pooled observational data in each of the ILM and TAM conditions. We evaluated the goodness of fit based on the Kolmogorov-Smirnov test, and confirmed that data were well fitted by the cumulative Gaussian function (ps > .10). Using the psignifit program implemented in MATLAB (Wichmann & Hill, 2001a, 2001b), we calculated bootstrap confidence 95% intervals bv resampling and refitting each psychometric function 10000 times. Estimated regression intercepts at d' = 0 and their 95% confidence intervals were shown in Fig. 3b. The results showed that when the d' = 0, both proportions of ILM and TAM were significantly larger than the chance level, although the proportion of ILM was larger than that of TAM.

#### Discussion

The results showed that both the proportions of ILM and TAM were above chance level when cue stimuli were invisible (d' = 0), suggesting that the invisible cue stimuli caused both ILM and TAM. The results in the ILM condition were consistent with a previous study (Blanco & Soto, 2009). Moreover, the results in the TAM condition were also consistent with our prediction. Therefore, the processing of the TAM as well as ILM cues were incompletely suppressed by continuous flash suppression, even when the visibility of the cues were ultimately lowered.

However, it was a critical reservation that we did not actually observe the performance of all of the observers at d' = 0 in Experiment 1. We merely estimated the performance by fitting a cumulative Gaussian function to pooled data: For some of observers, continuous flashes were not strong enough to reduce the visibility of the ILM/TAM cue stimuli and thus these cue stimuli were not always suppressed to a subthreshold detection level. To resolve this issue, in Experiment 2 we employed stronger masks than the ones used in Experiment 1. This allowed us to specify luminance contrasts which guaranteed supra- and subthreshold detection of the cue



*Observers* Three naive observers (KY, KS, and QK) and one of the authors (YY) participated in Experiment 2. They reported that they had normal or corrected-to-normal visual acuity.

Method

*Apparatus and Stimuli* Apparatus and stimuli used in Experiment 2 were identical to those used in Experiment 1 except for the followings: The luminance of each cell of continuous flashes was randomly selected from 0 to 80.7 cd/m<sup>2</sup> and the swap rate was at 10 Hz. Michelson contrast of the masks were 0, .031, .063, .125, .25, .5, .7, .8, .9, and 1. The luminance of the ILM and TAM stimuli was 42.9 cd/m<sup>2</sup>; however, only for YY 43.3 cd/m<sup>2</sup> of the luminance was used in the ILM condition to ensure supraliminal as well as subliminal detection performances for the cue stimuli.

**Procedure** Observers' tasks were identical to those used in Experiment 1. Trials were blocked based on one of ten levels of contrasts from 0 to 1 and motion type (ILM and TAM). Each block consisted of two conditions for cue location (left and right)  $\times$  15 replications and 30 trials of the no cue condition. Hence, each observer performed 1200 trials in total. In each block, the trial order



Fig. 3. (a) Relationship between the proportions of illusory motion and perceptual sensitivity of the cue stimulus (d') in the ILM and TAM conditions in Experiment 1. (b) Estimated proportions of illusory motion when the cue stimulus was invisible (d' = 0) in the ILM and TAM conditions in Experiment 1. Error bars denote 95% confidence intervals.

stimuli for each observer. In next experiment, we again tested the effect of the visibility on ILM and TAM by using the supra- and subthreshold cue stimuli.

was randomized. The order of the blocks was also randomized for each observer. It took about two hours for each observer to complete the experiment.

#### Results

We calculated the proportions of trials in which the observers reported the rightward motion in the left, right, and no cue conditions



Fig. 4. (a) The proportion of rightward motion as a function of mask contrast in the ILM and TAM conditions in Experiment 2. Data of the mean and each observer were shown. Error bars denote standard errors of the mean. The vertical arrow indicates estimated 75% detection threshold of each observer. (b) The mean proportion correct as a function of mask contrast in the ILM and TAM conditions in Experiment 2. Error bars denote standard errors of the mean bias in the supra- and subthreshold conditions of the ILM and TAM conditions in Experiment 2. Error bars denote standard errors of the mean.

for the ILM and TAM cues. Fig. 4a shows the proportion of rightward motion reports as a function of mask contrast.

Moreover, we calculated the proportion correct for the detection of the ILM and TAM cues. Fig. 4b shows the mean proportion correct as a function of mask contrast. We fitted a logistic function to the proportion correct obtained from each observer for the ILM and TAM cues and estimated 75% detection threshold in mask contrast: .023 (YY), .02 (KY), .03 (KS), and .018 (QK) in the ILM condition and .151 (YY), .036 (KY), .042 (KS), and .063 (OK) in the TAM condition. Based on the calculated threshold, we divided the data (the proportions of rightward motion reports and proportion corrects) into supraand subthreshold conditions. Α one-sample *t*-test showed that mean proportion of correct detection in the suprathreshold condition was significantly higher than 0.5 (chance level) in the ILM [t(3) = 9.36, p < .003] and TAM conditions [t(3) = 25.98, p < .0002], while that in the subthreshold condition was not significantly different from 0.5 in the ILM [t(3) = 2.79, p]> .06] and TAM conditions [*t*(3) = 1.97, *p* < .14].

Then, we calculated bias in motion judgment by subtracting the proportion of rightward motion reports in the no cue condition from the one in the left and right cue conditions. Fig. 4c shows the mean bias in the ILM and TAM conditions. For ILM, a two-way analysis of variance (ANOVA) of bias with visibility (supra- and subthreshold) and cue location (left and right) as within-participant factors was carried out. The ANOVA showed a significant main effect of cue location [F(1, 3) = 381.01, p < .0004] and the significant interaction [F(1, 3) = 123.32, p]< .003]. However, a main effect of visibility was not significant [F(1, 3) = 1.86, p > .26]. Post-hoc tests on the interaction showed significant simple main effects of cue location in the suprathreshold [F(1, 6) = 430.73, p < .0001; Cohen's d = 5.06]and subthreshold cue conditions [F(1, 6) = 10.43], p < .02; Cohen's d = 1.90]. Moreover, there were significant simple main effects of visibility in the left [F(1, 6) = 23.19, p < .004; Cohen's d = 1.84] and right cue conditions [F(1, 6) = 50.68, p]< .0005; Cohen's d = 4.73].

For TAM, a two-way ANOVA of bias with visibility and cue location as within-participant factors was carried out. The ANOVA showed a significant main effect of cue location [F(1, 3) = 120.38, p < .003] and the significant interaction [F(1, 3) = 780.48, p < .0002]. However, a main effect of visibility was not significant [F(1, 3) = 1.29, p > .33]. Post-hoc tests on the interaction showed significant simple main effects of cue

location in the suprathreshold [F(1, 6) = 336.10, p < .0001; Cohen's d = 4.85] and subthreshold cue conditions [F(1, 6) = 7.50, p < .04; Cohen's d = 1.61]. Moreover, there were significant simple main effects of visibility in the left [F(1, 6) = 38.75, p < .0009; Cohen's d = 4.04] and right cue conditions [F(1, 6) = 15.90, p < .008; Cohen's d = 1.78].

Furthermore, as in Experiment 1, we calculated the proportions of trials in which the observers reported the illusory motion of the bar from the cue side in the cue-present trials of the ILM and TAM conditions, as a function of mask contrast. A logistic function was fitted to the proportion of each observer for the ILM and TAM cues. We calculated 95% bootstrap confidence intervals by resampling and refitting each psychometric function 10000 times. We estimated regression intercepts at 100% and 200% of the threshold mask contrast and their 95% confidence intervals in each observer. At 200% of the threshold mask contrast, the lower limits of 95% confidence interval of both estimated proportions of ILM and TAM in all observers were above .50 (Fig. 5). An estimated proportion correct at 200% of threshold mask contrast was  $.61 \pm .04$  in the ILM condition and  $.55 \pm .01$  in the TAM condition. One-sample t-tests (two-tailed) revealed that the mean proportion correct in each of the ILM and TAM conditions at 200% of threshold mask contrast was significantly smaller than .75 (ps < .04), ensuring that both cues were presented at a subthreshold level. Taken together, the results indicated that ILM and TAM were significantly induced by both suprathreshold and subthreshold cues.

#### Discussion

Experiment 2 replicated the findings of Experiment 1. Specifically, the cue stimuli which were presented at the subthreshold levels could significantly induce both ILM and TAM. These results again suggest that both ILM and TAM occur even when the cues were rendered invisible by continuous flash suppression.

#### General discussion

The objective of the present study was to examine whether the cue visibility that was controlled by continuous flash suppression affected ILM and TAM. A previous study showed that a peripheral cue that was rendered invisible by object-substitution masking could trigger ILM (Blanco & Soto, 2009). On the other hand, it was unclear whether invisible cues could induce TAM. Employing continuous flash



Fig. 5. The estimated proportion of illusory motion from cue and its 95% confidence interval (error bars) at a 200% threshold mask contrast for each observer.

suppression, the present study demonstrated that invisible cue stimuli induced both ILM and TAM when the cue invisibility was ensured with d'(Experiment 1) and detection threshold (Experiment 2).

The phenomenon observed in the present study is a bit different from so-far reported contextual modulation effect that is induced by invisible stimuli. Several previous studies have demonstrated that invisible contextual stimuli caused the change in appearance of a visible stimulus. For example, Kawabe and Yamada (2009) showed that invisible peripheral motion could induce motion contrast in visible central ambiguous motion. Similar kinds of contextual modulation of visible stimuli by invisible stimuli have been reported elsewhere (Cai, Zhou, & Chen, 2008; Clifford & Harris, 2005; Kanai, Tsuchiya, & Verstraten, 2006). These studies have focused on a perceptual contrast between visible and invisible stimuli on the basis of spatial integration. In contrast, the present study showed that invisible cue stimuli altered the appearance of a visible static bar. It is thus possible that the effects of invisible stimuli on the appearance of visible stimuli are not limited to spatial contrast of orientation or motion, but are observed in the phenomena (ILM and TAM) which are not related to spatial contrast effects, but are mediated by higher-order motion processing.

As a possible explanation of the present results, one can argue that ILM and TAM are processed in the monocular pathway. It has been suggested that the early component of visual processing that occurs monocularly (*i.e.* before binocular fusion) is severely suppressed (Blake, Tadin, Sobel, Raissian, & Chong, 2006; Maruya, Watanabe, & Watanabe, 2008) but not abolished by an interocular mask (Cai et al., 2008).

Because in the present study ILM and TAM were observed even when the visibility of cue stimuli were suppressed by continuous flash suppression which was a kind of the interocular masking, it was possible that the monocular pathway at least partially contributes to these illusory motion percepts. However, Hikosaka et al. (1996) have observed that ILM occurred even when a cue and a bar stimulus was presented to different eyes, indicating that at least ILM is processed in the binocular pathway that is susceptible to the interocular masking. Moreover, it is difficult to clearly say that a phenomenon which is suppressed by continuous flash suppression is always processed in the monocular pathway; because although it is equivocal whether the visual processing for emotional stimuli is monocular or binocular, the emotional stimuli which are rendered invisible by continuous flash suppression can still affect the visual orientation discrimination (Jiang, Costello, Fang, Huang, & He, 2006) or time perception of visual stimuli (Yamada & Kawabe, in press). Thus, it is hard to conclude as to whether ILM and TAM are processed in the monocular or binocular pathway at this stage.

The suppression of visual transients by continuous flash suppression may provide a more rigorous explanation for the present study. In Motoyoshi and Hayakawa (2010), an invisible orientation annulus without visual transients caused the orientation contrast in a central visible orientation patch. That is, even though the visual signals without the transients do not enter the visual awareness, they still effectively influence on-going visible events in the spatial vicinity. In the present study it is possible that continuous flash suppression effectively reduced the transients of neural signals sent to higher-order motion processing. Hence, the neural signals could not cause the visual awareness for the cue stimuli. However, they were enough to stimulate higher-order motion processing. We suggest that this is why the invisible cue stimuli caused ILM and TAM.

A more reliable, precise measurement of subjective invisibility may be required in assessing the influence of invisible on visible information. Though the present results demonstrated that invisible cues induced ILM and TAM, it was unclear that the cue stimuli was completely invisible. We used an indirect measure of visibility, that is, an estimated intercept at a null sensitivity point (or d' = 0) that was extrapolated by a regression technique (e.g., Abrams & Greenwald, 2000; Draine & Greenwald, 1998; Greenwald et al., 1995). Based

on this technique, we inferred that perceptual sensitivity for cue stimuli was nonlinearly related to mask contrast. However, a true relationship between them around a null sensitivity point is unknown (Hannula, Simons, & Cohen, 2005). Moreover, in Experiment 2, we set a 75% correct response as a threshold for the detection of cue stimuli, and the weak but significant illusory motion percepts were obtained in the subthreshold condition (i.e. at a mask contrast of 200% threshold). On the other hand, it is still possible to argue that the weak illusory percepts may have stemmed from the data of slight trials in which the cues were accidentally visible. Thus, it is precise to conclude that what the present results demonstrated was that the subthreshold (but sometimes visible) cues contributed to the generation of illusory motion percepts. In light of these issues, it is necessary to devise the measurement of cue invisibility to precisely investigate relationship among the visual transients. visual awareness, and motion processing.

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