

# Inhibition of target detection in apparent motion trajectory

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Letter discrimination performance is degraded when a letter is presented within an apparent motion (AM) trajectory of a spot. This finding suggests that the internal representation of AM stimuli can perceptually interact with other stimuli. In this study, we demonstrated that AM interference could also occur for pattern detection. We found that target (Gabor patch) detection performance was degraded within an AM trajectory. Further, this AM interference weakened when the differences in orientation between the AM stimuli and target became greater. We also revealed that AM interference occurred for the target with spatiotemporally intermediate orientations of the inducers that changed their orientation during AM. In contrast, the differences in phase among the stimuli did not affect the occurrence of AM interference. These findings suggest that AM stimuli and their internal representations affect lower visual processes involved in detecting a pattern in the AM trajectory and that the internal object representation of an AM stimulus selectively reflects and maintains the stimulus attribute.

Keywords: apparent motion, object representation, target detection, orientation, phase

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## Introduction

When two or more inducing stimuli in different locations are alternately turned on and off, we perceive motion between them (Kolers, 1972; Wertheimer, 1912). In this apparent motion (AM) phenomenon, smooth motion perception, indistinguishable from real motion, can occur when the spatiotemporal properties of the stimuli are optimal (Korte, 1915). It has been hypothesized that the internal representations of AM stimuli are established along the AM trajectory even when there are no physical inputs, and these representations mediate AM perception (Kolers, 1972; Kolers & von Grünau, 1976; Shepard & Judd, 1976; Shepard & Zare, 1983). In fact, recent psychophysical studies have demonstrated that letter discrimination performance is impaired when the letters were presented in an AM trajectory (Hogendoorn, Carlson, & Verstraten, 2008; Yantis & Nakama, 1998), supporting the idea that the

internal representation of AM stimuli can interfere with our perception of other physical inputs.

However, the levels of perceptual processing that are involved in AM interference remain unclear. Because AM interference has been revealed by using letter discrimination performance as an index, it is possible that AM interference would occur only at a relatively high processing stage (e.g., letter processing). However, some brain imaging studies have reported that observation of the AM trajectory containing no physical inputs elicited neural activation not only in the human motion processing area (Liu, Slotnick, & Yantis, 2004) but also in the primary visual cortex including V1 (Muckli, Kohler, Kriegeskorte, & Singer, 2005), similar to the neural activation elicited when actual physical input was presented. This activation in V1 was assumed to be triggered by a feedback modulation from the motion processing area (Sterzer, Haynes, & Rees, 2006; Wibrall, Bledowski, Kohler, Singer, & Muckli, 2009) and, thus, could cause our subjective AM

perception. These findings suggest that AM interference could be found with more basic perceptual processes than letter discrimination.

The current study specifically addressed this issues, asking whether AM interference could occur at visual processes lower than shape identification or recognition (Hogendoorn et al., 2008; Yantis & Nakama, 1998). Specifically, we investigated whether the detection performance for targets changed in the AM trajectory. Furthermore, we examined whether the consistency of lower level visual properties (stimulus orientation and phase) between the inducers and target could affect detection performance. We found that performance was degraded when a target was presented within an AM trajectory but not when the target was slightly offset from the AM trajectory or when AM was not perceived (Experiment 1). Moreover, AM interference for target detection weakened when the differences in orientation between the AM stimuli and target became greater (Experiment 2). We also revealed that AM interference occurred for the target with intermediate orientation of the inducers that changed their orientation during AM (Experiments 3 and 4). In contrast, the differences in phase between the stimuli had no effect (Experiments 5 and 6). These findings suggest that AM stimuli and their internal representations affect lower visual processes involved in detecting a pattern in the AM trajectory and that AM interference selectively reflects the consistency of an object's feature—even a spatiotemporally intermediate object's feature interpolated in the AM trajectory—between the AM stimulus and target.

## Experiment 1

In the first experiment, we investigated target detection performance along an AM trajectory to determine whether AM interference could occur for relatively low visual processes (pattern detection). Whereas the visibility of stimuli decreases with increased retinal eccentricities, sensitivity to motion remains constant (Koenderink, van Doorn, & van de Grind, 1985). We therefore manipulated the eccentricity of the stimuli to reveal a situation where AM interference for the target detection occurred effectively.

## Methods

### Participants and apparatus

Written consent was obtained from each participant before all the experiments began. The experiments were approved by the local ethics committee of Rikkyo University. One author (S. H.) and four paid volunteers (undergraduate students in Rikkyo University) participated in the first experiment. The four volunteers were naive to the purpose of this experiment. All had normal or corrected-to-normal vision.

The stimuli were presented on a linearized CRT display (EIZO FlexScan T776, 19 inches) with a resolution of  $1280 \times 960$  pixels and a refresh rate of 75 Hz. An Apple Power Mac G4 and MATLAB (The Mathworks) with the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) were used to control the experiment. The participants placed their heads on a chin rest and reported their responses using the “1” (indicating target-present) or “3” (indicating target-absent) key on a numeric keyboard.

### Stimuli

We presented Gabor patches with horizontal stripes ( $1.5 \times 1.5$  deg, 1.5 cycle/deg,  $\sigma = 0.25$  deg) as visual stimuli (Figure 1A) against a gray background ( $30 \text{ cd/m}^2$ ). The luminance of inducers for AM ranged from 0.1 to  $60 \text{ cd/m}^2$  (from  $-100$  to  $100\%$  in Weber contrast), and the target's luminance ranged from 15 to  $45 \text{ cd/m}^2$  (from  $-50$  to  $50\%$  in Weber contrast). The inducers and target were aligned vertically. The distance between the inducers was 6 deg. The target was presented in between the inducers so that the distance between the target and inducers was 3 deg. The inducers' duration was 80 ms, and interstimulus intervals (ISIs) were 106 ms. The target was presented at an intermediate temporal position of the inducers for 26 ms. The ISIs between the target and inducers were 40 ms. A black ( $0.1 \text{ cd/m}^2$ ) fixation circle consisting of three rings was also presented on the left of the inducers and targets.

### Procedure

After the presentation of the fixation for 1000 ms, the inducers were presented as shifting from either the upper to the lower end or vice versa. Each trial comprised 20 AM sequences in which AM stimuli were perceived as moving back and forth, divided into three phases: pre-target, target, and post-target. In the pre-target phase, only the inducers appeared. The length of the pre-target phase was randomly assigned from 6 to 13 sequences in each trial to prevent participants from predicting the timing of the target onset. In the subsequent target phase, the target was present in half the trials and absent in the other half. Thereafter, the remaining sequences containing only the presentation of the inducers were presented as the post-target phase. There were three conditions: In the first condition, the spatial position of the target fell within the AM trajectory of the inducers (AM-on-path, Figure 1B). In the second condition, the horizontal position of the inducers was displaced rightward relative to the target by 2 deg (AM-off-path). This was a control condition to distinguish the obtained effect from misdetection by eye movements or attentional shift. Finally, in the third condition, two inducers simultaneously flickered so that AM was not perceived (FL). This served as a control for a possible masking effect induced by transient signals (e.g., Kanai & Kamitani, 2003) from the inducers to the target. The eccen-

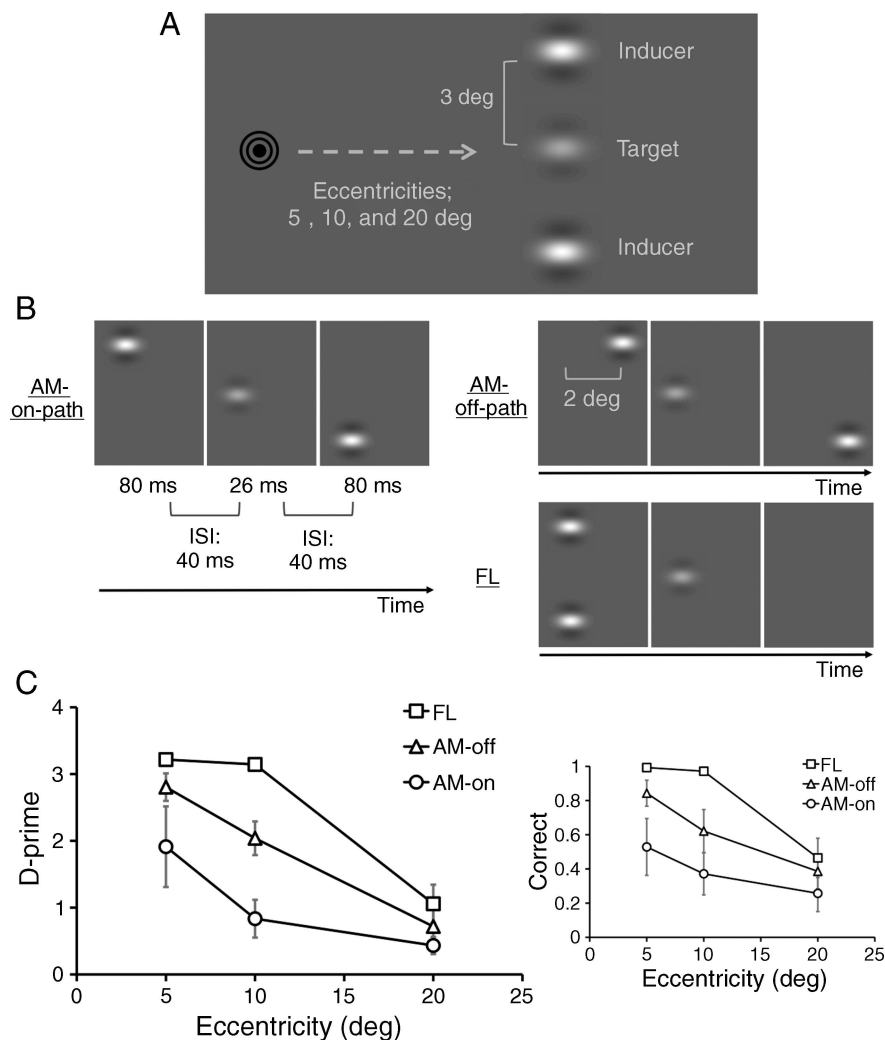


Figure 1. Schematics of the stimuli and results in Experiment 1. (A) Stimuli. (B) Conditions. (C) *D*-primes (left) and proportion of correct responses for target-present trials (right). Error bars denote the standard errors of the means.

tricity of the target was 5, 10, or 20 deg. The task of the participants was to report whether they perceived the target.

The experiment consisted of two sessions. In the practice session, the participants completed 36 trials: conditions (3)  $\times$  eccentricities (3)  $\times$  target (2; present/absent)  $\times$  repetitions (2). The main session consisted of 360 trials: conditions (3)  $\times$  eccentricities (3)  $\times$  target (2)  $\times$  repetitions (20). The conditions, eccentricities, and target presentations were introduced in a random order in each trial and counterbalanced among the participants.

## Results and discussion

First, we calculated the average proportion correct for the target-present (Figure 1C) and target-absent trials. Then, as an index of detection sensitivity to the target, we computed *d*-primes on the basis of the signal detection

theory (Macmillan & Creelman, 2004). The responses of target-present were regarded as “hits” in the trials with a target and as “false alarms” in the trials without a target. The proportions of hits and false alarms with 0% or 100% values were corrected as  $1/n$  or  $(n - 1) / n$ , respectively, where  $n$  was the total number (20 times) of presentations (Anscombe, 1956; Sorkin, 1999).

The resultant *d*-primes are shown in Figure 1C. A two-way repeated-measures analysis of variance (ANOVA) was conducted with conditions (3)  $\times$  eccentricities (3). This analysis revealed a significant main effect of conditions ( $F(2,8) = 24.02, p < 0.001$ ). A post-hoc test (Tukey’s HSD) revealed that the *d*-primes became smaller in the order of the FL, AM-off-path, and AM-on-path conditions ( $p < 0.05$ ). A main effect of eccentricities ( $F(2,8) = 97.64, p < 0.001$ ) was also significant; a post-hoc test found that the *d*-primes became smaller in the order of 5, 10, and 20 deg of eccentricities ( $p < 0.05$ ). However, the

interaction between the factors did not reach significance ( $F(2,8) = 2.02$ ,  $p = 0.14$ ).

The results showed that detection sensitivity to the target decreased when the target was presented in the AM trajectory. One might assume that the presentation of inducers will trigger misdetection by eye movements, attentional shift, or inducer's transient signals. However, because the  $d$ -prime in the AM-on-path condition was smaller than that in the other conditions, the effect of AM interference could be distinguished from generalized misdetection. These findings suggest that the internal representation of AM stimuli can interfere with the target detection performance in the AM trajectory. It clearly appears from Figure 1C that the target detection performance reached floor level at 20 deg of eccentricity irrespective of the conditions. In addition, the AM interference in target detection seemed most obvious at 10 deg of eccentricity. Therefore, in the subsequent experiments, we generally used stimuli presented at 10 deg of eccentricity.

## Experiment 2

In the second experiment, we examined whether the consistency of lower stimulus properties between the inducers and target could affect the target detection performance in the AM trajectory. Specifically, we manipulated the orientation of the target relative to the AM stimuli.

## Methods

One author (S. H.) and four paid volunteers (undergraduate students in Rikkyo University) participated in this experiment. The newly recruited volunteers were naive to the purpose of this experiment. All had normal or corrected-to-normal vision.

The orientation of the inducers was 0 deg (horizontal). In contrast, the orientation of the target was 0,  $\pm 15$ ,  $\pm 45$ , or 90 deg (vertical; Figure 2A). The eccentricity of the inducers and targets was 10 deg for the volunteers but 20 deg for the author because his detection performance reached ceiling level at 10 deg of eccentricity. Both the AM-on-path and FL conditions were included.

In the practice session, the participants completed 32 trials: conditions (2)  $\times$  orientations (4)  $\times$  target (2; present/absent)  $\times$  repetitions (2). The main session consisted of 320 trials: conditions (2)  $\times$  orientations (4)  $\times$  target (2)  $\times$  repetitions (20). The total number of the trials was equal (10 trials in each) between  $+15$  and  $-15$  deg or  $+45$  and  $-45$  deg of orientations. Except for these differences, the

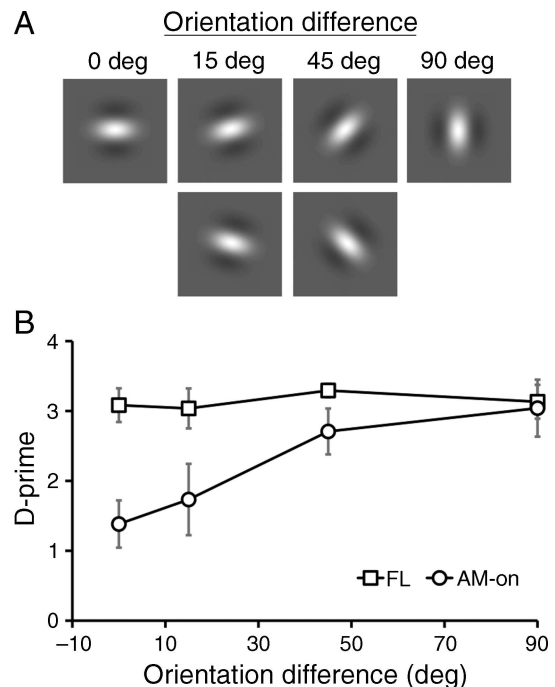


Figure 2. Schematics of the stimuli and results in Experiment 2. (A) Stimuli. Orientation was manipulated from 0 to 90 deg. (B) Result. Error bars denote the standard errors of the means.

apparatus, stimulus parameters, and procedures were identical to those in Experiment 1.

## Results and discussion

Similar to Experiment 1, we calculated the  $d$ -primes. False alarms were pooled and averaged among target-absent trials in each condition (Figure 2B). A two-way repeated-measures ANOVA was conducted with conditions (2)  $\times$  orientations (4). This analysis revealed a significant main effect of conditions ( $F(1,4) = 11.54$ ,  $p < 0.05$ ) and orientations ( $F(1,4) = 6.98$ ,  $p < 0.01$ ). The interaction between these factors was also significant ( $F(3,12) = 6.61$ ,  $p < 0.01$ ). A simple main effect of the conditions revealed that the  $d$ -primes of the AM-on-path condition were smaller than those of the FL condition at 0 ( $F(1,16) = 21.88$ ,  $p < 0.001$ ) and 15 ( $F(1,16) = 12.85$ ,  $p < 0.005$ ) deg of orientations. Regarding a simple main effect of the orientations in the AM-on-path condition ( $F(3,24) = 13.27$ ,  $p < 0.001$ ), a post-hoc test (Tukey's HSD) revealed that the  $d$ -primes in 0 and 15 deg of orientations were smaller than those in 45 and 90 deg ( $p < 0.05$ ).

The results showed that sensitivity to the target decreased only when the difference in orientation was within 15 deg between the AM stimuli and target. Such an orientation-tuned effect is consistent with estimates of the bandwidth of narrowly tuned low-level orientation channels (e.g., Campbell & Kulikowski, 1966; for a recent overview,

see Goveanlock, Taylor, Sekuler, & Bennett, 2009). This pattern of results thus indicates that AM interference reflects the low-level coding of a basic stimulus property, with interference occurring only when the target stimulus falls within the narrow channel that would detect inducing stimuli.

## Experiment 3

The third experiment investigated whether detection performance was impaired for a target with a spatiotemporally intermediate stimulus property of inducers in the AM trajectory. Here, the inducers' orientations were either fixed (at +45 deg or −45 deg) or different (+45 deg to −45 deg or vice versa). In the latter case, the stimuli were perceived as changing their orientation during AM. We also presented the target with ±45- or 0-deg orientation. Based on the result of Experiment 2, we could predict that AM interference would be less for a target with 0-deg orientation when the inducers' orientation was consistent. Moreover, if inducers' spatiotemporally intermediate orientation could be represented in the AM trajectory, detection performance for a target with 0-deg orientation would be also degraded when the inducers' orientation changed during AM.

## Methods

One author (S. H.) and four paid volunteers (undergraduate students in Rikkyo University) participated in

this experiment. The newly recruited volunteers were naive to the purpose of the experiment. All had normal or corrected-to-normal vision.

While the orientations of the inducers were fixed at either +45 deg or −45 deg in inducer-consistent trials, these were +45 and −45 deg in inducer-inconsistent trials (Figure 3). The orientation of the target was consistent with that of the inducer in ±45-deg target trials. We also presented a target with 0-deg (horizontal) orientation (0-deg target trials). Both the AM-on-path and FL conditions were included.

In the practice session, the participants completed 32 trials: conditions (2) × inducer's consistency (2) × target's orientations (2) × target (2; present/absent) × repetitions (2). The main session consisted of 320 trials: conditions (2) × inducer's consistency (2) × target's orientations (2) × target (2) × repetitions (20). The inducers' and target's orientations were randomly assigned in each trial and counterbalanced among the conditions. Except for these differences, the apparatus, stimulus parameters, and procedures were identical to those in Experiment 2.

## Results and discussion

False alarms were pooled and averaged among target-absent trials in each condition and each inducer's consistency. Regarding the calculated  $d$ -primes (Figure 3), we conducted a three-way repeated-measures ANOVA with conditions (2) × inducer's consistency (2) × target's orientations (2). This analysis revealed a significant interaction among the factors ( $F(1,4) = 9.14, p < 0.05$ ). There were significant simple interactions between conditions

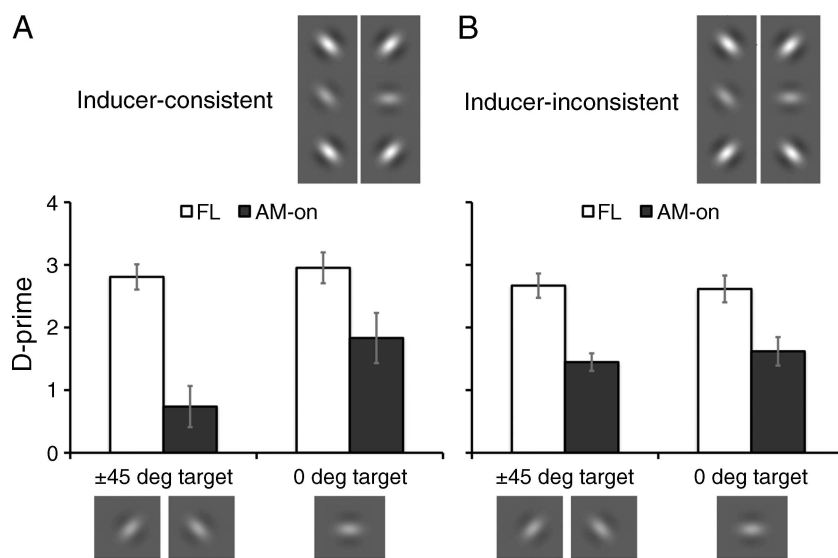


Figure 3. Schematics of the stimuli and results in Experiment 3. (A) Inducer-consistent and (B) inducer-inconsistent trials. Error bars denote the standard errors of the means.

and target's orientations in the inducer-consistent trials ( $F(1,8) = 9.66, p < 0.05$ ) and between inducer's consistency and target's orientations in the AM-on-path condition ( $F(1,8) = 18.86, p < 0.005$ ).

With regard to the simple interactions, we found that detection performance was more degraded for the target with  $\pm 45$ -deg rather than 0-deg orientation in the inducer-consistent trials (45 deg or  $-45$  deg) of the AM-on-path condition. On the contrary, the performance was equally impaired for all the targets when the inducers changed their orientations ( $+45$  deg and  $-45$  deg) during AM. A simple main effect of target's orientations in the inducer-consistent trials of the AM-on-path condition showed that the  $d$ -prime of the  $\pm 45$ -deg target trials was smaller than that of the 0-deg target trials ( $F(1,16) = 8.43, p < 0.05$ ). In contrast, a simple main effect of target's orientations in the inducer-inconsistent trials of the AM-on-path condition was not significant ( $F(1,16) = 0.76, p = 0.40$ ). These results show that AM interference can occur for the stimulus with not only the inducers' orientation but also their intermediate orientation information, indicating that the spatiotemporally intermediate feature of the AM stimulus can also be interpolated in the AM trajectory.

It was also demonstrated that detection performance for the target with the inducers' orientation showed stronger degradation when the inducers' orientations were consistent rather than when they changed during AM. A simple main effect of inducers' orientations in the  $\pm 45$ -deg target trials of the AM-on-path condition showed that the  $d$ -prime of the inducer-consistent trials was smaller than that of the inducer-inconsistent trials ( $F(1,16) = 8.43, p < 0.05$ ). This might suggest that the internal representation of AM stimuli could be robustly established in the AM trajectory due to spatiotemporal summation of consistent inducers' information.

It should also be noted that, unlike Experiment 2, AM interference was observed even when the inducer's orientation was consistent and the inducers' and target's orientations were different by 45 deg. A simple main effect of conditions showed that the  $d$ -primes of the AM-on-path condition were smaller than those of the FL condition in all the inducers' consistency and target's orientations ( $F(1,16) = 18.86 (p < 0.001)$  in the inducer-consistent and  $\pm 45$ -deg target trials,  $8.61 (p < 0.005)$  in the inducer-consistent and 0-deg target trials,  $10.22 (p < 0.005)$  in the inducer-inconsistent and  $\pm 45$ -deg target trials, and  $6.82 (p < 0.05)$  in the inducer-inconsistent and 0-deg target trials). This could be simply explained by oblique effect on the inducers' orientation: Since orientation discrimination sensitivity to a stimulus becomes worse when stimulus orientation deviates from the horizontal or vertical direction (Heeley & Timney, 1988), AM interference with inducers containing 0-deg orientation (Experiment 2) could show sharper sensitivity to the differences in the inducers' and target's orientation relative to the inducers with  $\pm 45$ -deg orientation.

## Experiment 4

In Experiment 3, we found that AM interference occurred equally for the targets with the inducers' orientation and those with their intermediate orientation when AM stimuli changed their orientation during AM. Based on this result, one might assume that the orientation changes of AM stimuli induced broader orientation tuning of AM interference, not the spatiotemporal interpolation of the intermediate features of the AM stimulus. The fourth experiment tested this possibility. The inducers' orientations were always different ( $+45$  deg to  $-45$  deg or vice versa). The target's orientations were either 0,  $\pm 22.5$ ,  $\pm 67.5$ , or 90 deg. While all the target's orientations were different from the inducers' orientations, only the former two could be represented in the AM trajectory (Figure 4). Thus, if not the broader orientation tuning but the spatiotemporal interpolation played a key role, AM interference would be observed, particularly for the targets with 0 and 22.5 deg of orientations.

## Methods

One author (S. H.) and four paid volunteers (graduate and undergraduate students in Rikkyo University) participated in this experiment. The newly recruited volunteers were naive to the purpose of the experiment. All had normal or corrected-to-normal vision.

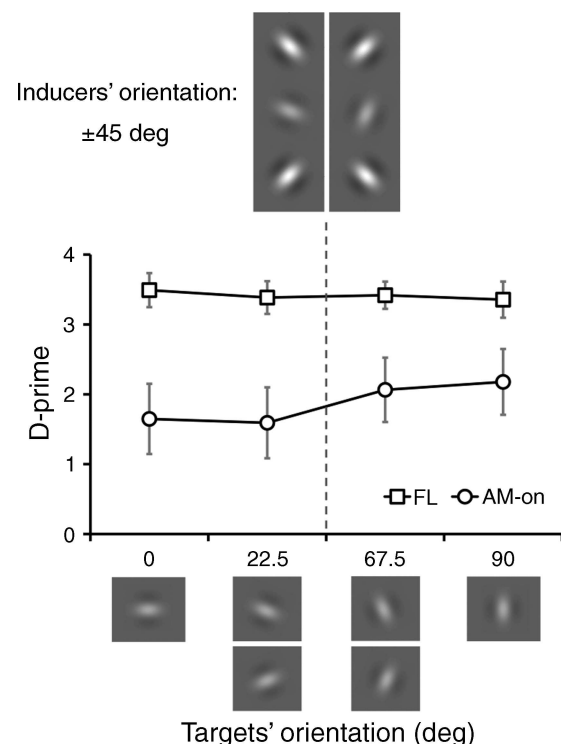


Figure 4. Schematics of the stimuli and results in Experiment 4. Error bars denote the standard errors of the means.

The orientations of the inducers were  $+45$  and  $-45$  deg (Figure 4). The orientation of the target was either 0, 22.5,  $\pm 67.5$ , or 90 deg. Both the AM-on-path and FL conditions were included.

In the practice session, the participants completed 32 trials: conditions (2)  $\times$  target's orientations (4)  $\times$  target (2; present/absent)  $\times$  repetitions (2). The main session consisted of 320 trials: conditions (2)  $\times$  target's orientations (4)  $\times$  target (2)  $\times$  repetitions (20). The inducers' and target's orientations were randomly assigned in each trial and counterbalanced among the conditions. Except for these differences, the apparatus, stimulus parameters, and procedures were identical to those in Experiment 3.

## Results and discussion

False alarms were pooled and averaged among target-absent trials in each condition. Regarding the calculated  $d$ -primes (Figure 4), we conducted a two-way repeated-measures ANOVA with conditions (2)  $\times$  target's orientations (4). This analysis revealed a significant interaction between the factors ( $F(3,12) = 4.02$ ,  $p < 0.05$ ). Simple main effects of the conditions revealed that the  $d$ -primes of the AM-on-path condition were smaller than those of the FL condition in all the target's orientations: 0,  $\pm 22.5$ ,  $\pm 67.5$ , and 90 deg of orientations ( $F_s(1,16) = 33.33$ , 30.59, 17.46, and 13.19, respectively ( $p < 0.005$ )). For a simple main effect of the target's orientation in the AM-on-path condition ( $F(3,24) = 6.06$ ,  $p < 0.005$ ), the post-hoc test revealed that the  $d$ -primes in the 0 and  $\pm 22.5$  deg of orientations were smaller than in the  $\pm 67.5$  and 90 deg of orientations ( $p < 0.05$ ).

While detection performance was degraded for all the target's orientations, stronger degradation was observed especially for the two target's orientations (0 and  $\pm 22.5$  deg) that could be represented in the AM trajectory. We, therefore, could conclude that AM interference occurred dominantly for the spatiotemporally intermediate features of the AM stimulus interpolated in the AM trajectory.

## Experiment 5

In this experiment, we further investigated the effect of consistency between target and inducers for a lower level stimulus property other than orientation. Specifically, we manipulated the spatial phase information of the target to determine whether differences in phase between the inducers and target could affect target detection performance for targets falling along the AM trajectory.

## Methods

One author (S. H.) and four paid volunteers (undergraduate students in Rikkyo University) participated in

this experiment. The newly recruited volunteers were naive to the purpose of the experiment. All had normal or corrected-to-normal vision.

The phase of the inducers was always 0 deg (white center), while that of the target was either 0,  $\pm 45$ ,  $\pm 90$ , or 180 deg (black center; Figure 5A). Similar to Experiment 2, the eccentricity of the inducers and target was 10 deg for the volunteers and 20 deg for the author because his detection performance reached ceiling level at 10 deg of eccentricity. Again, both the AM-on-path and FL conditions were included.

In the practice session, the participants completed 32 trials: conditions (2)  $\times$  phases (4)  $\times$  target (2; present/absent)  $\times$  repetitions (2). The main session consisted of 320 trials: conditions (2)  $\times$  phases (4)  $\times$  target (2)  $\times$  repetitions (20). The total number of trials was equal (10 trials in each) between  $+45$  and  $-45$  deg or  $+90$  and  $-90$  deg of phase. Except for these differences, the apparatus, stimulus parameters, and procedures were identical to those of Experiments 1 and 2.

## Results and discussion

False alarms were pooled and averaged among target-absent trials in each condition. With regard to the calculated  $d$ -primes (Figure 5B), we conducted a two-way repeated-measures ANOVA with conditions (2)  $\times$  phases (4). This analysis revealed a significant main effect of conditions

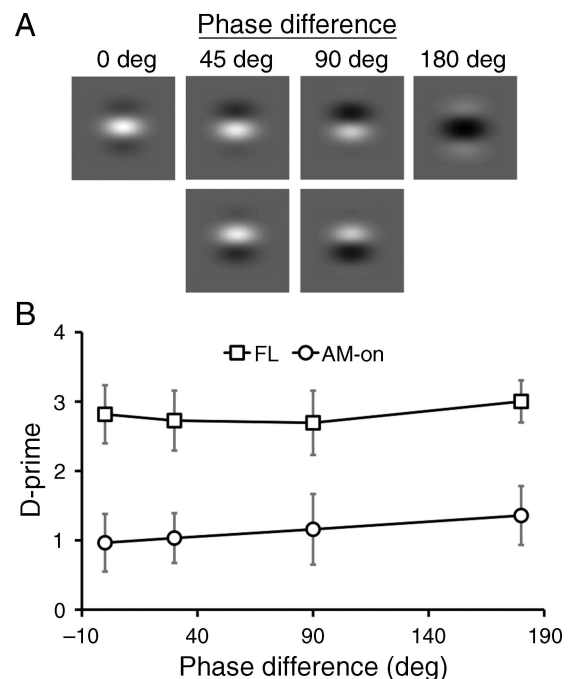


Figure 5. Schematics of the stimuli and results in Experiment 5. (A) Stimuli. Phase was manipulated from 0 to 90 deg. (B) Result. Error bars denote the standard errors of the means.

( $F(1,4) = 384.37$ ,  $p < 0.001$ ). However, a main effect of phases ( $F(1,4) = 2.79$ ,  $p = 0.09$ ) or the interaction between the factors ( $F(3,12) = 0.29$ ,  $p = 0.83$ ) was not significant. These results suggest that, unlike the object's orientation information, differences in the object's spatial phase information could not affect the magnitude of AM interference.

## Experiment 6

In Experiment 5, we did not find any effect of phase difference on the extent of AM interference. Although one could suggest that the discrimination of phase differences was difficult in the periphery, previous research has shown that at least some phase differences, such as that between 0 and 180, should remain discriminable in the periphery even in complex stimuli (Bennett & Banks, 1987, 1991). Thus, we investigated whether the object's phase differences themselves could be discriminated in the current experimental situation as Experiment 6A.

Moreover, one might assume that the object's phase differences did not affect the magnitude of AM interference due to the basic uncertainty of the stimuli in the peripheral visual field. In order to investigate this possibility, we replicated Experiment 4 at 5 deg of eccentricity instead of 10 deg (Experiment 6B).

## Methods

One author (S. H.) and four paid volunteers (undergraduate students in Rikkyo University) participated in Experiment 6A, and another four paid volunteers participated in Experiment 6B. The newly recruited volunteers were naive to the purpose of the experiment. All had normal or corrected-to-normal vision.

In Experiment 6A, the participants were asked to report whether or not the target was different from the inducer. The discrimination performances for orientation and phase were separately tested into two blocks. The order of the blocks was counterbalanced among the participants. In each block, the inducer and target had 0 deg of orientation or phase (60 trials) in half the trials (same trials). In the other half, the target contained three different deviations (15, 45, and 90 deg for orientations and 45, 90, 180 deg for phases) from the inducers for 60 trials: deviations (3)  $\times$  repetitions (20) (different trials). In each trial, only one of the inducers was presented at either the upper or lower position (Figure 6A).

In Experiment 6B, we tested the target detection performance for the target with the manipulation of object's phase information at 5 deg of eccentricity. Except for these differences, the stimuli, apparatus, and procedures were identical to those in Experiments 2 and 5.

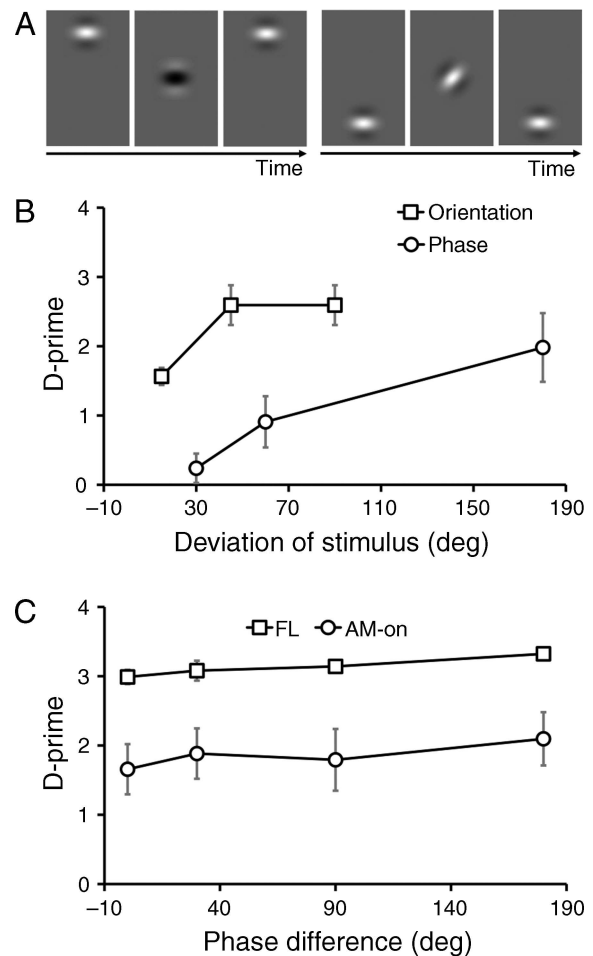


Figure 6. Schematics of the stimuli and results in Experiment 6. (A) Schematics of stimulus presentation for phase and orientation. (B) Results in Experiment 6A. (C) Results in Experiment 6B. Error bars denote the standard errors of the means.

## Results and discussion

As for Experiment 6A, we calculated  $d$ -primes for the “different” responses in the different trials as hits and those in the same trials as false alarms (Figure 6B). With regard to orientation, a one-way repeated-measures ANOVA revealed a main effect ( $F(2, 6) = 17.92$ ,  $p < 0.005$ ). A post-hoc test (Tukey's HSD) showed that the  $d$ -prime in 15 deg of deviation was lower than that in the others ( $p < 0.05$ ). With regard to phase, the ANOVA revealed a main effect ( $F(2, 6) = 21.91$ ,  $p < 0.005$ ). A post-hoc test showed that the  $d$ -prime in 180 deg of deviation was higher than that in the others ( $p < 0.05$ ).

As with Experiment 5, we calculated  $d$ -primes for the data of Experiment 6B (Figure 6C). A two-way repeated-measures ANOVA with conditions (2)  $\times$  phases (4) revealed a significant main effect of conditions ( $F(1,3) = 12.94$ ,  $p < 0.05$ ) and that of phases ( $F(1,3) = 6.30$ ,  $p < 0.05$ ). However, the interaction between the factors was not significant ( $F(3,9) = 0.29$ ,  $p = 0.83$ ).

Experiment 6A confirmed that the difference between 0 and 180 deg of phases could be distinguishable without continuous AM sequences for our specific stimulus configurations. The results, therefore, clearly showed that differences in phase, as well as those in orientation, could be discriminated. Moreover, the same pattern of results with Experiment 5 was replicated in Experiment 6B where the stimuli were presented at 5 deg of eccentricity instead of 10 deg. These findings indicate that the results of Experiment 5 could not be explained simply by the absence of sensitivities to the stimuli at the peripheral visual field.

On the basis of the findings in Experiments 5 and 6, it appears that AM interference is not modulated by all aspects of stimulus differences coded at the lowest levels. In other words, differences in orientation information do influence AM interference, while AM interference is not influenced by the consistency of the object's spatial phase.

## General discussion

The current study investigated whether the detection performance for targets changed along an AM trajectory. We found that target detection performance was degraded only along the AM trajectory (Experiment 1) and only when AM was perceived. This pattern of results indicates that AM stimuli and their underlying object representations can interfere with the detection of physical stimuli. Furthermore, AM interference declines with increasing difference in orientation between the AM inducers and target (Experiment 2). We also found that AM interference occurred for the target with intermediate orientations of the inducers that changed their orientations during AM (Experiments 3 and 4). On the contrary, phase differences between the AM inducers and target had no effect (Experiment 5), even when those phase differences are highly discriminable (Experiment 6). These findings imply that AM interference selectively reflects the consistency of an object's feature—even a spatiotemporally intermediate object's features interpolated in the AM trajectory—between the AM stimulus and target.

One might suspect that the effect of eye movements or attentional shifts induced by the alternation of the inducing stimuli could have driven the AM interference effect. However, the decrement of target detection performance along the AM trajectory (the AM-on-path condition) was clearly distinguishable from that in the AM-off-path condition in which the target position deviated from the AM trajectory. Thus, the results of the experiments could not be explained simply by eye movements or attentional shifts. The involvement of the transient signals induced by the inducers around the target (e.g., Kanai & Kamitani, 2003) might also be considered as leading to the AM interference

effect. We can, however, dismiss this possibility because the suppression of target detection was not observed when the inducers simply appeared and AM was not perceived (the FL condition).

The results of the current study suggest that the internal representation of AM stimuli degraded the target detection performance along the AM trajectory. Thus far, it has been reported that letter discrimination performance was impaired in an AM trajectory (Hogendoorn et al., 2008; Yantis & Nakama, 1998). These previous findings seemed to suggest that the internal representation of AM stimuli directly interfere with a relatively high-level perceptual stage in terms of letter processing. In contrast, our current study clearly demonstrates that perceptual sensitivity decreases for the elemental targets along the AM trajectory. Our results, along with those from brain imaging studies (e.g., Muckli et al., 2005), suggest that the letter interference seen in previous studies could also be the result of interference as lower level visual processing stages; in this conceptualization, the AM letter interference might have been caused by degraded letter visibility due to decreased target detection. We could, therefore, consider that AM interference certainly can occur for basic lower level aspect of visual processing, like pattern detection.

A significant finding was that AM interference reflects the consistency of the object's properties between the AM stimuli and target. When the orientation of the AM stimuli and target differed significantly, AM interference did not occur. Moreover, AM interference did occur even for the target with intermediate orientations of the inducers. These results imply that internal object representation in the AM trajectory contains or maintains the object's feature of AM stimuli and interferes with another object on the basis of the consistencies of the features. Such a conclusion is consistent with suggestions from previous studies using more subjective methods that internal representations mediate AM perception and persist throughout the AM trajectory, where there are no physical inputs (Kolars, 1972; Kolars & von Grünau, 1976; Shepard & Judd, 1976; Shepard & Zare, 1983). Our findings provide further information regarding the manner in which internal representation contributes to AM perception: The internal representation could act much as a physical instantiation of the AM inducers and mask the perception of physical inputs containing similar object properties to maintain continuous AM perception.

Consistent with the current study, previous studies suggest that internal representations of moving stimuli and stimulus' low-level features can be spatiotemporally maintained along motion trajectory: Object's features can be attributed and integrated among stimuli in a motion trajectory (trajectory integration) with regard to luminance (Shimozaki, Eckstein, & Thomas, 1999), color (Nishida, Watanabe, Kuriki, & Tokimoto, 2007), size (Kawabe, 2008), motion (Boi, Ögmen, Krummenacher, Otto, & Herzog,

2009), and vernier offset (Otto, Öğmen, & Herzog, 2006). However, some phenomenal aspects seem to be different between trajectory integration and AM interference. In trajectory integration, motion information induces perceptual changes to *perceived stimuli* by attribution/integration of a physically presented moving objects' feature, especially when continuous motion is perceived among all moving stimuli (Breitmeyer, Herzog, & Öğmen, 2008; Otto, Öğmen, & Herzog, 2009). In AM interference, the target becomes an *unperceived stimulus* based on the consistency of an object's feature between target and inducers in the motion trajectory where moving stimuli were not physically presented. As a consequence, motion perception is maintained only between inducers against a transient onset of the target. Based on these facts, we could consider that trajectory integration and AM interference separately demonstrates counterpart processes in perceptual interaction between object and motion processing: Trajectory integration shows the contributions of motion perception to the spatiotemporal maintenance/summation process of an object's low-level feature. In contrast, AM interference demonstrates that the spatiotemporal maintenance/interpolation process of a low-level feature can establish continuous motion perception of a single object.

It is also noteworthy that the effect of stimulus consistency on AM interference occurred selectively. Although orientation information affected the magnitude of AM interference, phase information did not. Interestingly, this same pattern of stimulus consistency has been seen in masking experiments using physical stimuli: Masking can be abolished by increasing the orientation difference between target and mask (Campbell & Kulikowski, 1966; Govenlock et al., 2009), but masking is not necessarily abolished by contrast reversal (a 180-deg phase shift; Foley & Chen, 1999; Georgeson & Georgeson, 1987). In addition to the fact that orientation selectivity exists in motion perception, orientation information would be highly related to pattern detection (e.g., Nothdurft, 1991). On the contrary, phase information could be considered a dominant cue for shape perception (Piotrowski & Campbell, 1982). We could also speculate that an object's shape information is not well processed in AM perception (e.g., Burt & Sperling, 1981), because AM perception has limited capacity for attentional processing load (Dawson, 1991). In line with this idea, it was suggested that internal object representation contained coarse shape (depth) information (Hidaka, Kawachi, & Gyoba, 2008, 2009). However, it is also worth noting that the availability of shape information for AM perception changes depending on the situation (e.g., Sekuler & Bennett, 1996). It may also be considered that the selectivity of AM interference could be observed for an object's high-level (curvature, depth, shape type, and so on) as well as low-level features. Detailed aspects of the object's feature selectivity in AM interference will be tackled in future research.

## Conclusion

The current study investigated whether AM interference occurs in low-level perception. We found that target detection performance was inhibited when a target was presented along an AM trajectory. Further, this AM interference weakened when the difference in the object's orientation information between the AM stimuli and target became greater. Moreover, AM interference occurred even for the target with spatiotemporally intermediate orientations of the inducers. In contrast, the difference in the object's phase information had no effect. These results were not explained simply by eye movements, attentional shifts, or inducers' transient signals. The present findings suggest that there is an internal representation of AM stimuli that moves along the path of AM, and the representation can inhibit the perception of the physical stimuli and maintain motion perception of a single object along the AM trajectory. Furthermore, the internal representation contains or maintains information about an object's property that is essential for AM perception and its inhibition mechanism that mirrors processes seen for physical stimuli.

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## References

- Anscombe, F. J. (1956). On estimating binomial response relations. *Biometrika*, 43, 461–464.
- Bennett, P. J., & Banks, M. S. (1987). Sensitivity loss in odd-symmetric mechanisms and phase anomalies in peripheral vision. *Nature*, 326, 873–876. [PubMed]
- Bennett, P. J., & Banks, M. S. (1991). The effects of contrast, spatial scale, and orientation on foveal and

- peripheral phase discrimination. *Vision Research*, 31, 1759–1786. [PubMed]
- Boi, M., Ögmen, H., Krummenacher, J., Otto, T. U., & Herzog, M. H. (2009). A (fascinating) litmus test for human retino- vs. non-retinotopic processing. *Journal of Vision*, 9(13):5, 1–11, <http://www.journalofvision.org/content/9/13/5>, doi:10.1167/9.13.5. [PubMed] [Article]
- Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision*, 10, 433–436. [PubMed]
- Breitmeyer, B. G., Herzog, M. H., & Ögmen, H. (2008). Motion, not masking, provides the medium for feature attribution. *Psychological Science*, 19, 823–829. [PubMed]
- Burt, P., & Sperling, G. (1981). Time, distance, and feature trade-offs in visual apparent motion. *Psychological Review*, 88, 171–195. [PubMed]
- Campbell, F. W., & Kulikowski, J. J. (1966). Orientational selectivity of the human visual system. *The Journal of Physiology*, 187, 437–445. [PubMed]
- Dawson, M. R. W. (1991). The how and why of what went where in apparent motion: Modeling solutions to the motion correspondence problem. *Psychological Review*, 98, 569–603. [PubMed]
- Foley, J. M., & Chen, C. C. (1999). Pattern detection in the presence of maskers that differ in spatial phase and temporal offset: Threshold measurements and a model. *Vision Research*, 39, 3855–3872. [PubMed]
- Georgeson, M. A., & Georgeson, J. M. (1987). Facilitation and masking of briefly presented gratings: Time-course and contrast dependence. *Vision Research*, 27, 369–379. [PubMed]
- Govenlock, S. W., Taylor, C. P., Sekuler, A. B., & Bennett, P. J. (2009). The effect of aging on the orientational selectivity of the human visual system. *Vision Research*, 49, 164–172. [PubMed]
- Heeley, D. W., & Timney, B. (1988). Meridional anisotropies of orientation discrimination for sine wave gratings. *Vision Research*, 28, 337–344. [PubMed]
- Hidaka, S., Kawachi, Y., & Gyoba, J. (2008). Depth representation of moving 3D objects in apparent motion path. *Perception*, 37, 688–703. [PubMed]
- Hidaka, S., Kawachi, Y., & Gyoba, J. (2009). The representation of moving 3-D objects in apparent motion perception. *Attention, Perception & Psychophysics*, 71, 1294–1304. [PubMed]
- Hogendoorn, H., Carlson, T. A., & Verstraten, F. A. J. (2008). Interpolation and extrapolation on the path of apparent motion. *Vision Research*, 48, 872–881. [PubMed]
- Kanai, R., & Kamitani, Y. (2003). Time-locked perceptual fading induced by visual transients. *Journal of Cognitive Neuroscience*, 15, 664–672. [PubMed]
- Kawabe, T. (2008). Spatiotemporal feature attribution for the perception of visual size. *Journal of Vision*, 8(8):7, 1–9, <http://www.journalofvision.org/content/8/8/7>, doi:10.1167/8.8.7. [PubMed] [Article]
- Koenderink, J. J., van Doorn, A. J., & van de Grind, W. A. (1985). Spatial and temporal parameters of motion detection in the peripheral visual field. *Journal of the Optical Society of America A*, 2, 252–259. [PubMed]
- Kolers, P. A. (1972). *Aspects of motion perception*. Oxford, NY: Pergamon Press.
- Kolers, P. A., & von Grünau, M. (1976). Shape and color in apparent motion. *Vision Research*, 16, 329–335. [PubMed]
- Korte, A. (1915). Kinematoskopische untersuchungen. *Zeitschrift für Psychologie*, 72, 193–296.
- Liu, T., Slotnick, S. D., & Yantis, S. (2004). Human MT+ mediates perceptual filling-in during apparent motion. *NeuroImage*, 21, 1772–1780. [PubMed]
- Macmillan, N. A., & Creelman, C. D. (2004). *Detection theory: A user's guide* (2nd ed.). New Jersey: Lawrence Erlbaum Associates.
- Muckli, L., Kohler, A., Kriegeskorte, N., & Singer, W. (2005). Primary visual cortex activity along the apparent-motion trace reflects illusory perception. *PLoS Biology*, 3, e265. [PubMed]
- Nishida, S., Watanabe, J., Kuriki, I., & Tokimoto, T. (2007). Human visual system integrates color signals along a motion trajectory. *Current Biology*, 17, 366–372. [PubMed]
- Nothdurft, H. C. (1991). Texture segmentation and pop-out from orientation contrast. *Vision Research*, 31, 1073–1078. [PubMed]
- Otto, T. U., Ögmen, H., & Herzog, M. H. (2006). The flight path of the phoenix—The visible trace of invisible elements in human vision. *Journal of Vision*, 6(10):7, 1079–1086, <http://www.journalofvision.org/content/6/10/7>, doi:10.1167/6.10.7. [PubMed] [Article]
- Otto, T. U., Ögmen, H., & Herzog, M. H. (2009). Feature integration across space, time, and orientation. *Journal of Experimental Psychology: Human Perception and Performance*, 35, 1670–1686. [PubMed]
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, 10, 437–442. [PubMed]
- Piotrowski, L. N., & Campbell, F. W. (1982). A demonstration of the visual importance and flexibility of spatial-frequency amplitude and phase. *Perception*, 11, 337–346. [PubMed]
- Sekuler, A. B., & Bennett, P. J. (1996). Spatial phase differences can drive apparent motion. *Perception & Psychophysics*, 58, 174–190. [PubMed]

- Shepard, R. N., & Judd, S. A. (1976). Perceptual illusion of rotation of three-dimensional objects. *Science*, *191*, 952–954. [PubMed]
- Shepard, R. N., & Zare, S. L. (1983). Path-guided apparent motion. *Science*, *220*, 632–634. [PubMed]
- Shimozaki, S. S., Eckstein, M., & Thomas, J. P. (1999). The maintenance of apparent luminance of an object. *Journal of Experimental Psychology: Human Perception and Performance*, *25*, 1433–1453. [PubMed]
- Sorkin, R. D. (1999). Spreadsheet signal detection. *Behavior Research Methods, Instruments, & Computers*, *31*, 46–54. [PubMed]
- Sterzer, P., Haynes, J. D., & Rees, G. (2006). Primary visual cortex activation on the path of apparent motion is mediated by feedback from hMT+/V5. *NeuroImage*, *32*, 1308–1316. [PubMed]
- Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. *Zeitschrift für Psychologie*, *61*, 161–265.
- Wibral, M., Bledowski, C., Kohler, A., Singer, W., & Muckli, L. (2009). The timing of feedback to early visual cortex in the perception of long-range apparent motion. *Cerebral Cortex*, *19*, 1567–1582. [PubMed]
- Yantis, S., & Nakama, T. (1998). Visual interactions in the path of apparent motion. *Nature Neuroscience*, *1*, 508–512. [PubMed]