

## Attention alters the appearance of motion coherence

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Selective attention enhances visual information processing, as measured by behavioral performance and neural activity. However, little is known about its effects on subjective experience. Here, we investigated the effect of transient (exogenous) attention on the appearance of visual motion, using a psychophysical procedure that directly measures appearance and controls for response bias. Observers viewed pairs of moving dot patterns and reported the motion direction of the more coherent pattern. Directing attention (via a peripheral precue) to a stimulus location increased its perceived coherence level and improved performance on a direction discrimination task. In a control experiment, we ruled out response bias by lengthening the time interval between the cue and the stimuli, so that the effect of transient attention could no longer be exerted. Our results are consistent with those of neurophysiological studies showing that attention modulates motion processing and provide evidence of a subjective perceptual correlate of attention, with a concomitant effect on performance.

Attention is the mechanism that allows us to selectively process the vast amount of information that we receive and to guide our behavior. Visual spatial attention can be deployed overtly, accompanied by eye movements to the relevant location, or covertly, without such eye movements. Covert attention can be either directed to a particular location voluntarily (sustained or endogenous attention) or drawn to a location via external stimulation, such as an abrupt onset (transient or exogenous attention; Yantis, 2000). The two types of attention differ with regard to their temporal dynamics (Jonides, 1980), degree of automaticity (Cheal & Lyon, 1991; Müller & Rabbitt, 1989), and possible neural mechanisms (Corbetta & Shulman, 2002). It is well established that attention improves performance (accuracy and response time) on many tasks. However, an important issue, debated by psychologists and physiologists alike for over 100 years, yet rarely investigated, is whether attention changes one's subjective experience of the visual world.

A major obstacle to answering this question had been the lack of an effective method for measuring subjective experience. It is important to distinguish a change in perception from a response bias that may arise due to task specifics and demand characteristics. Recently, we implemented a paradigm for studying the effect of attention on apparent contrast (Carrasco, Ling, & Read, 2004) and spatial resolution (Gobell & Carrasco, 2005), dimensions in which attention affects performance (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Lee, Itti, Koch, & Braun, 1999;

Yeshurun & Carrasco, 1998). In this paradigm, observers are shown two stimuli and are asked to "report property  $x$  of the stimulus that is greater/lesser in property  $y$ ." That is, they use the perceived relative values of property of  $y$ —the primary interest of the experiment (e.g., contrast or spatial frequency)—as an indicator of which stimulus to report on property  $x$  (e.g., orientation). The critical manipulation is that the observers are asked not to directly rate their subjective experience on property  $y$  but to make a decision about another stimulus property,  $x$ . This procedure and further control experiments ruled out response bias (Luck, 2004; Treue, 2004). We have found that attention increases apparent contrast and spatial frequency.

These studies addressed the effects of attention on the appearance of static stimulus properties. It is unknown, however, whether attention also affects the appearance of dynamic stimulus properties. A fundamental dynamic dimension is visual motion. Most of our visual information involves motion, because of various types of movement: eye movement, observer movement, and object movement (Gibson, 1979). In addition to forming a major component of our perceptual world, motion is also critical to guiding our locomotion and interaction with other objects. Such ecological considerations suggest that it is important to understand how attention affects motion perception and, in particular, whether transient attention alters the appearance of motion. This was the primary goal of the present study.

The secondary goal of the present experiment was to examine the effect of transient attention on the perception of motion as assessed by performance in a direction discrimination task. Previous studies have shown that sustained attention affects performance in motion-related tasks. For instance, *sustained* attention lowers coherence threshold in direction discrimination in humans (Dobkins & Bosworth, 2001), as well as increases the accuracy in motion detection in monkeys (Cook & Maunsell, 2002).

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However, it is still unknown whether *transient* attention affects the perception of motion coherence. Hence, while assessing appearance, we simultaneously measured performance in a direction discrimination task. As coherence increases, the motion signal becomes stronger, and the direction of motion is more salient. We reasoned that if attention increases apparent coherence, it should also improve performance on the direction discrimination task.

## METHOD

### Subjects

Twelve observers participated in Experiment 1; 2 were authors, and the remaining 10 were naive as to the purpose of the experiment. Ten observers participated in Experiment 2, 9 of whom had participated in Experiment 1.

### Visual Stimuli

The stimuli were presented on a 19-in. CRT monitor refreshed at 100 Hz. Background luminance was set at 20 cd/m<sup>2</sup>. The peripheral cues consisted of two black dots, one above and one below the horizontal meridian (3° from the horizontal meridian, 8° from the vertical meridian), and the neutral cue was a single black dot in the center of the screen (dot size: 0.5°, <1 cd/m<sup>2</sup>). The moving random dot pattern (RDP) contained 40 dots (size: 0.1°) in a 5° aperture, which were shown at maximum luminance (100 cd/m<sup>2</sup>). Coherence of the RDP was controlled by the proportion of dots that moved in a single direction; these dots moved continuously at 4°/sec, and the rest of the dots were plotted at random locations every 20 msec (these dots did not move along any particular direction). A small black fixation point was presented throughout in the center of the screen. The observers were stabilized with a chinrest and viewed the stimuli from a distance of 57 cm.

### Design and Procedure

The events in a single trial are illustrated in Figure 1. A brief auditory tone indicated the beginning of each trial. After 500 msec, cues appeared for 50 msec, in the left, right, or center of the screen (neutral cue). An interval of either 30 msec (Experiment 1) or 450 msec (Experiment 2) followed the cue offset. Two moving RDPs were then presented for 150 msec, one to the left and one to the right of fixation on the horizontal meridian at 8° of eccentricity. To prevent forward masking from the cues, the locations of the peripheral cues did not overlap with the RDPs. One dot pattern always moved at 50% coherence (*standard*), while the other dot pattern could move with one of nine levels of coherence (*test*; 10%–90% in 10% steps). Both patterns moved independently in one of four directions at a small offset from the horizontal meridian. The observers were asked to “report the direction of motion of the more coherent pattern” by pressing one of four keys on a computer keyboard with each hand (left hand, “f,” “d,” “r,” and “e” keys; right hand, “j,” “k,” “u,” and “i” keys). The motion directions (upper left, upper right, lower left, and lower right) were directly mapped to the four keys (see the bottom diagram in Figure 1). Thus, if the observer pressed the “f” key, it indicated that the left pattern appeared to have higher coherence, and it moved in the lower right direction. After training, the observers reported no difficulty in using the stimulus–response mapping. The observers were instructed to maintain central fixation at all times. All the conditions, created by fully crossing factors within subjects (cue type, standard/test locations, and coherence level), were equiprobable and resulted in 1,296 total trials for each observer, divided into 12 blocks of 108 trials each. The observers completed the experiment in two sessions on different days. Each session contained 6 blocks and lasted 1 h.

The task reduced response bias because the observers were not directly responding with regard to perceived coherence, but we can

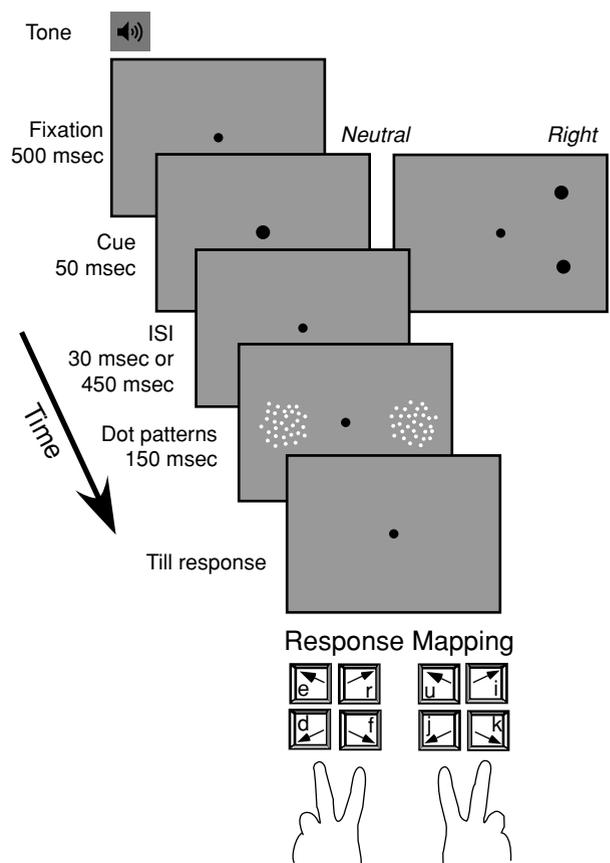


Figure 1. Schematic of the experimental procedure.

index perceived coherence from the direction discrimination. Cue location (left, right, and central), the locations of the standard and test, and their directions of motion were randomly assigned on each trial. The cues were thus totally uninformative regarding the correct response, and the observers were explicitly told so prior to the experiment. This procedure further reduced possible response bias, since the observers had no incentive to use the cue to guide their responses. Nevertheless, peripheral cues capture attention involuntarily even when they are uninformative (Jonides, 1980; Müller & Rabbitt, 1989; Pestilli & Carrasco, 2005).

A training phase of only neutral-cue trials preceded the experiments. The purpose of the training was twofold: to familiarize observers with the coherence judgment of RDPs and to titrate their performance on the direction discrimination. The direction offset from the horizontal meridian was adjusted during training, so that direction discrimination stabilized at around 75% correct for the 50% coherence standard stimulus. The direction offset ranged from 5° to 12° across observers.

In Experiment 1, we did not monitor eye movement, because the total durations of the cues and RDPs were brief enough to prevent goal-directed saccades (Mayfrank, Kimmig, & Fischer, 1987). In Experiment 2, although the interval between the cue and the RDP presentation was long enough for eye movements to take place, there was no incentive for the observers to move their eyes, given the uninformative nature of the cue. Nevertheless, we monitored the observers' eye position with an infrared video camera system (ISCAN, Burlington, MA). Videos of the left eye were viewed later to detect breaks from fixation, which happened rarely (<0.1%). Trials on which fixation was broken were discarded from the analyses.

### Data Analysis

We fitted the psychometric function with a four-parameter Weibull function:

$$\psi = \gamma + (1 - \gamma - \lambda) \left( 1 - \exp \left[ - \left( \frac{x}{\alpha} \right)^\beta \right] \right),$$

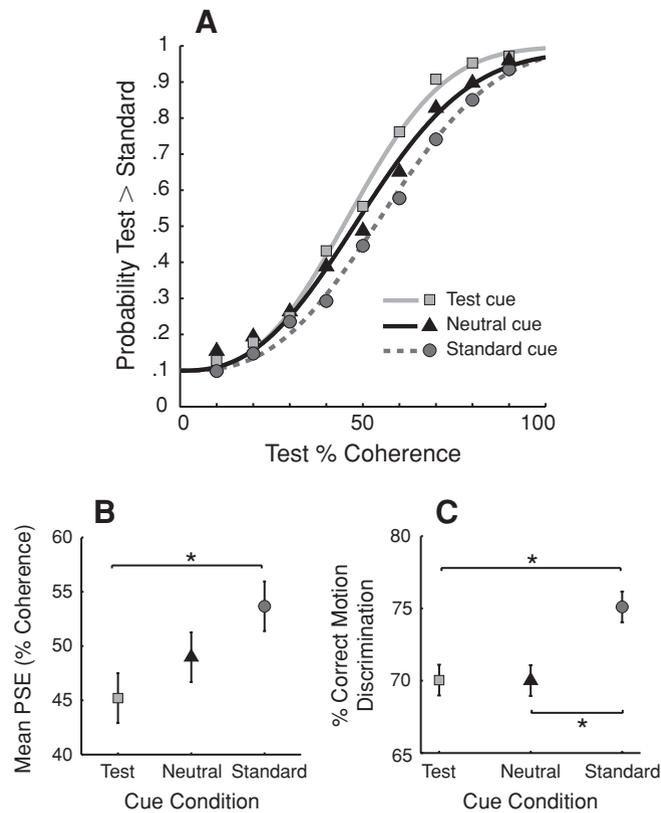
where  $\psi$  is the proportion,  $x$  is the coherence,  $\alpha$  is the location parameter,  $\beta$  is the slope, and  $\gamma$  and  $\lambda$  are lower and upper asymptotes, respectively. The  $\gamma$  and  $\lambda$  parameters were constrained between 0 and 0.1. Fits were performed using maximum likelihood estimation, and chi-square log-likelihood hypothesis tests were conducted comparing models including cue condition (full model) and excluding cue condition (constrained model; Wichmann & Hill, 2001a, 2001b).

## RESULTS

Figure 2A shows the psychometric functions for the coherence judgment averaged across observers for Experiment 1. The curves are Weibull fits to the averaged psychometric functions. Trials were collapsed across the absolute location (left vs. right) of the cue and RDPs and

were classified as standard cued, test cued, or neutral (48 trials per data point), which were within-subjects conditions. When the test was cued, the curve shifted to the left of the neutral curve; when the standard was cued, the curve shifted to the right. Thus, at all test coherence levels, the observers were more likely to report that the test had higher coherence when it was cued than when the standard was cued. The three curves were significantly different from each other, as assessed by a log-likelihood test [ $\chi^2(8) = 155, p < .001$ ]. These data indicate that the peripheral cues increased perceived coherence.

We also fitted individual observers' data and evaluated the reliability of the effect across observers. The asymptote parameters were constrained to limits of 0 and 0.1 (as opposed to fixing them at 0), to improve fit and stability of the point of subjective equality (PSE) estimates (defined as 50% threshold). Goodness of fit was evaluated using deviance scores (Wichmann & Hill, 2001a), which compute log-likelihood ratios between a fully saturated, zero residual model and the data model. A score above the critical chi-



**Figure 2.** Results from Experiment 1. (A) Psychometric functions of apparent coherence plotting the probability that the test stimulus would be chosen as more coherent than the standard stimulus (which had a fixed 50% coherence) against the coherence of the test stimulus (data averaged across 12 observers). Lines are maximum likelihood Weibull function fits. (B) Mean point of subjective equality (PSE; corresponding to 50% threshold) as a function of cue condition. (C) Mean percent correct for motion discrimination when the standard stimulus was chosen as more coherent. Error bars in panels B and C are pooled standard errors from the ANOVA (Loftus & Masson, 1994). Asterisks in panels B and C indicate significant differences in paired comparisons ( $p < .05$ ).

square value indicates a significant deviation between the fit and the data. The observer deviance scores, for all three cue conditions in both experiments, were generally non-significant (63/66 fits), relative to a  $\chi^2(9)$  critical value of 16.9. For Experiment 1, the average deviance score was 6.9 (range, 2.1–17.9); for Experiment 2, the average deviance score was 7.5 (range, 1.0–14.5). Figure 2B plots the mean PSE values for the neutral, standard-cued, and test-cued conditions. The means were significantly different from each other, as assessed with a repeated measures ANOVA [ $F(2,22) = 4.53, p < .05$ ]. Post hoc paired comparisons indicated that the test cue PSE was significantly lower than the standard cue PSE [ $t(11) = 2.26, p < .05$ ]. No significant difference was found for the slope parameter of the fitted psychometric functions [ $F(2,22) < 1$ ].

Figure 2C shows the performance data in the direction discrimination task, plotting percent correct when the observers chose the standard to be of higher coherence. (The average number of trials per observer for each cuing condition was 185 for the test-cued, 200 for the neutral, and 224 for the standard-cued conditions.) These are trials in which the direction discrimination was made on the same physical stimulus: the 50% coherent standard. Performance was better when the standard was cued than in the other two conditions, which did not differ [ANOVA,  $F(2,22) = 9.34, p < .01$ ; test vs. standard paired comparison,  $t(11) = 3.68, p < .005$ ; standard vs. neutral paired comparison,  $t(11) = 2.78, p < .05$ ]. Analysis of the test stimulus responses was not feasible, due to low statistical power, given that the test had nine different coherence values.

### Control Experiment

Although our experimental procedure minimizes response bias, to further rule out response bias, we conducted a control experiment (Experiment 2). It is known that transient, stimulus-driven attention reaches its maximum effect around 100 msec and rapidly dissipates (Jonides, 1980; Müller & Rabbitt, 1989). In Experiment 1, the stimulus timing was designed so that the maximum cuing effect occurred during the RDP presentation. In Experiment 2, we lengthened the interstimulus interval (ISI) between the cue and the RDP to 450 msec, to allow attention to dissipate before stimulus presentation. On the one hand, if our results were due to attention, the cuing effect should disappear with a longer ISI. On the other hand, if our results were due to response bias, the effect should persist, because response bias should not be sensitive to a slight change of timing before stimulus presentation.

Figure 3A shows the group-averaged psychometric function for Experiment 2. The slight difference among the three curves reached significance [ $\chi^2(8) = 20.35, p < .05$ ], but the order of the functions is inconsistent with an attention effect; that is, cuing did not increase perceived coherence. Figure 3B shows the PSE values from fitting individual data, which showed no reliable difference [ $F(2,18) < 1$ ]. The slope parameter also did not show any significant difference [ $F(2,18) < 1$ ].

Lastly, direction discrimination performance did not differ among the three conditions, as is shown in Figure 3C

[ $F(2,18) = 3.29, p > .05$ ]. (The average number of trials per observer for each cuing condition was 209 for the test-cued, 200 for the neutral, and 201 for the standard-cued conditions.) Note that the eyetracking procedure did not affect performance; identical results were obtained when the same observers performed Experiment 2 without eye tracking (data not shown).

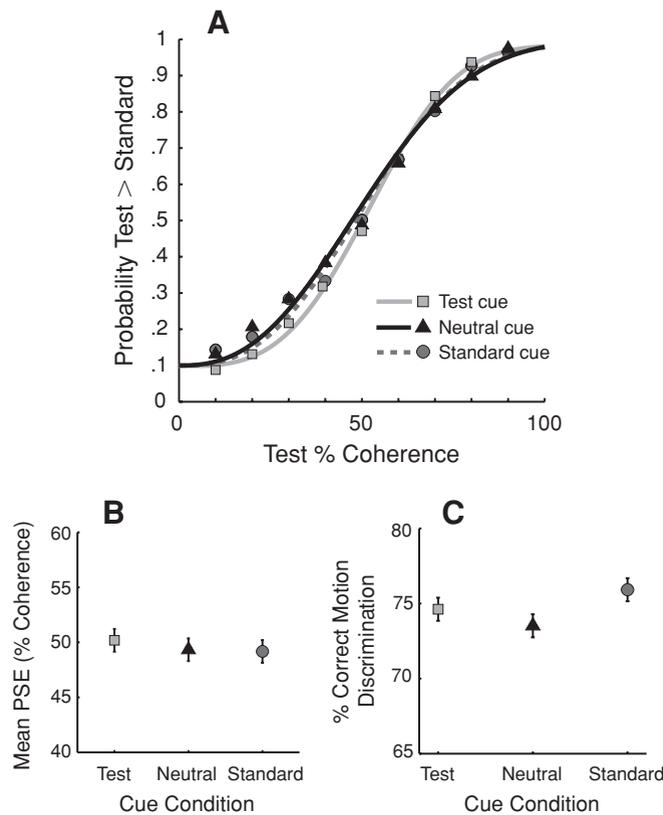
## DISCUSSION

The question of whether attention changes subjective appearance was raised over a century ago by psychologists and physiologists such as James, Wundt, Fechner, and Helmholtz and has been a source of debate ever since, but it has seldom been addressed experimentally (Prinzmetal, Nwachuku, Bodanski, Blumenfeld, & Shimizu, 1997; Tsai & Shalev, 1996; Tsai, Shalev, Zakay, & Lubow, 1994). Recent evidence indicates that attention alters the appearance of the static stimulus properties of contrast (Carrasco et al., 2004) and spatial frequency (Gobell & Carrasco, 2005).

However, it is unknown whether attention also alters the appearance of dynamic stimulus properties. Although previous studies have shown that attention affects motion processing (Beauchamp, Cox, & DeYoe, 1997; Chaudhuri, 1990; Cook & Maunsell, 2002; Martínez-Trujillo & Treue, 2002; Rezec, Krekelberg, & Dobkins, 2004; Treue & Maunsell, 1996), the present study is the first in which the phenomenological correlates of such effects have been examined. Our results weigh in on this age-old question by showing that attention also alters a dynamic stimulus property. In particular, attention enhances the subjective appearance of motion coherence.

Our paradigm allowed us to simultaneously measure the effect of attention on appearance and performance. We found that along with a change in appearance, attention produced a concomitant improvement in performance on direction discrimination. It is noteworthy that in the majority of studies on attention and motion, illusory motion perception has been examined (e.g., Chaudhuri, 1990; Rezec et al., 2004), with very few examining the perception of real motion (Cook & Maunsell, 2002; Dobkins & Bosworth, 2001). Our performance results converge with these earlier findings by indicating that spatial attention also benefits the perception of real motion. These performance results further argue against response-bias-based explanations of the appearance data, since response bias should not produce a change in discrimination performance.

Our results also complement neurophysiological studies of spatial attention and motion processing, which have documented attentional modulation of the motion-sensitive MT/hMT+ areas in monkeys and humans (Beauchamp et al., 1997; Cook & Maunsell, 2002; Treue & Maunsell, 1996). Because these areas are strongly implicated in the processing of global motion (i.e., coherence; Newsome, Britten, & Movshon, 1989; Newsome & Pare, 1988), we suggest that these neural modulations due to attention produce phenomenological consequences, as has been demonstrated here. That is, the increased firing rate in MT/hMT+ due to attention may be interpreted by the brain as if the stimulus is



**Figure 3.** Results from Experiment 2 (500-msec stimulus onset asynchrony between cue and stimuli). Data are in the same format as in Figure 2. (A) Psychometric functions of apparent coherence (data averaged across 10 observers). (B) Mean point of subjective equality (PSE) as a function of cue condition. (C) Mean percent correct for direction discrimination.

of higher coherence (see also Cook & Maunsell, 2002). A similar proposal in the domain of contrast has been put forth recently (Reynolds & Chelazzi, 2004; Treue, 2004). According to the *linking hypothesis*, the attentional enhancement of neural firing is interpreted as if the stimulus has a higher contrast. This proposal is supported by converging evidence from neurophysiological (Martinez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000), psychophysical (Carrasco et al., 2004; Carrasco et al., 2000; Lu & Doshier, 1998), and neuroimaging (Liu, Pestilli, & Carrasco, 2005) studies (for a review, see Carrasco, 2006).

The present study lends further support to the linking hypothesis by demonstrating analogous effects in the domain of motion coherence, a stimulus feature predominantly associated with the dorsal visual stream. The plausibility of the linking hypothesis relies on the fact that attentional modulation occurs in very early stages of visual processing, which provide sensory input to the rest of the brain. Thus, it might be difficult for the brain to “know” whether the enhanced neural signal is due to attention or to an increase in stimulus intensity. Indeed, from an ecological point of view, such a distinction might not be necessary: As long as a stronger signal improves

task performance, knowing the origin of this improvement may not confer additional evolutionary advantage.

Our results indicate that attention increases apparent coherence. Given that attention also increases apparent contrast (Carrasco et al., 2004), one might argue that the observed coherence effect is mediated by increased apparent contrast. This argument is weakened in light of recent psychophysical and neurophysiological studies showing that at high contrast, perception of motion strength is impaired for relatively large stimulus size, due to surround suppression (Pack, Hunter, & Born, 2005; Tadin & Lappin, 2005). Consequently, it could be argued that attentional enhancement of stimulus contrast might lead to an impaired perception of motion coherence—the opposite of what we found. Two additional considerations also argue against the possibility that the coherence effect is mediated by contrast. First, although attention has been shown to increase contrast appearance for grating stimuli, it is not clear whether the same effect applies to moving random dot stimuli. Indeed, attention was found to have no effect on the contrast sensitivity for a first-order motion stimulus (Lu, Liu, & Doshier, 2000).<sup>1</sup> Second, the motion system has a very high contrast sensitivity; that is, responses saturate at very low contrast (Sclar, Maunsell,

& Lennie, 1990; Tootell et al., 1995). For example, contrast threshold on motion detection with RDP stimuli is around 5% (rms) for a wide range of coherence levels (Fine, Anderson, Boynton, & Dobkins, 2004). Given that the RDP stimuli in this study were at 50% rms contrast (once performance had reached asymptote), even if attention increased contrast sensitivity for RDP, it could not account for the improved performance in direction discrimination.

To conclude, our experimental paradigm provides an objective method by which to evaluate subjective experience. This study demonstrates that attention increases the appearance of motion coherence and improves concomitant performance in a direction discrimination task.

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## NOTE

1. The moving RDP is a type of first-order motion stimulus.

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