

# New binary direction aftereffect does not add up

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Neural adaptation and inhibition are pervasive characteristics of the primate brain and are probably understood better within the context of visual processing than with any other sensory modality. These processes are thought to underlie illusions in which one motion affects the perceived direction of another, such as the direction aftereffect (DAE) and direction repulsion. The DAE describes how, following prolonged viewing of motion in one direction, the direction of a subsequently viewed test pattern is misperceived. In the case of direction repulsion, the direction difference between two transparently moving surfaces is overestimated. Explanations of the DAE appeal to neural adaptation, whereas direction repulsion is accounted for through lateral inhibition. Here, we report on a new illusion, the binary DAE (bDAE), in which superimposed slow and fast dots moving in the same direction are perceived to move in different directions following adaptation to a mixed-speed stimulus. This new phenomenon is essentially a combination of the DAE and direction repulsion. Interestingly, the magnitude of the bDAE is greater than would be expected simply through a linear combination of the DAE and direction repulsion, suggesting that the mechanisms underlying these two phenomena interact in a nonlinear fashion.

Keywords: binary direction aftereffect (bDAE), direction aftereffect (DAE), direction repulsion, motion perception

## Introduction

The binary direction aftereffect (bDAE) is induced by adapting to a mixed-speed stimulus containing fast dots moving in one direction (say, right of vertical) and slow dots moving in a second direction (left of vertical). Following adaptation, observers are presented with a test stimulus, which also contains fast and slow dots, but this time, all dots move in the mean direction of the adapting stimulus (vertical). Although all dots in the test stimulus move in an identical direction, observers report seeing the slow and fast dots moving right and left of vertical, respectively (see [Figure 1](#)). The phenomenon is reminiscent of the transparent motion aftereffects described by van de Smagt, Verstraten, and van de Grind (1999) and Curran and Benton (2006); furthermore, previous findings suggesting the existence of two speed-tuned channels in the human visual system (Edwards, Badcock, & Smith, 1998; Heinrich, van der Smagt, Bach, & Hoffmann, 2004; van de Grind, van Hof, van der Smagt, & Verstraten, 2001; van de Smagt et al., 1999; Verstraten, Fredericksen, Van Wezel, Lankheet, & Van de Grind, 1996; Verstraten, van der Smagt, Fredericksen, & van der Grind, 1999) would predict the bDAE occurrence.

In this article, we investigate the contributions of the direction aftereffect (DAE) (Levinson & Sekuler, 1976) and direction repulsion to this new phenomenon. The DAE and direction repulsion are thought to be the result of neural adaptation and inhibition, respectively. [Figure 2](#) depicts a model of direction repulsion proposed by Hiris and Blake (1996). The circles

in the model represent units tuned to different directions, which have inhibitory interconnections. In this example of the model, two transparent motions are represented by the solid arrows, with one motion heading slightly left and the other slightly right of vertical. The inhibitory connections between the unit sensitive to each direction and its neighboring units result in the responsiveness of the unit tuned to upward motion being suppressed more than the responsiveness of the other units. This, in turn, leads to a shift in the population activity, resulting in an exaggeration of the angular separation of the two motions (depicted by the dashed arrows). The model can also, in principle, explain the DAE. Prolonged presentation of vertically upward motion would cause the upward-sensitive unit to adapt more than the other units. This leads once again to a shift in population activity in response to subsequent motion slightly off vertical, exaggerating its angular separation from vertically upward.

Whether or not the DAE and direction repulsion are expressions of the same neural mechanism(s) remains an open question. While the two phenomena show similar direction-tuning characteristics (Levinson & Sekuler, 1976; Patterson & Becker, 1996; Schrater & Simoncelli, 1998), as well as similar speed-tuning characteristics (Benton & Curran, 2003; Curran & Benton, 2003; Curran, Clifford, & Benton, 2006), there is as yet no consensus on whether they occur at the same or at different levels of motion processing. Opinion on the neural locus of direction repulsion is divided between two camps. Whereas one group argues that it occurs at the relatively early local motion extraction stage (Grunewald, 2004; Hiris & Blake, 1996; Marshak & Sekuler, 1979;

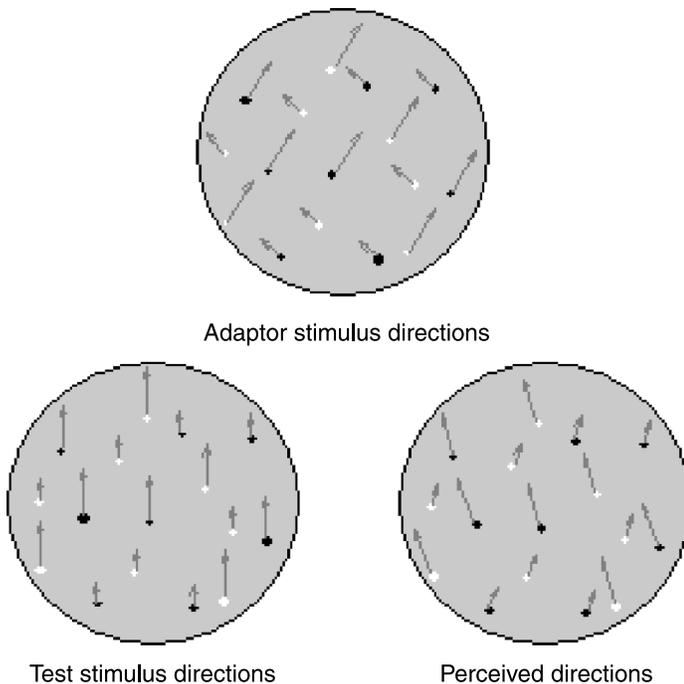


Figure 1. A schematic depiction of the bDAE. Observers adapt to slow and fast dots moving transparently across one another (top). Arrows indicate speed and direction, with fast and slow dots moving to the right and left of vertical, respectively. Next, observers are presented with slow and fast dots moving vertically (bottom left). The reported percept is of fast and slow dots moving left and right of vertical, respectively (bottom right).

Mather & Moulden, 1980), the other group advocates a later global-motion processing stage (Benton & Curran, 2003; Chen, Matthews, & Qian, 2001; Chen, Meng, Matthews, & Qian, 2005; Kim & Wilson, 1996, 1997; Wilson & Kim, 1994).

In contrast to direction repulsion, we are aware of only one study that attempts to identify the cortical location of adaptation underlying the DAE. Kohn and Movshon (2004) report that motion adaptation changes the direction tuning of macaque MT neurons consistent with the perceived repulsive nature of the DAE. However, as Kohn and Movshon point out, this does not necessarily mean that the DAE is a global-motion process. They note that their data can also be modeled by weakening feedforward input from V1 into a recurrent model of MT circuitry. This account assumes that adaptation in V1 weakens the input to those MT cells providing recurrent excitation more than it weakens the input to inhibitory MT cells. Recent data from our laboratories (Curran et al., 2006), suggesting that the DAE is driven by local motion detector adaptation, concur with this latter interpretation.

If the bDAE is a combination of both the DAE and direction repulsion, this raises the question of the manner in which neural activity underlying these two phenomena is combined. Here, we consider two plausible combinatorial scenarios. In the first case, the bDAE is a result of a simple linear combination of direction repulsion and the DAE.

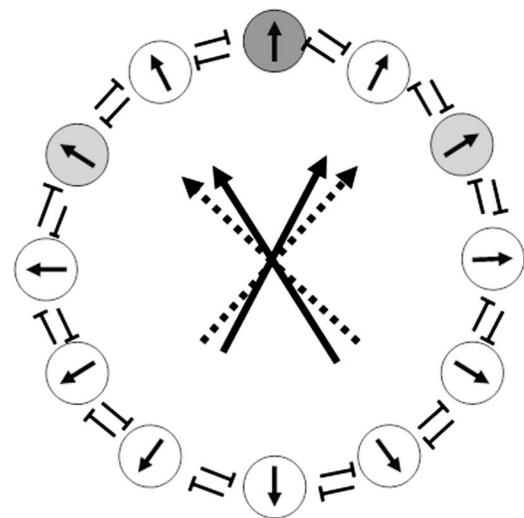


Figure 2. Hiris and Blake's (1996) model of direction repulsion (see text for details).

Alternatively, it is produced by the two effects combining in a nonlinear fashion.

Let us consider the simple linear combination model, which might operate as follows. The initial test stimulus contains no direction difference, yet the DAE results in a direction difference of, for example,  $10^\circ$ . The subsequent signal (now encoding a  $10^\circ$  direction difference) feeds into the processes responsible for direction repulsion. These act upon the DAE-induced direction difference, resulting in motion repulsion, thereby creating a direction difference of, for example,  $20^\circ$ . Thus, direction repulsion adds a further  $10^\circ$  to the initial DAE-induced direction difference. In this model, if the size of the DAE (i.e.,  $10^\circ$ ) is known, then the bDAE can be predicted by measuring the direction repulsion resulting from a  $10^\circ$  difference.

If, on the other hand, the effect follows a nonlinear combination rule, its magnitude should be significantly different to that predicted by a linear combination rule, as described above. Before addressing the nature of the underlying interaction between the DAE and direction repulsion, we first measured the magnitude of the bDAE.

## Experiment 1: Measuring the bDAE magnitude

### Observers

Three experienced psychophysical observers, one of the authors and two others who were not informed of the purpose of the experiment, participated in the experiment.

### Apparatus and stimuli

The adaptor and test stimuli were random dot kinematograms (RDK), presented within circular apertures ( $7.96 \text{ deg}^2$ ),

with each RDK containing equal numbers of black and white dots against a mean luminance background. Dot density in each stimulus was set to 64 dots/deg<sup>2</sup>. Stimuli were presented on a Sony G520 monitor. Mean luminance was 33.6 cd/m<sup>2</sup>, and viewing distance was 138 cm. The monitor was driven by a Cambridge Research Systems VSG 2/5 graphics board at a frame rate of 120 Hz. Stimuli were viewed binocularly.

## Procedure

During the initial motion adaptation phase (60 s duration), observers were presented with a transparently moving random-dot, mixed-speed stimulus in which 50% of the dots moved at 7 deg/s and the remaining dots moved at 2 deg/s. In addition to the difference in their speed, the dots also differed in their direction. Thus, the fast dots moved in a direction 25° to one side of vertical (upward), and the slow dots' direction was 25° to the other side of vertical. A central fixation spot was presented throughout the experiment. In the test phase immediately following adaptation, observers were presented again with a mixed-speed stimulus with each dot moving at either 7 or 2 deg/s. The duration of the test stimulus was 400 ms. The direction of one of the speed sets remained fixed at 90° (vertical up), and the other was varied from trial to trial. Observers' task was to judge whether the latter dot set was moving left or right of vertical. Test phases alternated with adaptation "top-up" phases of 10 s duration. The motion direction of the dot set being judged was chosen by an adaptive method-of-constants procedure (adaptive probit estimation), a method that dynamically updates the set of stimuli being presented depending on the observer's previous responses (Treutwein, 1995; Watt & Andrews, 1981). The stimulus values are selected to optimize the estimation of the point of subjective equality (PSE), in our case the direction of the set of dots being judged when it was perceived as moving vertically up. Half the psychometric functions were gathered using an adapting stimulus in which the fast and slow dots moved left and right of vertical, respectively, and half the functions were gathered with the adapting directions switched, thus controlling for any potential difference between subjective and objective measures of vertical. The interval between switching the fast and slow dots' directions was at least 2 hr. Each observer generated four psychometric functions per condition (7 and 2 deg/s test dots), with each psychometric function being derived from 64 trials. Prior to each block of trials, observers were informed of which speed set (slow or fast) they were to make direction judgments of.

## Results

Because the results were similar across all observers, we pooled their data. The results are plotted as the paired bars on the left of Figure 3 (bottom plot). Each bar represents

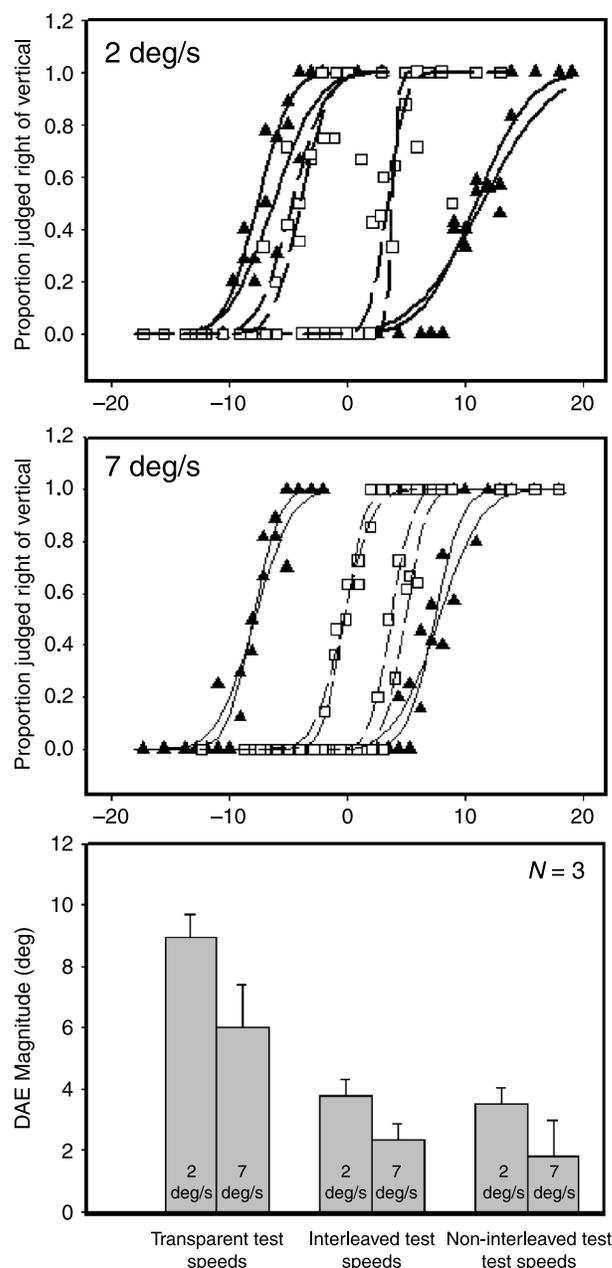


Figure 3. Results from Experiments 1 and 2. The top and middle plots show sample psychometric functions for one of the observers (W.C.). Solid lines plus triangles and dashed lines plus squares are for Experiment 1 and the interleaved condition of Experiment 2, respectively. Negative and positive x-axis values denote directions to the left and right of vertical up, respectively. Psychometric functions to the left of center were obtained when the adapting dots with the same speed as the test dots moved 25° to the left of vertical; psychometric functions to the right are from those conditions in which the adaptor moved 25° to the right. The bottom plot shows results that were averaged across observers. The leftmost bar pair measures the magnitude of the fast and slow components of the bDAE (Experiment 1). The center and rightmost bars measure the DAE of the slow and fast speed sets when each was presented in isolation following adaptation (Experiment 2). Error bars in this figure as well as in subsequent ones denote 1 SE.

the mean of 12 PSEs. Note that a positive value indicates that the perceived direction of the test speed in question was repelled from the direction of its identical speed in the adapting stimulus. The test stimulus directions were misestimated by approximately  $9^\circ$  and  $6^\circ$  for the slow and fast dots, respectively. Thus, our initial data confirm the subjective observation of a bDAE.

Recall that, in this experiment, observers made direction judgments of the same speed set (fast or slow) in any given block of trials. It could be argued that the bDAE found was simply a consequence of attention brought on by the prior “priming” of the observers. Indeed, the adaptation literature shows that attention has a significant impact on motion aftereffects (see Alais, 2005, for a review). For instance, Lankheet and Verstraten (1995) reported that the perceived MAE direction following adaptation to two transparent motions moving in opposite directions is influenced by attention. Thus, if observers attended to one of the two directions in the adapting stimulus, the perceived MAE was reported to be in the direction opposite the attended direction. It could be argued that the results of Experiment 1 are simply a consequence of prior knowledge allowing observers to attend preferentially to the same speed in the adapting stimuli as that on which they made direction judgments in the test stimuli. In other words, when making direction judgments of the fast dots in the test stimulus, observers may have attended to the fast dots in the adapting stimulus. Although none of our observers reported using such a preferential attention strategy, it is important that this potential artifact is controlled for. We address this issue in the following experiment.

## Experiment 2: An artifact of attention?

### Procedure

The adapting stimuli were identical to those used in Experiment 1. However, the mixed-speed test stimuli of Experiment 1 were replaced with single-speed stimuli in which all dots moved at either 7 or 2 deg/s. The observers’ task was to judge whether the test pattern was moving left or right of vertical. Observers were tested with two conditions: one in which the slow and fast test stimuli were randomly interleaved during each block of trials and the second condition in which a given block of trials contained either just the fast test stimulus or just the slow test stimulus. Test stimulus dot density was half that of the adapting stimuli. If the results of Experiment 1 are explicable in terms of observers using a selective attention strategy, then the noninterleaved condition should produce a stronger DAE than the interleaved condition. This is because, in the interleaved condition, the observer does not know from trial to trial which test speed will be presented following adaptation top ups.

In the noninterleaved condition, the observer always knows which test speed will be presented, allowing a selective attention strategy to be used. The same three observers as in Experiment 1 were tested.

### Results

The data from this experiment are plotted in Figure 3, thus permitting a direct comparison to be made with the results of Experiment 1. The psychometric functions (top two plots) are sample functions for one observer. The filled triangles plot responses from Experiment 1, and the unfilled squares plot responses from the interleaved condition of Experiment 2. The extent to which psychometric functions are offset from zero is an indication of DAE magnitude. The bottom plot of Figure 3 shows results that are averaged across observers. The center pair of bars plots the DAE magnitude for the slow and fast patterns when they were randomly interleaved during testing; the pair of bars on the right of the figure plots DAE magnitude when the two speed patterns were tested separately. The first thing to note is that there is no difference in DAE magnitude between the interleaved and noninterleaved test speed conditions. Thus, one can conclude that the bDAE of Experiment 1 was not modulated by attention based upon prior knowledge.

A particularly striking outcome of this experiment is the reduced DAE magnitude for both speed test patterns relative to that found in Experiment 1. Indeed, the strength of the effect is well under half of that reported in Experiment 1. Given that the only difference between the test stimuli in these two experiments is the number of directions contained in each pattern—two directions in Experiment 1 and one direction in Experiment 2—the much larger effect in Experiment 1 must be a consequence of a second motion direction being present (an alternative explanation, ruled out in the next experiment, is that the illusion strength simply decreases over time). There are two possible explanations for the larger effect when a second motion direction is present. Recall that, in Experiment 1, one of the speed sets in the test stimulus moved vertically up in every trial. However, because of the speed-specific DAE effects, its perceived direction would be off-vertical. Now, it is possible that, in the absence of any explicit vertical cues, observers used this speed set as a reference for upward vertical. Because *both* speed sets would undergo a DAE, this would result in a greater measured DAE than when just one test direction is present. This explanation fits neatly with the pattern of results reported above. A second, alternative explanation for the increased effect when two directions are present in the test stimulus is that an additional interaction between the motions occurs in the form of direction repulsion. In this scenario, the initial adaptation causes a shift in population activity (DAE), say, along the lines discussed in the Introduction section. This is then followed, during the test phase, with a further shift in population activity (direction repulsion) caused by inhib-

itory interactions between units sensitive to the test directions. One way to test which of these two accounts is correct is to measure the effect with stimuli that contain an explicit reference to vertical. The next experiment does just that.

### Experiment 3: Misreferenced vertical?

#### Procedure

The stimuli and task were identical to [Experiment 1](#), with just one exception. A white vertical line (length,  $0.3^\circ$  of visual angle) extended from the top and from the bottom of both the adapting and test stimuli. Observers were told to make their direction judgments relative to this line. Two observers were tested, one of the authors and one observer who was not informed of the purpose of the experiment.

#### Results

The bar charts in [Figure 4](#) plot the results for both observers. The white triangles record the strength of the effect for the same observers in [Experiment 1](#), and the black triangles record its magnitude in the “interleaved test speed” condition of [Experiment 2](#). For one observer, W.C., the magnitude of the effect is similar to that found in [Experiment 1](#). Although there is some reduction in the effect’s strength for observer D.A., it is substantially greater than that found in the interleaved test speed condition of [Experiment 2](#), with differences of 98% and 55% for the 2 and 7 deg/s conditions, respectively. Thus, the data clearly show that the difference in illusion strength between [Experiments 1](#) and [2](#) cannot be accounted for by observers misreferencing vertical in [Experiment 1](#).

The results of this experiment demonstrate that the bDAE is a combination of the conventional DAE and direction repulsion. In the final experiment, we investigate whether these two effects are combined in a linear or nonlinear fashion.

### Experiment 4: The bDAE results from nonlinear combination of the DAE and direction repulsion

#### Procedure

This final experiment sought to establish if direction repulsion and the DAE combine in a linear or nonlinear fashion.

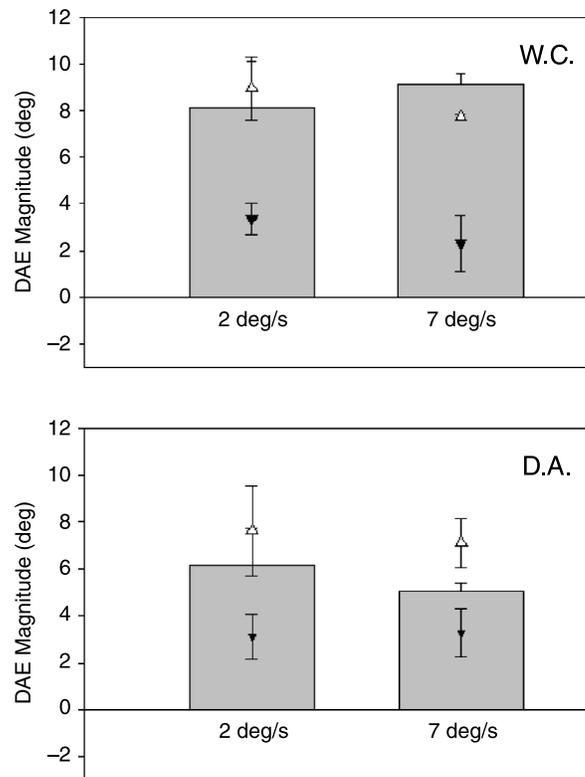


Figure 4. Results from [Experiment 3](#), in which observers were provided with an explicit reference to vertical. The left and right bars measure the slow and fast components, respectively, of the bDAE. The white triangles record the strength of the effect for the same observers in [Experiment 1](#), and the black triangles plot data from the interleaved test speed condition of [Experiment 2](#).

To answer this question, we measured the magnitudes of the DAE and direction repulsion individually. In a third condition (which we refer to as the “combined” condition), we measured the combination of the two effects. In both the DAE and combined conditions, observers adapted to a mixed-speed stimulus (7 and 2 deg/s) with all dots moving in the same direction— $45^\circ$ . Different test stimuli were used for the two conditions. In the DAE condition, test stimuli contained dots moving in a single direction and at the same speed—2 deg/s. The test stimulus direction varied from trial to trial and, as before, observers judged whether it was moving left or right of vertical. Test stimuli in the combined condition contained two motion directions—a “fixed” direction, which remained constant across trials, and the “target” direction, which varied across trials. Observers judged whether the target direction was moving left or right of vertical. The fixed direction was set at  $60^\circ$ , a direction intermediate between the adaptor and horizontal.

Careful consideration was given to test stimuli in the direction-repulsion condition. It is important to ensure that the fixed-direction component of this condition is *comparable* with, but not necessarily identical to, the fixed-direction component of the combined condition. This will be appreciated when one considers the order in which the

DAE and direction repulsion occurs, a point that we first raised in the [Introduction](#) section. Recall that the fixed-direction component of the combined test stimulus is set at 60° (i.e., 15° offset from the adaptor). If the DAE precedes direction repulsion, then, following adaptation, the visual system will register the direction of the fixed-direction dots as being greater than 15° from the adaptor. This “direction signal” will then feed into neural activity underlying the direction-repulsion component of the combined condition. In this scenario, to compare like with like, the fixed direction used in the direction-repulsion condition would have to be greater than that used in the combined condition. We know from previous studies that an adaptor test direction difference of 15° results in a DAE magnitude of between 5° and 25° (Levinson & Sekuler, 1976; Patterson & Becker, 1996; Schrater & Simoncelli, 1998). Thus, to compare like with like, the fixed-direction dots would have to be set to between 65° and 85°. Of course, the DAE may not precede direction repulsion; in which case, it would be reasonable to use the same fixed direction for the combined and direction-repulsion conditions. Given these different scenarios, we opted to use four fixed-direction conditions in the direction-repulsion condition—60°, 70°, 75°, and 80° (see [Figure 5](#)).

### Results

[Figure 6](#) plots the data obtained from two observers, one of the authors and a naive observer. The black and white bars in Panels a and b plot the strength of the DAE and

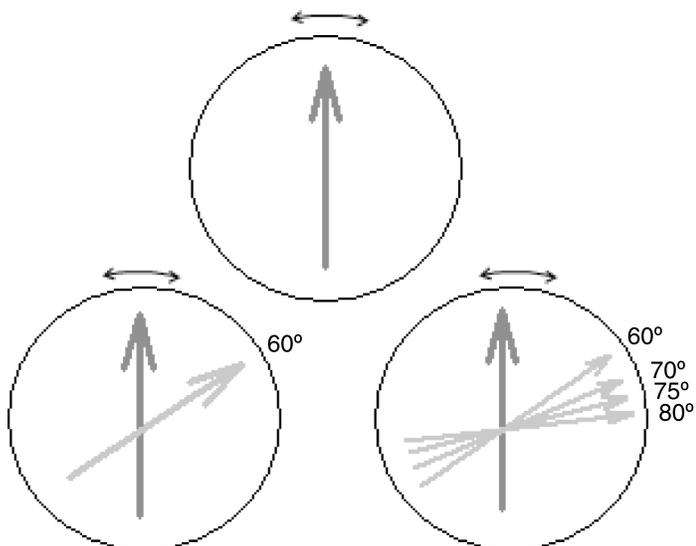


Figure 5. Test stimulus dot directions used in [Experiment 4](#). In the DAE condition (top), all dots moved in the same direction. In the combined condition (bottom left), the fixed-direction dots always moved 60° from vertical. In the direction-repulsion condition (bottom right), repulsion was measured as a function of four fixed directions: 60°, 70°, 75°, and 80° (see text for details).

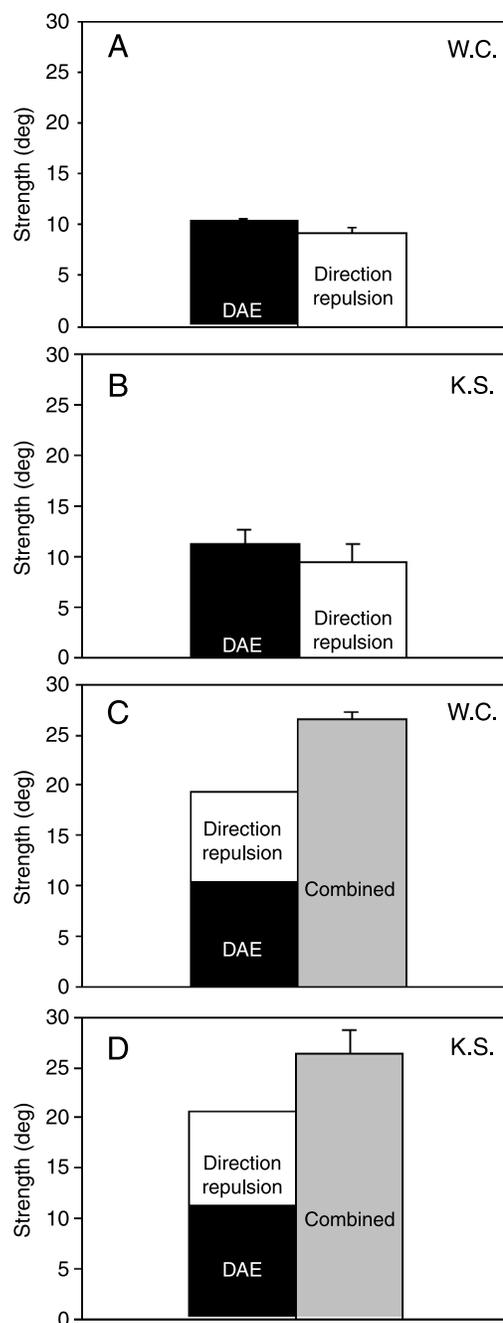


Figure 6. The black and white bars in Panels a and b plot the strength of the DAE and direction repulsion, respectively. The stacked bars in Panels c and d are used to indicate the combined magnitude one would predict based on a simple linear combination of the DAE and direction repulsion. The gray bars are a measure of the combined magnitude of the two phenomena.

direction repulsion, respectively. The direction-repulsion measure is taken from the direction condition producing the largest effect (see [Table 1](#)). The stacked bars in Panels c and d plot the combined DAE and direction-repulsion data for each observer. This serves as a reference point against which to test whether or not the bDAE results from a simple linear combination of the two effects. The strength

Observer	Direction			
	60°	70°	75°	80°
W.C.	8.17° ( $\pm 0.37$ )	6.53° ( $\pm 0.77$ )	9.12° ( $\pm 0.64$ )	7.13° ( $\pm 0.22$ )
K.S.	6.32° ( $\pm 2.26$ )	8.81° ( $\pm 1.78$ )	4.16° ( $\pm 1.88$ )	9.43° ( $\pm 1.84$ )

Table 1. Results of the direction-repulsion condition of Experiment 4, in which the fixed-direction dots moved in one of four directions (standard errors are enclosed in parentheses).

of the bDAE is shown by the gray bar in Panels c and d. The data reveal that the bDAE is stronger than the combined DAE and direction repulsion by as much as 37% and 28% for W.C. and K.S., respectively. Thus, the bDAE results from a nonlinear combination of the DAE and direction repulsion.

## Discussion

We have described a new illusion, the bDAE. Observers adapt to a mixed-speed transparent stimulus in which the fast and slow components move in two directions lying to either side of vertical. If a test stimulus containing slow- and fast-moving dots is then presented, with all dots moving vertically, the fast and slow dots appear to move in different directions on either side of vertical. The dot directions are, in effect, repelled from the direction of the same-speed dots in the adapting stimulus. Our investigations have shown the bDAE to be a robust phenomenon that cannot be explained by appealing to attentional mechanisms (Experiment 2).

In addition to ruling out attentional factors, Experiment 2 also revealed that the bDAE strength was much greater than the DAE effect recorded when the test stimuli had only one speed. Experiment 3 ruled out the possibility that the greater strength of the bDAE was a consequence of observers misreferencing vertical. The only other plausible explanation for its greater magnitude is that the bDAE results from the combination of the DAE and direction repulsion. Our final experiment sought to determine the rules governing this integrative process. The results clearly show that the combination of the DAE and direction repulsion does not follow a simple linear rule; rather, they suggest a nonlinear combination of the two effects.

The results of Experiment 4 raise the interesting question of whether the DAE and direction repulsion are expressions of the same or different neural mechanisms. Whereas the results from this experiment do not distinguish between the two interpretations, results of recent and current experiments from our laboratories suggest that they are expressions of different neural mechanisms. Benton and Curran (2003) used a novel “speed-notch” paradigm to demonstrate that direction repulsion reflects inhibitory interactions between neural units sensitive to global motion.

More recently, we have used the same paradigm to demonstrate that the DAE is an expression of local motion detector adaptation (Curran et al., 2006). Thus, it appears that the bDAE is a consequence of interactions between different neural mechanisms underlying the DAE and direction repulsion. Furthermore, it is clear from our results that the effects of direction adaptation and direction repulsion interact in a nonlinear fashion.

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