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Integration of motion energy from overlapping random background noise increases perceived speed of coherently moving stimuli

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Abstract

The perception of visual motion can be profoundly influenced by visual context. To gain insight into how the visual system represents motion speed, we investigated how a background-stimulus that did not move in a net direction influenced the perceived speed of a center-stimulus. Visual stimuli were two overlapping random-dot patterns. The center-stimulus moved coherently in a fixed direction, whereas the background-stimulus moved randomly. We found that human subjects perceived the speed of the center-stimulus to be significantly faster than its veridical speed when the background contained motion noise. Interestingly, the perceived speed was tuned to the noise level of the background. When the speed of the center-stimulus was low, the highest perceived speed was reached when the background had a low level of motion noise. As the center speed increased, the peak perceived speed was reached at a progressively higher background noise level. The effect of speed overestimation required the center-stimulus to overlap with the background. Increasing the background size within a certain range enhanced the effect, suggesting spatial integration. The speed overestimation was significantly reduced or abolished when the center-stimulus and the background-stimulus had different colors, or when they were placed at different depths. When the center- and background-stimuli were perceptually separable, speed overestimation was correlated with perceptual similarity between the center- and background-stimuli. These results suggest that integration of motion energy from random motion noise has a significant impact on speed perception. Our findings put new constraints on models regarding the neural basis of speed perception.

New & Noteworthy

We found that random motion noise in a background-stimulus significantly increased the perceived speed of an overlapping center-stimulus, and the speed overestimation was tuned to the background noise level. Experimental characterizations suggest that the speed overestimation is due to integration of motion energies from center-stimulus and random background noise, and is reduced by visual segmentation cues. Our results reveal a new speed illusion and have implications on neural mechanisms underlying the perception of motion speed.

Introduction

The perception of visual motion is crucial for humans to interpret visual scenes and to interact with our environment. The neural substrates underlying visual motion processing have been studied extensively in primates. The velocity of a moving stimulus contains a direction vector and a speed scalar. The neural mechanisms underlying direction perception and the neural code for direction are fairly well understood (e.g. Salzman et al., 1990; Kohn and Movshon, 2004). However, the neural mechanisms underlying speed perception are less clear. To gain a better understanding of the neural mechanisms underlying speed perception, we conducted human psychophysics experiments to investigate how the perception of motion speed is influenced by visual context.

The perceived speed of a moving stimulus can be profoundly influenced by the context of visual scenes (Walker and Powell, 1974; Tynan and Sekuler, 1975). For example, when two target dots move at the same speed against a background of smaller dots which have a speed gradient and move in the same direction as the target dots, the two target dots appear to move at different speeds. The target dot that is moving faster than its surrounding background dots is perceived to be faster than the target dot that is moving slower than its surrounding dots (Loomis and Nakayama, 1973). In another example, when two overlapping random-dot patterns moving transparently in opposite directions, the perceived speed of one motion component is significantly faster than its veridical speed (De Bruyn and Orban, 1999; Krekelberg and van Wezel, 2013). Moreover, the perceived speed of a random-dot pattern moving within a circular aperture is influenced by motions in the surrounding region. When the speed of motion in the surround was increased, the perceived speed of the center stimulus was decreased regardless of the motion direction of the surround (Norman et al., 1996). In these studies, the visual context also moved in a specific direction and at a specific speed. These effects of visual context on the perceived speed may be explained as the results of interactions between different neural channels that are tuned to different motion directions and/or speeds. The effect of visual context on the perceived speed of a target stimulus is still unclear if the visual context only contains motion noise and does not move in a specific direction, nor at a specific speed.

It has been suggested that the motion coherence of a random-dot stimulus can influence the perceived speed of the visual stimulus (Edwards and Grainger, 2006; Benton and Curran, 2009). However, the previous results regarding the effects of motion coherence, in other words "motion noise", on perceived speed are mixed. A reduction of motion coherence (i.e. an increase in motion noise) has been shown to reduce (Freeman and Sumnall, 2002; Benton and Curran, 2009), to increase (Edwards and Grainger, 2006), or to have no effect (Zanker and Braddick, 1999) on the perceived speed. In these previous studies, the change of motion coherence simultaneously increased the noise level and reduced the signal strength of the same visual stimulus. It remains to be determined whether, and if so, how the noise level of visual context influences the perceived speed of a target stimulus.

In this study, we characterized how random motion noise in a background-stimulus influenced the perceived speed of an overlapping center-stimulus that moved coherently. We found that the perceived speed of the center stimulus increased significantly when the background contained random motion noise. We also showed for the first time that the perceived speed of a center-stimulus is *tuned to* the level of the background noise, and the tuning changed systematically with the speed of the center-stimulus. We conducted a series of experiments to characterize factors that influenced the speed overestimation. Our findings suggest that the speed overestimation is caused by integration of motion energies from overlapping center- and background-stimuli. Our results provide new constraints on models regarding the neural mechanisms underlying speed perception, and motivate future neurophysiological experiments to elucidate the nature of the neural code for speed.

Materials and Methods

Apparatus

Visual stimuli were generated by a Linux workstation using an OpenGL application and displayed on a 19" CRT monitor. The monitor had a resolution of 1,024 x 768 pixels and a refresh rate of 100 Hz. The output of the video monitor was measured with a photometer (LS-110, Minolta) and was gamma corrected. Stimulus presentation was controlled by a data acquisition and stimulus control program called "Maestro" (https://sites.google.com/a/srscicomp.com/maestro). The experimental control computer communicated with the stimulus presentation computer via a dedicated Ethernet link. Subjects viewed the visual stimuli in a dark room with a dim background illumination. The viewing distance was 57 cm. A chin rest and a forehead support were used to restrict head movements of the observers.

Subjects

Ten adult subjects, four males and six females, with normal or corrected-to-normal visual acuity participated in the experiments. Four subjects participated in the first and the second experiment. Among them, subjects J, M and Z were naïve about the purposes of the experiments and subject C is one of the authors. Subjects J, C and Z also participated in the fourth experiment. Three new subjects D, R, and S participated in the third experiment. Subject S and three additional subjects E, R and W participated in the fifth, sixth and seventh experiment. All aspects of the study were in accordance with the principles of the Declaration of Helsinki and were approved by the Institutional Review Board at the University of Wisconsin-Madison.

Visual Stimuli

Visual stimuli used in the first (i.e. the main) experiment are described below. Visual stimuli used in other experiments were variations of those used in the main experiment and are described together with the experimental procedures in the next section and in Results. In the main experiment, the “Test” stimulus was composed of two circular and concentric random-dot patches. The "center-patch" had a diameter of 5°, whereas the "background-patch" had a diameter of 7°. The center-patch overlapped with the center region of the background-patch (Fig. 1A). The random-dots were achromatic. Each random dot was 3-pixel (i.e. 0.114°) at a side and had a luminance of 4.5 cd/m^2. The background luminance was 0.05 cd/m^2. The dot density of the center- and background-patch was 2.7 dots/deg^2, respectively. The summed area of the random dots within either the center-patch or the background-patch occupied roughly 3% of the total area of the corresponding patch.

The random dots in the center-patch moved coherently (i.e. at 100% motion coherence) within a stationary aperture. The dots moved rightward at one of four stimulus speeds of 5, 10, 15, 20°/s. The lifetime of each dot was as long as the presentation duration. When a dot reached the boundary of the circular aperture, it would reappear on the other side of the aperture in the next monitor frame.

The dots in the background-patch moved randomly in all possible directions. The coherence level was varied between 0% and 100%. To generate a random-dot patch moving at N% motion coherence (after Newsome and Pare, 1988; Britten et al., 1992), N% of the dots were selected to move coherently at an assigned direction and speed, whereas the rest of the dots were repositioned randomly within the boundary of the stimulus. In this study, we assigned the speed of the random dots in the background-patch to 0°/s, such that the background dots did not move in any net direction. At N% coherence, N% of the dots in the background-patch were stationary, whereas the rest of the dots were repositioned randomly. The total number of background dots remained constant across different levels of motion coherence. The assignment of the stationary and randomly moving dots occurred at each monitor frame of 10 ms. At 100% coherence, all dots in the background-patch were stationary and therefore there was no noise. At 0% coherence, all dots in the background-patch were repositioned randomly at each monitor frame and therefore the noise level of the background was at its maximum. We defined the “noise level” of the background dots as 100% minus the coherence level. As the motion coherence of the background dots decreased from 100% to 0%, the noise level increased from 0% to 100%. We referred to the dots in the center-patch as the “signal dots” and the dots in the background-patch as the “noise dots”.

The “Comparison” stimulus (Fig. 1B) was the same as the center-patch in the “Test” stimulus, except that the stimulus speed of the Comparison stimulus was varied from trial-to-trial in a staircase procedure.

Procedures

Each experiment trial started with a subject fixated on a red spot on the video monitor. The fixation spot was shown in the center of visual stimuli throughout the stimulus presentation period. In Experiments 1, 2, 3, 4 and 6, subjects performed a temporal two-alternative forced choice (2AFC) task to discriminate the motion speeds of the Test and Comparison stimuli presented in two sequential intervals. The Test stimulus was presented for 800 milliseconds (ms), followed by an inter-stimulus interval (ISI) of 450 ms, and then the Comparison stimulus was presented for 800 ms (Fig. 1C). The red fixation spot then turned to white for 1.3 seconds, during which the subject was required to press one of two buttons to indicate whether the speed at the center region of the Test stimulus was faster or slower than the speed of the Comparison stimulus. The next experimental trial started after an inter-trial-interval of 1.5 seconds.

Except in Experiments 5 and 7, we used a staircase method to determine the perceived speed of the center-patch of the Test stimulus. In each staircase, the speed of the signal dots in the Test stimulus was fixed and the speed of the Comparison stimulus was varied adaptively at a step of 1°/s. The initial speed of the Comparison stimulus was set randomly within the range from 1°/s to twice of the veridical speed of the signal dots in the Test stimulus. When the subject reported that the comparison speed was faster (or slower) than the test speed in a given trial, the speed of the comparison stimulus was decreased (or increased) in the following trial. A "reversal" speed was reached when the subject switched from reporting the Comparison stimulus as faster to slower, or vise versa. The staircase was stopped after seven reversals and we determined the matching speed as the mean of the last four reversals. After a subject's performance was stabilized via practice, we conducted four staircases for each stimulus condition and calculated the mean matching speed.

In the first (i.e. the main) experiment, we measured the perceived speed of the center-patch as a function of the noise level of the background dots. We tested four speeds of 5, 10, 15, and 20°/s of the center-patch. For each of these test speeds, we varied the noise level of the background from 0% to 100%.

In the second experiment, we manipulated the configuration of the background-patch and examined its impact on the perceived speed of the center-patch. The "background" patch in this experiment 1) had a larger diameter than the center-patch as in the first experiment, 2) was an annulus and therefore did not overlap with the center-patch, or 3) had the same diameter as the center-patch.

In the third experiment, the center-patch overlapped with the background-patch as in the first experiment. We varied the diameter of the background-patch, while we kept the diameter of the center-patch at 5° as in the first experiment. Five background diameters of 7°, 8.5°, 10°, 13° and 16° were used. The speed of the signal dots in the center-patch was 10°/s.

In the fourth experiment, we placed the center- and background-patch either at the same depth (2-D condition) or different depths (3-D condition), and measured the perceived speed of the center-patch. Subjects wore anaglyph glasses made of red- and green-light filters (Wratten 2 Filters, #25, 58, Kodak). In the 2-D condition, the random dots of the center- and background-patch were shown in yellow and placed at the same depth of the fixation spot (i.e. zero disparity). In the 3-D condition, the center-patch was shown at the zero disparity, whereas the background patch was placed at a far disparity of 0.4°. Random dots of the background-patch were shown in red and green. All dots of the center- and background-patch had the same luminance of 4.5 cd/m^2, measured via the red and green filter respectively. As in the main experiment, the background luminance was

0.05 cd/m^2. In this experiment, the signal dots of the center-patch moved at one of three speeds of 10, 15, and 20°/s. The noise level of the background dots was set to 30%.

In the fifth experiment, subjects reported perceptual separability between the center-patch and the center region of the overlapping background. In each experimental trial, only one stimulus interval was used. The visual stimulus was the same as the Test stimulus used in the first experiment. Subjects reported whether they perceived two separate surfaces, or alternatively a single, integrated surface in the center region of the visual stimulus. The combination of four different center speeds and six different background noise levels at each center speed constituted a total of 24 randomly interleaved conditions. Each stimulus condition was repeated at least 10 times.

In the sixth experiment, we manipulated color difference between the center-patch and the background-patch. In the *chromatic condition*, the color of the random dots in the center-patch of the Test stimulus was red, whereas the color of the background random dots was green. The color of the Comparison stimulus was also red. Random dots in the center- and background-patch of the Test stimuli, and in the Comparison stimulus had the same luminance of 4.5 cd/m^2. In the *achromatic condition*, all dots were achromatic with a luminance level of 4.5 cd/m^2. Other aspects of this experiment were identical to Experiment 1. In a staircase procedure, subjects performed a temporal 2AFC task to discriminate the speeds of the Test stimulus and the Comparison stimulus.

In the seventh experiment, subjects performed a temporal 2AFC task to judge the perceptual similarity between the center- and background-stimuli. Each trial contained two stimulus intervals. The duration of each stimulus interval and the ISI were identical to those in the first experiment. The visual stimulus presented in each of the two time intervals was the same as the Test stimulus in the first experiment (Fig. 1B), and contained a center-patch and an overlapping background-patch. Visual stimuli in the two time intervals had the same center speed of 5°/s, but different background noise levels. Subjects were instructed to choose one of the two time intervals, in which the background stimulus appeared to be more similar to the center stimulus (see Results).

In each trial, two different background noise levels were picked for the two stimulus intervals from six noise levels of 0, 30, 45, 60, 80 and 100%. There were a total of 15 pair-wise comparisons (i.e. C_6^2). These trials were blocked together and repeated at least ten times. The results of two given background noise levels presented at different temporal sequences (i.e. which noise level was presented first) were pooled together. To quantify perceptual similarity between the center- and background-stimuli, we calculated the *relative similarity* (*RS*) at a given background noise level *i*:

$$RS_i = \frac{\sum_{j=1}^{n} P_{ij}}{n-1}, \quad j \neq i \; and \; i = 1 \; to \; n \qquad (1)$$

in which P_{ij} is the probability of a subject choosing a stimulus interval that had a background noise level of *i* when comparing with noise level j. *n* is the total number of background noise levels (*n* = 6). In other words, RS_i is the cumulated probability of a subject choosing background noise level *i* when comparing noise level *i* with all other noise levels, normalized by the total number of comparisons. The index *RS* is similar to the cumulated score of a soccer team in the world cup group-stage competition. Based on the team's cumulative scores in competing with all other teams in the same group, the team's relative strength in the group can be determined.

We also measured the “relative” perceived speed of the center-patch using the same approach that was used to measure relative perceptual similarity. The visual stimuli were identical to the experiment measuring perceptual similarity. Subjects were asked to report which stimulus interval contained a center-stimulus that appeared to move faster. A relative speed score was calculated using Eq. 1 for each background noise level. A higher score indicates that the center-patch of a given stimulus appears to move faster.

Results

Effects of background noise on the perceived speed of a center stimulus (Experiment 1)

We set out to test the hypothesis that the perceived speed of a coherently moving random-dot stimulus can be influenced by random motion noise of a background stimulus that did not move in a net direction, nor at a specific speed. *In the first experiment,* the visual stimuli contained a center-patch and a larger background-patch (Fig. 1A). The diameter of the center-patch was 5° and the diameter of the background patch was 7°. The signal dots in the center-patch overlapped with the noise dots in the same region of the background-patch. We found that, when the signal dots moved at 10°/s, the perceived speed was faster than their veridical speed (Fig. 2). The highest perceived speed averaged across four subjects was 14.5°/s, 45% faster than the veridical speed.

The perceived speed of the signal dots was *tuned* to the noise level of the background. When the signal dots moved at 10°/s, for all four subjects, the highest perceived speed was reached when the noise level of the background was at 60% (Fig. 2). At this noise level, 60% of the background dots were randomly selected and repositioned to random locations within the aperture of the background-patch at each monitor frame, and the remaining 40% of the background dots were stationary. When the background noise level was higher or lower than 60%, the perceived speed of the signal dots was reduced, but still higher than the veridical speed (Fig. 2). The perceived speed of the signal dots was the lowest when the background noise level was at 0% (i.e. when all the background dots were stationary). We referred to the background noise level at which the perceived speed of the signal dots was the highest as the “noise level at the peak-speed”.

The tuning of the perceived speed of the center-patch as a function of the background noise level varied with the speed of the signal dots in the center-patch (Fig. 3). When the speed of the signal dots was low, the peak perceived speed was reached at a low noise level of the background. As the speed of the signal dots increased, the noise level at the peak-speed increased progressively (Fig. 3 and Fig. 4A). We performed a two-factor repeated measure ANOVA, in which the two factors were the background noise level and the veridical speed of the signal dots, and the dependent variable was the perceived speed of the center-patch. The main effect of the background noise level on the perceived speed was highly significant [(F(4, 12) = 71.8, $p = 2.8 \times 10^{-8}$]. The interaction between the background noise level and the veridical speed of the signal dots was also significant [F(12, 36) = 4.5, $p = 2.0 \times 10^{-4}$].

Across the four speeds of 5, 10, 15 and 20°/s, the peak perceived speed was on average ~40% faster than the veridical speeds of the signal dots (Fig. 4B). In our temporal 2AFC task, the Test stimulus was always shown first, followed by the Comparison stimulus. To determine whether the overestimation of the speed might be due to an adaptation effect related to the presentation sequence of the visual stimuli, we did a control experiment using a Test stimulus without the noisy background. We found that, given the same temporal sequence of the Test and Comparison stimuli, the perceived speed of the Test stimulus without the background patch was nearly identical to the veridical speed (see the open squares in Fig. 4B). This ruled out the possibility that the speed overestimation was caused by an adaption effect induced by the center-patch of the Test stimulus.

Effects of stimulus configuration on speed overestimation (Experiment 2)

To provide insight into the possible mechanism underlying the speed overestimation, we manipulated the configuration of the Test stimulus *in the second experiment*. We first asked, for the speed overestimation to occur, whether it was necessary for the signal dots of the center-patch to overlap with the noise dots of the background-patch. We removed the center region of the background patch and kept only the noise dots in the remaining annulus region surrounding the center-patch (Fig. 5A2). When the signal dots and the noise dots did not overlap, the signal dots no longer appeared to move faster than the veridical speed. This was the case across different background noise levels when the speed of the signal dots was 10°/s (the red curve in Fig. 5B), and across different speeds of the signal dots (the red curve in Fig. 5C). These results indicate the necessity for the signal dots to overlap with the noise dots for the speed overestimation to occur.

When the background-patch had the same diameter as the center-patch and therefore the center- and background-patch overlapped completely (Fig. 5A3), the speed overestimation of the signal dots still occurred, but to a lesser extent in comparison with the situation when the background was larger (the blue curves in Fig. 5B, 5C). The effect of the stimulus configuration on the perceived speed was significant (one-way ANOVA, $F(2, 9) \geq 6$, $p < 0.05$). Although the background annulus by itself cannot make the speed overestimation to occur, in combination with the center region of the background-patch, the noise dots in the annulus can enhance the effect of the speed overestimation, suggesting spatial integration.

Spatial integration and speed overestimation (Experiment 3)

To characterize the extent of spatial integration, *in the third experiment*, we varied the size of the background-patch while we maintained the diameter of the center-patch at 5°. As in the first experiment, the center-patch overlapped with the center region of the background-patch. The speed of the signal dots in the center-patch was 10°/s. We set the background noise level to 60%, at which the peak perceived speed was achieved in the first experiment. Four new subjects participated in this experiment. One of them was excluded because this subject did not perceive the speed of the center-patch to be significantly faster than the veridical speed at the background diameter of 7°. Across the remaining three subjects, the speed overestimation was the largest when the background diameter was 8.5°. As the background diameter further increased, the speed overestimation declined (Fig. 6). These perceptual properties mirror the size tuning of neurons in the motion-sensitive, middle-temporal cortex (i.e. area MT) of primates. As the size of a visual stimulus increases, the response of a MT neuron initially increases as more excitatory region of the neuron's receptive field (RF) is stimulated and spatially integrated, and then the neuronal response starts to decline when the visual stimulus covers the suppressive surround of the RF (e.g. see Pack et al., 2005).

Effects of depth cues on speed overestimation (Experiment 4)

In the experiments described above, the center-patch and the background-patch were displayed in the same depth plane, which potentially allows integration of motion energies from the center-patch and the noisy background to occur. At the neuronal level, such integration is likely to occur within the RFs of motion sensitive neurons in the visual cortex. It has been shown previously that neural interactions between multiple motion signals located at different depths are weakened, in comparison to the situation when the motion signals are present in the same depth (Bradley et al., 1995). At the perceptual level, stimuli placed at different depths are easily segregated by the visual system and therefore are more difficult to be integrated than when stimuli are placed at the same depth. If the speed overestimation was caused by integration of motion energies from overlapping signal dots and noise dots, placing the center-patch and the background-patch at different stereoscopic depths should reduce the effect of speed overestimation due to potentially weakened integration across different depths. To test this prediction, we manipulated the stereoscopic depths of the visual stimuli *in the fourth experiment*. Subjects wore red/green anaglyph glasses to view the visual stimuli. We placed the signal dots of the center-patch at zero disparity (i.e. the same depth as the fixation spot) and the noise dots of the background-patch either at a far disparity of 0.4° (3-D condition) or at the same depth as the center-patch (2-D condition). The spatial extent of the background-patch and the center-patch were the same as in the first experiment, in which the diameter of the background-patch was 2° larger than the center-patch. In the 2-D projection of the visual stimuli, the signal dots overlapped with the noise dots at the center region of the background-patch. Under the 3-D condition, the subjects could reliably segregate the center-patch and the background-patch to different depths, when the signal dots moved at the speeds of 10, 15 and 20°/s, but not at the speed of 5°/s. We therefore used the speeds of 10, 15 and 20°/s for the signal dots in this experiment.

Under the 2-D condition, we found that the subjects perceived the signal dots to be faster than the veridical speed, as in the first experiment. However, when the center-patch and the background-patch were positioned at different depths, the speed overestimation of the signal dots was essentially abolished (Fig. 7). Under the 3-D condition, the signal dots of the center-patch and the noise dots of the background-patch were perceived as belonging to two separate surfaces at different depths. For each of the three speeds tested, the perceived speed under the 3-D condition was significantly slower than that under the 2-D condition (one-tailed t-test, $p < 0.01$, after Bonferonni correction for multiple comparisons). This effect can be conveniently demonstrated by having subjects first view the visual stimuli under the 3-D condition to establish the stereoscopic depths, and then quickly close one eye to view the visual stimuli monocularly. We tested four subjects with this simple demonstration. All of them reported that, when they closed one eye and hence lose the stereoscopic perception of the visual stimuli, the perceived speed of the center-patch suddenly increased. Together, the results of this experiment suggest that the speed overestimation was caused by interactions between overlapping signal dots and noise dots presented at the same stereoscopic depth.

Perceptual separability between the center-patch and the overlapping background (Experiment 5)

The abovementioned results are consistent with the idea that the overestimation of the center speed is related to integration of motion energies of the center- and background-stimuli. As alluded to above, it is likely that motion integration is influenced by perceptual separability between the center-stimulus and the background. We therefore measured perceptual separability of our visual stimuli in the 2-D condition to evaluate the relationship between perceptual separability and the speed overestimation.

The visual stimulus was the same as the Test stimulus used in the first experiment. Each experimental trial contained only one stimulus interval (see Methods). Following each trial, subjects indicated whether they perceived the center-patch and the background-patch as two separate surfaces, or alternatively as a single, integrated surface.

Figure 8 shows results from four subjects. These subjects also participated in Experiments 6 and 7 (see below). When the speed of the center patch was 5°/s, subjects could always segregate the center-patch from the overlapping background, regardless of the background noise level (Fig. 8, black curve). As the speed of the center-patch increased, it became harder to segregate the center-patch from the overlapping background. When the center speed was equal to or greater than 10°/s, the perceptual separability decreased as the background noise level increased (Fig. 8). These trends were consistent across subjects, despite individual differences in the background noise level at which subjects started to have difficulty segregating the center-patch from the overlapping background.

These results show that it is not necessary for the center-patch and the overlapping background to be perceived as a single, integrated surface for the speed overestimation of the center-stimulus to occur. For example, the center- and background patches were perceptually separable at the center speed of 5°/s, yet speed overestimation occurred at this speed (Fig. 3A). Furthermore, although the perceptual separability decreased monotonically with the background noise level (Fig. 8), the speed overestimation did not increase monotonically, but peaked at an intermediate noise level (Fig. 3). Together, these results provided two insights: First, motion integration pertinent to speed perception is not an all-or-none process, but rather occurs in a graded manner. Among a set of conditions in which the center-patch and background-patch are perceptually separable, some of the conditions are easier to separate than others, which may be linked to different levels of motion integration. Similarly, among a set of conditions in which the center-patch and background-patch are perceived as a single, integrated surface, some of the conditions appear to be more uniform and integrated than others, which again may be linked to different levels of motion integration. Second, perceptual separability may not be the only factor that determines speed overestimation. We further investigated the first point in Experiment 6, and the second point in Experiment 7.

Impact of color cues on speed overestimation (Experiment 6)

In this experiment, we investigated whether increasing perceptual separability by introducing a color difference between the center-patch and the background-patch had an impact on the speed overestimation. We hypothesized that introducing a color difference between the center-patch and the background would increase perceptual separability and reduce motion integration, and therefore reduce speed overestimation.

We manipulated the color difference between the center-patch and the background-patch. In the *chromatic condition*, the random dots in the center-patch of the Test stimulus were red, whereas the random dots in the background-patch were green. In the *achromatic condition*, all dots were achromatic. Other aspects of this experiment were identical to Experiment 1. In the chromatic condition, subjects could easily segregate the center-patch from the background-patch, regardless of the center speed and the background noise level.

We found that introducing color cues significantly reduced speed overestimation. Four subjects participated in this experiment. These subjects also participated in Experiments 5 and 7. We first tested the subjects using a center speed of 10°/s. In the achromatic condition, all four subjects overestimated the speed of the center-stimulus and the perceived speed was tuned to the background noise level and peaked at the noise level of 60%, consistent with the results from Experiment 1 (black curves in Fig. 9). In contrast, the speed overestimation was reduced, if not abolished, for all subjects in the chromatic condition (red curves in Fig. 9). We performed a two-way ANOVA, in which the two factors were the presence or absence of color cues, and the background noise level, and the dependent variable was the perceived speed of the center-stimulus. The main effect of color cues on the perceived speed was significant for all subjects [($F(1, 36) > 6.8$, $p < 0.013$]. The interaction between color cues and the background noise level was also significant for all subjects [$F(5, 36) > 5.8$, $p < 0.001$].

In the chromatic condition, the speed overestimation was also reduced in comparison to the achromatic condition across different speeds of the center-patch (Fig. 10), at noise levels of peak perceived speed as measured in Experiment 1. The main effect of color cues on the perceived speed was significant for all subjects [two-way ANOVA, ($F(1, 24) > 22$, $p < 10^{-4}$]. The interaction between color cues and the speed of center-patch was also significant [$F(3, 24) > 5.9$, $p < 0.005$]. These results confirmed our hypothesis.

Note that when the center speed was 5°/s, introducing color cues had minimum effect on the speed overestimation for three of four subjects (Fig. 10). A possible explanation is that, because at center speed of 5°/s it was already easy for subjects to segregate the center patch from the background, in other words separability may nearly asymptote, introducing color cues may therefore provide little extra benefit on separability at this speed.

Perceptual similarity between the center- and background-stimuli (Experiment 7)

Our working hypothesis is that the speed overestimation of the center-stimulus is caused by integration of motion energy from random noise in the background. Can the idea of motion integration explain our finding that the speed overestimation is tuned to the level of background noise? We reasoned that motion integration was more likely to occur when the perceptual appearances of the background-patch and the center-patch were similar. If the speed overestimation were caused by motion integration, perceptual similarity should also be tuned to the level of background noise. To test this prediction, we measured perceptual similarity between the center-patch and the background-patch at different background noise level. To avoid having perceptual separability confound the measurement of perceptual similarity across background noise levels, we performed this experiment using a speed of 5°/s, at which the center-patch and the background-patch were separable at all background noise levels (Fig. 8).

Subjects performed a temporal 2AFC task similar to that in Experiment 1. In this experiment, however, the Comparison stimulus had the same configuration as the Test stimulus, containing a center-patch and a larger, overlapping background-patch. The only difference between the Test stimulus and the Comparison stimulus was the background noise level. Subjects were instructed to choose one of the two temporal intervals in which the background stimulus was more similar to the center stimulus than that in the other temporal interval. Subjects were instructed to judge similarity based on the apparent appearance of the center-patch and background-patch. Factors such as the apparent (i.e. perceived) dot density, dot size, brightness of individual random dots, brightness of the background surface as a whole, apparent update rate of the random dots and the appearance of motion can all influence the perceived similarity. Subjects were instructed to evaluate similarity based on the overall appearance of the center-patch and the background-patch, taking these factors into consideration.

Figure 11 shows the results from four subjects. The perceived similarity between the center- and background-stimuli varied with the background noise level. With the center-patch moved at 5°/s, the background-patch appeared to be most similar to the center-patch at a noise level of 30%. This result was highly consistent across subjects (Fig. 11A). On average, the tuning of the perceptual similarity between the center-patch and the background-patch as a function of the background noise level (Fig. 11B) matched well with the tuning of the perceived speed (Fig. 3A).

Because the four subjects participated in this experiment did not participate in Experiment 1 and the methods employed to determine perceptual similarity (Experiment 7) and the perceived speed (Experiment 1) were different, we therefore measured the relative perceived speed of the center-patch for the four new subjects using the same approach as in Experiment 7. In this task, the visual stimuli were identical to the experiment measuring perceptual similarity. Subjects were asked to report which stimulus interval contained a center-stimulus that appeared to move faster than that in the other stimulus interval. Figure 12 shows consistent results from the four subjects. The tuning of the relative perceived speed (Fig. 12B) matched well with the tuning of the perceptual similarity (Fig. 11B), and with the tuning of the perceived speed measured in Experiment 1 (Fig. 3A). These results confirmed our prediction and are supportive of the idea that the speed overestimation is the result of motion integration.

Discussion

We found that a background-stimulus that contained random motion noise could increase the perceived speed of an overlapping center-stimulus that moved coherently. We also discovered that the perceived speed of the center-stimulus was tuned to the background noise level. The faster a center-stimulus moved, a noisier background was needed to give rise to the largest overestimation of the perceived speed. We found that the speed overestimation was significantly reduced or abolished when the center- and background-stimuli had different colors, or when they were placed at different depths. Our results suggest that integration of motion energies across overlapping stimuli in the same depth has a significant impact on speed perception, and that such integration is more likely to occur when the overlapping stimuli are perceptually similar.

Possible impact of integration and segmentation

The processes of integration and segmentation can influence motion perception considerably (Stoner et al., 1990; Murakami and Shimojo, 1993; Braddick, 1993; Nishida, 2011; Gaudio and Huang, 2012). One candidate explanation for our finding of the speed overestimation is related to image segmentation - the presence of a larger, noisy background may make the signal dots "stand out" and the speed overestimation occurs due to the apparent "contrast" between the *segmented* center and background stimuli. Alternatively, the visual system may *integrate* the motion energies of the signal dots from the center-patch and the non-directional noise dots from the background, and tag the greater motion energy to the signal dots, making them appear to move faster. When all the dots in the background-patch were stationary (i.e. at 0% noise level), the center-patch can be segmented from the background-patch. Our finding of a slight overestimation of the perceived speed at the 0% noise level is consistent with the previous finding that increasing the number of stationary reference markers leads to an increase of the perceived speed (Gogel and McNulty, 1983). However, when the noise level of the background-patch was greater than 0%, our results suggest that it was motion integration, rather than segmentation, that caused the speed overestimation. Edwards and Grainger (2006) have shown that an increase in motion noise gives rise to an increase in the perceived speed and interpreted their results as due to the amount of relative motion in the stimulus. If the speed overestimation found in our experiments was also caused by perceptual segmentation, one may expect to find less speed overestimation when the signal dots and the noise dots are more similar perceptually. However, our result is opposite to this prediction. Furthermore, we found that the speed overestimation still occurred when subjects could not segregate the center-stimulus from the background at high center-speeds and high background noise levels. It is worth noting that our visual stimulus was different from that used by Edwards and Grainger (2006). We kept the motion coherence of the center-stimulus unchanged, but varied the noise level of the background-stimulus by randomly repositioning the background dots. Edwards and Grainger (2006) used a random-walk stimulus and varied the proportion of signal dots and noise dots. These differences in visual stimuli make it difficult to directly compare our results with the previous study.

We found that the speed overestimation required the center-patch to overlap with the background-patch. Perceptually, it was easier to segment the signal dots from the noisy background when the signal dots and the noise dots were spatially separated in the center and the annulus regions (Fig. 5A2), than when they overlapped (Fig. 5A3). However, the speed overestimation occurred in the overlapping condition (Fig. 5A3), but not in the annulus condition (Fig. 5A2). Moreover, when the center-stimulus and the background-stimulus were shown in different colors or at different depths, under which conditions perceptual segmentation of the center- and background-stimuli was enhanced, the speed overestimation was significantly reduced or abolished (Figs. 7, 9 and 10). These results are also consistent with the idea that the speed overestimation is due to motion integration, rather than segmentation.

Our results emphasize a distinction between the neural process of motion integration and the perception of a single, integrated stimulus/surface. Our measurements of perceptual separability and similarity between the center- and background-stimuli (Figs. 8 and 11), and their relationships with the speed overestimation suggest that the neural integration of motion signals is a graded process and can occur even across overlapping, perceptually separable stimuli.

Possible impact of adaptation

Adaptation effects in the primary visual cortex and cortical area MT are strongly modulated by stimulus size (Wissig and Kohn, 2012; Patterson et al., 2014). Following adaptation with a large stimulus, surround suppression may be reduced (i.e. causing disinhibition) in a stimulus-specific manner. In most of our experiments, the background-stimulus had a diameter of 7°, which is comparable to the size of the large stimulus (7.4°)

used by Patterson et al. (2014), and Wissig and Kohn (2012). May the size-dependent effect of adaptation account for the speed overestimation that we have observed?

The following considerations suggest that the speed overestimation was not due to interaction between the effects of adaptation and surround suppression. First, when the background-patch had the same diameter as the center-patch, the speed overestimation still occurred albeit smaller (Fig. 5). This indicates that the speed overestimation was not caused by an adaptation effect induced by the stimulus surround. Second, in most of our experiments (except in Experiment 7), the Comparison stimulus only contained the center-patch presented on a black background, without an annulus surround. Since the Comparison stimulus did not receive surround suppression from the annulus region to begin with, any change in the adaption state in the annulus region elicited by the stimulus surround in the Test stimulus would likely have little effect on the neural responses to the Comparison stimulus.

Neural code of motion speed

Visual information is encoded in the activity of populations of neurons (McIlwain 1991; Pouget et al. 2000). In one scheme of neural coding, referred to as the "labeled-line code", the attribute of a visual stimulus is encoded by neuronal responses distributed across a population of neurons that have different preferences for the visual attribute (Groh, 2001). In a different coding scheme, referred to as the "rate code", a visual attribute is encoded by the firing rate of a population of neurons. More sophisticated coding schemes using Bayesian inference have also been suggested (Stocker and Simoncelli, 2006; Jogan and Stocker, 2015).

Neuronal activity in area MT of macaque monkeys is linked to speed perception. Many neurons in area MT are selective to motion speed (Dubner and Zeki, 1971; Maunsell and van Essen, 1983; Mikami et al., 1986; Lagae et al., 1993; Perrone and Thiele, 2001; Priebe et al., 2003). Trial-to-trial variations of neuronal responses in area MT correlate with speed perception (Liu and Newsome, 2005), and lesions of area MT impair speed discrimination (Pasternak and Perigan, 1994; Orban et al., 1995). Several lines of evidence suggest that the neural code for speed is consistent with labeled-line coding. MT neuron's response tuning to speed typically follows a log-normal function, rather than changes monotonically with speed (Nover and DeAngelis, 2005). Microstimulation of area MT biases speed perception toward the PS of the stimulated neurons (Liu and Newsome, 2005). Importantly, several perceptual illusions of motion speed can be explained by labeled-line coding (Churchland and Lisberger, 2001; Priebe and Lisberger, 2004; Boyraz and Treue, 2011; Krekelberg and van Wezel, 2013).

However, other lines of evidence suggest that a rate code may be used to represent motion speed. Krekelberg et al. (2006) showed that the underestimation of speed at low luminance contrast cannot be explained by a labeled-line code based on neuronal responses in area MT. Since the responses of MT neurons were weaker at lower contrast, a rate code of speed can account for this illusion. Furthermore, Liu and Newsome (2005) showed that, only when the stimulus speed was lower than the PS of a neuron, meaning that at an interval of the speed tuning curve that the firing rate increased monotonically with the stimulus speed, the choice probability was greater than 0.5; when the stimulus speed was higher than the PS, the choice probability was no longer significantly different from chance. In the medial superior temporal (MST) cortex, an area that is downstream to area MT and is also important for processing visual motion information, many neurons prefer fast speeds and their firing rates increase monotonically with speed over a wide speed range (Kawano et al., 1994; Churchland and Lisbeger, 2005). It is possible that MST neurons use a rate code for representing motion speed (Churchland et al., 2007). Komatsu and Wurtz (1989) reported that microstimulation in areas MT and MST increased the speed of pursuit eye movement, which can be explained by a rate code for speed, rather than a labeled-line code. The nature of the neural code for motion speed remains to be understood.

Our finding that the tuning of the speed overestimation shifts with the speed of the center-stimulus suggests that the interaction between the background motion noise and the coherent motion of the center-stimulus is specific to the spatiotemporal frequency contents of the visual stimuli. Although the background stimulus did not move in a net direction, nor at a specific speed, the random noise contained motion energy distributed in the spatiotemporal frequency domain (Adelson and Bergen, 1985; Watson and Ahumada, 1985). As the noise level of the background stimulus increases, the motion energy at higher spatiotemporal frequencies also increases. Supported by human psychophysical studies (e.g. van der Smagt et al., 1999), neurons that prefer a fast (or slow) speed are likely to be more sensitive to a high (or low) level of motion noise. Integration of motion energies from the center-stimulus and overlapping background noise would reshape the population neural responses and cause changes in perceived speed. Importantly, whether such neural integration can occur may depend on the perceptual similarity between the center-stimulus and the background noise, and is subject to the influences of visual segmentation cues such as color and depth.

One possible neural explanation of our results is that, neurons that prefer the speed of the center-stimulus would be strongly activated by the center-stimulus, and further activated by a background-stimulus that has a noise level “matching” the speed of the center-stimulus, in terms of perceptual similarity. As the result, the population neural responses distributed across neurons with different PSs would be elevated by the background noise, but the location of the peak response in the neuron population would remain unchanged. If the visual system decodes the stimulus speed based on the firing rates of the neuron population (i.e. a rate code), the perceived speed of a center-stimulus would be faster at a matching background noise level than at a non-matching noise level and the veridical speed.

An alternative neural explanation of our results is that, the background motion noise at the peak perceived speed of a center-stimulus may be most effective in driving the neurons that prefer speeds slightly higher than the speed of the center-stimulus. As the result, the population neural responses elicited by the combination of the center-stimulus and the background noise would be biased toward the neurons that have faster PSs than the speed of the center-stimulus. If the visual system decodes the stimulus speed based on a labeled-line code, the perceived speed would be faster than the veridical speed.

Our psychophysical results reported in this study provide new insight and guidance for the investigation of neural code for motion speed. The stimulus manipulation used in our study may allow future neurophysiological experiments to distinguish the abovementioned possibilities of coding motion speed. In future neurophysiological studies, it would be important to characterize how population neural responses elicited by a coherently moving center-stimulus in motion-sensitive cortical areas are changed by different levels of background motion noise. Our psychophysical results also indicate that the perceived speed of a coherently moving stimulus can vary depending on the coherence level of an overlapping background.

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Figures and Figure Legends

Figure 1. Visual stimuli and the experimental paradigm. Visual stimuli were composed of achromatic random dots. **A**. The "Test" stimulus was composed of a center-patch and a larger, concentrically placed background-patch. Random dots in the center-patch moved coherently to the right. Random dots in the background-patch did not move in a net direction, nor at a specific speed and were randomly updated at each monitor frame. **B**. The "Comparison" stimulus was the same as the center-patch of the Test stimulus, except that the speed of the Comparison stimulus was varied from trial to trial according to a staircase procedure. **C**. The temporal sequence of the experimental paradigm. The Test stimulus was presented first for 800 ms, followed by a 450-ms inter-stimulus interval (ISI) and the Comparison stimulus was presented for 800 ms. Subjects were instructed to determine whether the motion speed of the center-patch of the Test stimulus was faster or slower than the speed of the Comparison stimulus

Figure 2. The perceived speed of the center-patch speed was perceptually tuned to the noise level of the background dots. Results were from four subjects. The speed of the center-patch was 10°/s. A noise level of N% means that N% of the dots in the background-patch were repositioned randomly within the aperture of the background-patch at each monitor frame, whereas the remaining dots in the background were stationary. Note the different vertical scales for different subjects. Error bars represent standard deviations.

Figure 3. The tuning of the perceived speed of the signal dots to the background noise level varied with the speed of the signal dots in the center-patch. The speed of the signal dots: **A.** 5°/s, **B.** 10°/s, **C.** 15°/s, **D.** 20°/s. Results were averaged across four subjects. Error bars represent standard deviations.

Figure 4. A. The relationship between the background noise-level at the peak perceived-speed and the speed of the center-patch. **B**. The speed overestimation was due to the presence of the background-patch and was not due to the temporal sequence of the Test and Comparison stimuli. Error bars represent standard deviations. The solid circles in A and B are data replotted from Figure 3.

Figure 5. The impact of stimulus configuration on the perceived speed of the center-patch. **A.** Three stimulus configurations. **A1**. The "large-background" condition. The diameter of the background-patch was 7° and the diameter of the center-patch was 5°. The two patches overlapped in the center region of the background-patch. **A2**. The "annulus" condition. The center- and the background-patch did not overlap. **A3**. The "small-background" condition. The background-patch had the same diameter as the center-patch and the two patches overlapped completely. **B**. The perceived speed as a function of the background noise level. The speed of the center-patch was 10°/s. **C**. The perceived speed as a function of the motion speed of the center-patch. The noise level of the background-patch was 30%, 60%, 80% and 90% for the motion speed of 5°/s, 10°/s, 15°/s and 20°/s, respectively. At these motion speeds and noise levels, the peak speed overestimation was achieved under the large-background condition, as shown in Figure 3. Error bars represent standard deviations.

Figure 6. The impact of the background size on the perceived speed of the center-patch. The diameter of the center-patch was 5°. The background-patch was larger than the center-patch and the two patches overlapped in the center region of the background-patch. **A-C**. Results from individual subjects. **D.** Averaged results across three subjects. Note the different vertical scales for different panels. Error bars represent standard deviations.

Figure 7. The impact of the stereoscopic depths of the visual stimuli on the perceived speed of the center-patch. In the "2-D" condition, the center-patch and the background-patch were presented at the same depth plane. In the "3-D" condition, the center-patch was presented at the zero disparity, whereas the background-patch was presented at a far disparity. Error bars represent standard deviations.

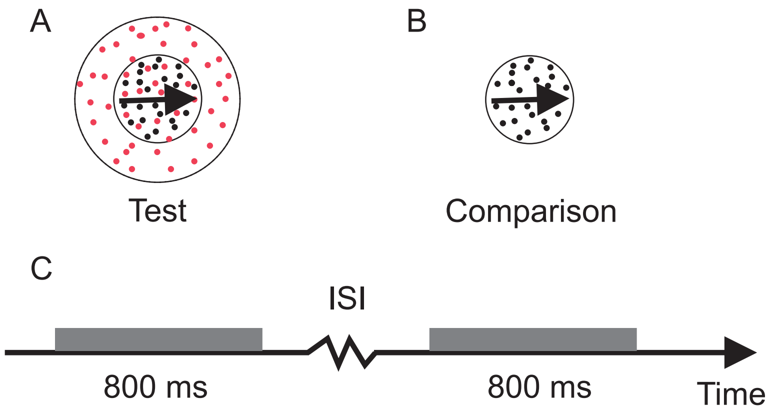
Figure 8. Perceptual separability between the center-patch and the overlapping background-patch as the background noise level and the speed of the center-patch varied. Ordinate indicates the ratio of experimental trials in which subjects perceived the center-patch and the overlapping background as two separate surfaces. Each panel shows results from one subject. Error bars represent standard deviations. Figure legends indicate speeds of the center-patch.

Figure 9. The impact of color cues on the perceived speed of the center-patch across different background noise levels. Black curves indicate results from achromatic condition. Red curves indicate results from chromatic condition. The speed of the center-patch was 10°/s. Each panel shows results from one subject. Note the different vertical scales for different subjects. Error bars represent standard deviations.

Figure 10. The impact of color cues on the perceived speed of the center-patch across different center speeds. Black curves indicate results from achromatic condition. Red curves indicate results from chromatic condition. The noise level of the background was 30%, 60%, 80% and 90% for the center speed of 5°/s, 10°/s, 15°/s and 20°/s, respectively. Each panel shows results from one subject. Note the different vertical scales for different subjects. Error bars represent standard deviations.

Figure 11. Perceptual similarity between the center-patch and the background-patch. Ordinate indicates the relative similarity score (see Methods), shown as a function of the background noise level. The speed of the center-patch was 5°/s. **A**. Results from individual subjects. **B**. Similarity scores averaged across four subjects. Error bars represent standard deviations. Figure legends indicate different subjects.

Figure 12. Relative perceived speed of the center-patch. Ordinate indicates the relative speed score (see Methods), shown as a function of the background noise level. A higher score indicates that the center-patch of the stimulus appears to move faster. The speed of the center-patch was 5°/s. **A**. Results from individual subjects. **B**. The relative speed score averaged across four subjects. Error bars represent standard deviations. Figure legends indicate different subjects.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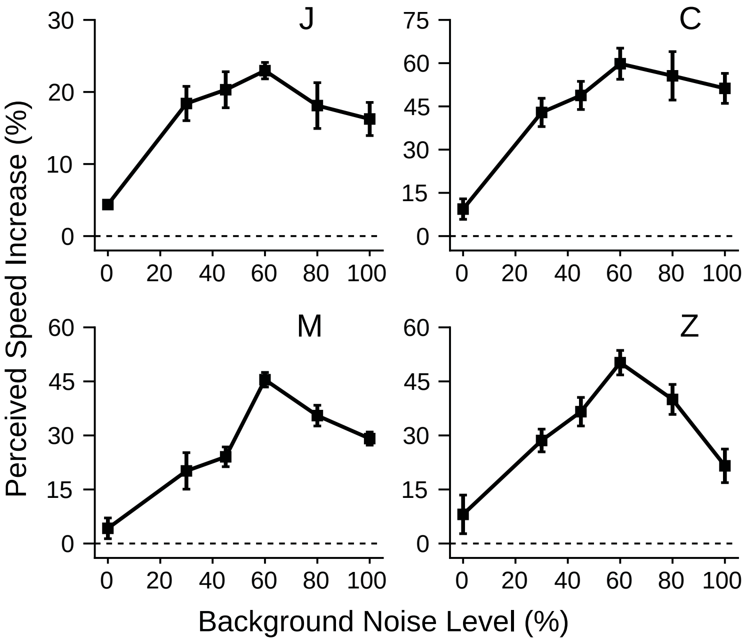
Time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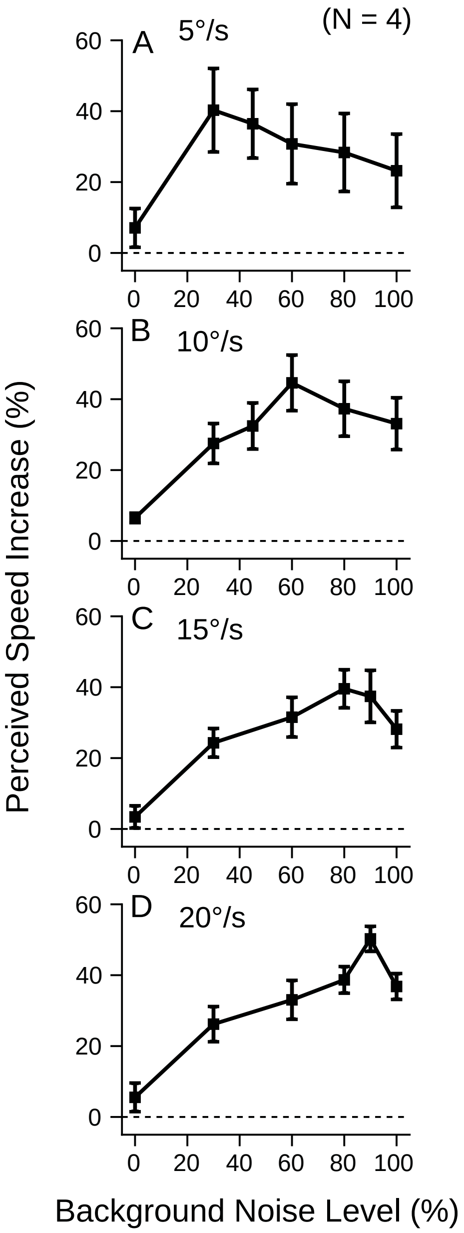
Background Noise Level (%)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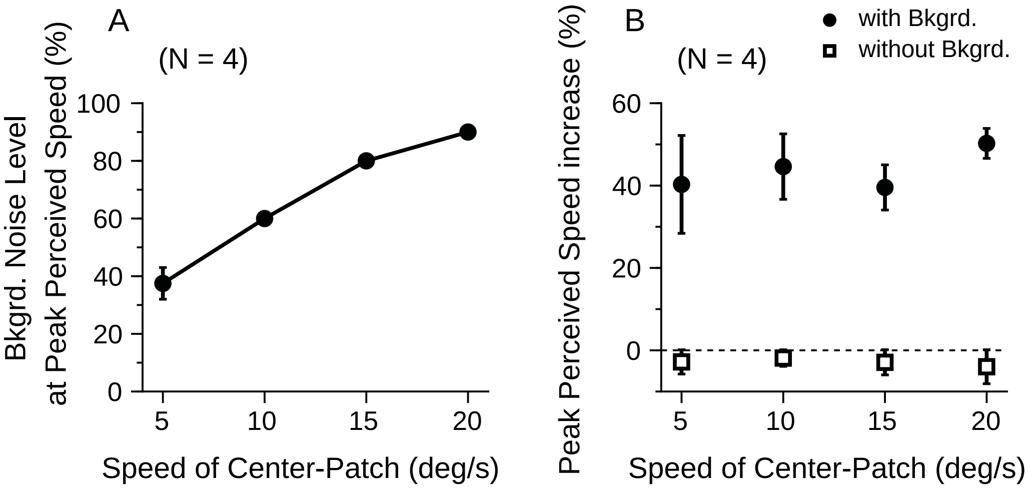
Perceived Speed Increase (%)
Background Noise Level (%)

A
(N = 4)
Bkgrd. Noise Level
at Peak Perceived Speed (%)
100
80
60
40
20
0
5
10
15
20
Speed of Center-Patch (deg/s)
B
● with Bkgrd.
□ without Bkgrd.
(N = 4)
Peak Perceived Speed increase (%)
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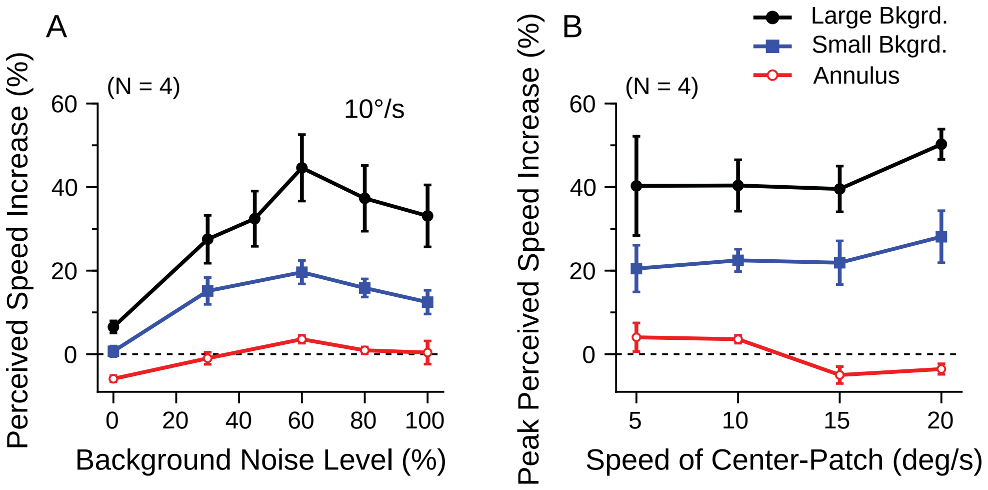
40
20
0
5
10
15
20
Speed of Center-Patch (deg/s)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B
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Small Bkgrd.
Annulus
(N = 4)
10°/s
Perceived Speed Increase (%)
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40
20
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0
20
40
60
80
100
Background Noise Level (%)
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Peak Perceived Speed Increase (%)
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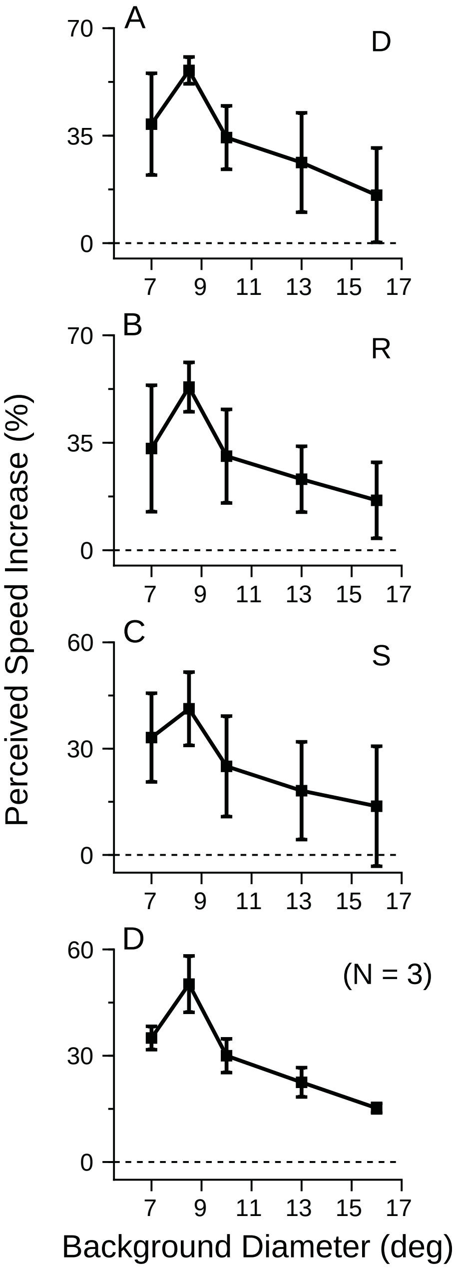
40
20
0
5
10
15
20
Speed of Center-Patch (deg/s)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R
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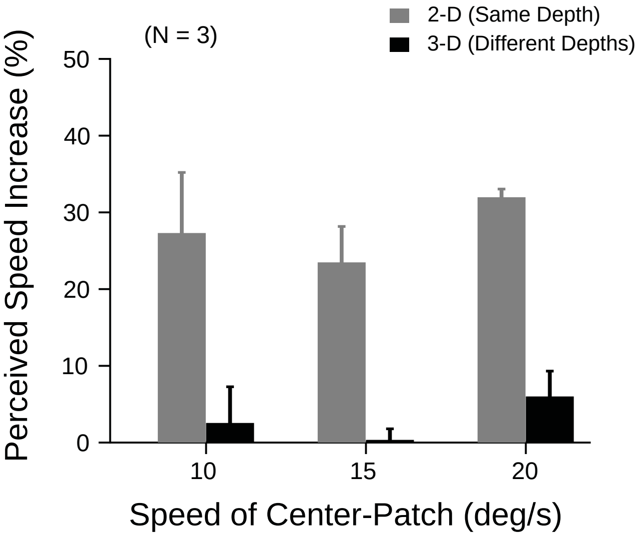
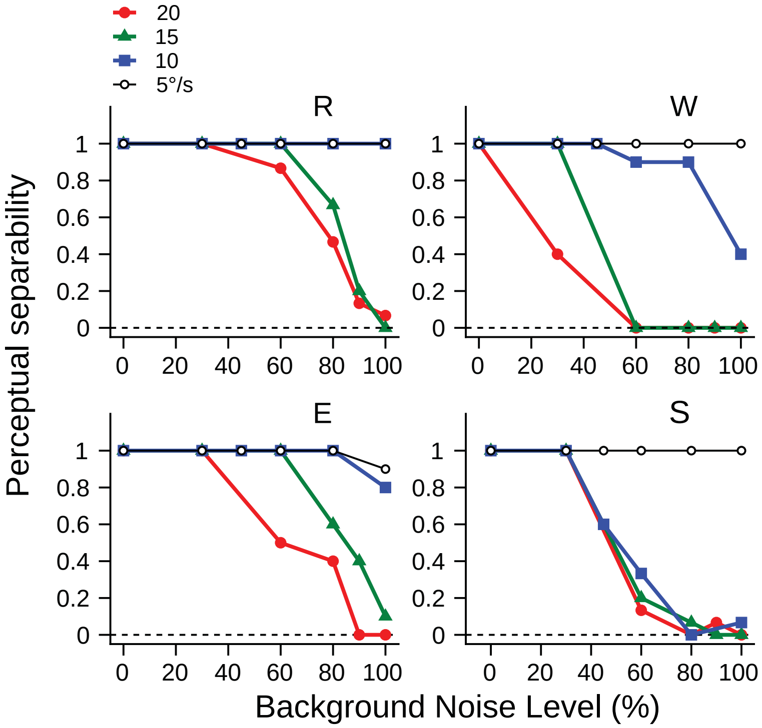
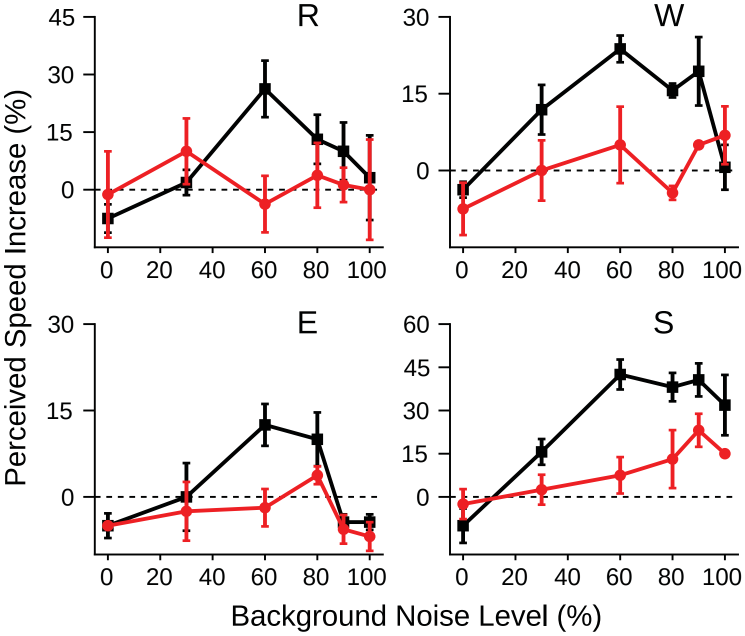
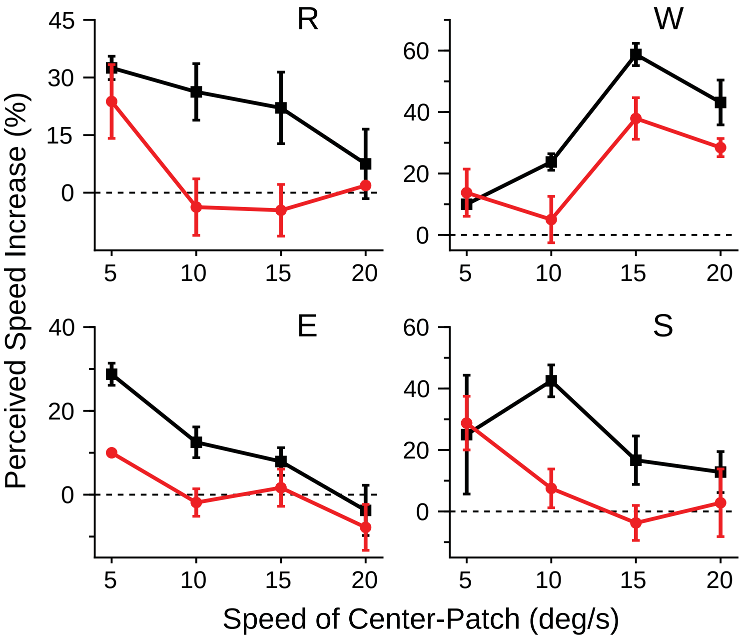
Perceived Speed Increase (%)
Background Diameter (deg)

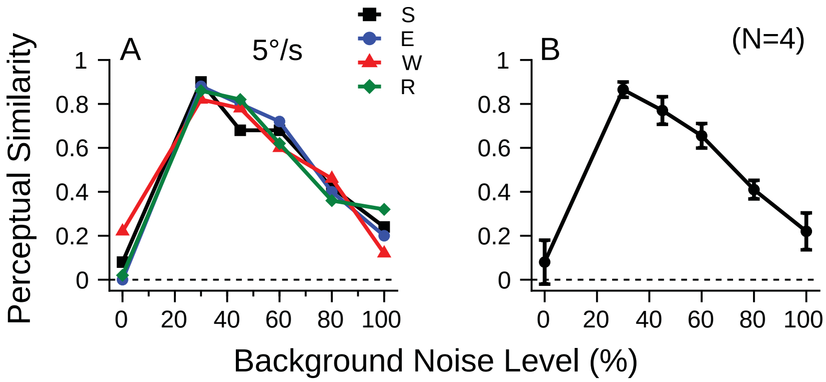

(N = 3)
2-D (Same Depth)
3-D (Different Depths)
Perceived Speed Increase (%)
50
40
30
20
10
0
10
15
20
Speed of Center-Patch (deg/s)

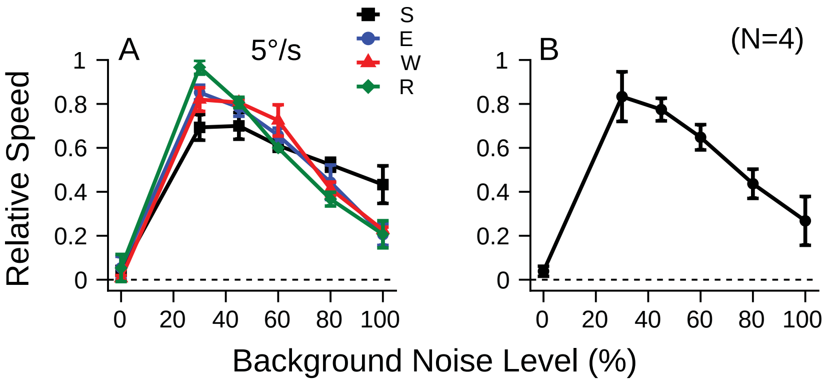

20
15
10
5°/s
R
W
E
S
Perceptual separability
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
Background Noise Level (%)


R
W
E
S
Perceived Speed Increase (%)
Background Noise Level (%)
45
30
15
0
60
0
20
40
60
80
100



R
W
E
S
Perceived Speed Increase (%)
Speed of Center-Patch (deg/s)
45
30
15
0
60
40
20
0
40
20
0
60
40
20
0
5
10
15
20


A
5°/s
S
E
W
R
B
(N=4)
Perceptual Similarity
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
Background Noise Level (%)


A
5°/s
S
E
W
R
B
(N=4)
Relative Speed
1
0.8
0.6
0.4
0.2
0
0
20
40
60
80
100
Background Noise Level (%)